Experience does not change the importance of wind support for migratory route selection by a soaring bird

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Abstract

Understanding how animals develop their ability to perform complex behaviors is fundamental to understanding their fitness and plasticity under global change. Migration can be a costly behavior in terms of time, energy, and mortality, and minimizing these costs is key to survival and reproduction. Thermal soaring birds rely on airflow to offset their energetic costs of flight. Their migratory routes are a record of movement decisions to negotiate the atmospheric environment and achieve efficiency, for example by flying in prevailing winds. We expected that, as individuals gain more experience, these movement decision will also increasingly favor the best thermal uplift conditions, which allow them to fly with minimal energy expenditure. We quantified how route choice during autumn migration of young European honey buzzards (*Pernis apivorus*) was adjusted to wind support and uplift over up to four years of migration and compared this to the choices of adult birds. We found that wind support was important in all migrations. However, we did not find an increase in the use of thermal uplifts. The young birds varied their responses to airflow, yet they may require more than four years to attain a stable, optimal behavior.

Keywords— behavioral development, bird migration, step selection function, *Pernis apivorus*

1 Introduction

Migration is a challenging behavior during which environmental conditions affect fitness through survival and breeding success [1, 2, 3]. Migrating birds move through the air, which is in motion itself. Thus, the most important way for them to offset the energetic costs of movement is to ride airflow. Winds subsidize flight costs when birds move in the same direction as them (wind support), but increase costs of flight when flowing in the opposing direction (headwinds) or perpendicular to the birds' headings (crosswinds) [4, 5]. Birds can also take advantage of rising air (uplift) [6, 7, 8].

Thermal soaring birds are among the most dependent on the dynamics of airflow due to their prohibitively high energetic costs of powered flight [9]. Under optimality theory [10], soaring birds will respond to the costs and benefits of airflow by optimizing their travel within it—by taking advantage of wind support and uplift while avoiding headwinds and crosswinds. This is reflected in their small-scale movement decisions, which determine the energetic costs of larger scale movement behaviors, such as migration [11]. The migratory routes of these birds should be characterized by wind support [12, 4] and uplift [13, 9] to be optimal. Yet in many species migratory routes vary in space and time within and between individuals [14, 15], with first-year migrants performing less optimally than more experienced birds [16, 17, 18, 19].

Few studies have been able to demonstrate whether these differences between juveniles and adults develop through a continuous process or a rapid acquisition of behavior [20, 21, 22], and none has investigated improvements in the use of airflow to optimize migration route choice. We expect that juvenile birds are able to use wind from an early age [23], as flying with tailwind is not a complex task. In contrast, soaring flight is complex, requiring the integration of cognitive processes (perception of the environment to locate thermals) and motor skills (adjusting flight speed and body angle within thermals) and is learned and perfected over time [6]. We therefore expect that younger migrants are not able to take advantage of thermals as efficiently as adults and that their small-scale movement decisions during migration reflect this.

We use a long-term data set of GPS-tracked European honey buzzards to compare the influence of airflow on route choice during successive migrations by juvenile birds. Juvenile and adult honey buzzards differ in their migratory timing and routes. Adults depart the breeding grounds sooner [24] and make long detours around water bodies [25]. Juveniles depart after adults, which leaves them unable to learn from informed conspecifics. They move with prevailing winds, apparently using compass direction and wind to determine their routes [23] and are more likely to cross the sea [25].

We investigate how juvenile birds select airflow along their migratory routes over consecutive years and ask how they adjust their route selection as they gain experience. We then compare this to route selection by adults. We expect the adult behavior to represent an attempt at optimality, and thus that as young birds gain experience their responses approach those of the adults.

We expect that (i) wind support is an important determinant of route selection regardless of experience, and (ii) birds increasingly select their routes on the basis of uplift availability as they age.

