

24 **Abstract**

25 **Background:** For soaring birds, the ability to benefit from variable airflow dynamics is crucial,
26 especially while crossing natural barriers such as vast water bodies during migration. Soaring
27 birds also take advantage of warm rising air, so-called thermals, that allow birds to ascend
28 passively to higher altitudes with reduced energy costs. Although it is well known that soaring
29 migrants generally benefit from supportive winds and thermals, the potential of uplifts and other
30 weather factors enabling soaring behavior remains unsolved.

31 **Methods:** In this study, we GPS-tracked 20 Red Kites, *Milvus milvus*, from the central
32 European population that crossed the Adriatic Sea on their autumn migration. Migratory tracks
33 were annotated with weather data (wind support, side wind, temperature difference between air
34 and surface – proxy for thermal uplift, cloud cover, and precipitation) to assess their effect on
35 Red Kites' decisions and soaring performance along their migration across the Adriatic Sea and
36 land.

37 **Results:** Wind support affected the timing of crossing over the Adriatic Sea. We found that
38 temperature differences and horizontal winds positively affected soaring sea movement by
39 providing lift support in otherwise weak thermals. Furthermore, we found that the soaring
40 patterns of tracked raptors were affected by the strength and direction of prevailing winds.

41 **Conclusion:** Thanks to modern GPS-GSM telemetry devices and available data from online
42 databases, we explored the effect of different weather variables on the occurrence of soaring
43 behavior and soaring patterns of migratory raptors. We revealed how wind affected the soaring
44 pattern and that tracked birds could soar in weak thermals by utilizing horizontal winds, thus
45 reducing energy costs of active flapping flight over vast water bodies.

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49 **1. Introduction**

50 Wind is an important environmental factor affecting birds' migratory route selection and overall
51 performance during migration and barrier crossings (1–4). Especially for soaring birds, the
52 ability to benefit from variable airflow dynamics is crucial due to the higher energetic costs of
53 powered flight (5). Wind flowing in the same direction as the migrant (tailwind) subsidizes
54 energy costs by supporting the bird in its movement. In contrast, winds of opposite (headwind)
55 or perpendicular direction (side wind) might increase the energy costs of flight by reducing
56 migrant speed or by drifting it away from its aimed direction (6,7). Soaring birds also take
57 advantage of warm rising air, so-called thermals, that allow birds to ascend passively to higher
58 altitudes with reduced energy costs (8,9). Although soaring migrants generally benefit from
59 supportive wind and thermals (7,8), how they respond to dynamic weather conditions over a
60 sea remains unsolved.

61 The open sea is considered a significant migratory barrier for all terrestrial, particularly
62 soaring, birds (10). Over open water, winds tend to blow stronger than over land, as ocean and
63 sea present a smooth surface that allows the wind to blow without interruption (11). Dynamic
64 weather conditions, strong winds, and the inability to regain energy create hazardous conditions
65 for sea-crossing soaring migrants. Moreover, the occurrence of thermals that can provide
66 energy-free lifts is considered to be relatively low at sea (12). In recent studies, the temperature
67 difference between surface and air (ΔT) has been used as a proxy for the occurrence of thermals
68 (1, 13). Positive ΔT values correspond to a warmer surface than the air temperature, where a
69 warmer surface heats the air that is pushed up by colder and denser air, creating an uplift.
70 Negative values represent sinking air (14). Soil particles generally have a lower thermal
71 stability than water, meaning that the land surface is more efficiently heated or cooled than
72 water. This different physical characteristic explains why thermals, which are essential for
73 soaring migrants, are formed stronger on land than over sea (15). The costs of sea crossings are

74 reflected in studies of birds that fly along the coasts (16) or perform long detours on their
75 migration and use shorter over-water passages to avoid long crossings of open seas (12, 17).
76 However, there is evidence that some soaring migrants soar in thermals that occur over the sea
77 and thus reduce the energy costs of such crossing (18).

78 Studies that investigated the presence of uplift (13,18–20) explored them as an
79 important source of passive altitude gain in soaring migrants. Nourani et al. (7) found that
80 weather conditions over open sea during different seasons can create more suitable migratory
81 corridors for soaring migrants than those that occur over land. A few years later, using high-
82 frequency GPS data, Duriez et al. (18) presented the first evidence of soaring behavior in raptors
83 over the sea. This finding presented the idea that soaring migrants benefit from uplifts over a
84 sea more than expected. However, Nourani et al. (13) conducted a study that found that sea-
85 crossing soaring migrants prefer to select areas with prevailing wind support over areas with
86 possible occurrence of uplifts. Although these studies brought precious information that built
87 the foundation of modern understanding of how soaring migrants overcome open sea, they did
88 not explore if the presence of soaring behavior is conditioned by the presence of uplifts *per se*
89 (13,18–20), mainly due to the lack of fine-scaled GPS data. Therefore, the potential of uplifts
90 and other weather factors that can enable the soaring behavior of soaring migrants, allowing
91 them to travel across natural barriers with lower risk and energy outcomes, merits further
92 research.

