Experience reduces reliance on conspecifics for route selection by a collectively migrating soaring bird

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ABSTRACT

Migration can be an energetically costly behavior with strong fitness consequences in terms of mortality and reproduction. The fact that costs and benefits may change with age and experience raises the question of whether experience changes the criteria that individuals use to select their migratory routes. Here we investigate the effect of age on route selection criteria in a collectively migrating soaring bird, the white stork (*Ciconia ciconia*). We perform step selection analysis on a longitudinal data set tracking 158 white storks over up to nine years to quantify how they select their routes on the basis of the social and atmospheric environments, and to examine how this selection changes with age. We find clear ontogenetic shifts in route selection criteria. Juveniles choose routes that have good atmospheric conditions and high conspecific densities. Yet, as they gain experience storks' selection on the availability of social information reduces—after their fifth migration experienced birds also choose routes with low conspecific densities. Thus, our results suggest that as individuals age, they gradually replace information gleaned from other individuals with information gained from experience, allowing them to shift their migration timing and increasing the time scale at which they select their routes.

Keywords: Ontogeny, Social migration, Movement ecology, *Ciconia ciconia*

MAIN

Seasonal migration is a model trade off. Despite its coming with substantial costs and risks [1, 2, 3, 4, 5, 6], many animals undertake migration to maintain access to resources for reproduction and survival [7, 8, 9, 10]. Optimal performance during migration demands adequate balancing of the cost-benefit ratio. This ratio may change over the course of an individual's lifetime depending on gained skills and shifting priorities [11, 12]. Thus, what defines optimal performance may not be the same for animals of different ages [13].

Older individuals often outperform juveniles in exploiting resources [14, 15, 16, 17] and in saving energy [18, 19]. In the case of migration, these skills might have been obtained early in life during exploration [20, 21, 22] when there was not yet time pressure due to reproduction. Immature animals may not need to return to breeding grounds quickly and be unable to afford energetically-demanding rapid travel or unable to reduce movement costs. Thus, immature animals may take slower or less energetically rewarding routes [23] and invest more in opportunities to learn how to balance their costs and benefits [24]. In contrast, adults may face pressure to reach breeding grounds early and thus benefit more from investing energy than time, leading them to travel more quickly or travel shorter

distances to less profitable non-breeding areas [25]. These differences may also lead to shifts in migration timing and thus to changes in the environmental conditions that different ages travel under [26, 27, 28].

Knowledge regarding where to go or how to move efficiently can come from individual experience through trial and error [29], but when obtaining this information asocially becomes costly, individuals may switch to exploiting social information [30]. Social information can reduce an individual's personal investment of time and effort in acquiring knowledge of the environment [31, 32, 33]. Thus, social information can give animals easier access to information than trial and error does and provide a lifeline to animals facing challenging conditions.

Social information is also error prone. Social information's value depends on how many asocial learners are present and how quickly its accuracy decays over space and time [34, 30, 35]. Young individuals often lack the information provided by experience, thus social information may be of greater value to them than it is to experienced individuals [36]. Just as the optimal balance of investing time or energy may change with age, how much to rely on social inputs versus individual experience may also change. Even when individuals of any age are equally capable of using social information [37], age may be a factor in whether or not individuals are equally likely to use it [38, 39].

Quantifying how the social environment affects migratory decisions has proven difficult because of the vast spatial scale over which migrations can occur and the difficulty of accounting for the presence of conspecifics [40, 41]. How route choice is influenced by the social environment and whether this influence changes as individuals age remain poorly understood. Animals can learn their migratory routes by traveling with informed conspecifics [42, 43, 44, 36]. The age of an individual may also affect how it moves through its environment [45, 46]. Experienced individuals may be able to move more efficiently [16, 19].

One system to study the effect of age on migratory route selection is soaring-gliding birds. These large, heavy birds have high costs of transport and cannot afford to undertake long journeys using flapping flight [47]. Thus, soaring birds rely on the environment to offset their costs of transport. They do this by soaring upwards on atmospheric uplifts and then gliding down to cross distance [48]. Soaring birds cannot afford to migrate without using uplifts, thus for them to approach optimality they must choose migratory routes that provide uplift [49, 50]. Not all individuals are capable of behaving optimally. Inexperienced soaring birds may not be able to locate the invisible uplifts they need to plot the most favorable routes. In this case, social information regarding when and where uplifts are available may be of value [51, 47]. A pre-requisite to the use of social information is access to it, which requires traveling in flocks. Many soaring birds do migrate together in large numbers [52, 53, 54]. However, although we know of pulses of migrants in the air during certain times of the seasons [55, 56], their impact on migratory decision-making at the individual level has not been studied before.