2 Methods

2.1 Study system

We used existing data from a study of honey buzzards breeding in southern Finland (for details see Vansteelant et al. [23]). Between 2011 and 2014, nine adults of unknown age and 28 fledglings were equipped with Argos or GPS transmitters; they were then tracked for up to seven years. Five of the fledglings suffered mortality or tag failure before completing their first migrations and were removed from the analysis. For the remaining 23 fledglings, we analyzed the autumn migrations from Finland to sub-Saharan Africa (electronic supplementary material, S1). In addition, five adults of unknown age transmitted four or five autumn migrations. We analyzed the fourth and fifth transmitted routes of these five adults. Hereafter we define birds of unknown age that have completed at least five autumn migrations as "adult".

2.2 Step-selection functions

2.2.1 Track processing

The transmitters varied in sampling rate from median one to four hours. We re-sampled the tracks, so that time intervals between steps were consistent within each individual across years.

We analyzed route selection using step-selection functions [26, 27], which model movement as a series of discrete steps between consecutive locations, comparing conditions at locations that the birds used to those that were available but forgone.

We generated a stratified data set (electronic supplementary material, S2) for the step selection analysis. For each step along the migratory route (i.e. used step), we generated 100 available steps. We determined the locations of available steps by randomly sampling from gamma distributions fitted to the step lengths and von Mises distributions fitted to the turn angles in the empirical data for each track (using the "amt" package [28] in R [29]; electronic supplementary material, S3). This choice of turn angles accounted for the birds' direction of migration, as most of the available points were in this direction. Each set of alternative steps also included points in other directions. This range of available points enabled the models to summarize the

available conditions without overestimating the impact of wind support, which could occur if all alternative steps were in the same direction.

2.2.2 Environmental data

We annotated all used and alternative locations using the Movebank Env-DATA service [30] to obtain data from the European Centre for Medium-Range Weather Forecasts (ECMWF) Global Atmospheric Reanalysis (ERA5). For each location we retrieved east/west and north/south wind velocities (m/s), and vertical velocity of pressure (Pa/s). All predictors are measured hourly at 0.25 degree (roughly 30 km) resolution and linearly interpolated at 925 mB pressure level (roughly 762 m asl). Because pressure is lower with increasing altitude, negative vertical velocity values indicate uplift [31]. We then calculated wind support along each used and available step [32] (electronic supplementary material, S4 & S5).

2.2.3 Model fitting

We fitted conditional logistic regression models separately for each individual track [33]. To make the coefficients of these models comparable, we standardized the predictor variables across the whole data set (by calculating z-scores). Because wind support and uplift are not mutually exclusive, we also investigated the effect of the interaction between the two. Wind support, vertical velocity, and their interaction were predictors of whether a step was observed or alternative, with each matched set of one observed and 100 alternative steps as strata. To evaluate the performance of our model we fitted it to 80% of the full data set and then evaluated how well it predicted the remaining 20% by calculating root mean square error (RMSE) ("caret" package [34]). RMSE is in the units and the range of the dependent variable (0 and 1), with values close to zero indicating closeness of the fitted curve to the data.

2.2.4 Null modeling

We carried out permutation tests [35] to assess whether the observed effect of airflow differed from random. Our null prediction was that used and available locations were random with regard to airflow. We pooled all of the data for each migration and randomized the identification of locations as either used or available within the strata 101 times ("mosaic" package [36]), thus maintaining the spatiotemporal structure of the routes. Then we fitted our conditional logistic regression model to each set of randomized data, extracted the coefficients, and compared our observed coefficients to the distribution of alternatives. We determined the significance level (at $\alpha = 0.05$) of the difference between observed and random coefficients by counting the coefficients with values more extreme than the observation and dividing this by the number of permutations.

3 Results

Due to high juvenile mortality and/or tag failure, of our 23 first-time migrants only five transmitted a second autumn migration, four a third, and just two transmitted a fourth autumn migration. Our model fit the full data well with a root mean squared error (RMSE) of 0.152.

Regardless of experience, most of the individuals used wind support for route selection (figure 1). When all individuals in each migration were considered together, this trend of reliance on wind support was significant in all but the fourth migration (table 1; electronic supplementary material, S6).