93 Knowing how birds adapt their flights across migratory barriers remains an open and
94 important question for understanding the evolution of migratory routes and sea-crossing
95 strategies. In this paper, we try to answer this question by investigating fine-scaled GPS data
96 obtained from Red Kites (*Milvus milvus*, a middle-size European raptor) that crossed the vast
97 open waters of the Adriatic Sea (approximately 200 km) on their autumn migration from Central
98 Europe to southern Italy. Red Kites from Central Europe winter in different Mediterranean

99 countries of Europe (21). Most birds from this population migrate through the continent, and
100 only a small part cross over the Adriatic Sea (21), where the katabatic Bora wind blows in the
101 southwestern direction (22). These cold katabatic winds can be beneficial for crossing migrants
102 not only by creating favorable wind support but also by bringing high-density air that decreases
103 the frequency of energetically costly flapping flights (23) and thus can create reliable freeway
104 for the small part of the Central European population during autumn migrations (24). Most birds
105 from this population migrate through the continent, and only a small part cross over the Adriatic
106 Sea (21), where the katabatic Bora wind blows in the southwestern direction (22). These cold
107 katabatic winds can be beneficial for crossing migrants not only by creating favorable wind
108 support but also by bringing high-density air that decreases the frequency of energetically costly
109 flapping flights (23) and thus can create reliable freeway for the small part of the Central
110 European population during autumn migrations (24).

111 Our study offers an opportunity to explore how soaring migrants, well adapted for flying
112 in continental lowland and hilly areas, face the environmental conditions of the vast open sea
113 and land terrain during their annual migratory movement. Here, we aim to determine 1) what
114 weather conditions affected the timing of soaring migrants to overcome the Adriatic Sea, 2)
115 what weather conditions enabled the soaring behavior of soaring migrants, and 3) how weather
116 conditions affected soaring patterns over land and sea. The individual decision to engage in sea
117 crossing and no evolutionary adaptations for life over sea makes Red Kites the perfect model
118 species to study the plasticity of flight behavior in land-dwelling soaring raptors over open
119 waters. Based on previous studies, we expect that wind support will play a significant role in
120 the decision to initiate sea crossing (13,16,19). We further assume the soaring behavior to be
121 enabled primarily by the presence of thermals and potentially by horizontal winds (1).

122

123 **Material and methods**

124 **Bird tagging and data collection**

125 In this study, we explore the behavior of 19 Red Kites from the central European breeding
126 population (Austria, Czech Republic, and Slovakia) that crossed open waters of the Adriatic
127 Sea during their autumn migration movements. Red Kites were fitted with telemetry loggers
128 with solar panels as nestlings (20 g; Ecotone, Poland, www.ecotone.pl and Ornitela, Lithuania,
129 www.ornitela.com). The average weight of tagged nestling was 950 ± 47 g, meaning that the
130 logger represented approximately 2.1 % of their body weight, under the recommended 3 %
131 threshold (25,26).

132 Loggers were fitted onto the backs of the birds using harnesses (backpacks) consisting of a
133 6 mm Teflon ribbon encircling the body by two loops around the bases of the wings and joined
134 in front of the breastbone. Loggers function in GPS (Global Position System)/GSM (Global
135 System for Mobile Communication) systems. Ecotone loggers were set to collect one position
136 fixed per 1–6 h, and Ornitela loggers were set to collect data in the range from 1 fix per 15
137 minutes to 1 hour or in a 5-minute burst (1 fix per second) followed by a 10-15-minute pause
138 to limit the battery drain. Accelerometer and magnetometer data (in g-force/1000 and
139 milliGauss (mG), respectively) were collected only for Ornitela loggers in the same frequency
140 as GPS positions. We used ArcGIS Pro (Esri, Redlands, CA, USA) to analyze the coordinates
141 of bird positions and create migration maps. The raw datasets analysed during this study are
142 available in Movebank Data Repository (27).

143 **Data processing, migration characteristics**

144 We processed positional data (coordinates) for each bird individually. These data were
145 separated into migration modules. The sea crossing was defined as the migration period
146 between the first and last location above the water body.

147 Most individuals ($n = 14$) that reached the western seashore of Croatia rested by the
148 shore for at least two days before crossing the Adriatic Sea (in 24 cases out of 38 crossings).

149 Thus, to test if weather conditions affected the decision to cross, we compared weather data
150 (see below for the specific variables used) from the days of resting by the shore and the day of
151 crossing. The meteorological data for the resting days were annotated for the coordinates
152 recorded from 6:00 to 13:00 (the time range when our birds initiated the crossing). For the
153 crossing, we chose coordinates recorded from 6:00 until the bird's distance from the shore
154 exceeded the arbitrarily chosen threshold of 10 km. We chose this threshold as some resting
155 birds explored the area above the Adriatic Sea within this distance but did not depart. If more
156 than one location per hour was obtained, we averaged the weather variables per hour. We
157 obtained 324 records from resting days and 56 records for days of initiating the sea crossing.

158 Red Kites exhibited soaring and non-soaring behavior during both sea and land
159 crossings. We followed the approach described by Williams *et al.* (28) and Duriez *et al.* (18) to
160 sort the flight behavior into three categories of movement: soaring, gliding, and flapping.