White storks (*Ciconia ciconia*) are model soaring migrants [57, 58]. White storks are limited in where they are able to move and tend to use low, open areas where thermal uplift is likely to form [59]. During migration, white storks travel in large flocks [52, 60], which gives them the opportunity to use social information to locate energy resources [51]. In spite of their collective movement, white storks display variation in where and when they travel [52, 61, 62], making them an ideal model for studying individual decision making in a collective context. We are beginning to understand how learning shapes migration over an individual stork's lifetime [12], but we do not yet know how experience interacts with the need to access flocks during migration. Here, we address this gap using long-term GPS tracking data of white stork migration. We use step selection analysis to quantify how storks select their routes on the basis of conspecific density and uplift availability, and how this changes with age.

We expect to observe a shift in the impact of social influences on route choice as individuals age. We predict that inexperienced individuals rely more on the benefits of collective movement and thus select routes to increase the availability of flocks. As they gain experience, storks may shift from relying on social information to using memory and experience, which is matched by a shift to reduced selection for high conspecific densities. Because white storks are obligate soaring birds, we also expect that they select their migratory routes to maximize uplift and minimize their flight costs. We expect that inexperienced individuals are less able to locate and to exploit strong uplift than

experienced birds.

RESULTS

To understand how white storks select their migratory routes, we analyzed the trajectories of 158 individuals tracked over up to nine consecutive years of migration (Table S3). We conducted step-selection analysis with generalized linear mixed models [63] using thermal uplift (proxied by the convective velocity scale [64]), the utilization distribution of 397 migrating white storks (our estimate of conspecific density), and number of years of experience as predictors of whether a location was used or unused. Because an animal's optimal decisions may differ between seasons, we built separate models for fall and spring. Both models had good predictive performance; the fall model fit with a root mean square error (RMSE) of 0.138 and the spring model fit with an RMSE of 0.140.

Route selection results

Route selection by white storks was influenced most strongly and positively by the density of migrating conspecifics ($p < 0.001$, Fig.1 A & B, Table S1) regardless of uplift or of how many migrations an individual had completed. We also found a significant interaction between age and conspecific density, indicating that experience plays a role in selection on conspecific density ($p < 0.001$, Fig.1 A & B Conspecifics X Migrations). In addition, storks selected routes to maximize uplift regardless of conspecific densities or age (fall $p < 0.001$ and spring $p = 0.002$, Fig.1). Age did not significantly affect this selection on uplift (fall $p = 0.351$ and spring $p = 0.058$, Fig.1).

