

1 **Causes and consequences of facultative sea crossing in a soaring migrant**

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21

## 22 **Abstract**

- 23 1. Studying the causes and consequences of route selection in animal migration is  
24 important for understanding the evolution of migratory systems and how they may be  
25 affected by environmental factors at various spatial and temporal scales. One key  
26 decision during migration is whether to cross “high transport cost” areas, or to  
27 circumvent them. Soaring birds may face this choice when encountering waterbodies  
28 where convective updrafts are weak or scarce. Crossing these waterbodies requires  
29 flying using energetically costly flapping flight, while circumventing them over land  
30 permits energetically cheap soaring.
- 31 2. We tested how several atmospheric factors (e.g., wind, thermal uplift) and geographic,  
32 seasonal and state-related factors (sex and age) affected route selection in migrating  
33 white storks (*Ciconia ciconia*). We used 196 GPS tracks of 70 individuals either  
34 crossing or circumventing the north-easternmost section of the Mediterranean Sea, over  
35 Iskenderun Bay in southern Turkey.
- 36 3. We found that westward and southward winds promoted a cross-bay journey in spring  
37 and autumn, respectively, acting as tailwinds. Also, overall weaker winds promoted a  
38 sea crossing in spring. Sea crossing was associated with flapping flight and higher  
39 values of Overall Dynamic Body Acceleration (ODBA) and resulted in higher ground  
40 speed than travel over land.
- 41 4. The combined environmental conditions and the effects of route selection on  
42 movement-related energy costs and speed were likely responsible for an increase in the  
43 time spent flying and distance travelled of migrating storks that decided to cross the  
44 bay during spring. Notably, daily travel distances of spring migrants crossing the bay  
45 were 60 kilometres longer than those of land-detouring birds, allowing them to reach  
46 their destination faster but likely incurring a higher energetic flight cost. No such  
47 benefit was found during autumn.

48        5. Our findings confirm that atmospheric conditions can strongly affect bird route  
49            selection. Consequently, migration timing, speed and movement-related energy  
50            expenditure differed considerably between the two migratory seasons and the two route  
51            choices, highlighting a time-energy trade-off in the migration of white storks.

52

53    Key words: bird migration, environmental effects, flight modes, geographical barriers, route  
54    selection, season-related behavioural responses, time-energy trade-offs, white stork

55

## 56 **1. Introduction**

57 Environmental conditions during long-distance bird migration are known to affect migration  
58 timing, flight performance and energy expenditure (Becciu et al., 2019; Shamoun-Baranes,  
59 Liechti, & Vansteelant, 2017). Still, how migration route is influenced by atmospheric and  
60 geographical factors is much less clear. Route selection over ecological barriers such as large  
61 waterbodies may depend on weather and geographical features (Alerstam, 2001; Becciu et al.,  
62 2019; Efrat, Hatzofe, & Nathan, 2019; Eisaguirre et al., 2018; Nourani, Yamaguchi, Manda, &  
63 Higuchi, 2016), affecting migration time and energy expenditures, with consequences for  
64 animal fitness (Shamoun-Baranes, Bouten, & Van Loon, 2010; Shamoun-Baranes et al., 2017).  
65 Large terrestrial soaring birds depend on local atmospheric conditions during their flight, since  
66 they utilize thermal uplifts to gain height and later glide towards their destination (Norberg,  
67 1990). During soaring flight, the birds stretch and do not flap their wings, allowing them to  
68 save energy while covering large distances (Sapir, Wikelski, Mccue, Pinshow, & Nathan,  
69 2010). Usually, soaring birds avoid flying over waterbodies where thermals are typically weak  
70 and rare (but see Duriez, Peron, Gremillet, Sforzi, & Monti, 2018; Nourani, Vansteelant,  
71 Byholm, & Safi, 2019). Yet, in some cases soaring birds are forced to switch to the  
72 metabolically demanding flapping flight (Hedenström, 1993; Norberg, 1990; Sapir et al., 2011),  
73 such as when flying over areas with low availability of thermals. These areas can be regarded  
74 as “high transport cost” areas (Alerstam, 2001). We note that differences in transport cost may  
75 be caused by additional factors, such as variable wind conditions experienced by the birds when  
76 travelling over different areas (Alerstam, 2001; Efrat et al., 2019). Besides increasing the  
77 transport cost, barrier crossing versus barrier circumvention (i.e., facultative barrier crossing)  
78 may shorten migration distance, with possible consequences for migration time saving  
79 (Alerstam, 2001; Efrat et al., 2019).

80 Weather conditions may affect the timing and the location of the crossing in obligatory sea  
81 crossing during migration (Agostini, Panuccio, & Pasquaretta, 2015; Bildstein, 2006; Bildstein,  
82 Bechard, Farmer, & Newcomb, 2009; Meyer, Spaar, & Bruderer, 2000; Nourani et al., 2016).

83 For example, Oriental honey-buzzards (*Pernis ptilorhynchus*) that crossed the sea between the  
84 mainland and Japan were affected by wind conditions and the geography of the study area  
85 (Nourani et al., 2016; Yamaguchi, Arisawa, Shimada, & Higuchi, 2012). Wind conditions also  
86 affected the propensity of several species of soaring migrants to cross the area of the strait of  
87 Gibraltar in locations where the cross-sea travel was not the shortest possible (Meyer et al.,  
88 2000). Compared to the latter situations of obligatory sea crossing, causes and consequences of  
89 a facultative sea-crossing decision in soaring migrants were rarely studied to date (Kerlinger,  
90 1984).

91 We investigated the flight behaviour of the white stork, *Ciconia ciconia*, a large soaring bird  
92 and a long-distant migrant, as it passed through the Iskenderun Bay (“the bay” hereafter) in the  
93 north-eastern corner of the Mediterranean Sea. We found that about half of the birds crossed  
94 the bay over water while the other storks circumvented it over land. We examined how  
95 meteorological conditions affected migration route selection (bay crossing vs. overland detour)  
96 and furthermore explored the consequences of route selection for migration travel distance and  
97 movement-related energetics due to changes in the prevalence of the two flight modes (soaring  
98 vs. flapping) used by the birds. Large differences in flight energetic costs between the two flight  
99 modes (Sapir et al., 2010) imply a possible trade-off between different benefits and costs of  
100 facultative sea-crossing behaviour. For example, over-sea shortcutting may involve high  
101 prevalence of energetically expensive flapping flight whereas the longer overland detour might  
102 be associated with low-cost soaring flight. We consequently hypothesize that cross-sea flight is  
103 selected only when specific meteorological conditions prevail, such as tailwinds, which  
104 increase the benefit-(shorter travel time)-to-cost (high energetic costs due to flapping) ratio of  
105 crossing the bay. We therefore tested how wind speed and direction, temperature and thermal  
106 availability affected the decision of the storks to cross the bay. We furthermore considered the  
107 sex and the age of the individuals because intrinsic individual attributes may play an important  
108 role in determining movement decisions in general (Nathan et al., 2008), and specifically in  
109 migrating white storks (Rotics et al., 2016; Rotics et al., 2018). Also, we considered the timing

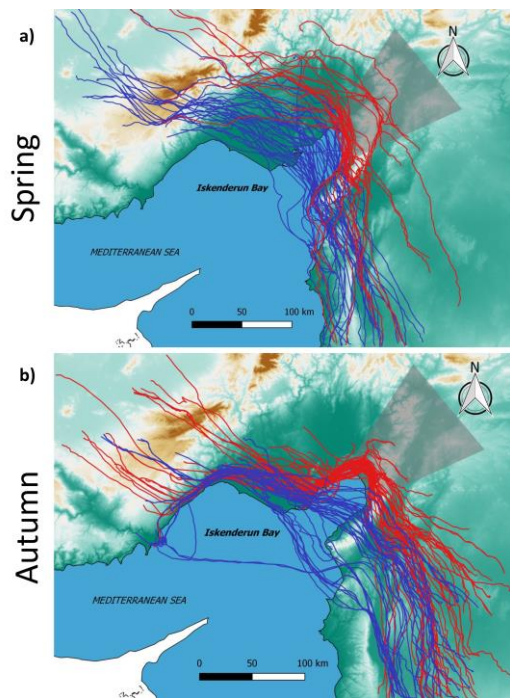
110 of bird passage through the study area within the season. We additionally explored time and  
111 energy consequences of route selection. We hypothesize that sea-crossing behaviour is not  
112 random and depends on both extrinsic and intrinsic factors that could affect individual fitness.  
113 We specifically predict that: (a) tailwinds will facilitate sea-crossing flight, and increase the  
114 speed of migration (Becciu, Panuccio, Catoni, Dell’Omo, & Sapir, 2018; Nourani et al., 2016).  
115 (b) Early-spring migrants will show higher sea-crossing propensity due high motivation to  
116 arrive earlier at their breeding grounds, and more so in males (Rotics et al., 2018). Further, we  
117 expect juveniles which are less prone to risk to travel through a safer land detour (Harel et al.,  
118 2016; Rotics et al., 2016). Early-spring migrants may further show higher sea-crossing  
119 propensity due to poor thermal conditions over land in early spring (Rotics et al., 2018;  
120 Shamoun-Baranes et al., 2003). (c) Sea-crossing flight will be beneficial to the migrants,  
121 shortening their route distance and time compared with land detour, consequently allowing  
122 them to allocate the saved time to cover more distance at the end of the migration day. (d) Sea-  
123 crossing flight will require flapping as opposed to soaring during land detour and consequently  
124 will be metabolically more costly (Sapir et al., 2010; Wilson et al., 2019). (e) Sea crossing will  
125 not be the outcome of individual consistency in route choice over the years, which is a strategy  
126 that might have developed with experience or with individual preference (Vardanis, Klaassen,  
127 Strandberg, & Alerstam, 2011; Vardanis, Nilsson, Klaassen, Strandberg, & Alerstam, 2016),  
128 but rather mainly depend on local meteorological conditions before deciding whether to cross  
129 the sea. Therefore, we suggest that facultative sea-crossing behaviour could be the outcome of  
130 a time-energy trade-off during white stork migration, in which the birds may trade off energy  
131 expenditure for migration speed.