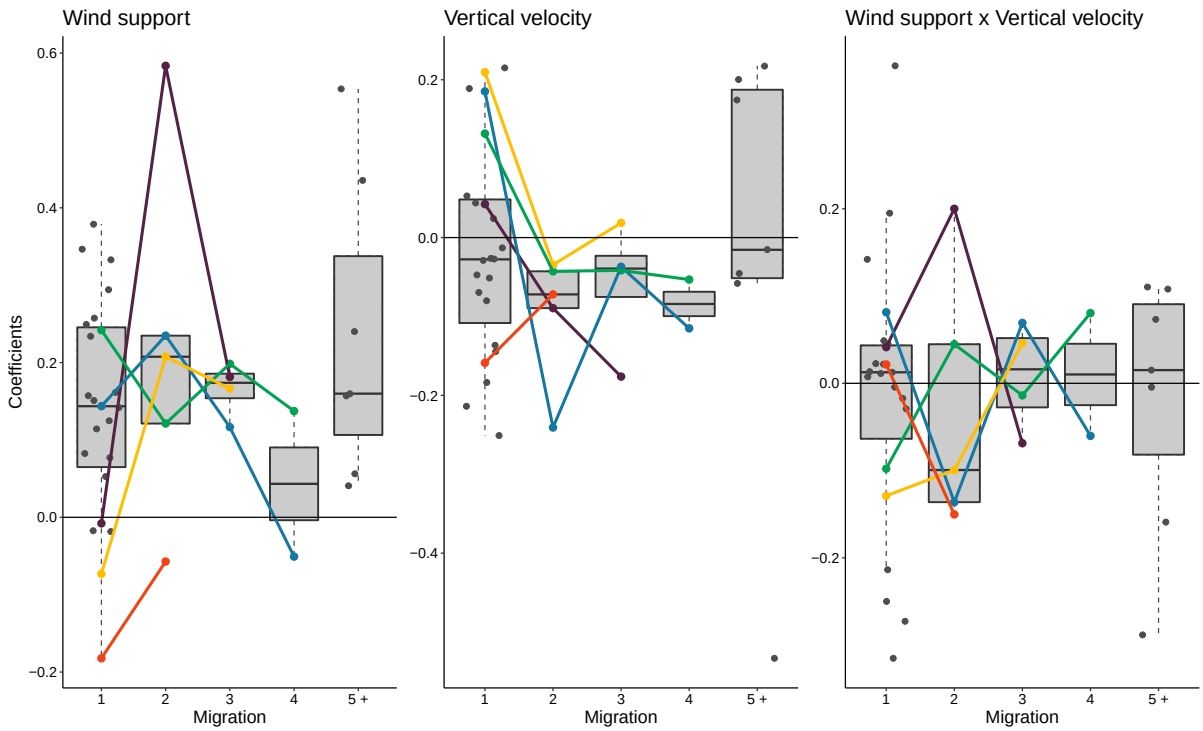

Figure 1: The importance of wind support, uplift (vertical velocity), and their interaction to route selection over migrations. Negative values of vertical velocity correspond to rising air. We fitted separate conditional logistic regressions for each track and extracted the coefficients for each predictor. Coefficients of individuals tracked in multiple years are connected by lines and highlighted in color.

Young individuals tended to select locations where uplift (negative vertical velocity) was available (figure 1). In contrast, adults showed a near-zero average effect. However, overall there was no significant effect of uplift on route selection in any migration (table 1).

The effect of the interaction between uplift and wind support on route selection was close to zero on average (figure 1). We found no significant difference between used and available locations in the effect of the interaction for any age (table 1).

Table 1: Our predictions regarding the pattern of importance for each atmospheric variable, coefficients (β) from conditional logistic regression models predicting used vs. available locations with wind support, vertical pressure velocity, and their interaction, and whether our observation matched our prediction. Significance is calculated by comparing the observed coefficient to the distribution of coefficients from permuted data.