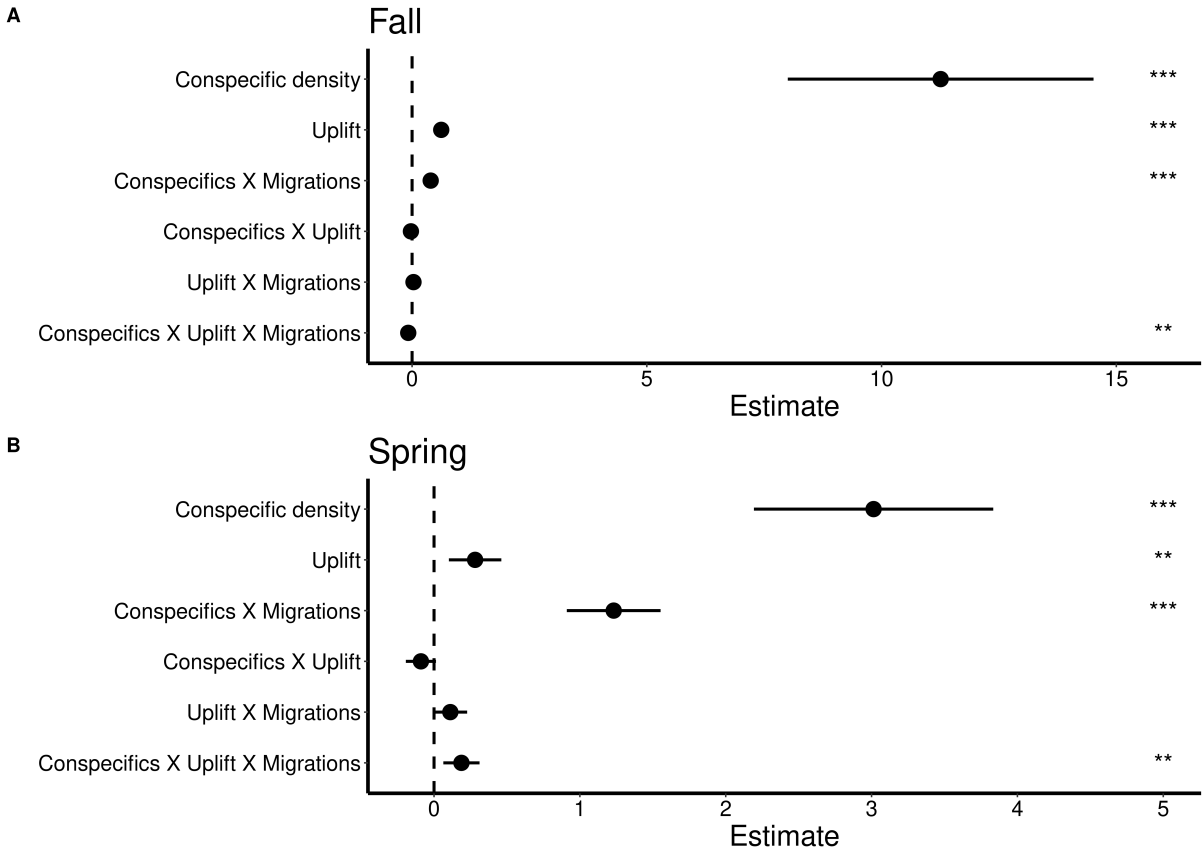

Fig.1. The interaction of conspecific density, uplift, and age predicts route selection. In both seasons, the availability of other storks, the availability of uplift, the interaction of conspecific density with age, the interaction of all three variables are significant predictors of route selection. Posterior means (centered and scaled) and 95% credible intervals for the fixed effects in the glmm for A) fall and B) spring migrations. Asterisks indicate the p-value ranges: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*).

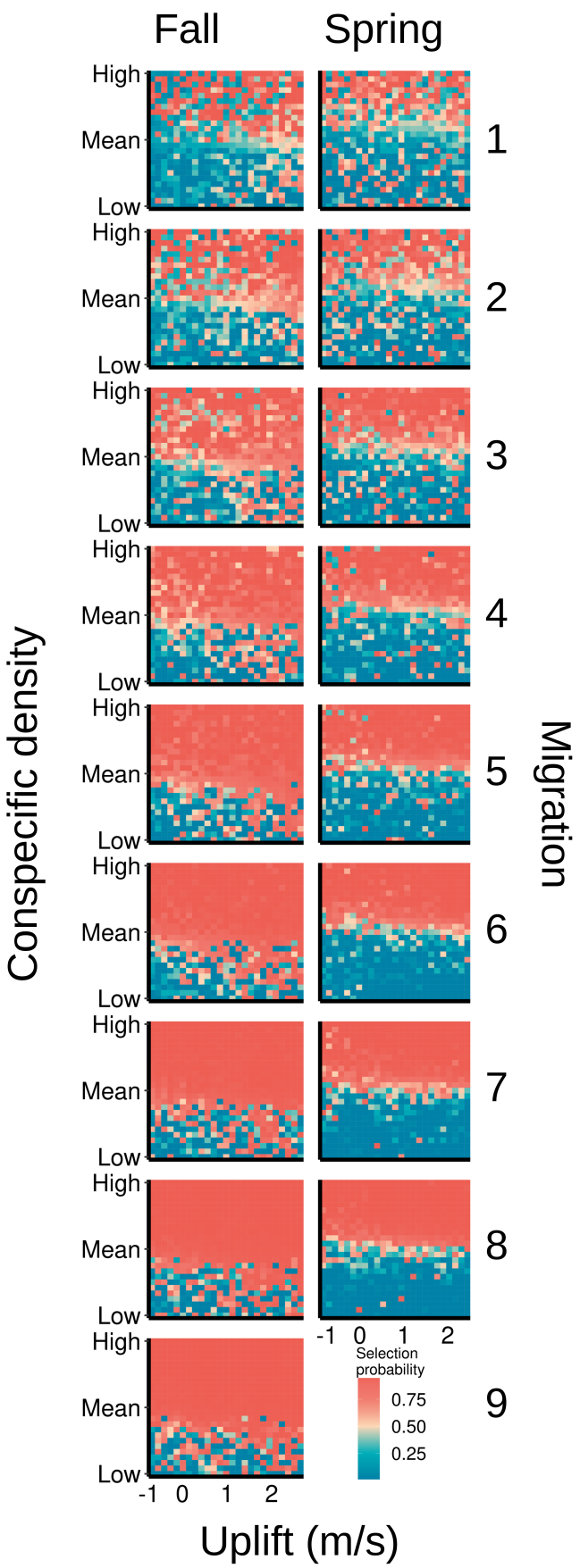

Fig.2. The strength of selection depends on both age and season. Over consecutive fall migrations, white storks grew less selective on conspecific density at all uplift velocities. In the fall, storks tended to be less selective on conspecific density than in the spring, and older birds became non-selective on conspecific density where strong uplift was available. In spring, storks were only slightly less selective on conspecific density where strong uplift was available.

Model predictions and timing

Next, we used our fitted models to predict route selection across the spectrum of environmental conditions in each season to explore the significant interaction of conspecific density, uplift, and age.

Fall

Our fall model predicted that young birds had high selection probabilities (> 0.75) at high conspecific densities. But this preference shifted as birds aged, i.e. older birds also had high selection probabilities at low conspecific densities (Fig.2). This suggests that older birds were not as selective with regard to conspecific densities compared to younger birds.

Storks had high selection probabilities at low conspecific densities (below the mean) when and where strong uplift was available (> 1.5 m/s). This indicates that in the fall storks will select for favorable atmospheric conditions even when this means experiencing less favorable conspecific densities.