161 The high resolution of the datasets made it easy to detect circling and ascending behavior,
162 indicating thermal soaring. However, we used 3-axis accelerometer and magnetometer data for
163 more systematic behavior classification and the sensor analysis software Framework4, available
164 from <https://framework4.swan.ac.uk/>. Firstly, we omitted locations with recorded speeds lower
165 than 1 km/h to eliminate roosting points. After that, we used the 3-axis accelerometer data to
166 identify between active/flapping flight (strong oscillations in vertical z-axis) and passive flight
167 (gliding/soaring - smooth in vertical z-axis between 800-1400 mG) (18, 28). Once we selected
168 the passive flight, we used the 3-axis magnetometer data to sort out thermal soaring (oscillations
169 in the x-axis) and gliding (smooth x-axis) (18, 28). After annotation, we projected the dataset
170 in ArcGIS Pro and checked if the annotated behavior matched the projected data. For our
171 purposes, we only used data from soaring and flapping flights. We did not include gliding flight
172 because soaring migrants can glide in variable conditions once they reach the required altitude,
173 regulating their airspeed and sink ratio (29), and we were interested in exploring suitable

174 weather conditions for soaring over the flapping flight. After removing data annotated as
175 gliding, we again projected the data in ArcGIS Pro. We chose only segments with more than
176 10 points in 1s intervals with clear soaring or non-soaring patterns. We recorded in total 3 394
177 (7 807) and 1 757 (12 712) GPS positions in 1s intervals for flapping and soaring flight over
178 the sea (land), respectively. For each individual, we calculated the climb rate of burst collection
179 as the difference between the segment's maximal and minimal heights above sea level. We
180 observed three different soaring patterns over sea and land. We divided them into three groups
181 by the trajectory shape: a) staircase – diameter of turns > 10 m, b) spiral - diameter of turns $<$
182 10 m, and c) s-shape - no full turns observed. Each GPS burst with recorded soaring behavior
183 was categorized into these three groups. Few segments contained both staircase and spiral
184 patterns were observed. In this case, we annotated the segments by the most frequent pattern.

185 **Weather data**

186 Weather data, such as u and v components of wind – vectors of speed and direction of the wind
187 used to calculate wind support and side wind, air temperature, sea/land surface temperature,
188 cloud cover, and total precipitation were obtained for each GPS position via the ENV-data track
189 annotation service provided by Movebank (30) by ECMWF ERA5 reanalysis database with a
190 temporal and spatial resolution of 1h and 0.25° , respectively. We used the bilinear interpolation
191 method for wind components and the nearest-neighbour method for temperature, precipitation,
192 and cloud cover. Before extracting data, we explored the birds' altitude while crossing. Weather
193 data of the sea crossings were extracted for each coordinate in real-time, and a pressure level of
194 1000 mb corresponded to an altitude of around 150 m. We extracted data separately for one
195 individual at a pressure level of 925 mb as it flew over the sea at a much higher altitude. To
196 assess the effect of weather on an individual's decisions to cross over the sea, we used the
197 weather data from 100 m above the surface. As the birds migrated over land in higher altitudes,
198 for this position, we obtained the weather data at a pressure level of 925 mb, corresponding to

199 an altitude of around 760 m. Wind support and side wind were calculated by function
200 NCEP.tailwind using RNCEP package (31), which calculates wind support and forward and
201 sideways movement according to the equation of Tailwind (Tailwind = wind speed * cos (α),
202 where α is the angle of the wind from the direction of travel). The azimuth of direction travel
203 was measured in ArcGIS Pro. For sea crossing - between birds' first and last location over the
204 sea, and for land crossing – between breeding site and crossing point at Croatian coast. Equation
205 Tailwind considers wind support as the flow component moving parallel to the specified
206 direction (tailwind), with negative values indicating flows against the specified direction
207 (headwind). We also calculated the temperature difference (ΔT) between surface and air as a
208 meaningful proxy for uplift over water (13). We calculated ΔT as the difference in temperature
209 between the surface and the air in mean altitudes of birds' flight (either 150 or 760 m).

210 **Statistical analysis**

211 We performed the Mann-Whitney U test and Chi-square tests to test the differences between
212 flight metrics during sea crossing and flying over land (wind support, side wind, temperature,
213 altitude, and climb rate). Before any statistical analyses, we run the Shapiro–Wilk test to
214 evaluate the normality of the data. To assess the effect of weather on an individual's decision to
215 cross overseas in relation to flow assistance, side wind (in absolute values), precipitation,
216 temperature, and total cloud cover, we used a binomial Generalized Linear Mixed Model
217 (GLMM) where the probability of departure was a binomial response variable. In these models,
218 we included data from all 20 birds. To model the effect of weather on birds' movement across
219 sea and land during autumn migration, we used another series of binomial GLMM models
220 where the occurrence of soaring was a binomial response variable (soaring behavior = 1,
221 flapping behavior = 0). In these models, only birds with telemetry loggers set to burst collection
222 were included in the soaring models over sea and land ($n_{\text{individuals}} = 4$) due to the high frequency
223 of coordinates recording. We analyzed the possible occurrence of soaring behavior in relation

224 to wind support, side wind (in absolute values), cloud cover, and temperature difference (ΔT)
225 between surface and air. We did not include precipitation in this model, as there was no
226 precipitation during crossings. Firstly, we wanted to use all recorded locations with a frequency
227 of 1 location per second. However, our models showed high autocorrelation of residuals.
228 Therefore, we used one location per 30 seconds and averaged annotated meteorological data.
229 Based on previous findings that sea crossing birds prioritized tailwind and areas with a high
230 tailwind and ΔT (13), we fitted soaring models with interactions among these two variables.
231 Two additional binomial GLMM models were used to test if weather conditions can predict
232 soaring patterns. As we observed two soaring patterns over land and sea, we ran two models,
233 one for each terrain, where the annotated soaring pattern was a binomial response. Again, we
234 used averaged data in 30-second intervals to avoid high autocorrelation of residuals. In models
235 regarding soaring vs. flapping behavior and soaring patterns over land, we observed a non-
236 linear relation between wind support and the dependent variable. Therefore, we included
237 polynomial terms for wind support in those models. In soaring models over sea, we observed a
238 linear relation between wind support and the dependent variable. We explain this difference by
239 absence of negative wind support (headwind) over a sea. We fitted our models in R software
240 using the 'lme4' package (32). We checked the dataset for multicollinearity and only used
241 variables that were not highly correlated ($r < 0.6$). We omitted cloud cover from soaring models,
242 as it was highly correlated with ΔT ($r = 0.83$). Before any analysis, we standardized the predictor
243 variables using the 'scale' function to make the coefficients of our models comparable. We
244 located outliers within independent variables and included them in our models. Weather
245 conditions can reach extreme values; therefore, removing outliers could alter our study's aim of
246 assessing the bird's response to changing weather conditions. In every model, an ID of birds
247 was added as a random factor to control for variations in individuals. Model estimates were
248 obtained by averaging the best-supported models with ΔAIC (Akaike information