variable	migration	prediction	observation (coef ± s.e.)	significance	match
wind support	1	positive importance	β = 0.106 ± 0.0162	0	yes
	2		β = 0.143 ± 0.050	0	
	3	↓	β = 0.151 ± 0.062	0.010	
	4		β = 0.091 ± 0.055	0.069	
	5 +	positive importance	β = 0.117 ± 0.042	0	yes
vertical velocity	1	no importance	β = -0.011 ± 0.018	0.218	yes
	2		β = -0.037 ± 0.045	0.178	
	3	↓	β = -0.034 ± 0.057	0.396	
	4		β = -0.046 ± 0.074	0.525	
	5 +	negative importance	β = -0.005 ± 0.047	0.822	no
wind support	1	no importance	β = 0.011 ± 0.012	0.198	yes
x	2		β = -0.027 ± 0.046	0.554	
vertical velocity	3	↓	β = 0.005 ± 0.039	0.832	
	4		β = 0.032 ± 0.052	0.485	
	5 +	positive importance	β = -0.025 ± 0.038	0.446	no

4 Discussion

Our results show that over time young European honey buzzards change their responses to airflow, but that these changes are not in a clear direction and vary among individuals. As expected , wind support was always the most important predictor of route selection [23, 12, 4]. Contrary to our expectation, uplift was never an important predictor of route selection.

We did not find a difference between the behavior of the adults and that of the juveniles. Because soaring is energetically low-cost [37, 38], we expected adult birds to optimize their movement by supplementing wind support with thermal uplift when it is available. Adult honey buzzards migrating from the Netherlands have been shown to exploit uplift [39], but we did not find that the adults in our study demonstrated this presumably optimal behavior.

The birds tagged as adults in our study were in fact individuals of unknown ages. It may be that they were still immature and had not yet attained the optimal adult-like behavior that we expected. Another explanation may be that the uplift proxy we used (vertical velocity of pressure measured

at roughly 30 km resolution every hour) might have failed to capture the uplift conditions that the birds select, which are likely on the scale of tens of meters. To measure the proportion of a route spent soaring by individuals with differing levels of experience, data extracted from animals' movement are more reliable than proxies retrieved from weather models. This requires high temporal-resolution GPS data to capture circling flight [40] and/or tri-axial accelerometry data to capture flapping bouts [41], which are not currently available for the honey buzzards.

Contrary to our expectation, juveniles did not gradually improve their use of thermal uplifts for route selection as they gained experience. Selecting affordable migratory routes may be cognitively demanding, requiring adequate perception of and responses to a changing environment. Thus, improvement in using airflow to optimize soaring flight and migratory performance may be slow and gradual [20, 6, 22]. In long-lived species such as the European honey buzzard, individuals may spend years acquiring and then refining their flight skills and migratory route selection [42]. Our data may not be sufficient for capturing the developmental trajectory of honey buzzards toward optimal route selection. Data collected for many individuals over extended time periods are required to understand how complex, cost-saving behaviors develop.

Route selection behavior is more complex than simply reducing local energy expenditure, which was the basis of our expectations. Migratory decisions from departure time and travel speed to which routes to use are affected by many factors. Time is important among these as a currency governing migratory decisions along with energy; optimal migration is a compromise between minimizing time and maximizing energy gain [43, 44]. In addition, factors such as predator avoidance [45], availability of roost sites [46] and food [47], and extreme conditions [48, 1, 49] contribute to migratory decisions in ways not considered here and that may differ between ages.

Migration is a complex behavior that can be improved by experience [20, 18, 22]. We studied the ontogeny of migratory route selection in a long-lived, long-distance, soaring migrant in relation to airflow. We show that European honey buzzards use wind support to select migratory routes and that this does not change with experience. Our finding suggests that wind support is important for migration in all life stages of this species and we suspect that this may be the case in other obligate soaring species as well. This may have consequences for the longevity of the species in the face of shifting wind patterns driven by anthropogenic global warming.

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Ethics

Capturing of the birds was done under a ringing permit (permit 2604) issued by the Finnish Museum of Natural History. Attachment of tracking devices was permitted under the following licences issued by Finnish authorities: EPOELY/135/07.01.2013, ESAVI/2195/04.10.07/2014, PIRELY/49/07.01/2013, VARELY/73/07.01/2013, VARELY/215/2015.

Data Accessibility

Data and R scripts used for step selection and permutation analysis are available as electronic supplementary material.

Authors' Contributions

EN conceived the study and supervised the project. PB provided the data. WMGV assisted with data preparation. HB analyzed the data with input from KS and EN. HB wrote the first draft of the manuscript. All authors discussed the final results and commented on the manuscript.