As white storks age, their migration timing shifts (Fig.3 A), meaning that the environment that individuals of different ages experience during migration may not remain the same. This also means that the observed strength of selection depends not just on the storks' decisions but also on how variable the environment is at that time. Thus, we may see a lack of selectivity due to true absence of selection by the individual and/or due to an absence of options in its environment. For this reason, we also tested how much choice individuals of each age group had in which conditions to use.

When comparing stratum level variance in conspecific density, i.e. the variance in the conditions available to an individual at each time point, we found it to be significantly lower for older birds (Fig.3 B & Table S2). As they aged, storks experienced decreasing variability. This means that older birds had fewer choices. Thus, their reduced apparent selectivity might have been due to absence of options.

We found the opposite to be true of uplift. Older birds experienced increasing variability, which means that they had an opportunity to be selective that the younger birds did not. We found that the variance at each time point tended to increase as birds aged (Fig.3 C & Table S2). Yet, we did not find an effect of age on selection of uplift (Fig.1 A).

Spring

Our spring model showed a similar trend to our fall model. Young storks had high selection probabilities for high conspecific densities across all uplift conditions (Fig.2). As they aged, they had higher probabilities of selecting low conspecific densities, but not to the same extent as in the fall. This shift towards selecting lower conspecific densities was not continuous; it stabilized and older birds continued to avoid below-average conspecific densities.

Unlike in fall, storks did not choose low conspecific densities when strong uplifts were available. All ages were selective on uplift, but this did not lead to the pattern of high selection probabilities at low conspecific densities and strong uplift that we saw in the fall (Fig.2). This indicates that in the spring storks will select for favorable atmospheric conditions, but only with favorable conspecific densities.

As in the fall, older storks experienced lower variation in the available conspecific density in the spring (Fig.3 B & Table S2). As birds aged, they experienced decreasing variability, but to a lower extent than in the fall. That we did not detect as prominent a shift in spring as in fall may be influenced by our lower sample sizes in the spring (Table S3).

The variance in uplift also followed the same pattern as in the fall. Variance tended to increase as birds aged (Fig.3 C), but the distributions of variances were not significantly different from each other after spring two (Table S2). In the spring, older birds' selection on uplift might have been driven by both opportunity and requirement. The uplift available to them was more variable (Fig.3), which provided choices, and uplift was also less profitable overall than it was for younger birds (Figure S1), which could mean that older storks have to work harder to find rewarding patches.

Summary

As storks age they gain independence from flocking, as demonstrated by their reduced selection on conspecific density. They select migration times when they will not be able to select high conspecific densities. As storks age, they also improve in their ability to cope with sub-optimal uplift conditions — although all ages select on the availability of uplift, older birds have more heterogeneous uplift landscapes compared to the more predictable ones of younger birds.