249 criterion)(soaring models) or $\Delta AICc$ (decision to cross model) lower than two, using the
250 'dredge' function in MuMIn package (33). We calculated the predictive accuracy of each model
251 using the k-fold-cross-validation method with 10 folds via the 'performance_accuracy' function
252 in the 'performance' package (34). All statistical tests were performed using an α value of 5%,
253 and all mean values are presented (\pm standard deviation; SD) unless stated otherwise.

254

255 **Results**

256 **The decision to cross the sea**

257 In this study, we examined the migration behavior of Red Kites from Central Europe that
258 crossed the Adriatic Sea on their way to their wintering ground (Figure 1). In total, we recorded
259 34 autumn sea-crossings that took place from September to November (Table 1). In order to
260 explore what factors affected the decision to initiate a sea crossing, we examined the weather
261 conditions experienced by the individuals who rested on the western Croatian coast before
262 initiating the crossing over the Adriatic Sea. Results of the averaged model (accuracy 75 %)
263 showed that birds tended to initiate the crossing with a supportive wind (tailwind) and rested
264 by the coast if the adverse winds prevailed (Table 2a, Figure 2). Other factors included in the
265 model did not have statistical support.

266 **Flight behavior over the land and sea**

267 Migrating birds spent more time flapping and less time soaring when flying across the sea than
268 over land (Table 3). The ratio between GPS positions annotated as soaring and flapping flight
269 was reversed above these two terrains. ΔT was more than four times larger at land, reflecting
270 the lower occurrence of thermals over the sea (Table 3). Furthermore, the mean climb rate was
271 twice higher at land ($1.1 \text{ m} \cdot \text{s}^{-1}$) than at sea ($0.6 \text{ m} \cdot \text{s}^{-1}$) (Table 3). Regarding the wind conditions,
272 we found that Red Kites experience stronger wind support at sea during soaring and flapping

273 flight (Table 3). In contrast to sea crossing, at land, migrating birds experienced mainly negative
274 wind support (headwind) and stronger side wind during both flapping and soaring flight.

275 As we explored the soaring behavior of Red Kites, we observed variability in soaring
276 patterns among birds (Figure 3). Overland, birds employed two soaring patterns with either
277 spiral (4 365 GPS positions, Figure 3B) or staircase-like (8 288 GPS positions, Figure 3A)
278 trajectory, depending on the strength of wind support and side wind (Table 2e). The stronger
279 the wind support and side wind, the shorter the circular movement dimensions, the more
280 horizontal the overall trajectory, and as a result the distance between turns increased. In weak
281 to no wind support, birds soared in larger circular patterns, often overlapping each other.

282 Sea-crossing birds also employed two soaring patterns. The first pattern was observed
283 in all birds, and its trajectory was identical to the spiral soaring pattern employed over land in
284 the strong wind support and side wind (1 460 GPS positions) (Figure 3C). However, unusual
285 behavior was observed in three birds. One of them crossed the sea at higher altitudes (661 ± 230
286 m a.s.l.), while the others used typical altitudes in comparison to others (112 ± 90 m a.s.l.).
287 These birds used a unique S-shaped soaring pattern (297 GPS positions) when they soared up,
288 changing their airspeed without complete circulation movement (Figure 3D). During this
289 movement, birds experienced low ΔT (0.4 ± 0.3) and faced one of the strongest wind support
290 (9.4 ± 1.1 m. s⁻¹) and side winds (3.1 ± 0.5 m. s⁻¹) from all sea-crossing Red Kites. Results of
291 our model show that the wind support again conditioned the difference in occurrence between
292 these two soaring patterns, but not side wind (Figure 4, Table 2d).

293 When estimating what factors affected soaring behavior over land and sea, we found
294 differences in wind utilization. During sea-crossing, the soaring behavior was affected by the
295 presence of wind support, side wind, ΔT , and the interaction of wind support and ΔT (Table 2b,
296 Figure 5A). Our results showed that the stronger the wind support, ΔT , and side wind, the higher
297 the probability of soaring behavior at sea. The best model, with a predictive accuracy of 83 %,

298 predicted a 50 % probability of soaring at sea when the tailwind speed was 6 m. s⁻¹ and ΔT over
299 1° (Figure 5A). Interaction between wind support and ΔT showed that rising values of both
300 predictors increased the probability of soaring and that in low values of ΔT , the probability of
301 soaring was small regardless of the wind support. The probability of soaring was also small
302 while negative or weak wind support prevailed, regardless of the value of ΔT . When flying over
303 the land, wind support and ΔT had a significant effect on the probability of soaring (Table 2c,
304 Figure 5B). The highest probability of soaring was found with wind support between -5 to 6
305 m.s⁻¹, and outside this interval, the probability decreased. The effect of ΔT on the probability
306 of soaring was smaller in comparison to the sea. The probability of soaring was 50 % when the
307 surface was approximately 3 °C warmer than the air at the altitude that birds flew in (model
308 predictive accuracy 81 %). Interaction between wind support and ΔT showed no effect on
309 soaring over land.

