

Black Kites on a Flyway Between Western Siberia and the Indian Subcontinent

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Abstract

Background

The Black Kite (*Milvus migrans*) is one of the most widespread raptors in the World. The Palaearctic is populated by two migrating subspecies, *Milvus migrans migrans* and *Milvus migrans lineatus*, in the western and eastern part of this realm, respectively. The intergradation zone of *M. m. migrans*/*M. m. lineatus* covers large areas in-between. Migration routes of *M. m. migrans* from Europe to Sub-Saharan Africa and the Middle East are well known including large waterbodies as main environmental obstacle.

Methods

We tagged with GPS/SMS/GPRS telemetry loggers 13 and 6 Black Kite *pulli* in lowland around Biysk and in mountains around Kosh-Agach.

Results

Black Kites originating from Biysk migrated through the Western Circum-Himalayan Corridor. Black Kites originating from Kosh-Agach used the Trans-Himalayan Corridor crossing the Himalayas in altitudes of up to 6 256 m asl. The average total distance travelled of Black Kites from both subpopulations was 9 166 m without any significant differences between these subpopulations. Timing of autumn migration varied slightly among individuals in departure date (30 August \pm 9 days) and differed more in arrival date (26 October \pm 92 days). The timing of spring migration varied less in both departure date (17 April \pm 12 days) and arrival date (09 May \pm 14 days). Black Kites from both subpopulations wintered in low elevations of anthropogenic areas of Pakistan and India. Birds wintered on average for 190 days, and the mean area of individual home ranges was 4 704 km². During the breeding period, birds occupied mainly natural or semi-natural habitats in southwestern Siberia, where they spent on average 106 days with an average home range size 3 554 km².

Conclusion

Black Kites crossing the Himalayas fly and, moreover, stay for hours resting at night in the environment of mountains at altitudes over 5000 m. It seems that the vast breeding territory of Black Kites in the Palearctic realm is connected with the unusual behavioural flexibility of Black Kites to surmount various environmental obstacles on their migration routes.

Introduction

The Black Kite (*Milvus migrans*) is one of the most widespread raptors occurring in Eurasia, Africa, and Australia (1, 2). It shows unique ecological flexibility and can inhabit many habitats, including human-affected landscapes, using variable food sources as an opportunistic predator and scavenger (3–6). The Palaearctic is populated by two subspecies, *Milvus migrans migrans* (7–10) and *Milvus migrans lineatus* in the western and eastern part of this realm, respectively (7–10). Indian Subcontinent and Indo-China are

populated by *Milvus migrans govinda*; Australia, and the adjacent islands by *Milvus migrans affinis*. *Milvus migrans formosanus* inhabits the eastern part of China, Taiwan, and Hainan. Africa is populated by subspecies *Milvus migrans parasitus* *Milvus migrans aegyptius*.

The ranges of the Palaearctic subspecies contact each other with an opportunity for mutual hybridisations. The intergradation zone of *M. m. migrans*/*M. m. lineatus* covers large areas of Eastern Europe, Kazakhstan, and West Siberia and is gradually expanding (1, 11–15). The most active is the westward expansion so that the birds with the characters of *M. m. lineatus* already occur in Iberian Peninsula (16). Black Kites of these two subspecies seem to cross freely since birds in the intergradation zone exhibit a whole range of intermediate characters (13). Moreover, it is supposed that the *M. m. migrans*/*M. m. lineatus* mixed population meets the *M. m. govinda* in the Hindu Kush in Afghanistan and Pakistan; thus, the intergradation zone between all the three Eurasian subspecies may exist (13).

The Palaearctic *M. m. migrans* and *M. m. lineatus* are seasonal migrants. *M. m. migrans* from Europe winter in Sub-Saharan Africa and the Middle East. Its migration routes are well known (6, 17, 18). The migration of *M. m. lineatus* is poorly studied. Based on the phenotypes of observed birds, *M. m. lineatus* overwinters in India, Indo-China, and China (19). Black Kites (pure *M. m. lineatus*?) from the eastern part of Mongolia overwintered in north-eastern India and Myanmar (20, 21). *M. m. govinda* breeding on the Indian subcontinent is sedentary, and during winter, shares the territory with the Black Kites arriving from the eastern Palaearctic (2, 22). Japan is inhabited by a nearly sedentary *M. m. lineatus* population, which seems to undertake seasonal migrations confined to the Japanese Archipelago (23). *M. m. affinis* migrates seasonally within the Australian continent (24). *M. m. aegyptius* migrate south to the East African coast, and *M. m. parasitus* migrates from South Africa to Uganda (25, 26).

Telemetry data suggest that immature *M. m. migrans* do not return to their natal area after first overwintering and may keep outside until maturity, moving long within the nesting and overwintering territories (18, 27). Formations of large summer aggregations of immature Black Kites were reported from Siberia (28, 29). *M. m. migrans* start nesting when 3–5 years old (30). Natal dispersal of kites was studied mainly in *M. m. migrans*. These birds tend to return for nesting to the natal area. Natal philopatry is relatively high (5 km on average, however, it may exceed 100 km) (30). Recently, a distance of 198 km between the natal nest and a place of own breeding was documented in the Czech Republic (31). Breeding philopatry (philopatry of birds after their first breeding) of adult *M. m. migrans* and adult birds from intergradation zone *M. m. migrans*/*M. m. lineatus* were strongly associated with their previous nesting territories, preferring to return each year (29, 30).

Migration routes and winter quarters mainly remained the same in individual *M. m. migrans* in the first three years of their life (18). Surprisingly for birds in 2cy, it was found that summer quarters occurred at lower latitudes than predicted and a substantial proportion of birds of this age remained in their African winter quarters. Some birds in their 3cy returned to spend the summer period in the natal area, but many of these birds remained at lower latitudes north of their winter quarters. Similar behaviour has been described in some other raptors (*Circaetus gallicus*, *Pernis apivorus*) migrating from Europe to Africa and

back (32, 33). Circannual variations in the movement patterns of *M. m. migrans* have been extensively reviewed (6). During migration, tens of thousands of *M. m. migrans* are observed migrating across the Straits of Gibraltar, along the eastern coast of the Black Sea and in the Middle East; while, substantial numbers cross the central Mediterranean (including Italy, Sicily, and Tunisia) and the Bosphorus (6, 34). Few birds cross the Mediterranean Sea between the Peloponnese, Crete, and Libya (6). The crossing of large water bodies of the Mediterranean Sea and the Black Sea seems to be challenging environmental obstacles for *M. m. migrans* on the flyway from Europe to Africa (6, 35).

Black Kites, supposedly originating from the intergradation zone between *M. m. migrans* and *M. m. lineatus* migrate traditionally to winter in Iraq, Iran, and western Pakistan (11). Siberian *M. m. lineatus* migrate to winter in the Indian subcontinent regarding the 18° Northern Latitude, Myanmar, Indochina, and southern China (11). Recently, some individuals of *M. m. lineatus* of unknown origin were also observed wintering in Kazakhstan (36–38).