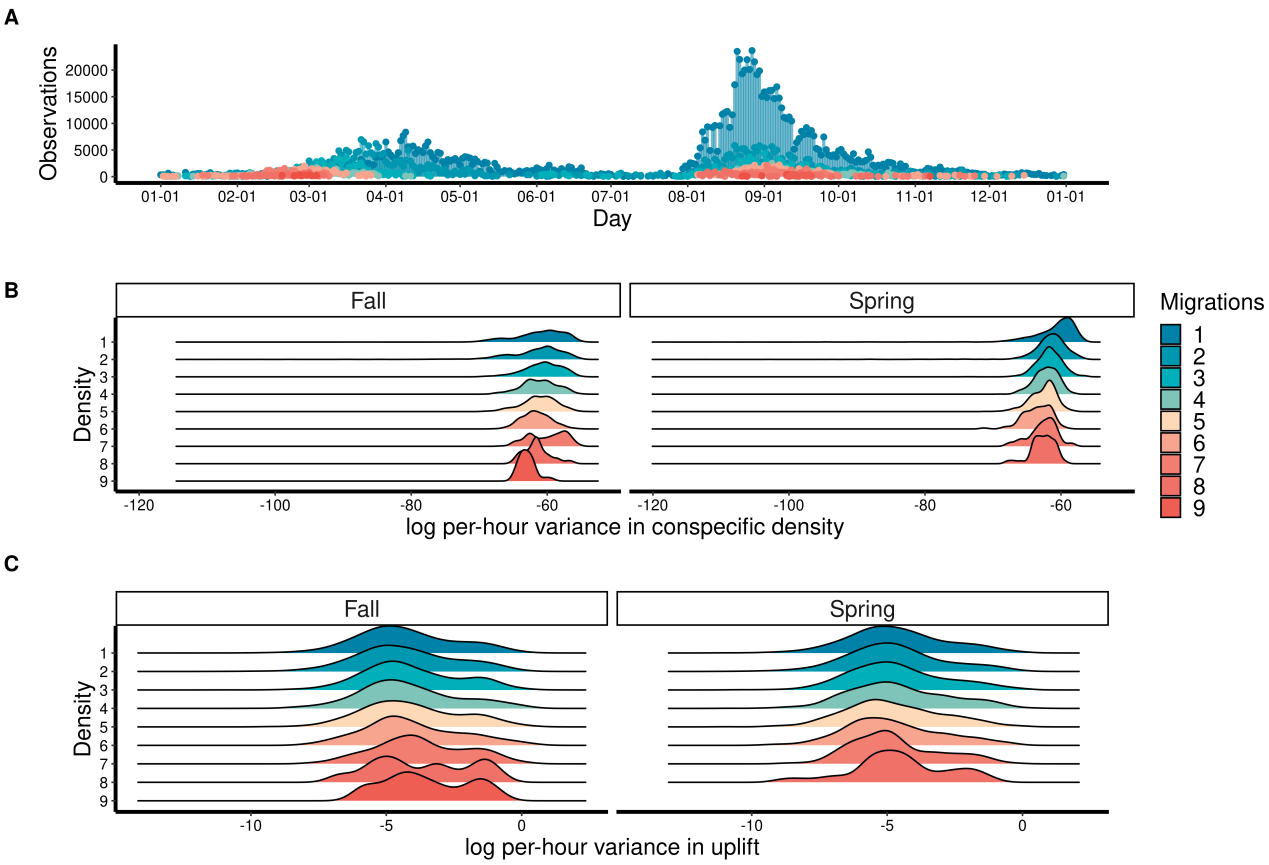

Fig.3. Different ages experience different environmental variability. A) Younger birds tended to migrate earlier in the fall and later in the spring than older birds did. B) The variance in available conspecific density reduced as storks aged and traveled when there are fewer other migrants. C) The variance in available uplift conditions increased as storks aged and traveled with cooler weather.

These patterns in environmental variability across age groups are most likely driven by differences in migration timing. Older storks tend to travel later in the fall and earlier in the spring than younger ones do (Fig.3 A), leading to less choice in conspecific density because there are fewer other migrants and more unpredictable uplift conditions because of cooler weather.

DISCUSSION

Here we investigated the effect of age on the use of access to social influences when selecting cost-efficient migration routes in a large soaring migrant. We quantified route selection on the basis of conspecific density and uplift availability by white storks. We found that, as we predicted, storks select routes depending on uplift conditions but grew less selective on conspecific density with age as they repeated their migrations.

We found that storks of all experience levels selected in favor of strong uplifts, but not to the extent of their selection on conspecific density. This indicates that their main route selection criterion is captured by conspecific density, and only once they have sufficient access to conspecifics do they select from the uplift that is then available to them. The distribution of this uplift is skewed towards positive values, indicating that storks are choosing to fly only when they can access favorable conditions, i.e. on sunny days regardless of wind (see supplemental file S2). To date, research on soaring migrants has tended to focus on the atmospheric energy resources available during flight [11, 49, 50, 65]. We find that even for large, obligate soaring birds, that have high cost of transport (Scacco et al. in prep.), migratory route selection does not depend solely on this dynamic energy landscape.

Route choices of migrants are influenced by a multitude of factors. For example, animals that pause migration for rest and refueling may need to consider available sleeping and foraging sites [66]. Predation during migration [67], disturbance [68], bad weather conditions [69], and health [70, 71] can also affect migratory decisions and may shape migratory routes. When migrating repeatedly, spatial memory most likely also plays a significant role in migratory route decisions, which could be quantified using a previous year's home range as a predictor [72]. Here we show that one additional driver of the decisions of this social migrant was the social landscape. This influence, however, decreased as birds grew older.

The reasons for the reduced importance of conspecific densities when selecting routes in older years may be two-fold. First, experienced individuals may indeed have a reduced dependence on joining flocks because they have gained enough knowledge to make informed movement decisions independently. Second, the fact that they shift their travel times means that they have limited choices regarding flocks, which they must cope with. We observed a reduced selection on conspecifics at the scale of hourly locations. But, storks are also selecting when to migrate. In fall, experienced birds delay travel, ignoring the peak of the departures. In spring, they advance their return to the breeding area to rush ahead of their competitors, meaning that they may actually be avoiding traveling when there is social information. Here we show that these choices at different temporal scales affect the availability of social and environmental support, revealing that storks may be choosing to have limited choices. Thus, as animals age, they can make decisions at longer time scales informed not only by their perception of the current environment, but also by experience [73].

Young birds may need conspecifics not just for finding good flight conditions, but also to learn routes [44, 36], to find breeding colonies [74, 75], or to find suitable wintering grounds [36]. Although here we only examined flight choices, these flights lead to suitable habitats. Thus, it is likely that these group flights lead to social learning that allows young birds to form spatial memories that can be retrieved in the following years. These experiences may allow older, more experienced individuals to be less sensitive to social guidance but more sensitive to competition and thus plot migrations that allow them to arrive at the opportune time. Effectively, this means that older birds are selecting at longer time-scales, producing the observed reduction in selectivity at the one-hourly scale.