Competing Interests

We declare we have no competing interests.

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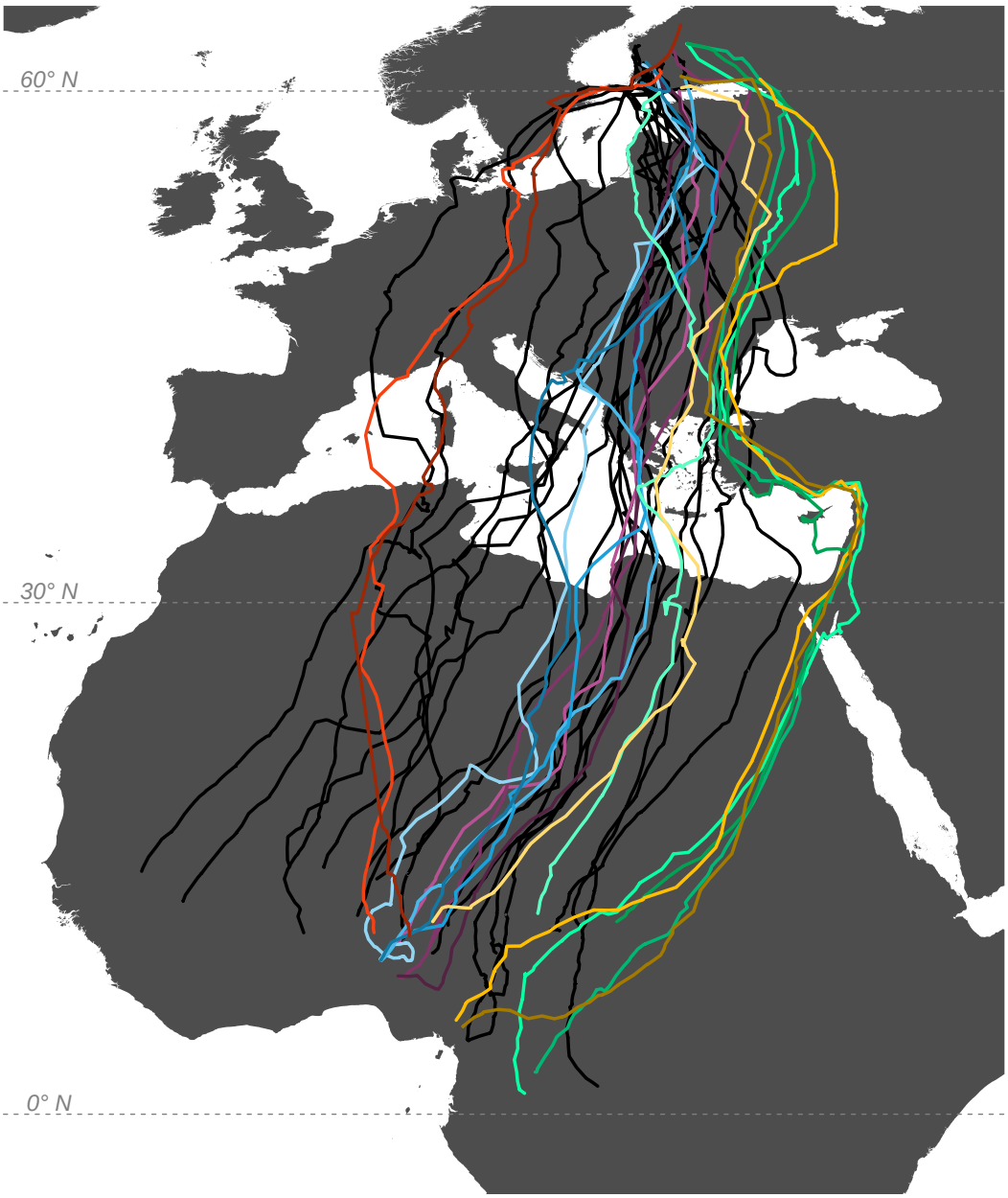
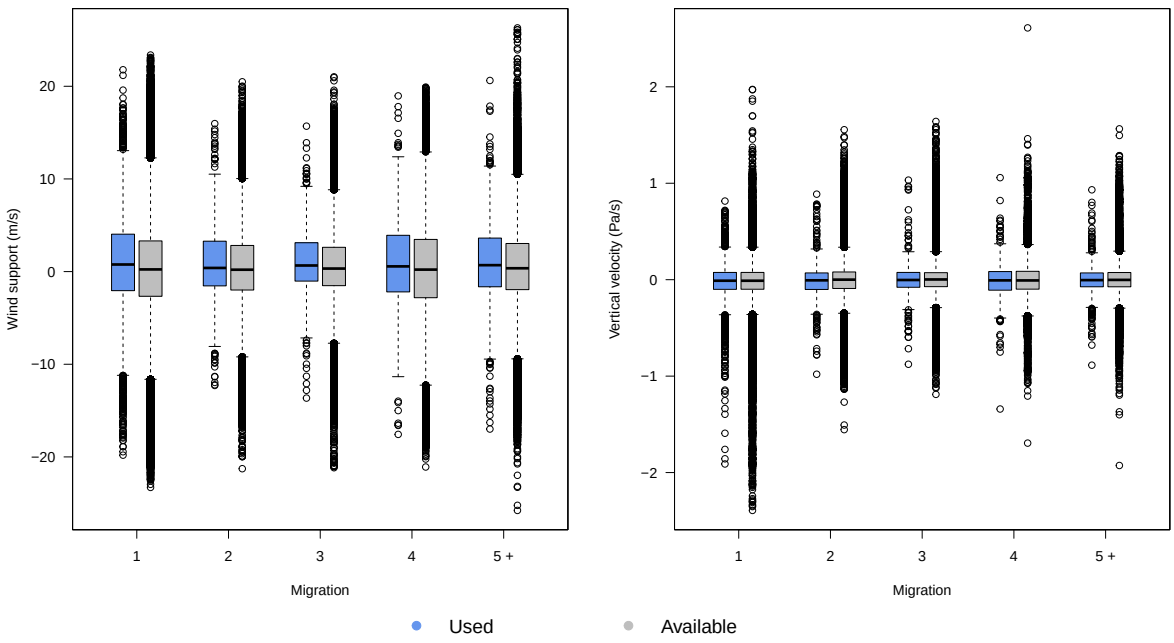
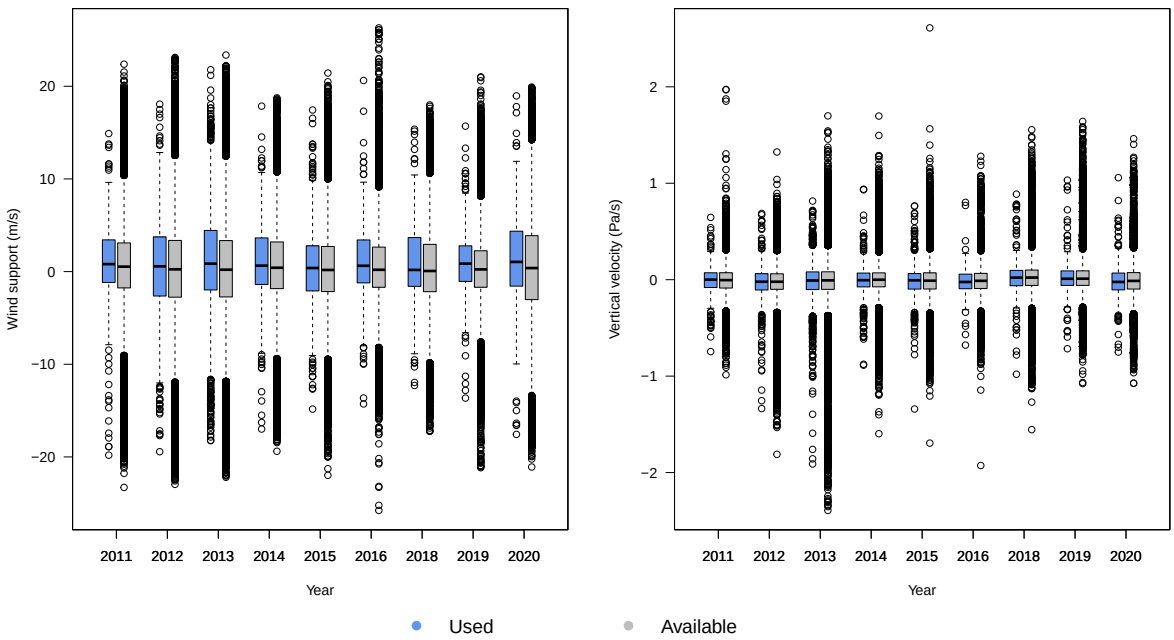
Supplemental materials