Migration routes of Black Kites from the Siberian part of Russia are mainly unknown. Some observations of Black Kites in autumn around Novosibirsk and the Kuznetsky Alatau Mountains indicated their direction of autumn migration to Kazakhstan, and aggregations of Black Kites on their autumn migration route through Kazakhstan were reported from Chokpak Pass (39–41). Between 2014 and 2018, Black Kites called Black-eared Kites (unfortunately, not specified if Kites originating from the intergradation zone between *M. m. migrans* and *M. m. lineatus* or pure *M. m. lineatus*) had been tagged with GPS transmitters at the landfill in Dehli, India (42). These pre-adult and adult Kites tagged in winter were tracked to reveal their migratory flyways. Kites migrated for 3300–4800 km along the narrow corridor between Dehli (winter quarters) and southern Siberia and western Mongolia (summer including supposedly breeding quarters), crossing the Himalayas at elevations up to more than 6500 m a.s.l. by the K2 of the Karakoram Range and travelled long periods at elevations above 3500 m. a.s.l. Previously, Black Kites were regularly observed during migration at various watch-sites in the Himalayan ridge in northwestern India, Nepal and the Tibetan Autonomous Region, western China (43).

Among atmospheric conditions, wind is known to strongly influence the speed of migration specifically during long-distance migration and overcoming of natural barriers (44–46). Flying with wind assistance may induce a decision to depart (47). Several studies have shown that both flapping and soaring migrants travel significantly faster when flying with tailwinds and are hindered by headwind and crosswinds (48, 49). Recent technological advances have made it possible to use tracking technology to record the flight path of wild birds and then determine from weather records the atmospheric conditions at the locations where the birds were recorded (50). This approach estimates key metrics needed for understanding the effect of wind on birds under natural conditions (46).

We studied Black Kites fledged in southwestern Siberia, Russia, which were tagged as *pulli* with GPS transmitters on nests in a) lowland area near Biysk, Altai Krai populated by Kites from the intergradation zone between *M. m. migrans* and *M. m. lineatus*, b) in a mountainous area near Kosh-Agach, Altai Republic populated by supposedly pure *M. m. lineatus*. The aims of the study were a) to reveal and to

compare migration routes of Kites from these two populations, b) to define the timing of autumn and spring migrations, c) to characterise sizes of their post-fledging area, home ranges in wintering quarters and summering (breeding) ranges, and d) to study in details, including weather conditions, the way how Kites crossed the extremely high elevations of the Himalayas as the leading environmental obstacle on their migration.

Materials And Methods

Birds

In total, 19 Black Kites (11 females, 8 males) from breeding populations in Western Siberia, Russia, were investigated in this study. Kites originated from two spatially separated breeding subpopulations. One subpopulation represents birds hatched in lowland around Biysk (Altai Krai), the second subpopulation represents birds hatched in the mountains around Kosh-Agach (Altai Republic) near the Mongolian border (Table 1).

DNA examination

Contour pin feathers (newly grown feathers, full of blood) were collected from the lower part of a chick body) and stored in 96% ethanol. The total DNA was isolated using the ExtractDNA Blood kit (Evrogene, Russia). The sex of tagged birds was determined by a method by Suh et al. (2011). A 699 bp fragment of the mitochondrial *cytB* gene was analysed to identify haplotypes (51). The *cytB* mitochondrial gene fragment (924 bp) was amplified using F3 (5'-CCACCCATCCTCAAATAA-3') and R8 (5'ATTGTGCGCTGTTTGGACTT-3'). We sequenced PCR fragments in both directions using a 3500 Genetic Analyser capillary sequencer (Applied Biosystems, USA) and aligned resulting sequences using the Vector NTI software (Thermo Fisher Scientific). In order to exclude contamination, operations with genomic DNA and with PCR products were performed in different rooms. In unclear cases, PCR and sequencing were repeated.

Satellite telemetry devices

Black Kites (*pullii*) were fitted with telemetry loggers in nests in 2018 (subpopulation A) and 2019 (subpopulation B). Loggers equipped with solar panels (20 g; Ecotone, Poland, and Ornitela, Lithuania; www.ecotone.pl, www.ornitela.com, respectively) were used to track the birds. Loggers were fitted onto the backs of the birds using harnesses (backpacks) consisting of a 6 mm Teflon ribbon encircling the body by two loops around the bases of the wings and joined in front of the breastbone. Loggers function in GPS (Global Position System)/GSM (Global System for Mobile Communication) systems. The GPS positions of the birds were collected according to individual settings (usually one position fixed per 1-6h). They were sent as SMS (Short Message Service) text messages by local mobile operators to the Ecotone and Ornitela Centers in Poland and Lithuania, respectively, where they were saved and archived. The coordinates of bird positions were analysed using GIS and the software ArcGIS 10.1 (Esri, Redlands, CA, USA) and QGIS (www.qgis.org).

Data processing, migration characteristics

We processed positional data (coordinates) from studied birds for each bird individually. These data were separated into yearlong modules from 01.07.20XY (in the first year from the date of tagging) to 30.06.20XY+1. The number of modules depends on the lifespan of each bird. We calculated the total distance travelled within the yearlong period and the number of temporary settlements areas (TSA) from these modules. We defined total distance travelled as distances between roosting places connected chronologically (daily local movements were not calculated within the migration movement = total distance travelled).

We defined TSA as a preferred place where a bird stayed for > 10 nights within 80 km². This template size was based on roost locations distributed within a 10-km diameter over 10 days, thus, all falling within 80 km² (18). Spring (pre-breeding) and autumn (post-breeding) migrations separate the winter and summer period. We defined the beginning of those migrations as a day when the bird left the ground for good. The end is defined as a day when the bird reached the summer or winter destination. During both migrations, birds tend to use stopovers, defined as a day with less than 50 km of a directed flight (42). The size of the post-fledging area (PFA), winter and summer grounds (home ranges) between migrations were calculated as a Kernel density estimate (KDE) 95%. The Himalayas flight-over was defined as the period of migration between the first and last day of migration with coordinates recorded by the foothill of the Himalayas with at least one coordinate recorded at over 5 000 m above the sea level. We calculated the length of trajectory segments leading parallelly along mountain ridges during the flight-over and compared them with the overall distance travelled during the flight over the Himalayas.

We defined checkpoints W1, W2 and W3 as night positions where birds stayed on 31 January of their 2cy (second calendar year), 3cy and 4cy, respectively. It represents where birds were wintering during this date during the first, second and third winter. We defined checkpoints S1, S2 and S3 as positions where birds stayed during the breeding period on 30 June of their 2cy, 3cy and 4cy, respectively. We used the positions during S1, S2, S3, W1, W2 and W3 to compare migration characteristics of individual birds between years of their life span and compare migrations among individual birds during the first, second and third years of their life. Natal dispersal distance was defined as the distance (using a straight line) between the birthplace (natal nest) and breeding place (30).

Meteorological data

Elevation data was downloaded from the mapping and analysing platform www.databasin.org "30 arc-second DEM of Asia" as a digital elevation model (DEM).

Weather data (wind, temperature and humidity) were obtained from the NCEP/DOE Reanalysis II dataset, using the RNCEP package (52) for the R-software. Weather data of flight over the Himalayas were extracted for each coordinate in real-time, and pressure level of 700 hPa corresponding to an altitude between 2 300 m and 3 150 m. Airspeed, flow-assistance and side wind were calculated by function NCEP:tailwind using RNCEP package, which calculates flow-assistance and forward and sideways

movement according to equation Tailwind (Tailwind = wind speed * cos (α), where α is the angle of the wind from the direction of travel). Equation Tailwind considers flow-assistance to be the component of the flow moving parallel to the specified direction (tailwind), with negative values indicating flows against the specified direction (headwind). Negative values of side wind speed represent the Eastern wind; positive values represent Western wind. We have extracted the weather data for coordinates recorded during post-breeding (n=1090) and pre-breeding (n=1310) migration over the Himalayas. We excluded coordinates recorded while roosting from the dataset.