Although we found a strong effect of conspecific density on route selection, our estimates of migrating stork densities may be too narrow. The breeding white stork population is abundant in Europe and spreads from the Southern borders of Spain all the way up to Southern Sweden, Denmark, and even the UK [76]. We know that migration timing is different among these different sub-populations [61]. This means that we might have underestimated the true availability of conspecifics because even if the birds in our study were unlikely to be traveling at a given time, there might have been birds from other populations that we could not monitor and that were in fact providing flocking opportunities to the tracked birds. Yet, in spring it may be essential to perform return migrations with individuals from the same breeding area. Thus, our estimate of conspecific densities may actually be realistic and capture what they experience and choose.

In the trade off that migration poses, older individuals can profit from past experience. We found that with age, white storks shifted their decisions away from the scale of an hour, most likely driven by the need to shift their travel times and arrival dates at the scale of weeks. Long-lived migratory species may travel to and from breeding grounds dozens of times. This affords them the opportunity to learn on early migrations and use experience to improve later ones [20]. Animals that travel in groups also have access to social information that can help them to negotiate their migrations and that may be of particular importance for inexperienced individuals [36]. We show that white storks select their migratory routes to increase their overlap with areas that have a high probability of hosting other storks at that time. Selection reduces as they age and migrate when there are fewer other migrants. This indicates that experienced storks do not need to seek out potential flocks. We expect that individuals of other species that migrate in groups also need the benefits of social groups less as they gain experience in saving and gaining energy, avoiding danger, and navigating to their goals.

METHODS

Movement data

We used existing data from several studies tracking white storks. In southwestern Germany, 464 juvenile white storks were tagged on the nest with solar GSM-GPS-ACC loggers between 2013 and 2022 (e-obs GmbH, Table S4, for details see [61, 77, 12]).

We only analyzed complete, long distance migrations along the western flyway by birds from the southwest German population. We defined migration using simple speed thresholds. The start and end of a migration were the first and last days with a total displacement of at least 40 kilometers within a week of moving more than 70 kilometers in a day. This double threshold accounts for the fact that storks may move slowly as they depart and arrive. We defined complete, long-distance migrations as those that ended at least 30 days before the bird died and that displaced the bird at least 3 degrees of latitude. Using these definitions resulted in 502 routes taken by 158 birds after filtering (Table S3). Routes marked as complete may include those for which birds died on a stopover site because whether the bird intended to (or would have decided to) continue migration after 30 days cannot be known.

Step selection functions

Step selection analysis views movement as a series of discrete steps between locations [78]. Each set of two locations is an observed step beginning and ending at observed locations. A set of alternative steps is generated beginning at the same observed location, but ending at alternative locations. These sets of one observed step and its alternatives are strata in the data set.

We down-sampled the birds' locations to once per-hour, then we generated 50 alternative locations over land for each observed one and annotated each location with the environmental variables (see supplementary file S2).

Environmental variables

We used two environmental covariates in our analysis: thermal uplift velocity, and the density of migrating conspecifics (a proxy for availability of social information en route). We also investigated the effect of wind support, but did not include it in our final models as we we found no evidence supporting its importance (see supplementary file S3).

For thermal uplift, we retrieved data from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-5 Global Atmospheric Re-analysis (0.25 degree and 1 hourly resolution). We estimated uplift velocity as:

$$w^* = [(\frac{\Phi \cdot w'\theta_v'}{\theta_v})]^{1/3},$$

where Φ is the geopotential at the highest pressure level below the boundary layer height (m^2 s^{-2}), w'θ_v' is the kinematic heat flux (K m s^{-1}), and θ_v is the virtual potential temperature at the highest pressure level below the boundary layer height (K) [64, 49, 79, 80] (for full calculations and code see supplementary file S4).

To proxy the potential to find flock mates on the landscape, we estimated conspecific density as the utilization distributions of migrating storks. The distributions did not take into account the year, natal population, experience level, or whether the routes were complete. We estimated these utilization distributions from recorded locations using auto-correlated kernel density estimates (AKDEs) [81] (in the "ctmm" package [82]). To make population-level distributions, we pooled the data from all storks that migrated from the southwest German population along with an additional 50 birds tagged in Spain, 79 in eastern Germany, and seven in France (397 migrated out of the 600, Table S4). We aligned the migratory locations (all locations between the start and end of migration, including non-flight segments) to the day, month, and hour, generating 3028 unique groups each with up to three observations from each individual that transmitted in that hour (for example, 12-21 12:00:00 to 12:59:00 UTC). To keep these distributions consistent and comparable, we built each AKDE on a 30 km x 30 km grid extending from 0° to 60° latitude and -20° to 20° longitude (using the Mollweide equal-area projection). However, the confidence did vary between distributions because the sample sizes were not the same in each hour (between 26 and 1428). Sample sizes differed particularly because there are unequal numbers of birds migrating at different parts of the year and because mortality meant our sample sizes were higher

in the fall (Fig.3 A). We generated one AKDE for each hour of the migrations of the 158 southwest German birds. Finally, we annotated each location with the average probability density of the grid cell where it fell (see supplementary code).