310

311 **Discussion**

312 Our study focused on soaring raptors' abilities to cross over barriers with a particular interest
313 in how weather conditions affected their soaring behavior over different terrains, as the ability
314 to perform soar-glide flight is crucial for soaring migrants (5). We found interesting results
315 showing that wind utilization of soaring migrants varied above different terrains, that horizontal
316 wind affected soaring patterns of tracked birds, and most importantly, that horizontal wind
317 played an important role in inducing soaring behavior in weak thermals over open waters.

318 **Soaring behaviour**

319 We found that the weather factors that affected the soaring performance of Red Kites differed
320 while flying above open waters and land. Our model showed that wind support, side wind, ΔT
321 and interaction of wind support and ΔT conditioned the presence of soaring behaviour over
322 open waters. Although no studies are exploring the effect of weather factors on soaring behavior

323 over a sea, Duriez et al. (18) reported that Ospreys *Pandion haliaetus* soared in thermal uplift
324 while crossing over the open sea, which offered an idea that thermals are more frequent over
325 the open seas than previously considered, and can play an important role for soaring migrants
326 in surmounting open waters. However, higher occurrences of flapping flights, lower flying
327 altitudes, and lower climb rates reported by our results indicate that their strength and
328 abundance are lower in comparison to thermals occurring over land. Nourani et al. (13) found
329 that soaring migrants were more affected by wind support than uplift while crossing overseas.
330 Considering all the factors mentioned above, it is highly probable that while sea crossing,
331 soaring migrants rely primarily on wind support rather than on the scarce occurrence of weak
332 thermals to reduce the time and energy required for completing their risky journey over open
333 waters (13,19,35).

334 By exploring the difference in soaring patterns observed above sea and land (Figure 3),
335 we found that the strength and direction of horizontal winds shaped soaring patterns. We
336 observed that during spring-like soaring, birds climbed through the air in the first quarter of the
337 sharp turn with a short diameter followed by horizontal flight – creating a spiral-like trajectory
338 caused by prevailing wind support and side wind (36,37). A similar trajectory was recorded in
339 Ospreys, which used thermals for soaring up during sea-crossing (17). This behavior connected
340 with sharp turns is possible due to the ability of these birds to fly at higher bank angles, which
341 considerably reduces their turning trajectory (38) and allows them to reduce the kinetic energy
342 loss while turning into a headwind and use it for the climb. The ability to perform sharp turns
343 can be crucial, especially for soaring migrants flying in the strong winds over the sea, because
344 while circling, the birds need to turn back to a supportive wind before losing all their kinetic
345 energy by the opposite wind in order to avoid an energetically costly flapping flight.

346 Three of the studied birds performed a unique pattern of soaring over the sea, where
347 they moved in an S-like shape, similar to the control flight observed in large soaring raptors

348 (39). We did not observe this soaring pattern over the land. Larger species of soaring raptors,
349 such as Turkey Vultures *Cathartes aura*, follow a characteristically tortuous flight path when
350 gliding at low altitudes, changing their vertical and horizontal direction while maintaining the
351 same altitude. This behavior was explained by the use of shear-induced turbulence generated in
352 areas where weather conditions are not optimal for the formation of thermals (39). Although
353 turbulences can explain this S-shaped soaring behavior, we observed an increase in altitude.
354 Therefore, we do not think that birds used shear-induced turbulence when soaring over the sea.
355 The three birds that performed this soaring pattern while facing strong wind conditions
356 supposedly benefited from the strong wind support and side wind. We assume that these birds
357 used their kinetic energy of movement gained by strong wind support to turn and climb up in
358 the side wind (now headwind from the birds' perception), using the higher air pressure on the
359 bottom of their wing as a force to push them up within short distances without the need of a
360 complete circular movement, reducing energy costs (14). We believe that this mechanism of
361 exchanging kinetic energy to climb was employed in all soaring behavior over the sea with
362 strong winds and explains the effect of wind support and side wind on the probability of soaring
363 behavior over sea shown by our model. We assume that, in this manner, sea-crossing birds were
364 able to soar up not only by using thermal uplift but also to horizontal winds in weak thermals
365 in a way similar to dynamically soaring seabirds (40). This assumption is supported by our
366 results, which showed that without sufficient wind support, the probability of soaring was
367 lower. Our finding provides the first evidence for the idea that soaring migrants have to utilize
368 horizontal winds to gain elevation in weak thermals, as proposed by Duriez et al. (18). Thus,
369 the preference for strong wind support would not only reduce the time and, with it, connected
370 energy costs (13,19,35) but also reduce the energy costs associated with frequent flapping flight.
371

372 Over the land, birds performed soaring behavior in the presence of thermals (high values of ΔT)
373 and in low to moderate wind support. As the wind support increased, the probability of soaring
374 decreased. Kites seemed to utilize this positive wind support to increase the distance travelled
375 while flapping, over elevation gain via soaring. When we explored the trajectories of migrating
376 Kites, we observed that birds often changed their heading and soared in the opposite direction.
377 After soaring up, birds reoriented back to their intended direction and glided/flapped through
378 the headwind that was prevailing over land during their autumn migration. Such behavior was
379 reflected in our model, which predicted that individuals also soared in a headwind. All in all,
380 Red Kites in this study showed great plasticity in response to changes in wind conditions along
381 their migratory route (7,29,41).