## 132 **2. Materials and Methods**

### 133 **2.1 Bird tagging and study area**

134 The white stork is a large long-distance migrant that breeds mainly in Europe and Western Asia,  
135 and the majority of its population over-winters in sub-Saharan Africa. The study took place at  
136 the area of Iskenderun Bay, Turkey (36.6330°N, 35.8786°E). White storks that migrate along  
137 the eastern Mediterranean flyway pass regularly over the study area twice a year. When  
138 encountering the bay, storks may choose to cross the bay, which is 30-45 km wide, or to  
139 circumvent it over land (Figure 1). From 2011 to 2014, we fitted solar-charged GPS transmitters  
140 with tri-axial acceleration (ACC) sensors (e-obs GmbH, Munich, Germany) to 62 adult and 84  
141 immature white storks in the state of Saxony-Anhalt, Germany (see Rotics et al., 2016, 2017  
142 for detailed methods regarding tagging and trapping protocols). Eight immature storks (birds  
143 in their first, second and third year of life) survived to the following years, allowing us to assess  
144 whether their behaviour changed with age. We found that the behaviour of 1<sup>st</sup>-year birds was  
145 similar to that of 2<sup>nd</sup>- and 3<sup>rd</sup>-year birds, in terms of sea crossing choice and day of passage over  
146 the study area (Figure S2), and consequently considered them in the same age class (juvenile)  
147 in the statistical analysis. Bird sex was determined by molecular methods (Rotics et al., 2018).  
148 The transmitters recorded GPS fixes every 5 minutes when solar conditions were good (95%  
149 of the time) or otherwise every 20 minutes. Every five minutes an ACC burst of 3.8 seconds  
150 was recorded at 10.54 Hz. Data were stored on-board and were downloaded via a VHF radio  
151 link upon locating the stork (Rotics et al., 2016). We excluded from the analysis tracks that did  
152 not present a clear route choice (storks that mostly followed the coast and cross less than 20 km  
153 over the bay), birds wintering at higher latitudes in the northern hemisphere (Rotics et al., 2017)  
154 and storks that did not cross the bay in one day (e.g. stopping over at the area of the bay).  
155 Consequently, we used data from 70 storks (39 adults and 31 immatures) that provided a total  
156 of 196 tracks (153 from adult and 43 from immature storks, 83 for spring and 113 for autumn  
157 migration). The maximum range of the storks' tracks that travelled through the Iskenderun Bay  
158 area during a single day defined the geographic boundaries of the study, which were

159 approximately 33.004° (westernmost longitude), 37.722° (easternmost longitude), 37.998°  
160 (northernmost latitude), and 34.963° (southernmost latitude).



161

162 **Figure 1.** Map of the study area showing the white storks' routes in (a) spring and (b) autumn. Blue routes depict  
163 sea crossing and red ones represent land detour. The shaded area is the bay-crossing stage named “ACROSS”, which  
164 is considered in the analysis of land-detouring birds (see Methods for details). The topography is depicted by a colour  
165 gradient from sea level (dark green) to mountains of about 3000 m a.s.l. (dark brown).

## 166 2.2 Movement parameters

167 Information regarding environmental data annotation of the birds' tracks is provided in the  
168 supporting online material (S1). We calculated ground speed ( $V_g$ ) based on the time interval  
169 between two consecutive locations and additionally calculated the angle ( $\sigma_i$ ) of each such  
170 segment relative to the previous segment. These parameters were calculated using the package  
171 “move” in R (Kranstauber, Smolla, & Scharf, 2018). Ground speed was subsequently averaged  
172 for the entire day during which the bay crossing took place. For every ACC burst we calculated  
173 the birds' Overall Dynamic Body Acceleration (ODBA), a valid proxy for activity-related  
174 energy expenditure (Wilson et al., 2019), and their flight mode (either flapping or soaring-  
175 gliding flight; see (Rotics et al., 2018) for details). Flight mode was annotated to each location



176 and the proportion of flapping flight out of the total was calculated (proportion of gliding was  
177 one minus proportion of flapping) for a pre-defined area or for the birds' daily travel over the  
178 area (see below the division of subsets). ODBA and the proportion of flapping flight are highly  
179 correlated (Spearman- $\rho = 0.92$ ,  $p < 0.001$ ). Flight height above ground was calculated by  
180 subtracting ground elevation (obtained from ASTER ASTGTM2 Global 30-m DEM data set)  
181 (Dodge et al., 2013) and geoid height (the elevation difference between ellipsoid and geoid  
182 earth models) from the ellipsoid height recorded by the GPS transmitter. Air speed ( $V_a$ ) was  
183 calculated for each segment of the individual tracks following Safi et al. (2013):  $V_a =$   
184  $\sqrt{(V_g - W_p)^2 + (W_c)^2}$ . A single trip was defined from a starting point established where the  
185 ground speed exceeded 5 m/s after a nocturnal staging to an ending point where ground speed  
186 was below 2 m/s after a day of flight. We calculated time spent flying and distance travelled as  
187 cumulative sum of time and distance intervals at the day of the bay area crossing and at pre-  
188 defined sections of the daily trip (see below).

### 189 **2.3 Data analysis**

190 Our analyses were done considering tracks within a single day, during the time window when  
191 the storks were migrating (03:00 - 17:00 UTC). We divided our dataset into different subsets  
192 depending on the position of the birds with respect to the bay on the day of crossing the study  
193 area within the following three sections: 1) BEFORE (from take-off to the "bay area" – see  
194 below), 2) ACROSS (over the "bay area" or its projection over land), 3) AFTER (from the "bay  
195 area" until landing). A minimum of three consecutive locations per section was required for  
196 including data from a given section. The "bay area" is considered as the water body itself plus  
197 its projection over land in a direction perpendicular to the GPS tracks (shaded area in Figure 1,  
198 see also Figure S1). We used averaged movement and environmental data per day and per each  
199 bay-crossing section (depending on the analysis) to avoid spatial and temporal correlation on  
200 the day when the storks passed over the study area. We assigned bird tracks to two categories,  
201 namely LAND and SEA, for land-detour and sea-crossing routes, respectively.

202 To test the first part of prediction (a), as well as prediction (b), we tested bird route choice  
203 before arriving at the bay using Generalized Linear Mixed Models (hereafter GLMMs) with a  
204 binomial response variable (route choice: 0=LAND; 1=SEA), separately for autumn and spring  
205 migration, in relation to environmental factors, ordinal date and individual factors (i.e. sex, age)  
206 as well as two random factors (calendar year and bird ID). To avoid multicollinearity issues,  
207 we chose the most biologically meaningful variable from pairs of variables with a Spearman  
208 rank correlation  $|\rho| > 0.6$ . This ensured that all the predictors in the GLMMs had a Variance  
209 Inflation Factor (VIF)  $< 3$  (Zuur, Ieno, & Elphick, 2010). We then tested all combinations of  
210 remaining variables in the global model and ranked the selected models according to the Akaike  
211 information criterion (Burnham & Anderson, 2002) using an automated stepwise model  
212 selection procedure in which models are fitted through repeated evaluation of modified calls  
213 extracted from the model containing all the meaningful variables, corrected for small sample  
214 sizes ( $AIC_c$ ) (Sugiura, 1978). Furthermore, we averaged all models with  $\Delta AIC_c < 7$  (Burnham,  
215 Anderson, & Huyvaert, 2011) and used the Akaike weights ( $w_i$ ) (Anderson, Burnham, &  
216 Thompson, 2000; Anderson, Link, Johnson, & Burnham, 2001) to assess the relative  
217 importance of the different variables. We used two global models, the first including E-W and  
218 N-S winds (but not  $W_p$  and  $W_c$ ), and the second with  $W_p$  and  $W_c$  (without E-W and N-S winds),  
219 and then used the one with the lowest  $AIC_c$  among them. We used 10-fold cross-validation with  
220 10 repetitions, where the best model was trained on 70% of the data and then applied to the  
221 remaining 30% of the data. These data subsets were chosen randomly for each repetition  
222 (Hastie, Tibshirani, & Friedman, 2009; Meijer & Goeman, 2013). From the repeated cross-  
223 validation we reported the ability of the best model to distinguish between land/sea-crossing  
224 decisions using the area under the curve (AUC) of the receiver-operating characteristic curve  
225 (with standard deviation), the logistic regression accuracy (defined as the ratio between the sum  
226 of correct predicted cases of sea crossing and land detour and the sum of correct and non-correct  
227 predicted cases), sensitivity (proportion of land-detour choices correctly classified) and  
228 specificity (proportion of sea-crossing choices correctly classified) (Fawcett, 2006). To test  
229 prediction (e), individual consistency in route choice was examined by calculating repeatability

230 across years (Intraclass correlation) using the rptR package (Stoffel, Nakagawa, & Schielzeth,  
231 2017).

232 To test the second part of prediction (a) and prediction (c), we used linear mixed models  
233 (LMMs) to examine the effects of route choice and environmental factors on the daily ground  
234 and air speeds. We found the optimal structure of the fixed component as described above for  
235 GLMMs, using AIC<sub>c</sub> in a multi-model selection framework. Also, we inspected GLMMs and  
236 LMMs residuals and considered the dispersion of the data (Zuur, 2009) using a simulation-  
237 based approach to create readily interpretable scaled (quantile) residuals for fitted (generalized)  
238 LMMs with the package DHARMA (Hartig, 2019). To test prediction (d) we additionally used  
239 LMMs to compare the two route choices in terms of time spent flying, distance covered, ground  
240 and air speeds, ODBA and proportion of flapping flight in of the daily travel and among the  
241 subsets (BEFORE, ACROSS and AFTER the bay). We report differences between route  
242 choices among the path segments using the *lsmeans()* R function of the package lsmeans (Lenth,  
243 2016). Model fitting and multi-model inference were carried out in the statistical environment  
244 R 3.5.1 (R Core Team, 2018) by the packages lme4 (Bates, Mächler, Bolker, & Walker, 2015)  
245 and MuMIn (Barton, 2019), while the cross-validation was done using the package caret (Kuhn,  
246 2019).