Statistical analysis

We estimated step-selection functions using generalized linear mixed models (using the *glmmTMB* package in *R* 4.3.1) [63, 83]. To ask how the roles of group availability and uplift in route selection change over time, we used conspecific density, uplift, a bird's experience level (1-9 migrations), and the interactions of the three as predictors of use case (used location or available location). We standardized the predictor variables across the whole dataset by calculating z-scores. We included individual as a random effect on the slopes. Finally, we assessed model fit using root mean square error (RMSE) [84], a comparison of the observed value to values predicted by the model. Small values of RMSE indicate good predictive ability.

The strength of selection is the difference between conditions along the observed and available steps [85, 86]. Thus, the strength of selection that we observe depends on the heterogeneity of the available conditions at each step. We explored whether the conditions that each age group experienced were equally heterogeneous by comparing the distributions of variance in each variable, each season, and each migration. First, we took the variance in the environment at each step (one observed and 50 available locations, a stratum in the model). Then, we used Kolmogorov-Smirnoff tests to detect differences between the distribution of per-stratum variance in each migration and the distribution of all other migrations' per-stratum variances pooled.

AUTHOR CONTRIBUTIONS

H.B.: formal analysis, investigation, methodology, visualization and writing—original draft; E.N.: conceptualization, methodology, validation and writing—review and editing; W.F. resources, funding acquisition, and writing—review and editing; A.F.: methodology, validation, resources, funding acquisition, supervision, and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

ETHICS

Permits for tagging and tracking the white storks were issued by the authorities of the Federal States (G-13/28 and G-268 15/47 by Regierungspräsidium Freiburg, 54-2532.1-14/14 by Regierung von Mittelfranken, MPI269 O-1/14 by Regierungspräsidium Tübingen, G15-20-032 by LUA Rheinland-Pfalz, ROB-55.2Vet-270 2532.Vet_02-17-95 by Regierung von Oberbayern).

DATA AVAILABILITY

The data used in this study will be made available upon acceptance of the manuscript. R scripts used for step selection analysis are available on *github* at https://github.com/hesterbronnvik/stork_route_selection_public.git.

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CONFLICTS OF INTEREST

We declare we have no competing interests.

SUPPLEMENTARY MATERIAL

Table S1. The model summary for the generalized linear mixed models predicting route selection in each season. We used the interaction of conspecific density, convective velocity scale, and the number of migrations an individual had completed as predictors of whether a location was used or unused in GLMMs.

Variable	Estimate	Upper	Lower	p-value
Fall				
Conspecific density	11.3	14.5	8.00	0.000
Uplift	0.621	0.708	0.534	0.000
Conspecifics X Migrations	0.396	0.563	0.229	0.000
Conspecifics X Uplift	-0.025	0.025	-0.074	0.325
Uplift X Migrations	0.030	0.093	-0.033	0.351
Conspecifics X Uplift X Migrations	-0.082	-0.031	-0.133	0.002
Spring				
Conspecific density	3.01	3.83	2.19	0.000
Uplift	0.282	0.461	0.102	0.002
Conspecifics X Migrations	1.23	1.55	0.910	0.000
Conspecifics X Uplift	-0.090	0.013	-0.193	0.088
Uplift X Migrations	0.112	0.227	-0.004	0.058
Conspecifics X Uplift X Migrations	0.188	0.312	0.064	0.003

Table S2. None of the distributions of variances of conspecific density matched the distributions of the others. The distributions of variances in both available conspecific density and available uplift increasingly differ from the others in the fall. Asymptotic two-sample Kolmogorov-Smirnov tests comparing the distribution of each migration's per-stratum variance in environment to the distribution of all the other migrations pooled.

	Uplift			**Conspecific density**		
Migration	Test statistic	p-value	sig.	Test statistic	p-value	sig.
Fall						
1	0.028	0.0002	yes	0.075	0	yes
2	0.020	0.1096	no	0.068	0	yes
3	0.046	0.0006	yes	0.085	0	yes
4	0.027	0.4639	no	0.095	0	yes
5	0.045	0.0414	yes	0.115	0	yes
6	0.063	0.0226	yes	0.199	0	yes
7	0.163	0	yes	0.160	0	yes
8	0.196	0.101	no	0.270	0.0069	yes
9	0.230	0.036	yes	0.538	0	yes
Spring						
1	0.035	0.0005	yes	0.323	0	yes
2	0.035	0.0013	yes	0.122	0	yes
3	0.015	0.8866	no	0.168	0	yes
4	0.044	0.1403	no	0.241	0	yes
5	0.049	0.1070	no	0.321	0	yes
6	0.059	0.1670	no	0.410	0	yes
7	0.080	0.2582	no	0.302	0	yes
8	0.123	0.5686	no	0.349	0.0001	yes