Statistical analysis

We performed the Mann-Whitney U test for testing the differences in pre-breeding and post-breeding migration and home-range characteristics and the pre-breeding and post-breeding Himalaya's flight-over characteristics. To assess the difference in total distance travelled, number of TSA, and the size of home ranges in summer and winter quarters over the years, we performed Kruskal-Wallis ANOVA test. Before any statistical comparison, we run the Shapiro-Wilk test for normality to assess the data distribution. To assess the effect of weather on bird's movement across the Himalayas, we used linear mixed models (LMMs) in R (53) using the 'lme4' package (54) to analyse the following dependent variables: bird ground speed and airspeed, in relation to flow-assistance and side wind during the flight over the Himalayas. We used LMM with bird ID as a random effect (as individuals could be tracked over multiple years). Only birds with telemetry loggers Ornitela, which flew over the Himalayas, were included in the LMM (K14 – K19) due to the high frequency of coordinates recording. The best supported LMM model was selected according to the lowest Akaike's information criterion for a small sample size (AICc). A difference in AICc (Δ AICc) between a model with a predictor and an intercept-only model greater than two was considered strong evidence for a particular model (55). All statistical tests were performed using an α -value of 5%, and all mean values are presented (\pm standard deviation; SD) unless stated otherwise.

Results

cytB haplotypes

Black Kites from Biysk belonged to haplogroup A (haplotypes A3 and A4) and haplogroup B (haplotypes B6, B6.1, B14, B19 and B19.1). Three families and 8 families had haplogroups A and B, respectively (Table 1). All Black Kites (5 families) from Kosh-Agach belonged to haplogroup B (haplotypes B6, B14, B19 and B19.1).

Migration routes and total distance travelled

Black Kites originating from Biysk migrated through the Western Circum-Himalayan Corridor (Figure 1). These birds flew through eastern Kazakhstan, Kyrgyzstan, Tajikistan and eastern Afghanistan to winter, mainly in northern and southern Pakistan and western India. After winter, birds flew over the same migration corridor back to Biysk area. Unlike Kites from Biysk, Black Kites originating from Kosh-Agach used a different migration route (Figure1). These birds flew over Tian Shan, and the Taklamakan Desert

in China, followed by Trans-Karakoram flight-over thought Jammu and Kashmir to winter in northern and western India and eastern Pakistan. After winter, birds flew over the same corridor back to Kosh-Agach area.

The average total distance travelled of birds from both subpopulations in the first year was 9 191 km (ranging from 6 431 to 12 478 km). During the first year, birds used on average 4 TSAs (ranging from 2 – 6). During the second year, birds travelled on an average total distance of 9 121 km (ranging from 7 422 – 11 268 km) using 5 TSAs (ranging from 4-7). The average total distance travelled in the third year was 6 839 (ranging from 6 594 – 7 084) using 5 TSA (ranging from 4 -5) (Table 2).

Five tagged birds survived and were tracked for multiple years. For those individuals, we compared the differences in the total distance travelled and the number of used TSAs. We found no significant difference in the total distance travelled ($P>0,05$) nor the number of TSA ($P>0,05$) used among the years. We also tested the difference in total distance travelled, and the number of TSA used between the two subpopulations without any significant results ($P>0,05$).

Timing of autumn and spring migrations

Timing of autumn migration varied slightly among individuals in departure date (30 August \pm 9 days) and differed more in arrival date (26 October \pm 92 days). The timing of spring migration varied less in both departure date (17 April \pm 12 days) and arrival date (09 May \pm 14 days). The tagged kites travelled relatively fast, completing a 2535–4842 km journey in 10–94 days, progressing by 62–253 km/day, with significantly faster speeds and lower need to rest in the pre-breeding migration (Table 3).

Post-fledging area and home ranges in winter and summer

The post-fledging area of tagged Kites varied from 1.7 km² to 1 567 km² with a mean of 396 \pm 432 km² (Table 4). Some birds left the nest and flew straightforward to the winter quarters. Others birds explored the area around the nest and departed for autumn migration with a slight delay. Black Kites from both subpopulations wintered in Indian Subcontinent in low elevations of anthropogenic areas of Pakistan and India (Figures 1 and 2). No bird remained in the Indian subcontinent during summer periods (Figure 3). Birds wintered on average for 190 days, and the mean area of individual home ranges was 4 704 km² (Table 4). On the contrary, during the breeding period, birds occupied mainly natural or semi-natural habitats south-western Siberia, where they spent on average 106 days with an average home range size 3 554 km² (Figures 1 and 2; Table 4). No bird remained in Siberia during the winter period (Figure 3). Although the mean area of home ranges was slightly smaller during the breeding season than in the nonbreeding winter period, we found no statistical difference in the spatial use ($p > 0.05$). Five tagged Black Kites survived and were tracked for multiple years (Table 4). For those individuals, we compared the differences in the area size of home ranges in the breeding (summer quarters) and nonbreeding season (winter quarters). We found no difference in spatial use over the years in neither the winter quarters ($p>0.05$) or summer quarters ($p>0.05$).

High-elevation crossing of the Himalayas and influence of the wind on the flight over the Himalayas

Timing of post-breeding and pre-breeding flight over Himalayas varied slightly among individuals in departure dates (19 September \pm 11 days; 28 April \pm 7 days) and arrival dates (20 September \pm 11 days; 29 April \pm 7 days). Black Kites originating from Koch-Agar travelled relatively fast, flying over the Himalayas (on average 571 km) in 2 days, progressing with average active speed of 31.7 km per travelling hour, flying from 6 to 10 hours per day. Active speed and number of traveling hours were slightly higher during pre-breeding flight-over. During the crossing of the Himalayas birds roosted for one night in average altitude of 4 246 m asl, ranging from 1 577 to 5171 m asl (Table 5, Figure 3).

Weather conditions significantly varied during the pre-breeding and post-breeding Himalaya flight-overs (Table 5). Noticeable was the difference in the tailwind speed, sidewind speed and percentage of parallel flight along the mountain ridge. While during the post-breeding flight-over, birds faced mostly a headwind and preferred to fly perpendicularly to mountain ridges and mountain valleys, on their pre-breeding flight-over, birds flew with a tailwind and preferred to fly parallelly along the mountain ridges and mountain valleys (Figure 4). The ground speed and airspeed of birds flying over the Himalayas in autumn were positively related to tailwind and side wind speed (Table 6a). Therefore, both winds increased the bird groundspeed and airspeed (Figures 4a and 5a). During the pre-breeding migration, the tailwind had a greater positive effect on both the ground- and airspeed of bird, which led to a higher speed increase. However, the side wind had a negative effect (Table 6b). Therefore, bird groundspeed and airspeed increased with tailwind and decreasing with stronger side wind during the pre-breeding flight over the Himalayas (Figure 4b and 5b).

Natal dispersal distance

Breeding behaviour was evident according to GPS positions in one black kite male (K 10) in its age of 3 years (4cy). Its supposed nest was in a distance of 14.6 km from its natal nest. The other male of this age or younger black kites showed no signs of breeding.