382 **Initiating sea crossing**

383 In autumn migration, Red Kites spent up to two weeks by the western coast of Croatia waiting
384 for suitable winds to initiate the Adriatic Sea crossing. During this time, birds could choose a
385 less risky route and fly through the continental part of northern Italy to reach their wintering
386 destination. However, they decided to wait and cross the Adriatic Sea in a prevailing wind
387 support. These birds waited for the Bora winds that blow from the direction of Croatia to Italy
388 (22). Because wind has a strong impact on flying costs (6), we suppose that such periodically
389 occurring winds create annual freeways that can be utilized by Red Kites and other soaring
390 migrants on autumn migration through the Adriatic Sea (13,18,24). Our results support previous
391 findings that showed the importance of supporting winds during migration and initiating
392 departures (7,20,42). By using this freeway, birds could benefit from supportive wind and reach
393 the wintering destination in southern Italy with less energy than by detouring over the continent,
394 at the expense of a possible later arrival to the wintering ground. A similar phenomenon was
395 observed on the Oriental Honey-buzzard *Pernis ptilorhynchus* (19). Suitable wind conditions

396 on autumn migration allowed these soaring raptors to perform long crossings over the East
397 China Sea and shorten their way to wintering ground (19).

398

399 **Conclusion**

400 In this study, we explored the effect of different weather factors on the soaring behavior of
401 soaring raptors, and we concluded that, although the principles of birds soaring in thermals have
402 been recently studied (38,42,43), there are still some knowledge gaps on weak-thermal soaring
403 behaviors that are essential for understanding birds' migratory capabilities. We found wind
404 support to be a key factor in the initiation of sea crossing and, surprisingly, along with side
405 wind, in the occurrence of soaring behavior over sea. Birds were able to soar in weak thermals
406 by utilizing horizontal winds, thus reducing the energy costs of active flapping during the
407 crossing. Red Kites, as a model species of land-dwelling soaring migrants, showed great
408 plasticity in utilizing winds over sea and land. By exploring the effect of different weather
409 variables on the occurrence of soaring behavior and soaring patterns, this study brings another
410 piece to the puzzle regarding the ability and capability of soaring raptors to cross over the open
411 sea.

412

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417 study.

418

419 **Ethical approval**

420 The telemetry study of Red Kites was undertaken under permits issued by local nature
421 protection authorities in Austria (MIL2-J-0812/012, GFL2-J-107/014, BHBRN-2019-
422 314986/5-PS), the Czech Republic (Permissions S-JMK 188552/2014 OŽP/Kuč, S-JMK
423 32177/2015 OŽP/Kuč, S-JMK 30634/2016 OŽP/Ško, S-JMK 177265/2017/OŽP/Ško) and the
424 Ministry of Environment of the Slovak Republic (Permissions MŽP SK 664/297/05-5.1pil and
425 MŽP SK 2944/2017-6.3) We observed no behavioural, survival or reproductive consequences
426 in Red Kites tagged with telemetry loggers. We performed all methods following the relevant
427 guidelines and regulations concerning study animals. We confirm that the study is reported in
428 accordance with ARRIVE guidelines (44).

429

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436 the REMARKABLE project.

437

438 **Authors' contributions**

439 JŠ and IL conceived the study and built the hypothesis. JŠ and ŠK processed and analyzed the
440 data. ESG supervised statistical analyses. JŠ wrote the manuscript. RR participated
441 substantially in the field part of the research and provided most of the telemetry loggers used in
442 the study. All authors revised and commented on the manuscript.

443

444 **Competing interests**

445 The authors declare no competing interest.

446

447 **Availability of data and materials**

448 The datasets analysed during the current study are available in the Movebank Data
449 Repository, <https://doi.org/10.5441/001/1.300> (Škrábal, year).

450

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563 **Figures and Tables**

564 **Table 1** - Estimates of autumn and spring sea crossing of tagged Red Kites from 2015 to 2022.

565 ^aNumber of migration episodes (number of tagged individuals).

566

567

Migration component	N^a	Autumn crossing Mean ±SD
Departure time	34 (19)	10:10 ± 3 h
Arrival time	34 (19)	13:35 ± 2.5 h
Departure date	34 (19)	03.10. ± 36 days
Average speed (km/h)	34 (19)	58 ± 13
Duration (hours)	34 (19)	3.2 ± 1 h
Route length (km)	34 (19)	189 ± 37

568 **Table 2** - Fixed effects on sea crossing probability, soaring probability and soaring pattern as
569 estimated by averaging our best GLMMs (ΔAIC or $\Delta AICc < 2$) with individual ID included as
570 a random factor (except d and e). GLMM – generalized linear mixed model, ID – identification
571 number, ΔT – difference between surface and air temperatures.

