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C : O (*Ciconia boyciana*)

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Abstract

Background: The Oriental Stork (, ò. , . ò.) breeds in southeastern Siberia and parts of northeast China, and winters mainly in southeast China. Although the autumn migration pattern of Oriental Storks has been previously described, di□erences between spring and autumn migration travel speed in relation to wind assistance were unknown.

Methods: Using GPS/GSM transmitters, we tracked the full migrations of 18 Oriental Storks during 2015–2018 to compare di□erences in autumn and spring migration patterns, and combined the satellite telemetry data with the National Center for Environmental Prediction Reanalysis data to explain the relationship between 850 mbar wind vectors and seasonal di□erences in travel speed.

Results: Di□erences in tailwinds contributed to significant di□erences in daily average Oriental Storks travel speed in spring (258.11 ± 64.8 km/day) compared to autumn (172.23 ± 49.7 km/day, < 0.001). Storks stopped significantly more often in autumn than spring (1.78 ± 1.1 versus 1.06 ± 0.9, < 0.05), but stopover duration (15.52 ± 12.4 versus 16.30 ± 15.1 days, respectively, = 0.3) did not di□er significantly. Tailwinds at 850 mbar pressure level (extracted from the National Center of Environmental Prediction Reanalysis data archive) significantly a□ected daily flying speed during spring and autumn migration. Tailwind conditions in spring (mean 4.40 ± 5.6 m/s) were always more favourable than in autumn when they received no net benefit (0.48 ± 5.6 m/s, < 0.001). Despite mean spring migration duration being less than autumn (27.52 ± 15.9 versus 32.77 ± 13.4 days, = 0.17), large individual variation meant that this duration did not di□er significantly from each other.

Conclusions: For long distance migratory soaring birds (such as storks), relative duration of spring and autumn migration likely relates to the interaction between imperative for earliest arrival to breeding grounds and seasonal meteorological conditions experienced en route.

Keywords: , ò. , . ò. , GPS/GSM tracking, Migration, Tailwind, Travel duration, Travel speed

Background

at weather conditions a ect the timing and flight behaviour of long-distance bird migration is well known (Shamoun-Baranes et al. 2017; Becciu et al. 2019). For instance, the migration of large terrestrial soaring birds may be a ected by local atmospheric conditions, as it is known that they prefer to use thermals to gain altitude before they glide towards their destination (Norberg

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2012). However, of all atmospheric conditions, wind has perhaps the greatest e ect on migration of birds (Liechti 2006; Mellone et al. 2012; Safi et al. 2013; Rotics et al. 2016; Vidal-Mateo et al. 2016). For example, Becciu et al. (2018) found that soaring birds exploit tailwinds to move faster, confirmed by Shamoun-Baranes et al. (2003) who showed the migration ground speeds of White Storks (*Ciconia ciconia*) increased with tailwinds in both spring and autumn, but that this decreased in headwinds. Moreover, migration intensity also increases in tailwind conditions (Erni et al. 2002; Fox et al. 2003; Becciu et al. 2019), even within seasons at the same site in response to di erent wind directions (e.g. Desholm et al. 2014).

Several studies have attempted to analyse relationships between weather factors at fixed locations (such as meteorological stations) and the migration of large soaring birds. Although not all studies have revealed an impact of wind on migration (for example, wind had no e ect on Osprey *Pandion haliaetus* migration; orup et al. 2006), many studies show selection for prevailing winds by large birds on, or about to undertake migration (Allen et al. 1996; Spaar and Bruderer 1996; Meyer et al. 2000).

As large, heavy soaring birds, storks are known to exploit tailwinds to aid their long distant movement (Becciu et al. 2018). Although the linkages between wind and migration are well studied for some species (Shamoun-Baranes et al. 2003; Vansteelant et al. 2015; Rus et al. 2017), no study has compared contrasting seasonal wind assistance on spring versus autumn migration of Oriental Storks (*Ciconia boyciana*), which is listed as an IUCN Endangered species (IUCN 2018). Despite a rich literature relating to the relative speed of spring versus autumn migrations (e.g. Alerstam and Hedenstrom 1998; Nilsson et al. 2013), there remain relatively few studies of the relative contributions of seasonal wind assistance to the speed and duration (i.e. the time taken to migrate between the breeding and wintering grounds) of spring and autumn migrations (e.g. Koelzsch et al. 2016). To address the knowledge gap for the Oriental Stork we therefore here present a study comparing the di erential e ects of wind parameters on a soaring bird during spring and autumn migration episodes.