247

### 248 **3. Results**

#### 249 **3.1 Route selection**

250 Migrating white storks crossed the Iskenderun Bay more often in spring (61.5%) than in autumn  
251 (39.8%). During the spring seasons of 2011 to 2015 storks crossed the Iskenderun Bay 51 times  
252 and detoured it 32 times. Adults preferred crossing the bay rather than detouring it ( $N_{\text{LAND}} =$   
253  $24$ ,  $N_{\text{SEA}} = 50$ ;  $\chi^2 = 9.13$ ,  $p < 0.01$ ), while an opposite trend was found in juveniles ( $N_{\text{LAND}} = 8$ ,  
254  $N_{\text{SEA}} = 1$ ). Juveniles travelled mostly over land also in autumn, ( $N_{\text{LAND}} = 25$ ,  $N_{\text{SEA}} = 9$ ;  $\chi^2 =$

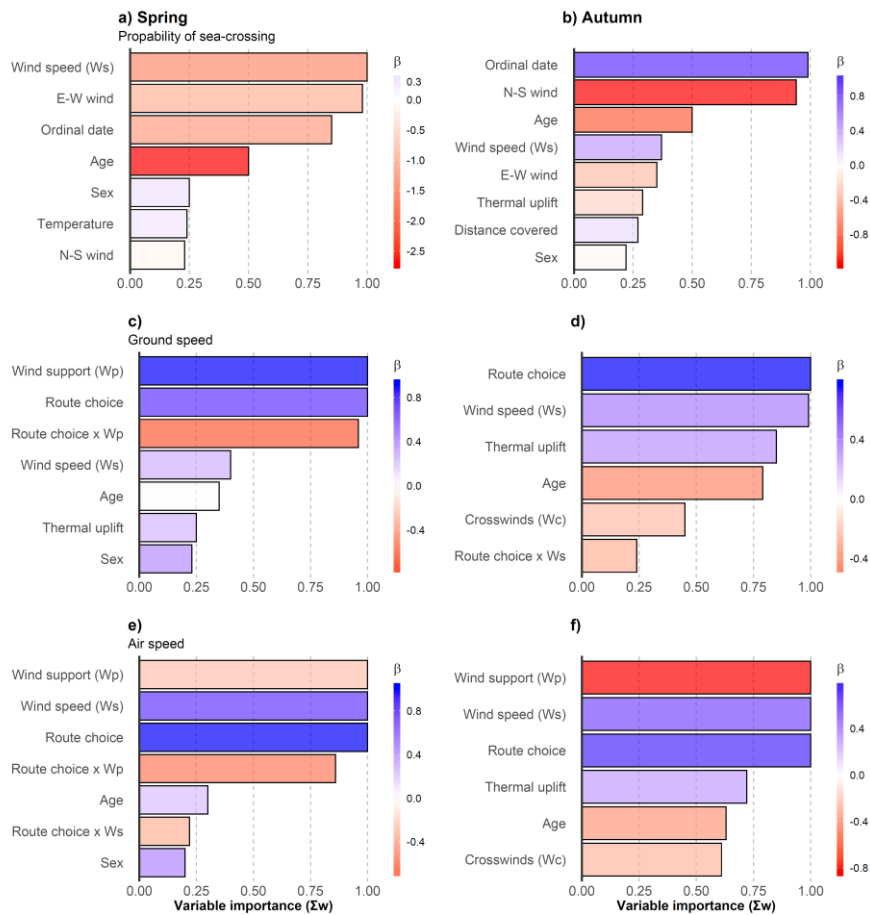
255 7.53,  $p < 0.01$ ), whereas adults did not show any route selection preference in this season ( $N_{\text{LAND}}$   
256 = 43,  $N_{\text{SEA}} = 36$ ;  $\chi^2 = 0.62$ ,  $p = 0.430$ ).

257 In spring, wind speed, E-W wind speed and the ordinal date were ranked as the most important  
258 variables influencing route selection (Figure 2a) such that sea crossing was facilitated by  
259 decreasing wind speed, increasing westward wind speed and earlier passage date (Figure S12-  
260 14; Table S3-5). The average ( $\pm$  SD) logistic regression accuracy of the best-ranked model  
261 following the testing of the data subsets was 0.86 ( $\pm$  0.13), with sensitivity<sub>LAND</sub> = 0.76 ( $\pm$  0.30)  
262 and specificity<sub>SEA</sub> = 0.92 ( $\pm$  0.14). The average ( $\pm$  SD) AUC was 0.96 ( $\pm$  0.09). Route choice  
263 of individual birds was not consistent among years ( $n = 44$ ; repeatability:  $r = 0.05 \pm 0.09$ ,  $p =$   
264 0.340).

265 In autumn, N-S wind and ordinal date were the most influential factors affecting route selection  
266 (Figure 2b). The probability of sea crossing increased with southward wind speed and when  
267 passing over the area relatively late in the season (Figure S15-17; Table S8-9). The average ( $\pm$   
268 SD) logistic regression accuracy of the best-ranked model was 0.74 ( $\pm$  0.14), with  
269 sensitivity<sub>LAND</sub> = 0.84 ( $\pm$  0.17) and specificity<sub>SEA</sub> = 0.60 ( $\pm$  0.27). The average AUC was 0.85  
270 ( $\pm$  0.15). Also in autumn, route choice of individual birds was not consistent among years ( $n =$   
271 67; repeatability:  $r = 0.0001 \pm 0.07$ ,  $p = 0.626$ ). Tables with model and variable rankings as  
272 well as the selected models are reported in the electronic supplementary material. In both  
273 seasons the best models with the lowest AIC<sub>c</sub> values were those that included E-W and N-S  
274 winds and not  $W_p$  and  $W_c$  ( $\Delta\text{AIC}_c = 3.41$  in spring and 5.98 in autumn).

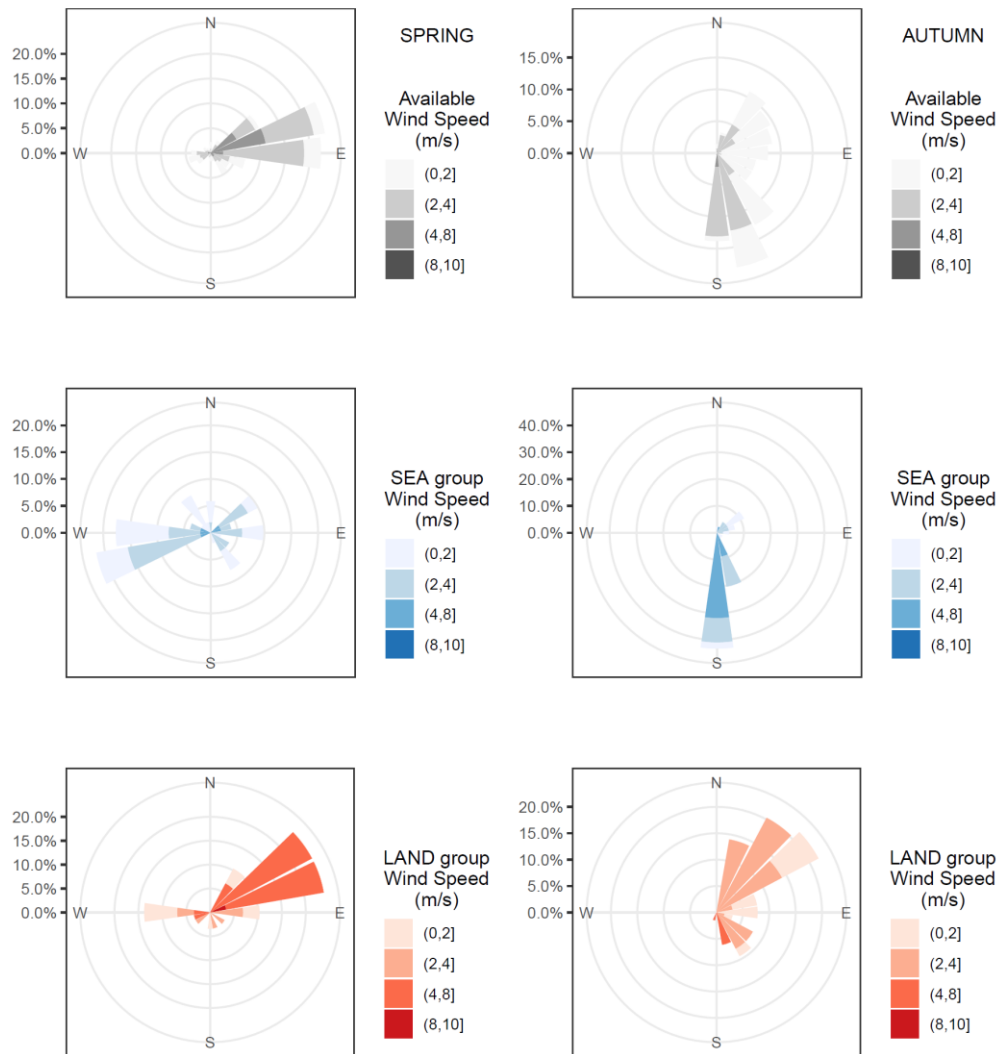
275 Figure 3 shows an overview of the winds available during the migration periods and the wind  
276 conditions (direction and speed) that the storks experienced before crossing or detouring the  
277 bay (BEFORE section; see also Figures S4-9).

278



279

280 **Figure 2.** Summary of predictor averaged coefficients ( $\beta$ ) ranked according to their predictive importance ( $\Sigma_w$ ) in  
 281 models with  $\Delta AIC_c < 7$ . Only results with a minimal  $\Sigma_w = 0.2$  are presented. Dependent variables are: probability  
 282 of sea crossing (a, b), ground speed (c, d) and air speed (e, f). The baseline levels of the binomial variables “Route  
 283 choice”, “Age” and “Sex” are land-detour (*LAND*), *adult* and *female*, respectively. See Tables S2-26 for a complete  
 284 overview of the models’ procedure and results.



285

286 **Figure 3.** Wind roses plots of available winds and those used by white storks over the area BEFORE the bay. The  
 287 available winds are depicted in grey tones, representing the daily averages of the entire period of migration window  
 288 ( $\pm 2$  days) for all the years of the study. The winds encountered by the storks before crossing the bay are depicted in  
 289 blue tones, and those encountered by the birds that detoured the bay are illustrated in red tones. Plots on the left are  
 290 from the spring, and those on the right are from the autumn. See also Figures S4-9.