Discussion

Subspecies status of examined Black Kites and their migration routes

We found different sets of *cytB* haplotypes in Black Kites from Biysk and Black Kites from Upper Altai close to Kosh-Agach. While in Kosh-Agach, the haplotypes were characteristic of *M. m. lineatus*, in the vicinity of Biysk, the haplotypes were characteristic for both subspecies *M. m. migrans* and *M. m. lineatus*, indicating a hybrid population from the intergradation zone between *M. m. migrans* and *M. m. lineatus* (51, 56). Lindholm and Forsten (57) were aimed at subspecies determination of Black Kites in Altai Krai (Barnaul area) and Altai Republic (area of Kosh-Agach) according to morphological features. They found that birds in the lowlands of Altai Krai, on average, were different from those in the higher

country of the Altai Republic. Black Kites from the lowlands of Altai Krai had some features of *M. m. migrans* (i.e., birds originated from the intergradation zone between *M. m. migrans* and *M. m. lineatus*). Black Kites from Altai were quite similar to the easternmost typical *lineatus* and were placed in that taxon (i.e., *M. m. lineatus*). This conclusion fits well with our observations, and it is consistent with our *cytB* haplotype results. We consider Black Kites tagged in Byisk as birds from the intergradation zone between *M. m. migrans* and *M. m. lineatus* and Black Kites tagged in Kosh-Agach as birds belonging to *M. m. lineatus*. Deep genomic study of Black Kites from various parts of their breeding area is needed to solve the genetic structure of their populations and hence, their species/subspecies status.

Raptors of several species were observed to migrate across the Himalayan region, and based on all data available, there were characterised four movement patterns of raptor migrating in this area: 1) Western Circum-Himalayan Corridor, 2) Eastern Circum-Himalayan Corridor, 3) East-to-West Southern Corridor and 4) Trans-Himalayan Corridor (43). We demonstrated that Black kites from Biysk (birds from intergradation zone between *M. m. migrans* and *M. m. lineatus*) used Western Circum-Himalayan Corridor and Black Kites from Kosh-Agach (*M. m. lineatus*) used Trans-Himalayan Corridor. Birds shared wintering ranges in the Indian subcontinent from both populations. We consider that the genetic background of the migration behaviour of Black Kites is strong, and the uniform behaviour of tracked birds from both studied subpopulations with different genetic history supports this hypothesis (see also Sergio et al. (17)). Nevertheless, variable routes of raptors (Peregrines, *Falco peregrinus*) migrating from Siberia to South Asia were demonstrated even if they had the exact genetic origin (58). Peregrines from a relatively small area close to the Popinga River, northern Siberia, used Western Circum-Himalayan Corridor (to winter in south Pakistan), Eastern Circum-Himalayan Corridor (to winter in Myanmar), and Trans-Himalayan Corridor (to winter in north India and Bangladesh).

Bird (including Black Kites) migration over high altitudes in the Himalayas

High-altitude flights of birds over the Himalayas is a highly challenging feat of performance underpinned by several specialised physiological traits. Flapping birds like Bar-headed Goose (*Anser indicus*) and Ruddy Shelduck (*Tadorna ferruginea*) can reach high altitudes during their migration across the Himalayas and Tibetan plateau because they can support the metabolic costs of flight as the low-density air becomes extremely hypoxic (59, 60). Like other migrating (soaring) birds, they may occasionally use updraft wind assistance to help offset flight cost (61). However, they experience periods of intense flapping flight that require extremely high heart rates, wing-beat frequencies, and metabolic power, such as during level flight at high elevation or during climbs that are not assisted by wind (59, 62). Bar-headed Geese can pass over the Himalayas in one day, typically climbing between 4000 and 6000 m in 7–8 hours, with a majority of climbing flights occurring during the night and early morning (63). Bar-headed Geese and Ruddy Shelducks fly up to 6443 m and up to 6800 m altitudes, respectively, but more commonly, both species remain below 5600 m (60, 62). Birds of both species selected an optimum flyway to avoid peaks and higher speed winds (they did not fly in specific wind speeds or directions during migratory flights or climbs) (60, 63). Bar-headed Geese typically travel through valleys of the

Himalayas and not over summits. Their maximum flight altitudes were 7290 m, and 6540 m for southbound and northbound individuals, respectively (61), Autumn migration of Bar-headed Geese breeding in Qinghai Lake, China and wintering in Indian lowland lasted for 50–90 days, and on their routes, the geese used 3–4 stopover sites in wetlands at Tibetan plateau and crossed the Himalayas in approx. 6000 m altitude (64).

Recently, it was revealed that most of the ducks wintering in India pass over the Himalayas (65). Flapping ducks as Eurasian Wigeon (*Anas penelope*), Gadwall (*Anas strepera*), Northern Pintail (*Anas acuta*), Northern Shoveler (*Anas clypeata*), and Garganey (*Anas querquedula*) usually flew overpasses at altitudes of 5070 m (Niti Pass) and 4310 m (Nathu Pass). However, they were able to reach altitudes up to 6830 m (Northern Shoveler) and 6930 m (Garganey). Before flying over the Himalayas, the ducks stopped at wetlands to replenish their fat reserves. Other flapping birds like Demoiselle Cranes (*Anthropoides virgo*) and some waders can also cross the Himalayas in high elevations during migrations. One tagged Demoiselle Crane avoided the Himalayas on its migration to the south from its summering range in Kazakhstan, and it flew using a western route over Hindu Kush, Pamirs, and Tien Shan wintering ground in India, three other Cranes, tagged in Mongolia, passed the Himalayas at elevations over 5000 m. They crossed the Tibetan Plateau within three days to reach wintering grounds in Indian lowland (66). Using geolocators and satellite tracking devices, it has been very recently demonstrated that waders Common Redshank (*Tringa totanus*) and Whimbrel (*Numenius phaeopus*) could also directly fly over the Himalayas on their migration (Li et al. 2020). Common Redshanks were flying at altitudes of potentially 3000–5000 m. Both Redshanks and Whimbrels benefited from wind assistance during migratory flights. The study suggested that the Himalayan mountain range may be less of a barrier than assumed.

Raptors are large or medium-sized land birds that primarily use soaring-gliding flight during migration (67). Soaring (up draught-assisted non-flapping flight) is an energetically efficient form of flight, and many long-distance migrants are so-called obligate soaring migrants (43). Up draught necessary for soaring flight includes thermals (pockets of warm rising air) and deflection (orographic) updraughts that occur when horizontal winds strike surface discontinuities, including mountains. The high-altitude terrain of the Himalayas precludes this type of pathway, and hence it is used by raptors (43). However, some raptors, especially falcons, use flapping flight on their migration across the Himalayas (58). Unfortunately, detailed studies using telemetry devices on raptors crossing the Himalayas are scarce. A study aimed at the Steppe Eagle (*Aquila nipalensis*) revealed that a bird tagged on a nest in Mongolia migrated to winter in a mountainous area in Uttarakhand State, India (68). It flew during migration up to 200 m relative to the ground, occasionally reached more than 1600 m. The highest altitude recorded was 7200 m asl. The altitude of the roost site on the day before the crossing of the Great Himalayas was 4630 m, and after the crossing, the eagle roosted at 4530 m.

We can compare our results mainly with a recent study aimed at Black Kites fitted with telemetry loggers in Delhi, India (42). It seems that Black kites tagged in Delhi originated, similarly like in our study, to two different populations: birds that used the Western Circum-Himalayan Corridor may belong to Black kites originating from the intergradation zone between *M. m. migrans* and *M. m. lineatus*, birds that used

Trans-Himalayan Corridor may belong to *M. m. lineatus*. Migration routes of these birds were distinct in our study as well as like in a study by Kumar et al. (42). The birds originating from Upper Altai (Kosh-Agach) crossed the Himalayas over Tian Shan Mts, Taklamakan Desert, and Karakoram Mts like the main portion of Black Kites tagged in Dehli.

These birds crossed the Himalayas in extremely high elevation up to 6 281 m asl and travelled long periods at elevations above 3500 m. Birds flew across the Himalayas for two days with a single stop to roost at elevations between 1 644 to 5 448 m asl.