e Oriental Stork has an estimated population of *c.* 3000 individuals and breeds along the Russia-China border, primarily in the Heilongjiang and Ussuri River basins and winters mainly in the middle and lower Yangtze River Floodplain in China (Wang and Yang 1995; Barter et al. 2004). Shimazaki et al. (2004) were the first to describe autumn migration timing and routes, breeding, staging and wintering areas of Oriental Storks based on 13 birds tracked using satellite telemetry during period 1998–2000. We here combine our own telemetry data from 18 instrumented Oriental Storks with modelled multi-year macro-scale wind patterns to understand seasonal di erences in migration strategies of the Oriental Stork by comparing the di erences in spring and autumn migration, and try to explain the observed seasonal differences in travel speed due to di erential tailwinds.

Methods

Animal capture and GPS tracking

We caught 18 juvenile Oriental Storks in Honghe National Nature Reserve (47° 47′ N, 133° 40′ E), Heilongjiang Province, China, during 2015 to 2018 (for full details see Additional file 1: Table S1) and equipped them with waterproof solar-charged battery-powered backpack mounted GPS transmitters. Devices recorded their latitude and longitude every 60–180 min (horizontal accuracy 9.6 ± 5.6 m SE in field tests, see Additional file 2: Supplementary Methods for full details) with date and time stamp, transmitted from the on-board memory every 8 to 24 h through the mobile phone network, for retrieval and analysis. All birds completed one autumn migration and the subsequent spring migration back to the summering areas, which form the basis for 36 individual migration episodes analysed here.

Segmentation of movement bouts to identify migration/stopover periods and sites

We used the methods described in Wang et al. (2018) to segment movement tracks into “fly” and “non-fly”, then we visualized the movement using Google Earth to pinpoint the arrival and departure time at each site. We define the cluster of non-fly durations of more than 48 h as a stopover (Koelzsch et al. 2016). Based on these movement segmentations, it is possible to establish arrival and departure time at breeding and wintering grounds, as well as stopover sites along the migration route. We calculated migration distance as the cumulative distance flown by each individual between the point of departure from breeding/wintering area to the point of arrival at wintering/breeding area, excluding local movements within the stopover sites. We estimated migration duration as the time taken between the point of departure from breeding/wintering area to the point of arrival at wintering/breeding area. We extracted the number of stopovers made by each individual and calculated the cumulative time spent at all of these during a single migration as stopover duration. Finally, we subtracted stopover duration from migration duration to obtain travel duration and divide migration distance by travel duration to derive travel speed.

Within each flight segment, distance travelled (km) was calculated from one point estimate to the next as the great circle distance between data points. Because the time between successive reliable location estimates

varied, we divided the distance between successive points by the time interval between them to calculate the flying speed at each point.

Meteorological data and calculations

In order to determine the degree of head and tail winds experienced by storks along their migratory journey, we generally followed the methods of Shamoun-Baranes et al. (2003). We used wind data at a pressure level of 850 mbar, obtained from the National Center of Environmental Prediction (NCEP) Reanalysis data archives. ese data have the advantage of being modelled at high spatial and temporal resolution across the entire globe based on actual real time observations, so data values are divided into four quality classes, dependent upon the relative degree of influence from observations or the model (Kalnay et al. 1996). e 850 mbar U and V wind components (i.e. instantaneous wind speed along the latitudinal and longitudinal orientations, respectively) used here are the most reliable of the generated variables. Although data can be accessed over specified spatial and temporal scales, we interpolated these data to points in space and time to coincide with stork movements. Data were extracted using R package "RNCEP" (Kemp et al. 2012), which contains functions to retrieve, organize, and visualize weather data from the NCEP/NCAR Reanalysis and NCEP/DOE Reanalysis II datasets.

Examination of the cumulative diurnal distribution of instantaneous flying speeds showed that Oriental Storks travel exclusively during daylight and roost at night, moving almost exclusively between 09:00 and 18:00 local time and that flying speed peaked at 14:00 local time (8 h ahead of UTC, see Additional file 1: Fig. S1). We confined our analysis to Oriental Storks flying at speeds greater than 4 m/s (Bengtsson et al. 2014) between 09:00 and 18:00 local time. In order to reduce variance in speed in relation to time of the day, or when several hours passed between reliable GPS locations, we estimated average daily flying speed between 09:00 and 18:00 local time. Average daily flying speed was calculated as the mean of all flying speeds from 09:00 and 18:00 local time each uesp07r daily