291

## 292 3.2 Flight speed

### 293 3.2.1 Ground speed

294 The storks' ground speed was 7% higher on average in autumn than in spring (LMM:  $\beta = -0.77$   
 295  $\pm 0.18$ ,  $t_{192} = -4.3$ ,  $p < 0.001$ ). Considering their daily track and regardless of the season, they  
 296 were 8% faster on average when crossing the sea than when flying over land (LMM:  $\beta = 0.7 \pm$

297 0.17,  $t_{192} = 3.99$ ,  $p < 0.001$ ). No difference in ground speed was found between adults and  
298 juveniles when data from the two migration seasons were pooled. In spring, white storks flew  
299 faster in tailwinds and slower under headwinds in general, but their route choice modulated  
300 their response (Figure 2c; Table S12-13). Over land, they increased their ground speed in  
301 tailwind (and decreased it under headwinds), but during sea crossing they maintained a rather  
302 steady ground speed regardless of wind support (Figure S3). In autumn, storks flew faster under  
303 stronger winds, thermal uplifts, crosswinds and when crossing the bay, compared to over-land  
304 flight. Also, adults flew faster than juveniles in this season (Figure 2d; Table S26). In spring,  
305 the best model with the lowest  $AIC_c$  value included  $W_p$  and not E-W winds ( $\Delta AIC_c = 11.45$ ).  
306 In autumn, the two selected models ( $\Delta AIC_c = 0$ ) included either  $W_p$  and  $W_c$  or E-W and N-S  
307 winds.

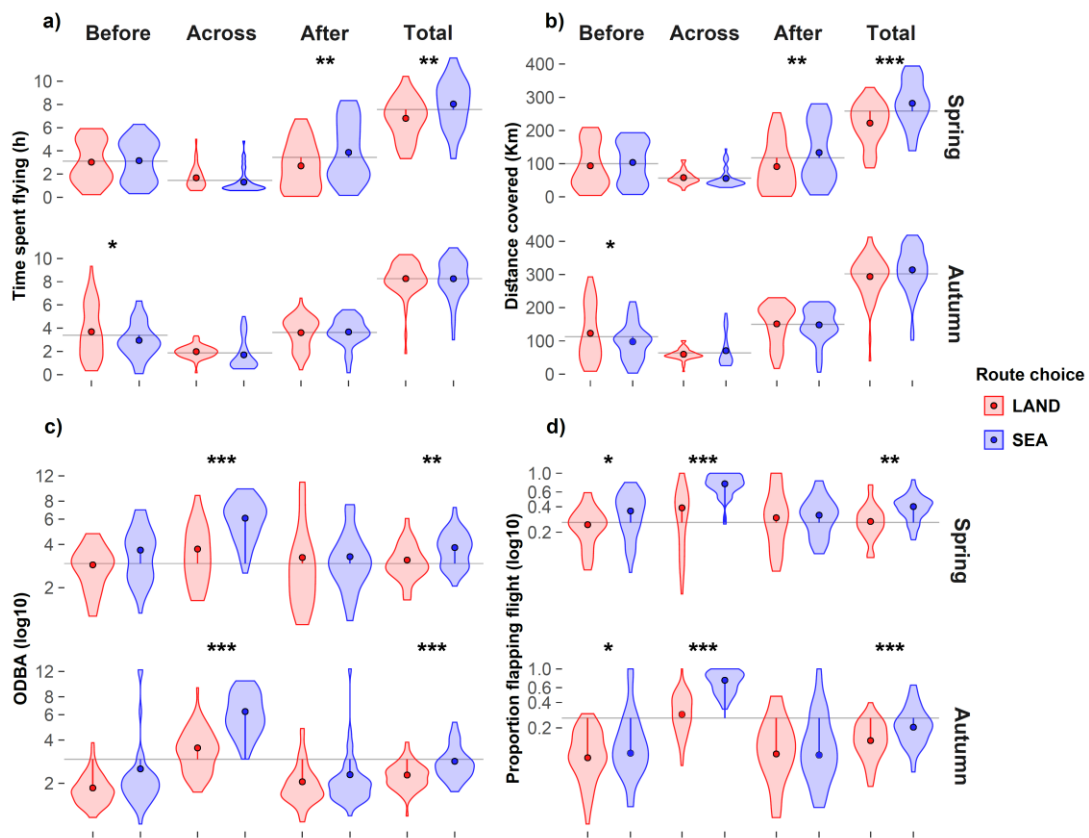
### 308 3.2.2 Airspeed

309 Overall, the storks' daily airspeed was 7% higher on average in spring than in autumn (LMM:  
310  $\beta = 0.55 \pm 0.19$ ,  $t_{192} = 2.89$ ,  $p < 0.01$ ), and adults were 9% faster on average than juveniles  
311 (LMM:  $\beta = -0.5 \pm 0.22$ ,  $t_{192} = -2.25$ ,  $p = 0.025$ ). Notably, considering data from both seasons,  
312 no significant difference in bird airspeed was found between detouring and bay-crossing storks.  
313 In spring, bay-crossing storks adjusted their airspeed to wind support (Figure 2e), decreasing it  
314 with tailwinds and increasing it with headwinds, while land detouring storks did not adjust their  
315 airspeed to wind conditions (Figure S3). Also, storks generally increased their airspeed with  
316 increasing wind speed (Figure 2e). In autumn, stork airspeed was higher under stronger  
317 headwinds, crosswinds and thermal uplifts and when crossing the bay (Figure 2f). In both  
318 seasons the best models with the lowest  $AIC_c$  values were those that included  $W_p$  and  $W_c$ , and  
319 not E-W and N-S winds ( $\Delta AIC_c = 11.89$  in spring and 40.81 in autumn).

### 320 3.3 Route choice and flight time, distance, energy and speed

321 We tested for differences in several flight parameters – namely time spent flying, distance  
322 covered, ODBA, proportion of flapping flight – between the two route choices (LAND or SEA)  
323 BEFORE, ACROSS and AFTER crossing the bay area, as well as over the entire daily path of

324 the birds (Figure 3, Table S1). We found that the distance covered and the time spent flying  
 325 depended on route choice. In spring, white storks that crossed the bay spent on average two  
 326 more hours flying (see also Figures S20-23) and covered 60 km more distance, with the main  
 327 difference found after crossing the bay, while in autumn the distance covered and the time spent  
 328 flying were similar between the two route choices (Figure 3a,b). The average distance covered  
 329 over the bay was 55.47 km (range: 28.12 – 144.33) in spring, and 70.50 km (range: 25.36 –  
 330 182.81) in autumn (Figure S10). ODBA and proportion of flapping flight were about 40%  
 331 higher in storks that crossed the bay in both seasons (Figure 3c,d and Figure 4) in the day that  
 332 included the cross-bay journey.



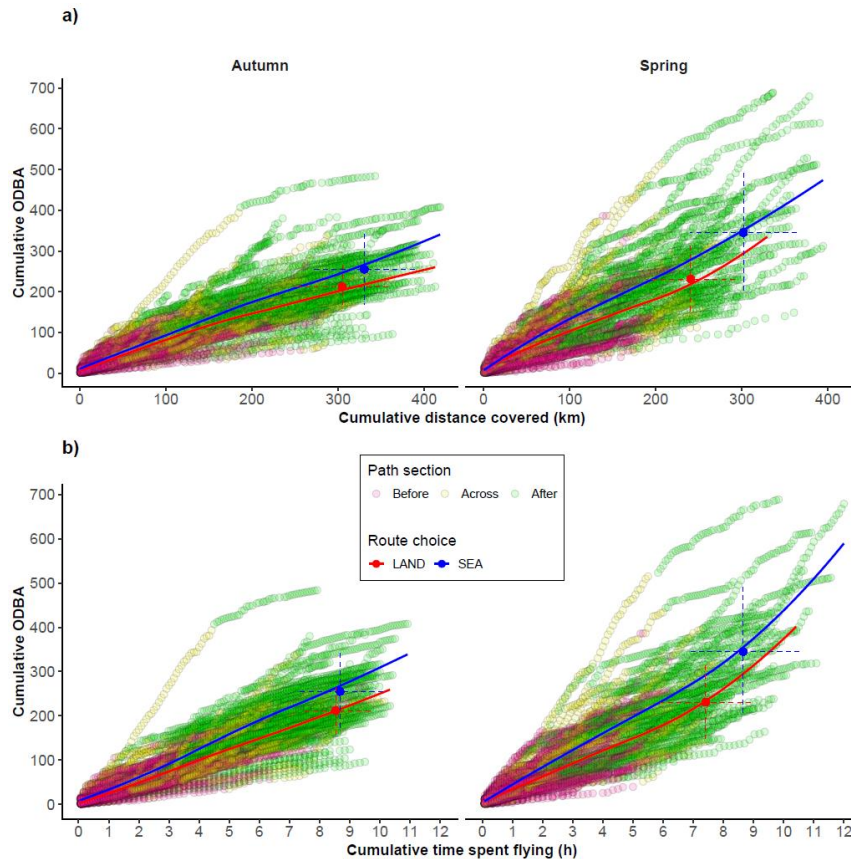
333

334 **Figure 4.** Summary statistics of (a) time spent flying, (b) distance covered, (c) Overall Dynamic Body Acceleration  
 335 (ODBA), and (d) proportion of flapping flight of migrating storks flying over Iskenderun Bay area, according to the  
 336 section of the flight path with respect to the bay (before, across or after) and the entire daily path, and by season.  
 337 Colours represent the two route choices: land-detour (red) and sea-crossing (blue). Horizontal grey lines are averages  
 338 per section and season (a, b) and overall average regardless of season and section (c, d). Dots are mean values and  
 339 the shapes represent the distributions of the data. Asterisks indicate the  $p$ -value ranges:  $p < 0.001$  (\*\*\*),  $p < 0.01$



340 (\*\*),  $p < 0.05$  (\*). See also Figure S6 and S7 for explanations regarding differences in time and distance between  
341 the two route choices over the bay area.