It seems that Black Kites crossing the Himalayas may have physiological adaptations that remain to be investigated. They fly and, moreover, stay for hours resting at night in the environment of mountains at altitudes over 5000 m with variable wind speed and direction, where the air density and partial pressure of oxygen is roughly half of that at sea level (59, 69). At the same time, the temperature can be very low, well below freezing year-round, which could require additional metabolic energy for thermogenesis. Maintaining water balance during flight should also be a major challenge in the dry air at high altitudes (59, 69).

Behavioural flexibility of immature Black Kites to stay somewhere in summer

Tagged Black Kites *M. m. migrans* from Europe wintered in sub-Saharan Africa north of the equator throughout the belt from Senegal and Gambia to Ethiopia in East Africa (18). Some of these Black Kites remained in tropical Africa during their first summer. Other birds moved north but to substantially lower altitudes than those of their natal areas. During the second year, all tagged Black Kites *M. m. migrans* wintered again in tropical sub-Saharan Africa. Their summer quarters were located north of the winter quarters, but no birds stayed during the summer in the natal areas. One tracked bird returned to its natal area and bred at the age of three years. Immatures Black Kites *M. m. migrans* stayed in summers in areas used for wintering or somewhere between winter quarter and natal areas. Surprisingly, no such behaviour was observed in tagged Black Kites from western Siberia, no matter if these birds originated from the population in Biysk or Kosh-Agach. These Black Kites regularly returned from wintering quarter in Indian Subcontinent to natal areas or more north to stay there in summer. It seems that high behavioural flexibility is apparent during summer stays of immature Black Kites.

In a previous study, Kumar et al. (42) reported that home ranges of Black Kites fitted with telemetry loggers in Dehli were larger during the breeding season than home ranges during the nonbreeding season using KDE 99% for the home range calculation. Our paper used for the home range size calculation KDE 95%. Unlike Kumar et al. (42), we found no difference in the size of the home range during the breeding and nonbreeding seasons.

Environmental influence on migration

Route configuration of Black Kites crossing the Himalayas seemed to be shaped by dominant wind support and barrier avoidance (42). Black Kites perform circular soaring in areas of higher predicted

thermal uplift and linear soaring in areas of higher predicted orographic uplift velocity (70). During the pre-breeding flight over Himalayas birds tend to fly parallelly along with the mountain ranges, through the mountain valleys using the up-lifting anabatic winds for soaring up to high altitudes and gliding with the possible strong south valley tailwinds (71). During the period of pre-breeding migration (from the end of April to the beginning of May, which correspond to the timing of spring migration of tagged Black Kites) with the warmest and driest surface condition, great ascending thermals are forming, creating a great opportunity for soaring birds to glide over Himalayas (72). While flying north along the mountain ridges, side wind, that mostly blows from the west (71), can break over the ridge creating a lee wind perpendicular to bird direction, that may have a negative effect on the birds' speed as the bird has to angle towards the sidewind (as shown by our results). In contrast with the pre-breeding Himalayas flight over, during the post-breeding Himalayas flight over birds tend to fly directly across the mountain ranges.

We assume that birds used thermals to stay as high as possible to glide along or against the lee winds to avoid the strong headwinds of the valley breeze (71). We found that Black Kites increased more their ground speed and less their airspeed when tailwinds prevailed. For soaring migrants, reducing airspeed under tailwinds allows the birds to attain low sink rate and by that to cover larger distances while decreasing the risk of reaching the ground or switching to energy-expensive flapping flight (73). However, during pre-breeding Himalayas flight over, birds noticeably increased their airspeed even during strong tailwind. We assume that this behaviour is caused by the abundance of great ascending thermals. Birds can therefore afford to increase their airspeed on the expense of higher sink rate in order to quickly pass the Himalaya barrier. We moreover found an asymmetric response of the birds to side wind, compensating when flying north towards the summer ground and drifting when flying south heading the winter quarters. Groundspeed increased in relation to side wind from the west during the post-breeding flight over and under easterly side wind during pre-breeding flight over. Bird response to crosswind was asymmetrical in relation to side wind and flight direction.

Effect of favourable weather conditions on the spring (pre-breeding) migration support our results. We found the spring migration to be significantly shorter in comparison with autumn (post-breeding) migration. Duration of the Himalayan flight-over was found to be the same, although the groundspeed was higher in pre-breeding flight-over, meaning that birds flying over the Himalayas on their way from winter quarters had a higher speed relative to the ground. Birds had similar speed relative to the air during both flight overs. Hence the wind played a major role in the overall speed during the flight-over. For aerial migrants, wind support can reduce both energy and time cost of migration considerably (74). A stronger tailwind that increases the birds' speed eases the Himalaya flight-over. Birds are less exhausted from the Himalayas flight over and arrive at summer destination much faster. During autumn migration, the weather conditions were less favourable, which reflected in the number of days spent in stopovers (mainly by the foothills of the Himalayas) and the overall duration of migration.

High behavioural flexibility of Black Kites to surmount environmental obstacles

The challenging environmental obstacles for Black Kites *M. m. migrans* migrating to winter in Africa are crossing large water bodies (35). Most migrating Black Kites *M. m. migrans* are reluctant to fly over large water bodies and cross transcontinental boundaries over the Strait of Gibraltar, the Bosphorus Strait, the Dardanelle Strait and the Bab-al-Mandeb Strait (6, 18, 75). However, some birds use unusual routes of migrating over large water bodies of the Mediterranean Sea and the Black Sea from Europe to Africa and from Europe to the Middle East. Raptors perform a soaring-gliding flight behaviour exploiting rising thermals and ridge lifts overland to reduce energetic expense. However, during migration, when crossing large water bodies, thermal updrafts are weak, and birds mainly use flapping (powered) flight, increasing both energy consumption and mortality risk (67). Black Kites crossing the large water bodies have to use flapping flight (18, 35). All routes over large water bodies are suboptimal for Black Kites, and they are supposedly used only by a minority of Black Kites originating from Europe since, for some of them, this route could be fatally unsuccessful (18). From this perspective, unusual observations of Black Kites on islands in the Atlantic Ocean, far from breeding territories and usual migration routes, are remarkable (76–78). One case of a long journey over the Red Sea was facilitated by the transport of the bird on board a cargo ship (27).

The challenging environmental obstacles for Black Kites *M. m. lineatus* migrating to winter in Indian Subcontinent is the crossing of the main Himalayan ridge, which was discussed above. It seems that the vast breeding territory of Black Kites in the Palearctic realm is connected with the unusual behavioural flexibility of Black Kites to surmount various environmental obstacles on their migration routes.

This high behavioural flexibility may also elucidate a new important wintering area for Black Kites in the Middle East. Black Kites with *M. m. lineatus* features were recorded for the first time in the Levant area in Syria (and perhaps also in Lebanon) during the beginning of the second half of the twentieth century (79, 80). Novel observations of the communal roosting of Black Kites during the winter months have been reported in south-eastern Europe, Egypt, and Turkey; however, their taxonomic subspecies status was not mainly investigated (81–86). Now, the Black Kite is the most common wintering raptor in Israel, and a proportion of kites wintering in Israel showed morphological characteristics of *M. m. lineatus*, likely representing the western outpost of wintering *M. m. lineatus* (87). Alternatively, these individuals may comprise birds from the broad intergradation zone between *M. m. migrans* and *M. m. lineatus* (88). It now appears that Black Kites with *M. m. lineatus* features supposedly originated from a large intergradation zone between *M. m. migrans* and *M. m. lineatus* can be found anywhere in Europe west of Russia (16). Recent data on numerous wintering of Black Kites in Georgia in an area of the Black Sea Basin correspond well with these data (89). Moreover, Black Kites with *M. m. lineatus* features can be found migrating from southern and eastern Africa as documented in South Africa on 3 November 1972 and Ethiopia on 18 November 2011 (90, 91). No significant environmental obstacles seem to complicate the migration of these Black Kites with features of *M. m. lineatus* (birds supposedly originated from the intergradation zone between *M. m. migrans* and *M. m. lineatus*, preferably from the European part of Russia).