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days; Fig. 3b) or stopover duration (16.30 ± 15.1 days versus 15.52 ± 12.4 days; Fig. 3d). However, Oriental Storks travelled significantly faster in spring (258.11 ± 64.8 km/day versus 172.23 ± 49.7 km/day; Fig. 3e), taking significantly less time travelling between wintering and breeding grounds than in autumn (10.99 ± 4.7 days versus 16.85 ± 7.9 days; Fig. 3e–f). Number of stopovers di ered significantly (1.06 ± 0.9 versus 1.78 ± 1.1; Fig. 3c), but since most birds stopped once during either season, the di erence is likely ecologically unimportant.

Daily flying speed was significantly related to tailwind at 850 mbar (GAM: df = 1.925, $F = 115.7$, $r^2 = 0.399$, $p < 0.001$, Additional file 1: Fig. S2). e di erence in seasonal tailwind was significantly related to the di erence in seasonal daily flying speed (GAM: df = 8.899, $F = 21$, $r^2 = 0.928$, $p < 0.001$, Fig. 4). e di erence in tailwind strength could explain the di erence of daily flying speed between spring and autumn migration. ere was a significant di erence between daily flying speed during tailwinds (34.28 ± 10.3 km/h) versus headwinds (22.74 ± 5.0 km/h, Wilcoxon signed-rank test: $p < 0.001$, Fig. 3h). ere was also a significant di erence between mean tailwind speed in spring (4.40 ± 5.6 m/s, significantly greater than zero, based on single sample *t*-test $p < 0.001$) compared to autumn (0.48 ± 5.6 m/s, independent *t*-test: $p < 0.001$, Fig. 3g, note that this latter value did not significantly di er from zero based on single sample *t*-test $p = 0.15$).

Discussion

e benefits of migrating with tailwinds have been widely reported in other large bird species, such as Honey