342



343

344 **Figure 5.** Visualization of cumulative sum of Overall Dynamic Body Acceleration (ODBA) in relation to cumulative  
345 distance covered (a) and cumulative time spent flying (b). The curves show the average relationships recorded from  
346 white storks that crossed the bay (blue) and those that circumvented it (red). Closed circles of these colours represent  
347 the mean ( $\pm$  SD) of each selected route choice (sea-crossing and over-land). Sequences of open coloured (see details  
348 below) circles depict data from white storks such that each sequence represents data from a single track across the  
349 bay area. The circles' colour depicts the section over which they were recorded, with respect to the Iskenderun Bay:  
350 BEFORE (violet), ACROSS (yellow) and AFTER (green) the bay (see also electronic supplementary material,  
351 Figure S1).

#### 352 **4. Discussion**

353 We highlight how important and consequential the choice of migration route is for soaring birds  
354 that either crossed a sea barrier or flew around it. Our findings uncover how migration route  
355 selection over a shorter path that is nonetheless characterized by a “high transport cost” is

356 undertaken. In our case, the birds must flap over the sea, while flying a longer over-land detour  
357 route is associated with a lower transport cost because the birds are able to soar over it. We  
358 explored the factors that modulate route selection in a large soaring migrant, the white stork  
359 and inspected route selection consequences for flight behaviour, migration speed and flight  
360 energetics. Specifically, wind influenced route selection (Figure 3) which in turn affected bird  
361 ground and air speed, as well as the birds' flight mode (soaring-gliding flight over land and  
362 flapping flight over the sea). Consequently, the combined effects of environmental conditions  
363 and route selection on energy costs and speed are likely responsible for the increase in the time  
364 spent flying and distance travelled of migrating storks that decided to cross the bay during  
365 spring. However, this longer daily migration distance came with a higher energetic flight cost,  
366 highlighting a likely time-energy trade-off in the migration of white storks. Yet, this benefit of  
367 sea crossing was found only in spring, allowing the birds to arrive earlier to their breeding  
368 grounds. The higher migratory motivation of those individuals that crossed the bay might have  
369 additionally played a major role in determining several aspects of their journey, including their  
370 daily travel duration. It is possible that the lower propensity of over-sea flights in autumn was  
371 based more on minimizing the risks during migration to reach the wintering grounds. Because  
372 route selection was strongly related to the local wind conditions at the day of passage, and was  
373 characterized by low repeatability, we hypothesize that route choice is not based on a fixed  
374 strategy of each individual but rather on a flexible selection with respect to local atmospheric  
375 conditions when arriving to the bay area. It is also noteworthy that the storks migrate in flocks,  
376 and thus route selection might not be an individual decision but rather a decision taken by the  
377 flock leaders (Flack, Nagy, Fiedler, Couzin, & Wikelski, 2018), possibly masking individual-  
378 related attributes. The lower rates of sea crossing in juveniles compared with adults could be  
379 related to their lower migratory experience (Rotics et al., 2016) and to lower migratory  
380 motivation since they do not breed. Possibly, juvenile birds trade off time and energy in a  
381 different manner than adults by responding more strongly to the negative aspects of the cross-  
382 bay flight.

383 Overall, we tested five predictions, how (a) tailwinds and (b) time pressure, sex and age could  
384 affect route choice, and how (c) sea-crossing could save time, possibly allowing extending the  
385 daily migration distance. We further tested whether storks have (d) higher energetic costs due  
386 to flapping flight while passing over the bay and whether (e) individual consistency played a  
387 role in bird route selection. Our first prediction (a) that tailwinds facilitate sea-crossing decision  
388 was confirmed. Decreasing wind speed, increasing westward winds in spring and increasing  
389 southward winds in autumn promoted sea crossing. The N-S and the E-W winds have a likely  
390 supporting effect in each season, since the crossing of the bay took place mostly from north to  
391 south in autumn and from east to west in spring. Similar results were reported by Meyer et al.  
392 (2000) for fall migration of soaring migrants crossing the Strait of Gibraltar with favourable  
393 southward and westward winds. In the same area Griffon vultures (*Gyps fulvus*) were also  
394 observed to cross the Strait of Gibraltar under weak winds or similarly with tailwinds (Bildstein  
395 et al., 2009).

396 Notably, we found contrasting responses to tailwinds between birds that selected the two routes  
397 in spring (see Figure S3). Specifically, birds that travelled over land increased their ground  
398 speed under tailwinds and decreased it under headwinds (see also Shamoun-Baranes et al.,  
399 2003), but kept a steady airspeed in both tailwind and headwind conditions. On the contrary,  
400 over the sea, when the birds employed flapping flight (see below), they adjusted their airspeed  
401 and maintained a quasi-steady ground speed, as observed in several studies of flapping birds  
402 and bats (Liechti, 1995; Sapir, Horvitz, Dechmann, Fahr, & Wikelski, 2014). No such  
403 differences in the birds' response to the wind were found in autumn. We found a general  
404 increase in ground speed and decrease in airspeed with increasing tailwinds, suggesting that  
405 storks probably partially drifted with the wind in their preferred direction (over sea or over  
406 land). This is supported by the fact that the tracks were experiencing mostly tailwinds and  
407 almost no headwinds (Figure S3), meaning that they probably adjusted their movement to  
408 exploit those winds along the daily route in order to undertake a sea crossing or a land detour  
409 (Figure 3).

410 Our second prediction (b) was supported by our results since early-spring migrants commonly  
411 crossed the bay while relatively late migrants mostly detoured over land (Figure 2a and S14).  
412 We note that the higher tendency to cross the sea in spring and mostly with westward winds  
413 may be related to less suitable thermal conditions over land in spring that hindered soaring  
414 flight, compared to autumn (Figure S11). Furthermore, soaring conditions likely improved with  
415 ordinal date in spring, possibly explaining the increasing tendency for a land detour with the  
416 progression of the spring (Figure S11). Notably, early-spring migrants are typically considered  
417 as ‘higher-quality’ individuals, with better body condition (Dittmann & Becker, 2003),  
418 breeding success (Smith & Moore, 2005), and flight performance (Matyjasiak, 2013), which  
419 might explain their higher rates of selecting the shorter but energy demanding sea-crossing  
420 route.

421 Our findings partially support our third prediction (c) that sea-crossing flight is beneficial as it  
422 saves travelling time (see also Figures S19-23), and extends the daily distance travelled. Our  
423 data suggest that this was the case only for spring but not for autumn. The results support the  
424 prediction (d) that sea-crossing is associated with higher movement-related metabolic costs,  
425 since sea-crossing birds mostly used flapping flight and had higher ODBA (and thus likely  
426 higher flight energetic costs) compared with overland detouring birds. As predicted (e), no  
427 individual consistency was found in bird route selection.

428 In autumn, choosing one route or the other had no benefits in terms of more distance covered  
429 after the bay, but due to the use of flapping flight when crossing the bay, the birds that flew  
430 over the sea likely had higher flight energetic costs compared with land detouring birds that  
431 mostly flew using soaring flight. However, one has to bear in mind that since we found an effect  
432 of the prevailing meteorological conditions on route choice, we could not compare storks that  
433 used the two alternative routes under similar weather conditions. Hence, our comparison of  
434 migration performance between overland versus sea-crossing tracks are limited by the specific  
435 weather conditions that prevailed in the area in which the storks selected their route.

436 Understanding how atmospheric processes impact migration movements is of fundamental  
437 importance in a time of climate change (La Sorte, Horton, Nilsson, & Dokter, 2018; Nourani,  
438 Yamaguchi, & Higuchi, 2017; Winkler et al., 2014). In Turkey, including in the area of  
439 Iskenderun Bay, wind speed and specifically the E-W component of wind speed decreased over  
440 the last decades (Dadaser-Celik & Cengiz, 2014), partially following changes in global  
441 circulation patterns and increasing surface roughness (Vautard, Cattiaux, Yiou, Thépaut, &  
442 Ciais, 2010). Our results indicate that migrants are sensitive to the dynamics of their aerial  
443 environment and their behaviour and movement properties are strongly affected by local  
444 meteorological conditions. Changing atmospheric patterns due to climate change may thus  
445 result in changes in migration route selection of migrating white storks, with possible  
446 implications for population dynamics (La Sorte, Fink, & Johnston, 2019) and conservation  
447 (Wilcove & Wikelski, 2008).

448

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461

462 **Authors' contributions**

463 P.B. and N.S. conceived the study and designed the methodology with the help of S.R., N.H.  
464 and R.N. S.R. and M.K. carried out the field work with the help of M.W. and D.Z. P.B. analysed  
465 the data and compiled all figures. P.B. and N.S. led the writing of the manuscript and all authors  
466 contributed to the revisions of the draft. S.R., N.H. and R.N. further contributed to data  
467 interpretation and manuscript revision. All authors contributed critically to the drafts and gave  
468 final approval for publication.

469

470 **Data availability statement**

471 The GPS-ACC data that was used in this study is available in Movebank Data Repository  
472 ([movebank.org](https://movebank.org)): <https://doi.org/10.5441/001/1.v8d24552> (Rotics et al., 2018), and  
473 <https://doi.org/10.5441/001/1.hn1bd23k> (Rotics et al., 2016).