Conclusion

By telemetry research and DNA analyse of Black Kites from Western Siberia we found differences in subpopulations of Black Kites from Upper Altai close to Kosh-Agach and Black Kites from Biysk, pointing at the intergradation zone between *M. m. migrans* and *M. m. lineatus* and revealing their migration routes. Black Kites *M. m. lineatus* migrating to winter in Indian Subcontinent are challenged by the crossing of the main Himalayan ridge. They fly and roost in the environment of mountains at altitudes over 5000 m in unfavourable weather conditions. They show a flexible response to the wind direction which helps them to overcome the environmental obstacle. Unusual behavioural flexibility of Black Kites to surmount various environmental obstacles on their migration routes seems to be connected with vast breeding territory and may also elucidate a new important wintering area for Black Kites. What is more, Black Kites crossing the Himalayas may have physiological adaptations that remain to be investigated.

Abbreviations

KDE – kernel density estimate, PFA – post fledging area, TSA – temporary settlement area, DEM – digital elevation model, GPS – global positioning system, SMS – short message service, GSM – groupe special mobile, PCR – polymerase chain reaction., LMM – linear mixed model.

Declarations

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Ethics approval and consent to participate

Black Kite trapping and tagging were approved by ...

Consent for publication

Not applicable for the section.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

IL, IVK, NGA, SVV conducted the field work including birds tagging. IL and JS wrote that paper and conducted the data analyses with guidance from all co-authors. The authors read and approved the final manuscript.

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Tables

Due to technical limitations, table 1-6 is only available as a download in the Supplemental Files section.

Figures

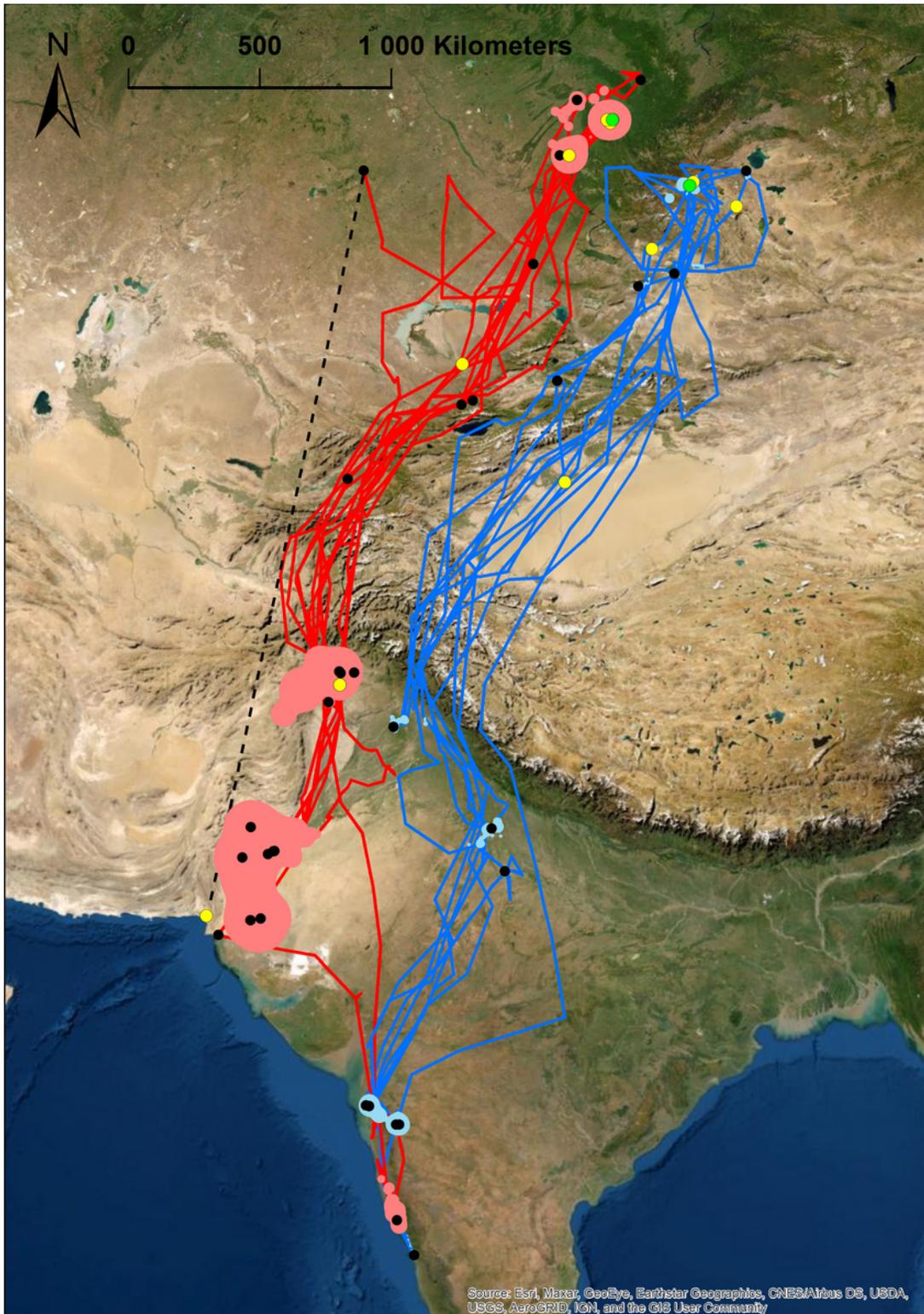


Figure 1

Migration routes and pre-breeding and post-breeding home ranges of Black Kites tagged in Biysk (red lines and rose polygons) and Kosh-Agach (dark blue lines and light blue polygons). Black dots represent temporary settlement areas. Green dots represent natal nests, yellow dots represent last recorded positions. Black dashed line represents the link between positions of K5 before and after a gap in data collection.