Model	Predictor	Estimate	Std. Error	z value	p value	P.A. %	R^2_c	R^2_m
a) Crossing	(Intercept)	-1.97	0.46	4.26	0.00	75	0.52	0.31
	Wind support	0.99	0.27	4.38	0.00			
	Side wind	0.30	0.19	1.58	0.11			
	Cloud cover	-0.07	0.20	0.38	0.70			
	Precipitation	-0.47	0.30	1.57	0.12			
b) Soaring over sea	(Intercept)	0.01	0.23	0.05	0.96	83	0.68	0.49
	Wind support	1.51	0.35	4.36	0.00			
	Side wind	1.65	0.48	3.44	0.00			
	ΔT	1.97	0.45	4.42	0.00			
	Wind support : ΔT	1.65	0.27	6.06	0.00			
c) Soaring over land	(Intercept)	0.15	0.08	1.87	0.06	81	0.18	0.10
	poly(Wind support,2)1	0.01	0.09	0.07	0.94			
	poly(Wind support,2)2	-0.27	0.10	-2.68	0.01			
	Side wind	-0.15	0.09	-1.71	0.09			
	ΔT	0.35	0.09	3.85	0.00			
	Wind support : ΔT	-0.15	0.13	-1.19	0.23			
d) Soaring pattern over sea	(Intercept)	-2.79	0.77	-3.60	0.00	80	0.72	0.54
	Wind support	3.42	1.47	2.31	0.02			
	Side wind	3.18	2.94	1.30	0.19			
	ΔT	3.82	2.61	1.21	0.22			
e) Soaring pattern over land	(Intercept)	0.61	0.11	5.37	0.00	68	0.26	0.12
	poly(Wind support,2)1	-0.60	0.13	-4.61	0.00			
	poly(Wind support,2)2	-0.80	0.14	-5.63	0.00			
	Side wind	-0.24	0.12	-2.03	0.04			
	ΔT	0.14	0.12	1.19	0.28			

572

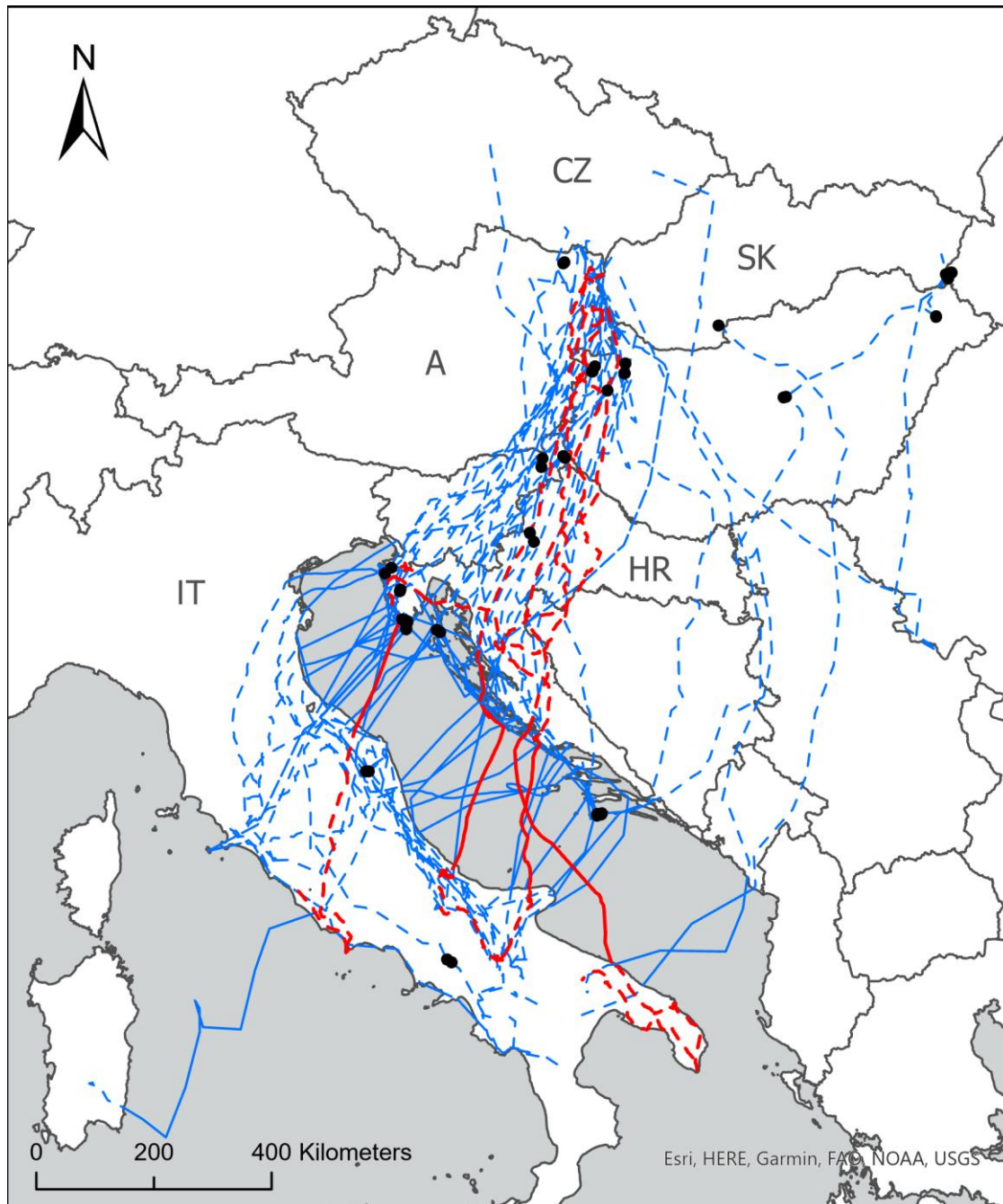
573

574 **Table 3** - Comparison of flight metrics during sea crossing and flying over land. Chi-square
 575 test and Mann-Whitney U tests of difference between behaviors at sea and over land. Means
 576 are presented \pm standard deviation with range in parentheses.