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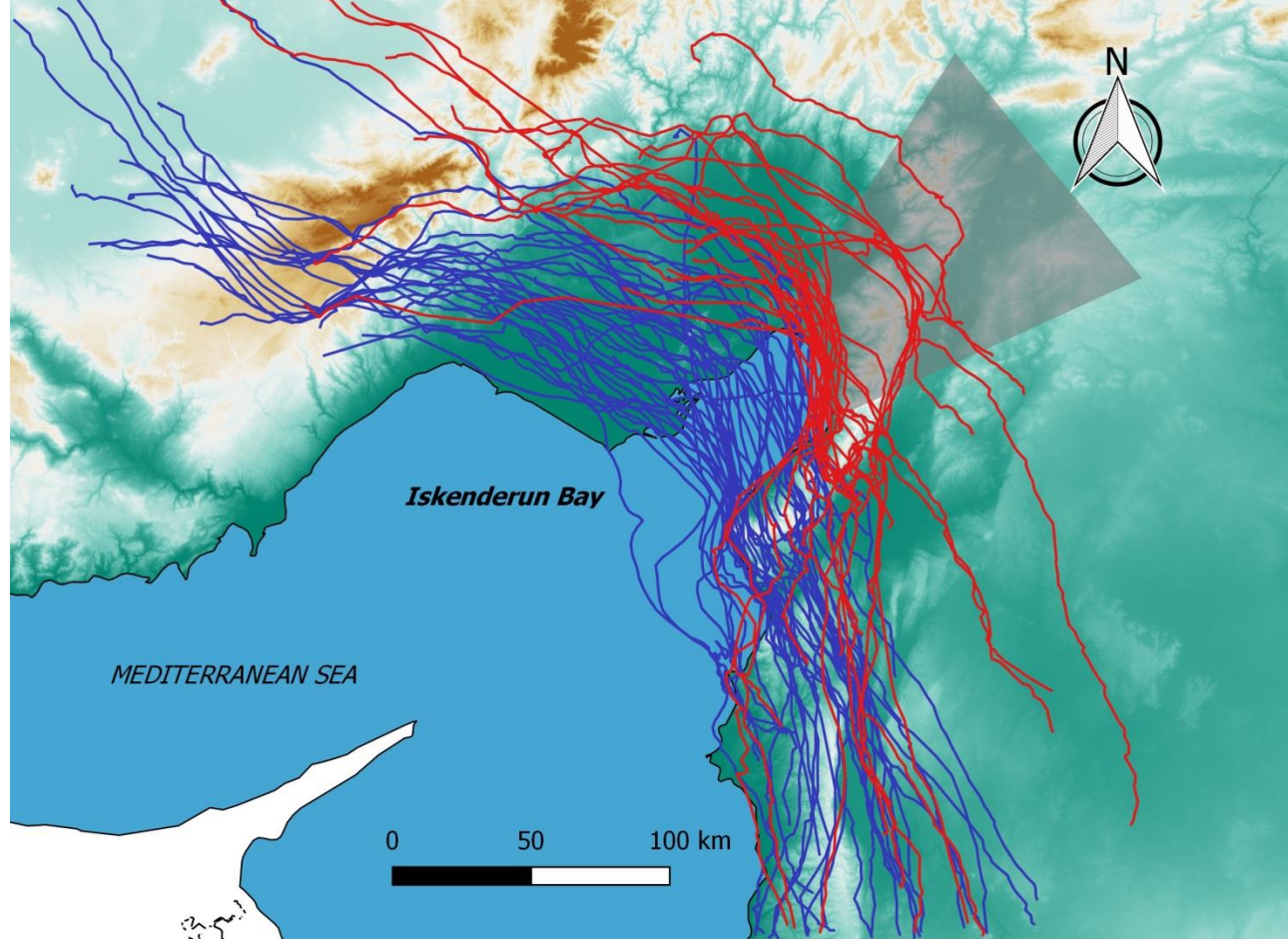
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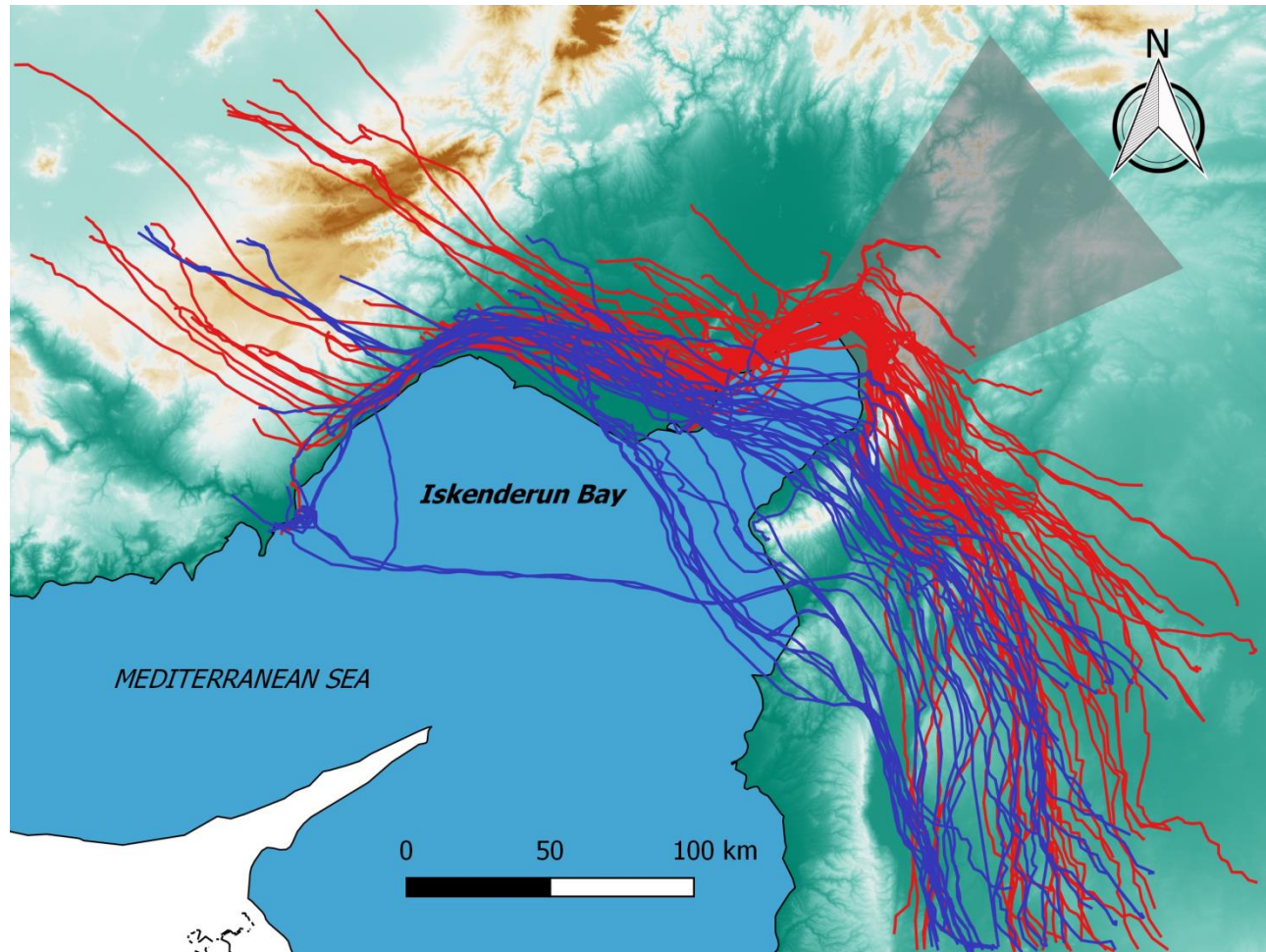
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a)  
Spring

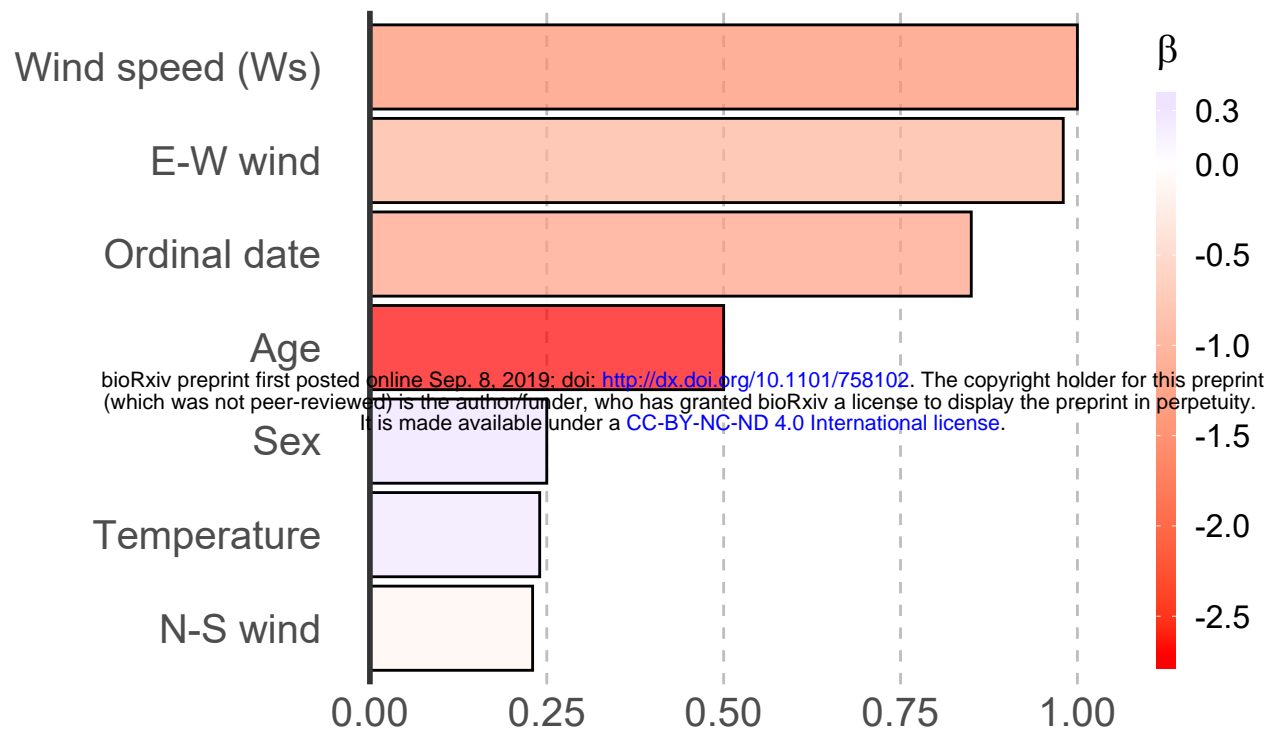
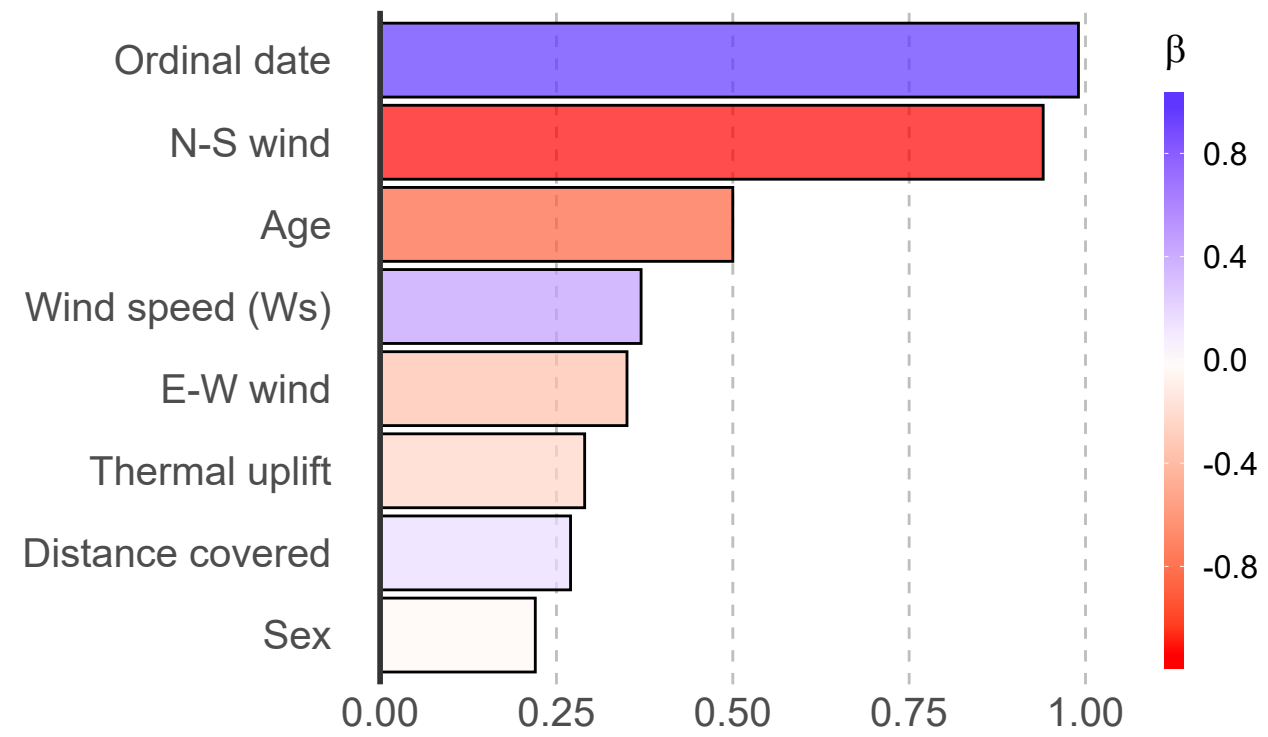