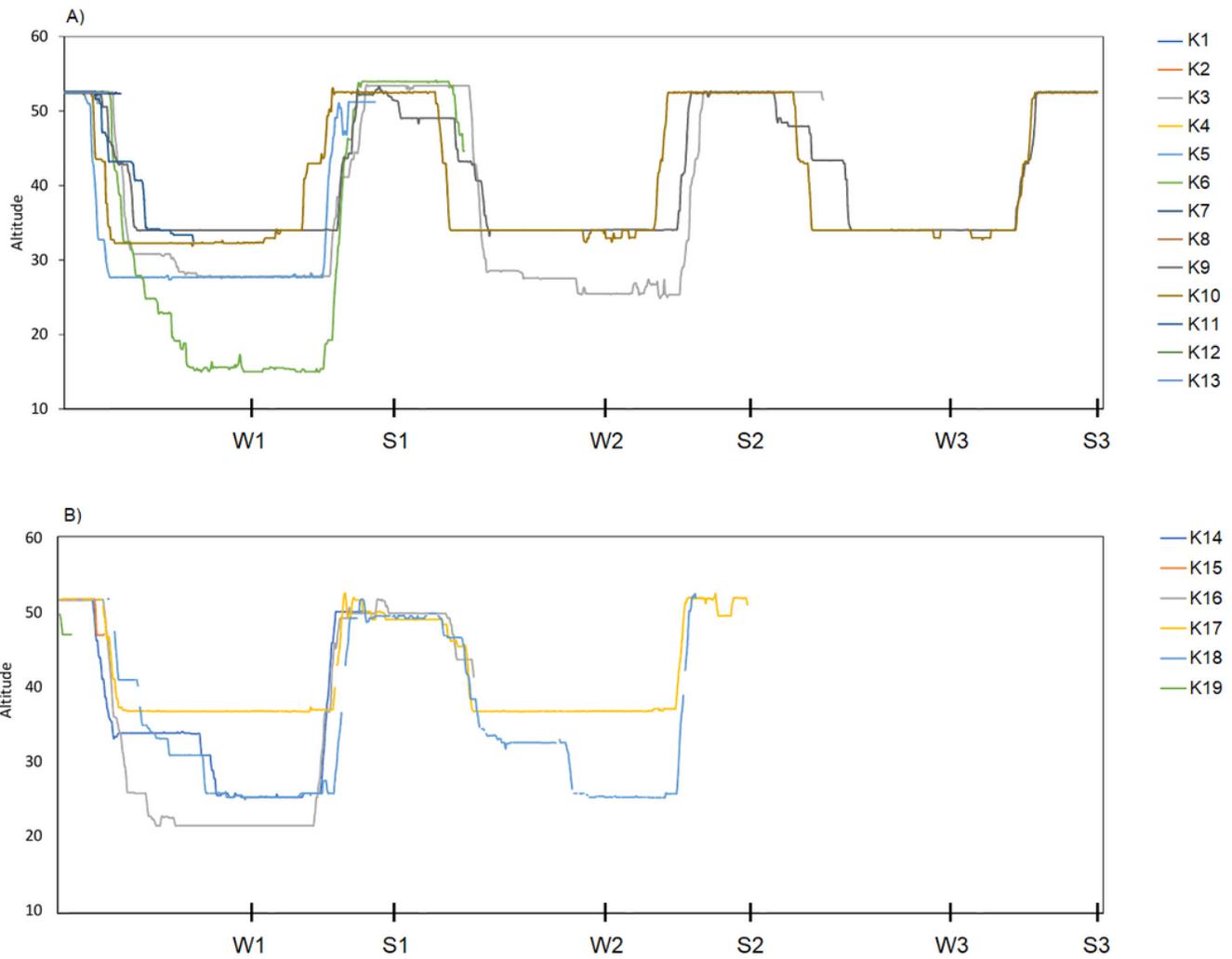


Figure 2

Latitudinal occurrences of tracked Black Kites throughout their lifespan. W1, W2 and W3 refer to the location of birds on 31 January in 2cy, 3cy and 4cy, respectively; S1, S2 and S3 refer to the location of birds on 30 June in 2cy, 3cy and 4cy, respectively. A, Black Kites from Biysk (lowland in southwestern Siberia); B, Black Kites from Kosh-Agach (Upper Altai).

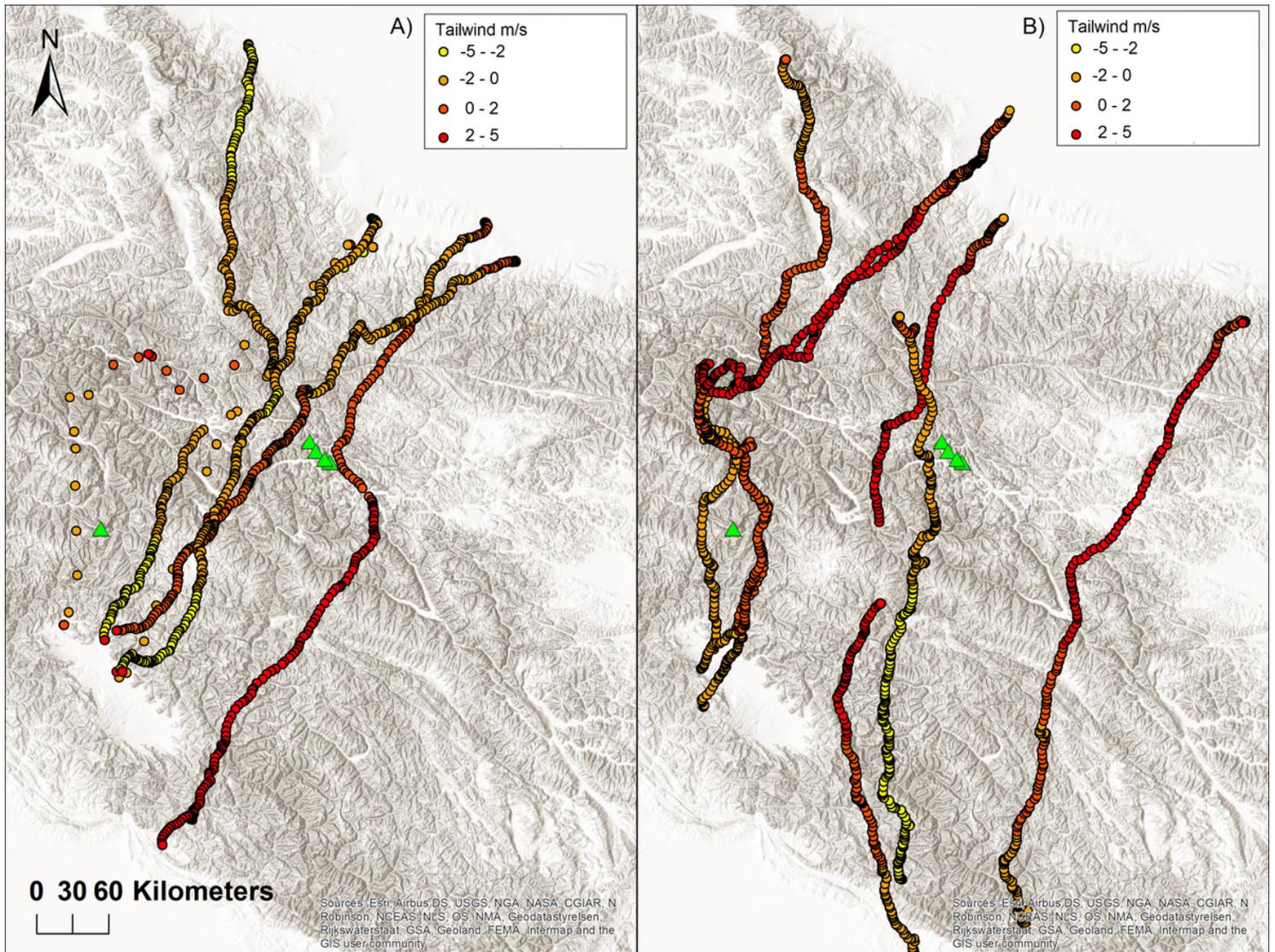


Figure 3

Elevation profile of lifelong journeys of tracked Black Kites. Green dots represent the nest, red dots represent highest roost points during migrations, yellow dots represent the last position collected due to the death of birds or signal loss, blue dots represent the last position collected of living birds. For W1, W2, W3 and S1, S2, S3 see Fig. 2