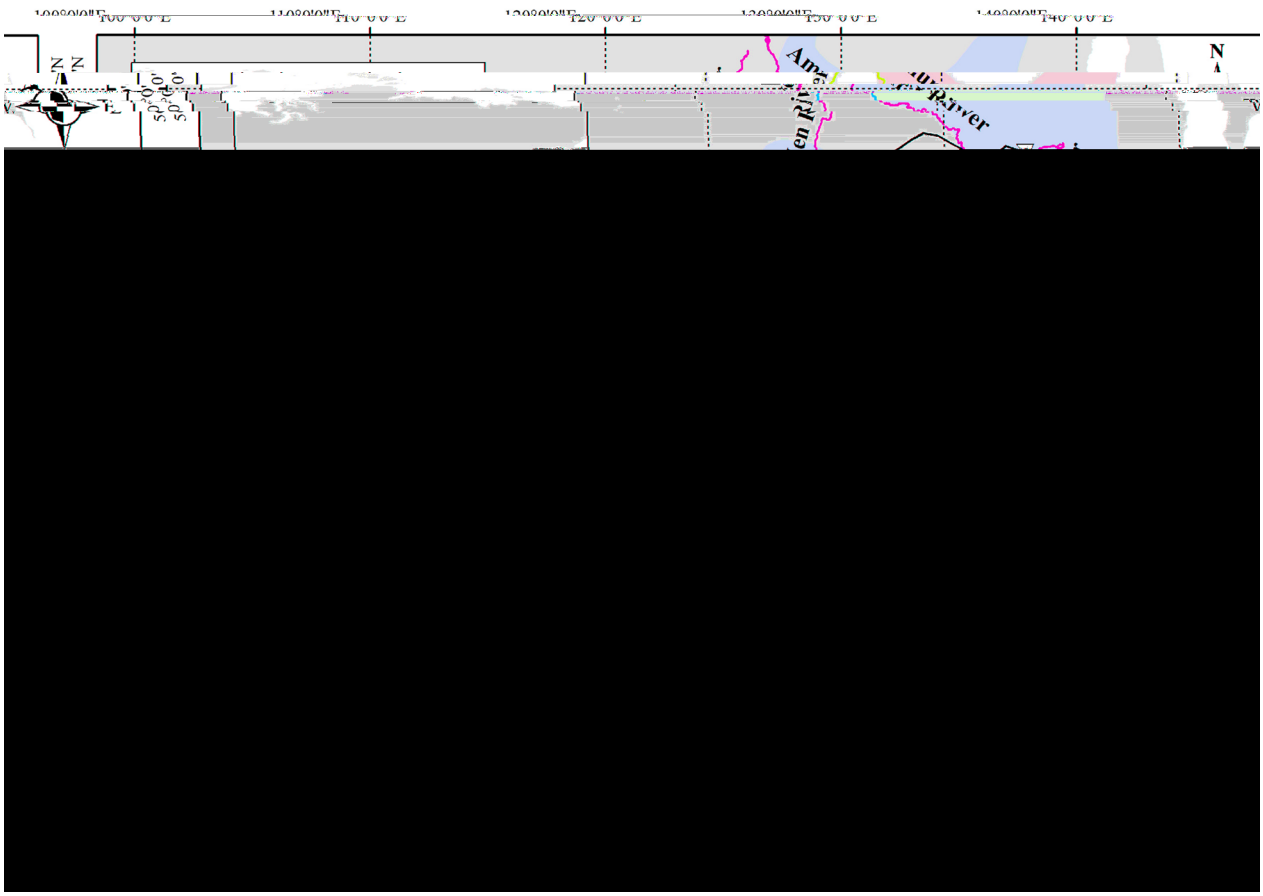

Fig. 2 Individual spring migration routes and stopover sites of 18 Oriental Storks (ò. ò.) derived from GPS/GSM telemetry devices. The distribution of breeding area and non-breeding area from BirdLife International

autumn. It is of course important to stress that our findings are from young Oriental Storks (which do not breed in their first year), and the behaviour of adults may be different from first year birds. In other species, age specific di erences in migration schedules have been demonstrated, usually becoming more similar to adult migration patterns with age (Hake et al. 2003; Mueller et al. 2013; Sergio et al. 2014). Generally, in large-bodied birds, males arrive earlier than females, which may reflect their need to secure a breeding territory (Rotics et al. 2018), but in our study we could not distinguish between the sexes and territorial defence was not relevant.

We found tailwind assistance explained seasonal differences in daily Oriental Storks flying speed. e tailwind strength (850 mbar) had a significant e ect on daily flying speed both in spring and autumn migration, but because tailwinds were on average stronger in spring (4.40 ± 5.6 m/s) than in autumn (0.48 ± 5.6 m/s when storks e ectively gained no net benefit from tailwinds throughout migration), spring daily travel speed was faster than in autumn. Liechti et al. (1996) found that the average ground speed of White Storks migration in southern Israel was higher in autumn than in spring, due to a di erence in prevailing tailwinds. Shamoun-Baranes et al. (2003) also found that tailwind had a significant impact on the average migration speed of White Storks in both spring and autumn, but in their study, autumn migration duration was shorter (26.1 ± 4.9 days) than spring (49.1 ± 15.0 days) compared to 32.77 ± 13.4 days and 27.52 ± 15.9 days respectively for Oriental Storks. Because of the large variation in migration duration between di erent individuals, this 5-day di erence failed to attain statistical significance. Shamoun-Baranes et al. (2003) also speculated that wind assistance may explain part of the seasonal di erence in mean migration speed in their European study of White Storks, where prevailing winds in spring were generally less advantageous than in autumn throughout their flyway.

Numerous studies of soaring birds have shown relationships between strength of tailwinds and speed of migratory birds. For example, peak movements or departures of migrants are associated with periods of favourable