b)  
Autumn

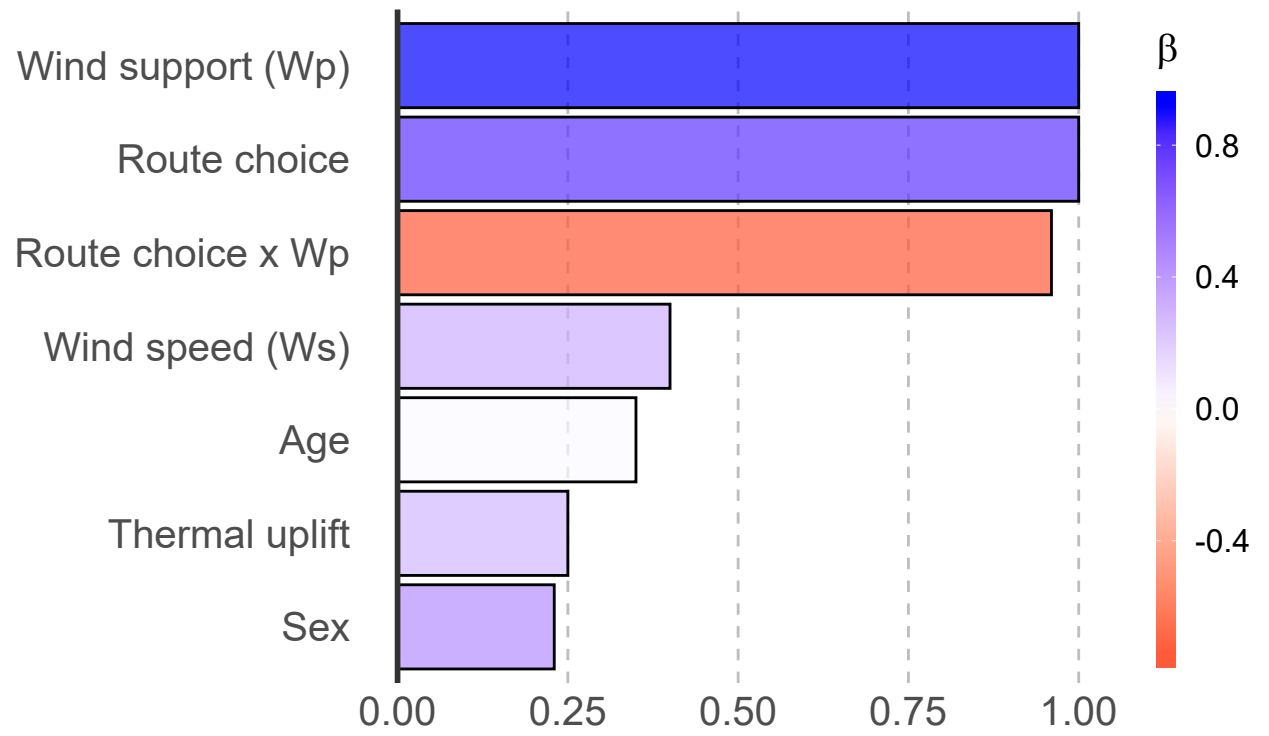
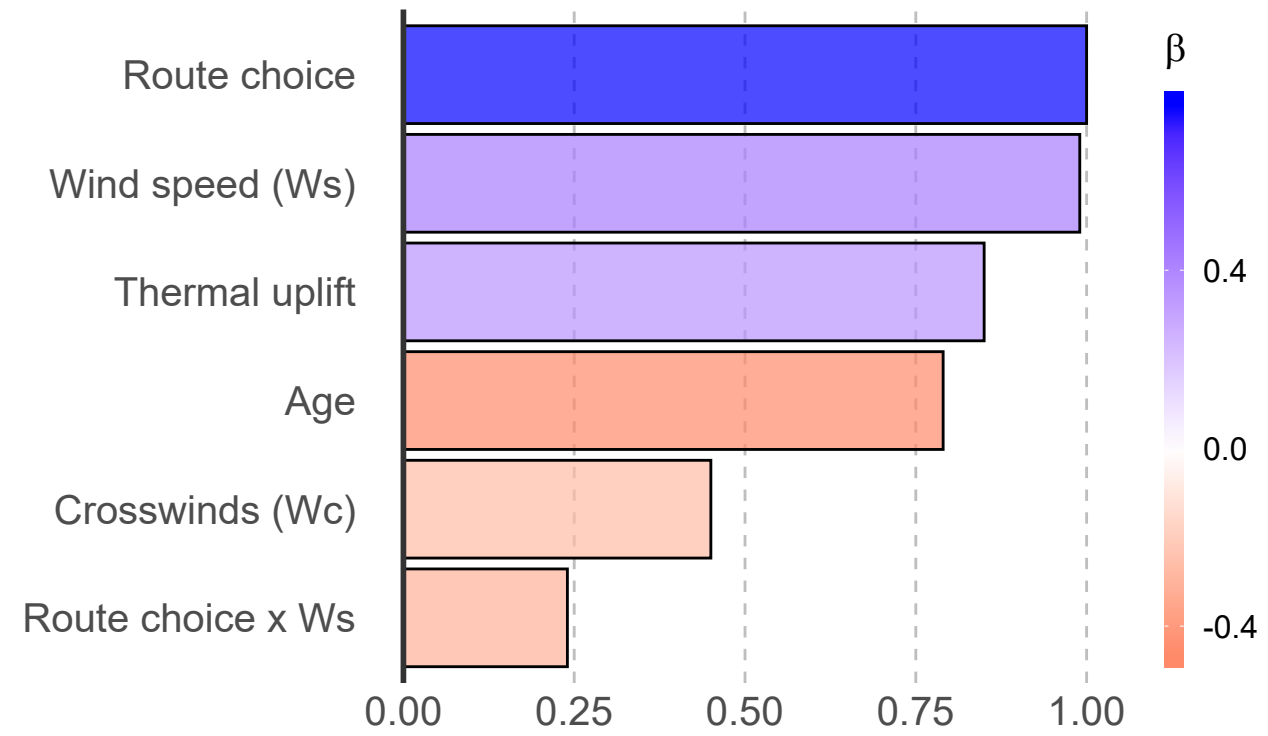