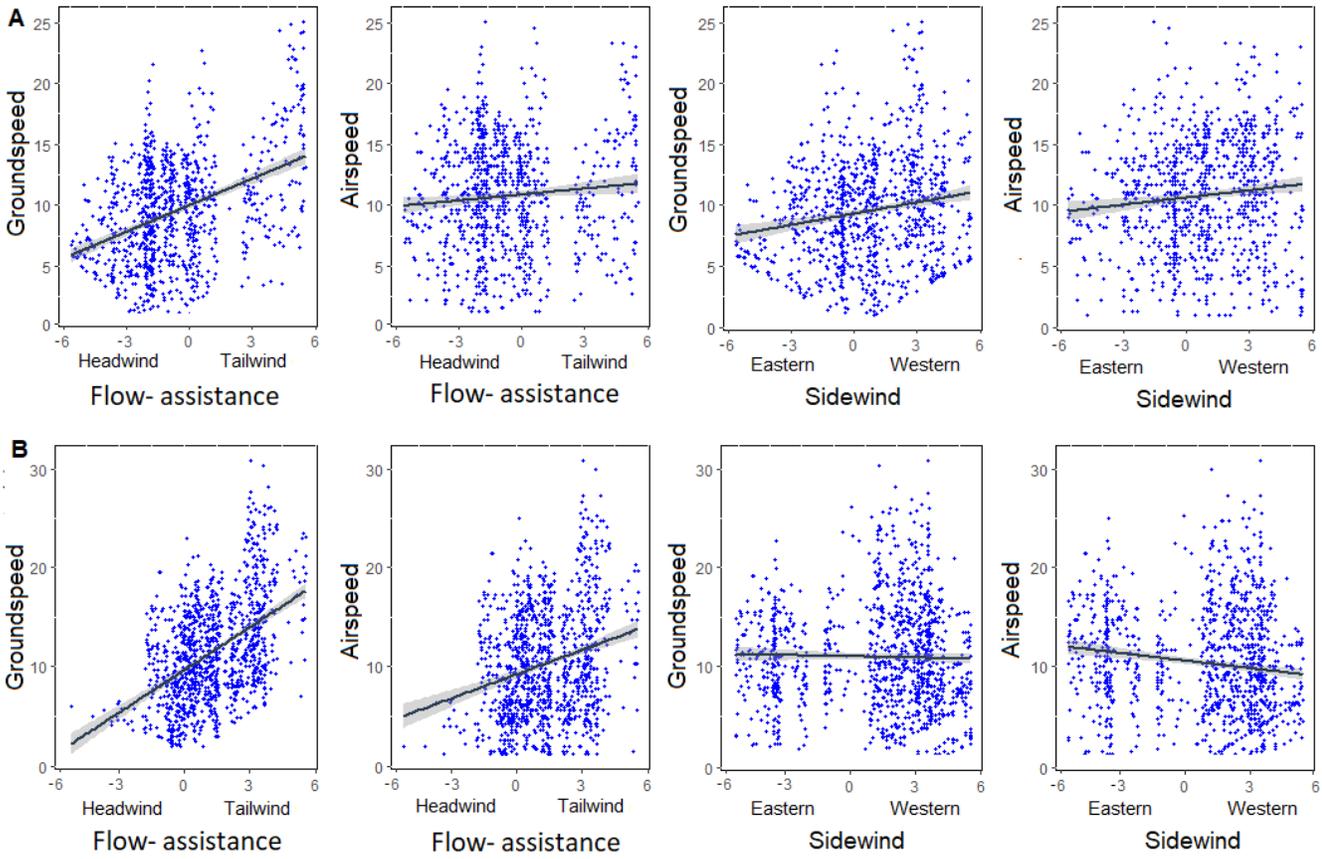


Figure 4

Post-breeding (A) and pre-breeding (B) flight over the Himalayas in relation to tailwind speed. Green triangles represent mountain peaks over 8 000 m.

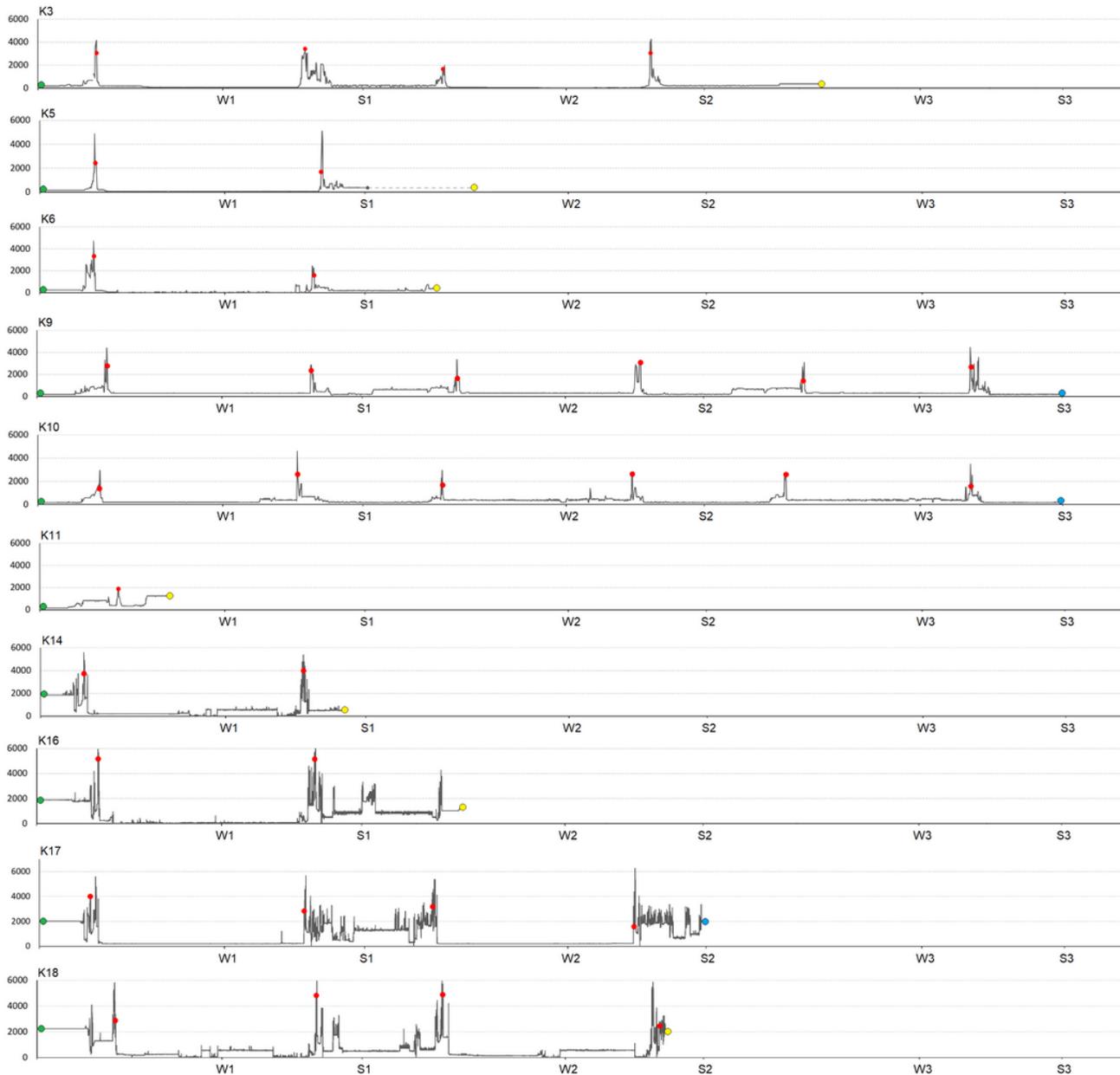


Figure 5

Black Kites groundspeed and airspeed fitted with linear regression lines (grey areas 95% CI) in relation to side wind and flow-assistance during the post-breeding (A) and pre-breeding (B) flight over the Himalayas.

Supplementary Files

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