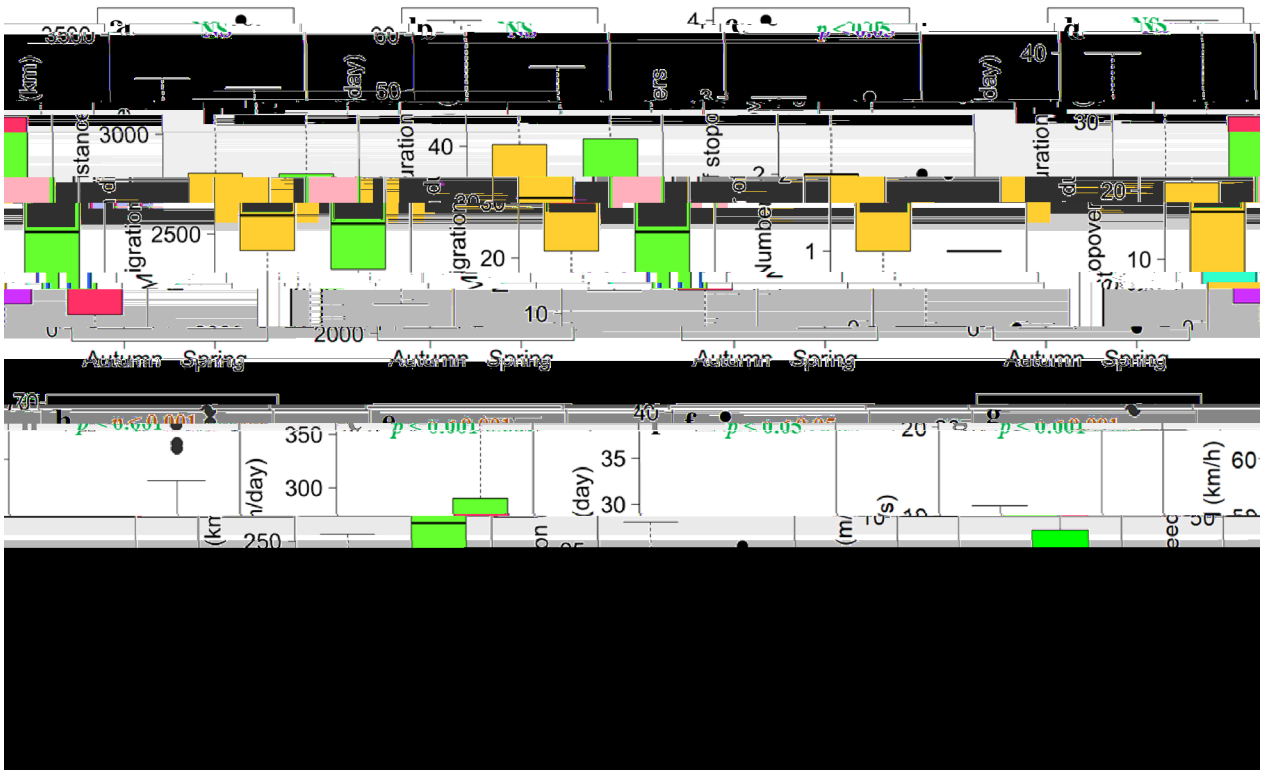

Fig. 3 Box plots (showing median, lower and upper quartiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles and outliers) illustrating the di□erences between spring (green) and autumn (orange) migration parameters of tagged Oriental Storks (, ò. , ò.) during migration. Individual graph plots show: **a** migration distance (km), **b** migration duration (day), **c** number of stopovers, **d** stopover duration (day), **e** travel speed (km/day), **f** travel duration (day). Also shown are **g** mean tailwind assistance experienced in autumn and spring and **h** mean autumn and spring daily flying speed in relation to headwind/tailwind. Probability levels for statistically significant di□erences between autumn and spring migration parameters are shown based on paired -tests and Wilcoxon signed-rank tests, "NS" indicates not significant

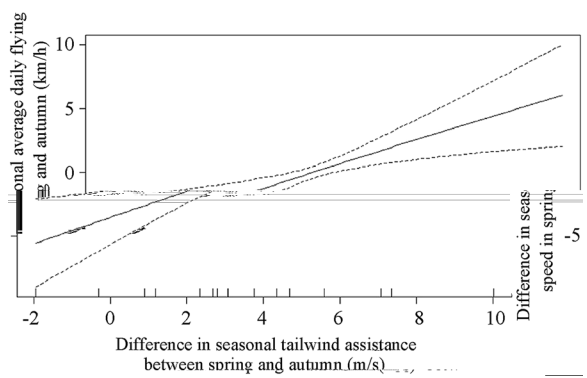

Fig. 4 GAM plot from the best fitting function of the di□erence in seasonal tailwind (-axis) on the di□erence in seasonal average daily flying speed (-axis). The scale of the ˆ -axis reflects the relative importance of covariate in the model. Dashed lines represent two standard error boundaries around the covariate. Vertical lines along the -axis represent a rugplot of data points used in the analysis to show the distribution of data points over the range of the di□erence in seasonal tailwinds

tailwinds (Allen et al. 1996; Spaar and Bruderer 1996; Meyer et al. 2000), while cross-country speeds of Steppe Eagles (*Aquila nipalensis*) increased with the increasing tailwind in southern Israel (Spaar and Bruderer 1996). Hence, wind direction and speed have the potential to substantially a ect daily travel speed (Vansteelant et al. 2015).

Oriental Storks are c. 40% heavier than White Storks (Dunning 2007), although structurally and ecologically they are very similar species. Hence, it seems highly likely that the reversal in relative duration of spring and autumn migration in these two species is linked to the degree and strength of tailwinds to which they are exposed during migration along their respective flyway corridors.