**a) Spring**

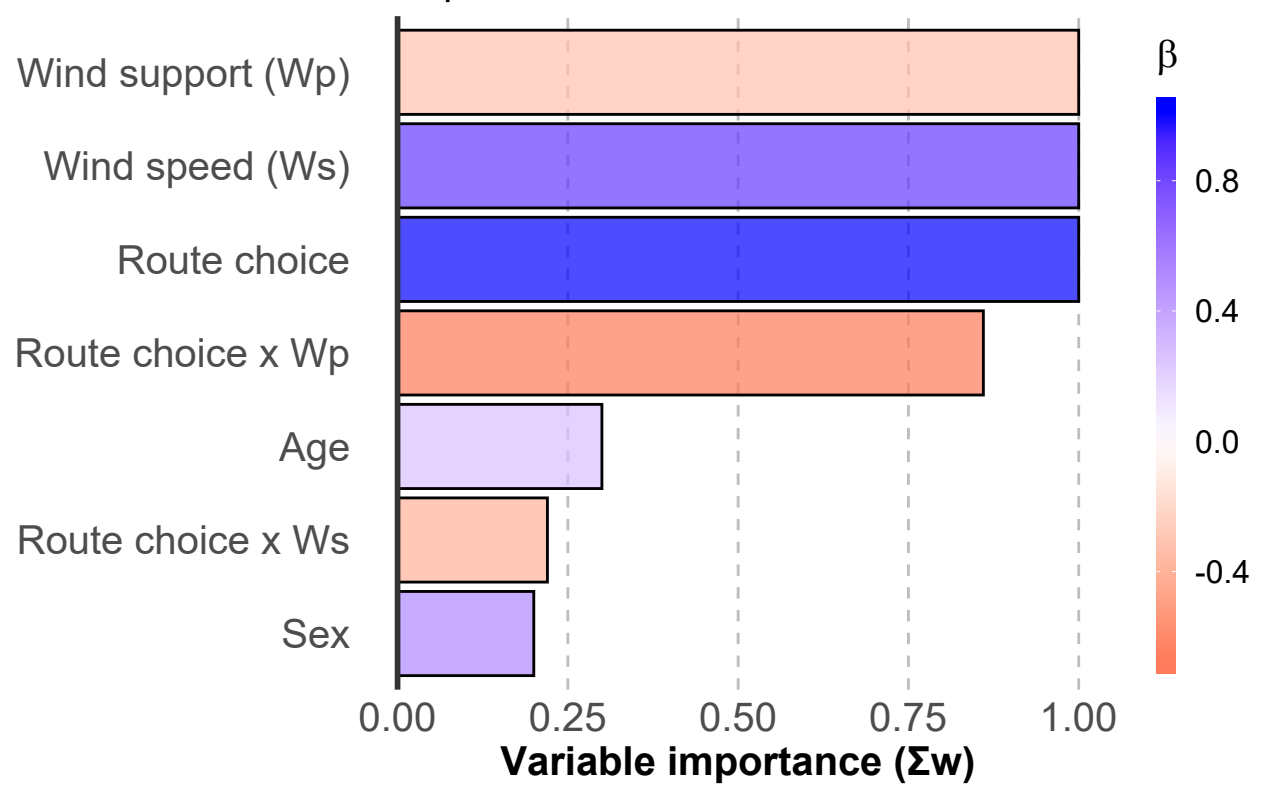
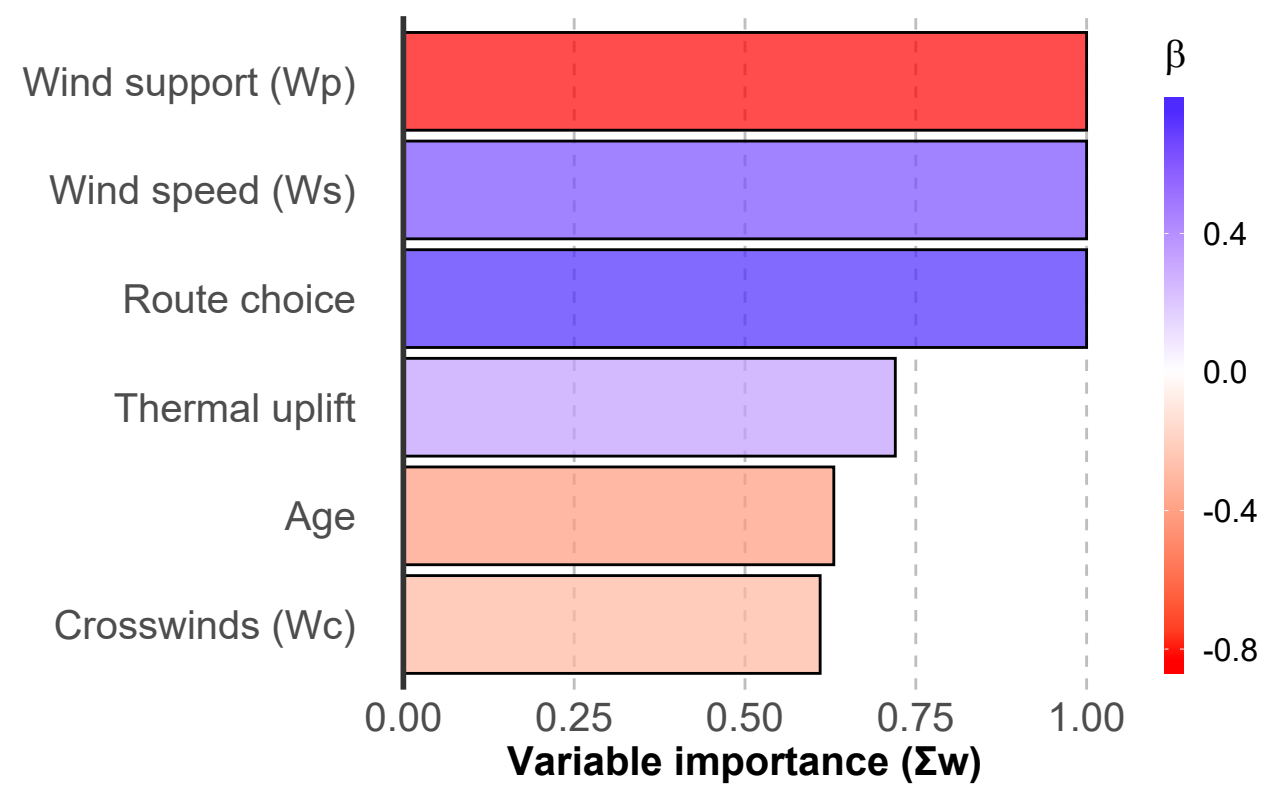
Propability of sea-crossing

**b) Autumn****c)**

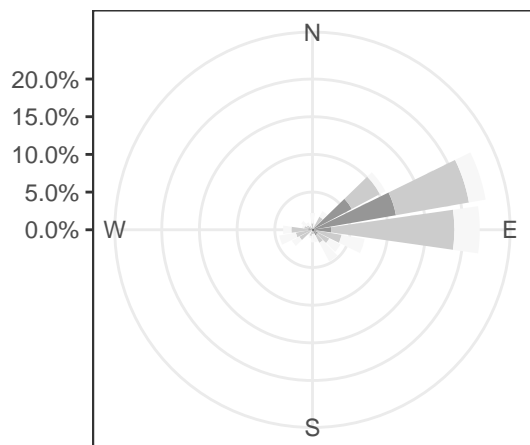
Ground speed

**d)****e)**

Air speed

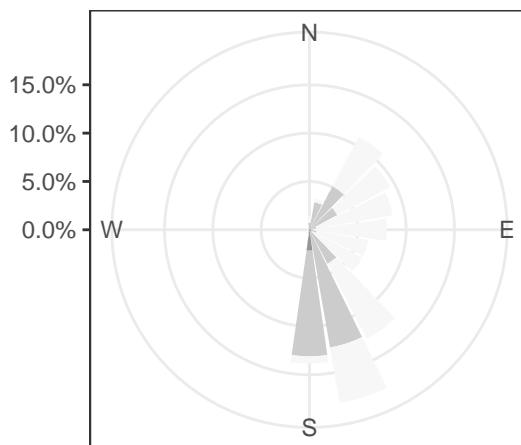
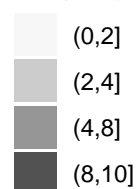
**f)**





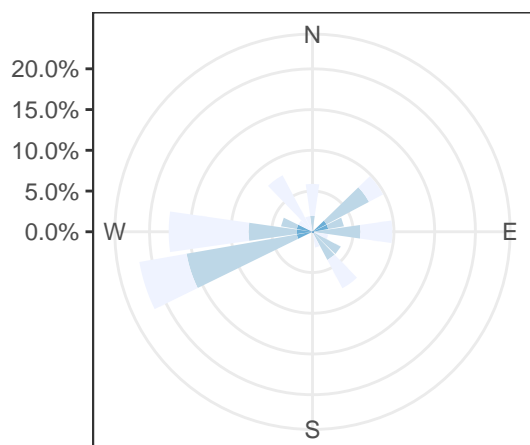
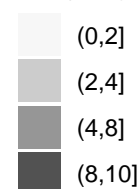
**SPRING**

**Available Wind Speed (m/s)**

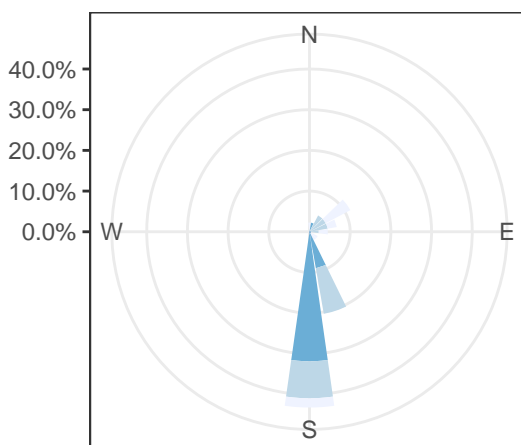
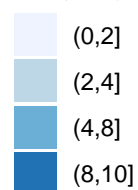


**AUTUMN**

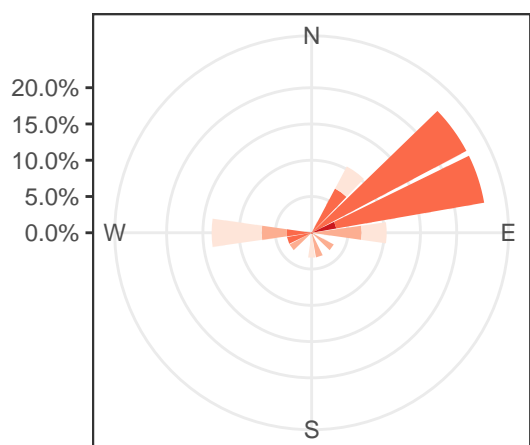
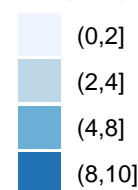
**Available Wind Speed (m/s)**



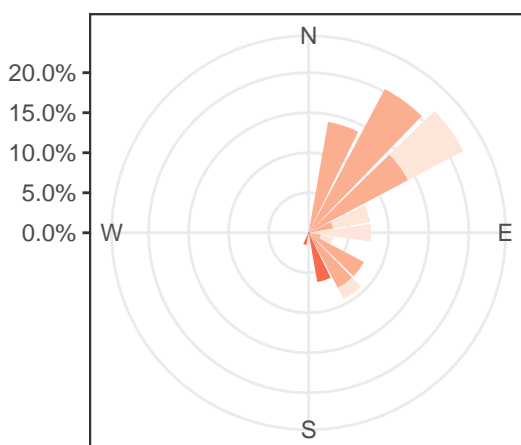
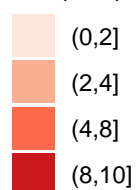
**SEA group Wind Speed (m/s)**



**SEA group Wind Speed (m/s)**



**LAND group Wind Speed (m/s)**



**LAND group Wind Speed (m/s)**