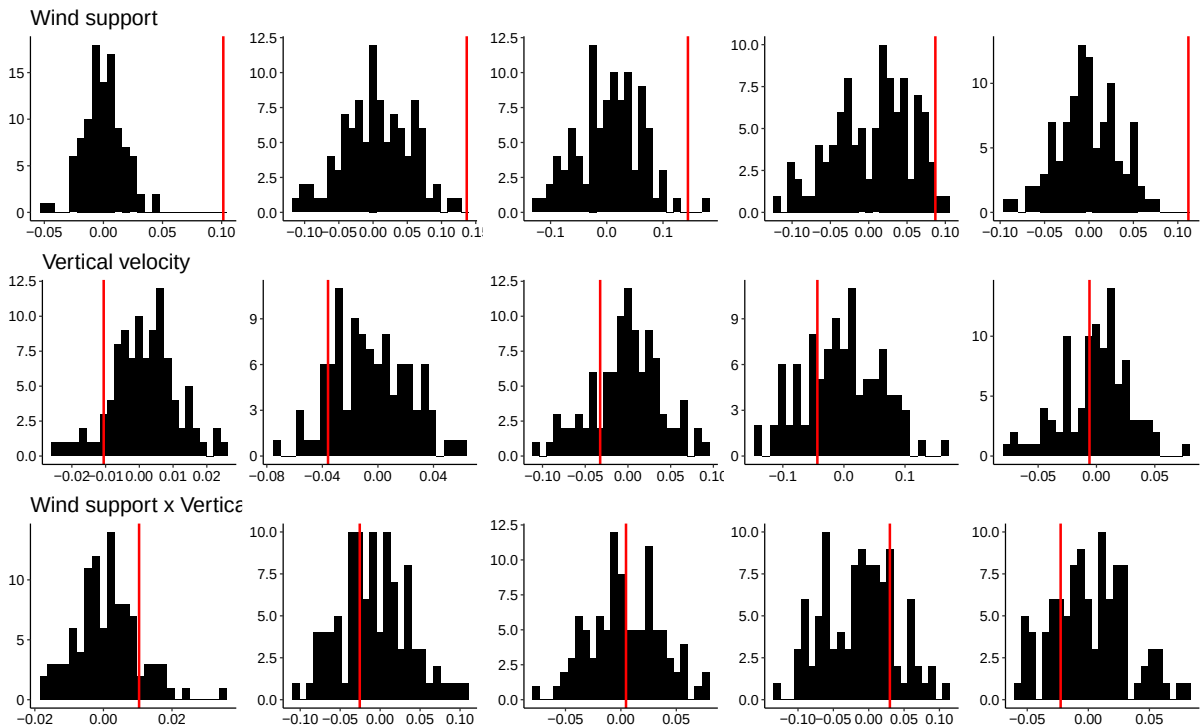
Supplemental material 1: The routes taken by individuals of known age. Routes of the individuals that transmitted only one migration are shown in black, those of the remaining five individuals are shown in colors matching figure 1. The first migrations of multi-year individuals are shown in pale shades that get darker in each consecutive migration.



Supplemental material 4: The distributions of wind support and vertical velocity of pressure at used (blue) and available (gray) locations in each migration.



Supplemental material 5: The distributions of wind support and vertical velocity of pressure at used (blue) and available (gray) locations in each year of tracking.



Supplemental material 6: Wind support is significantly higher than random at used locations in all but the fourth migration. Vertical velocity is never significant, nor is its interaction with wind support. Black lines show the distribution of coefficients from permuted data compared to observed coefficients in red.