Table S3. The number of tracks used for step-selection analysis. After filtering for migrants along the western flyway that survived at least one migration, we had data from 158 individuals. One of those did not contribute its first fall migration, but did contribute a first spring and second fall, accounting for the difference between number of individuals and number of tracks.

migration	fall	spring
1	157	76
2	50	53
3	33	28
4	18	16
5	17	14
6	11	11
7	8	6
8	2	1
9	1	0

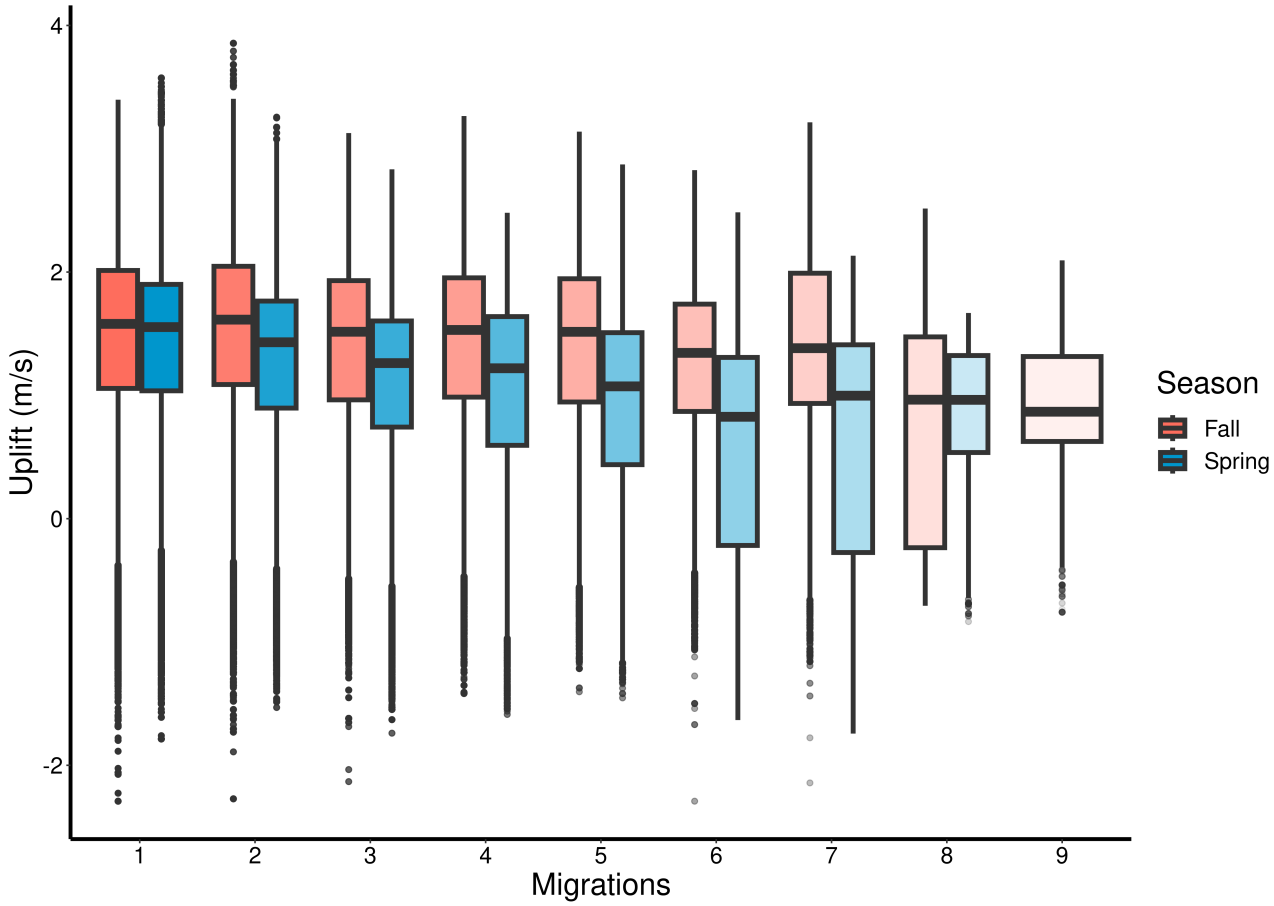

Figure S1. The distributions of uplift velocities differ based on season and age. Overall uplift velocities are fairly consistent in the fall. In the first spring migration, uplift is similar to uplift in fall. As birds age and advance their spring departures, their realized uplift velocities reduce.

Table S4. The sources of the tracking data. Sample sizes from each of the Movebank studies and how many were used for step-selection analysis in addition to the AKDEs.

study	individuals	tracks	analyzed
24442409	67	45	18
212096177	18	14	9
76367850	108	78	37
21231406	92	78	32
1176017658	153	113	54
173641633	26	17	8
1562253659	7	5	0
9648615	42	25	0
2204484313	38	11	0
10449318	41	4	0
2106043019	8	7	0

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