Competition for limited reproductive resources has been recognized as a major factor selecting for earliest arrival of territory holders in spring (Kokko 1999). Both Oriental and White Storks occupy traditional nest sites which can be highly limited in the landscape (Luthin 1987), so the incentive to return to defend such nest sites and their associated feeding territories is likely to favour

the earliest possible return of territory holders in spring, as predicted for such a species (Nilsson et al. 2013). Arrival times at the breeding ground are also negatively correlated with reproductive success in many species, so early avian arrival to breeding grounds ensures benefit from higher territory quality, nesting sites and reproductive success (Møller 1994; Smith and Moore 2005; Gunnarsson et al. 2006; Newton 2008; Janiszewski et al. 2013).

We therefore contend that comparing the duration of spring versus autumn migration in relation to theories about the imperative to arrive first to breeding areas to secure nesting resources is something of a straw man. ere is no doubt that both Oriental and White Storks have a similar imperative to arrive as early as possible to occupy and defend valuable nest sites, yet Oriental Storks show no significant di erence between autumn and spring migration duration, while White Storks take longer to complete spring migration than covering the same distance in autumn. is study and that of Shamoun-Baranes et al. (2003) show both species are dependent upon tailwind assistance to increase the speed of migration and both studies strongly imply that the seasonal headwind/tailwind ratio in spring versus autumn in Oriental and White Storks contributes to the duration of the migration episode.

We believe that the seasonal di erences in the travel speed of Oriental Storks during migration are related to the physical environmental conditions they encounter, which di er in spring compared to autumn. eir faster rate of travel on spring migration can be explained by stronger tailwinds during that season, yet there was no significant di erence in the overall duration of autumn and spring migration. e reason might be because the actual travel duration constitutes a relatively small part of overall migration duration, but the stopover duration (which contributes most to migration duration) showed much larger individual variation in spring than autumn. is seems to contrast with the White Storks, which took far longer to complete spring migration than when covering the same distance in autumn, potentially because of more favourable tailwinds in that season compared with headwinds that are encountered in spring (Shamoun-Baranes et al. 2003). is confirms that long distance soaring migrants may strive to shorten the duration of spring migration to ensure earliest arrival at breeding grounds to ensure territorial defence. However, storks are inevitably forced to migrate under the prevailing meteorological conditions in spring, which may di er radically between different flyway populations, dependent on the peculiar local weather patterns to which they are exposed. is finding also confirms the vulnerability of such populations to changes in prevailing atmospheric conditions under current climate change predictions if the prevailing seasonal wind patterns begin to change in the near future, as predicted that they will. Research indicates that changes in wind caused by global warming may have major impacts in the future (McInnes et al. 2011) which could potentially a ect migrating storks and other large-bodied avian species.

Conclusions

We studied the relationship between tailwind and travel speed of the Oriental Stork for the very first time. Although the autumn migration pattern of Oriental Storks has been described previously, our data are the first to show di erences between spring and autumn migration travel speed in relation to wind assistance. e results showed that the daily flying speed of Oriental Storks was seasonally a ected by di erences in the benefit gained from tailwinds throughout the migration episodes, which predictably di ered between spring and autumn.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40657-020-00196-8.

Additional le 1: Table S1. Summary table of details of 18 first year Oriental Storks (ò) fitted with solar-powered GPS/GSM telemetry devices attached with backpacks in China 2015–2018 all of which provided full information on spring and autumn migration used in the current analysis. **Table S2.** Summary table comparing the mean values of autumn and spring migration parameters generated from tagged 18 Oriental Storks (ò) fitted with solar-powered GPS/GSM telemetry devices in China 2015–2018, which provided full information on spring and autumn migration used in the current analysis. **Figure S1.** Boxplot showing instantaneous flying speeds of telemetry tracked Oriental Storks presented by each hour of the day, local timeeds of telemetry tracktarr of ;pA6.1M ng spn

Availability of data and materials
The datasets generated during and/or analysed during the current study are not publicly available due to storks in the flyway were highly threatened by illegal hunting, but are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
We declare that all field methods used in this study were approved by the Forestry Department of Heilongjiang Province under scientific research license (No.23 Hei Forest Protection (2018)). Field research was conducted with permission from the Bureau of the Honghe National Nature Reserve. The Honghe National Nature Reserve shared the tracking data during 2015-2017.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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