577

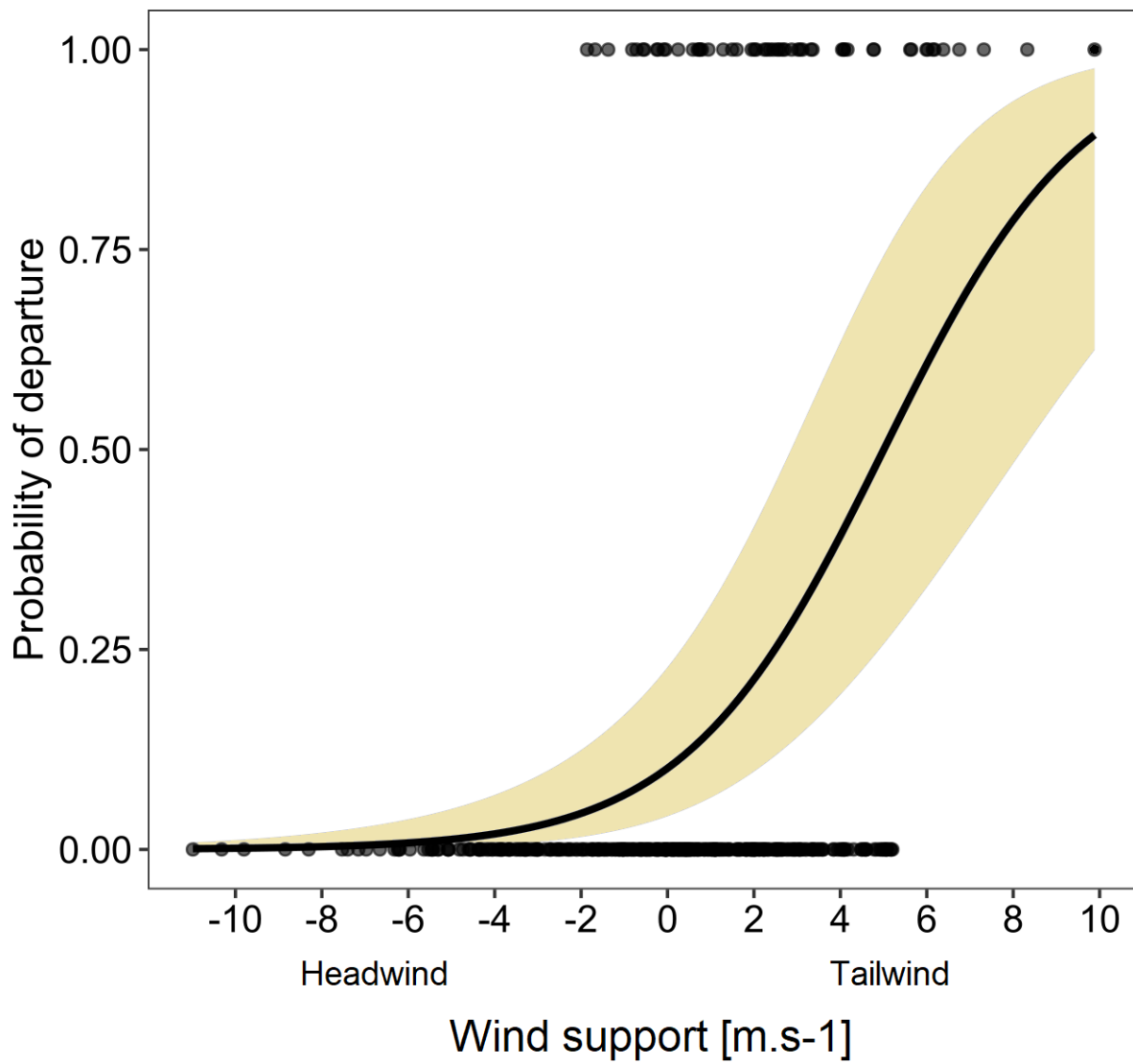
	Migration over sea	Migration over land	Test	578
Soar/Flap ratio	1/1.9	1.6/1		
Wind support while soaring (m. s ⁻¹)	4.8 \pm 2.3	-0.9 \pm 4.5	U = 9593, p < 0.05	
Wind support while flapping (m. s ⁻¹)	2.7 \pm 3.9	- 2.1 \pm 4.6	U = 4032, p < 0.05	
Side wind while soaring (m. s ⁻¹)	2.5 \pm 1.4	2.6 \pm 1.8	U = 4334, p < 0.05	
Side wind while flapping (m. s ⁻¹)	1.9 \pm 1.5	3.0 \pm 2.1	U = 7355, p < 0.05	
Δ T while soaring	1.1 \pm 0.5	5.4 \pm 1.8	U = 5793, p < 0.05	
Δ T while flapping	1.2 \pm 0.7	5.1 \pm 2.0	U = 9012, p < 0.05	
Mean altitude while soaring (m a.s.l.)	243 \pm 215 (43–906)	738 \pm 355 (63–2043)	U = 25137, p < 0.05	
Mean altitude while flapping (m a.s.l.)	101 \pm 129 (20–978)	1051 \pm 372 (247–2061)	U = 24435, p < 0.05	
Mean climb rate while soaring (m. s ⁻¹)	0.6 \pm 0.9 (0.1–1.5)	1.1 \pm 0.6 (0.2–2.8)	U = 239, p < 0.05	

579 **Figure 1** – Map of autumn migratory movement of twenty Red Kites from Central Europe that
580 crossed the Adriatic Sea . Dashed lines depict flight above the continent and full lines of sea
581 crossing. Red lines represent trajectory of four birds with 1s data collection that were used in
582 models comparing soaring and flapping flight. A – Austria, CZ – Czech Republic, SK –
583 Slovakia, IT – Italy, HR – Croatia.

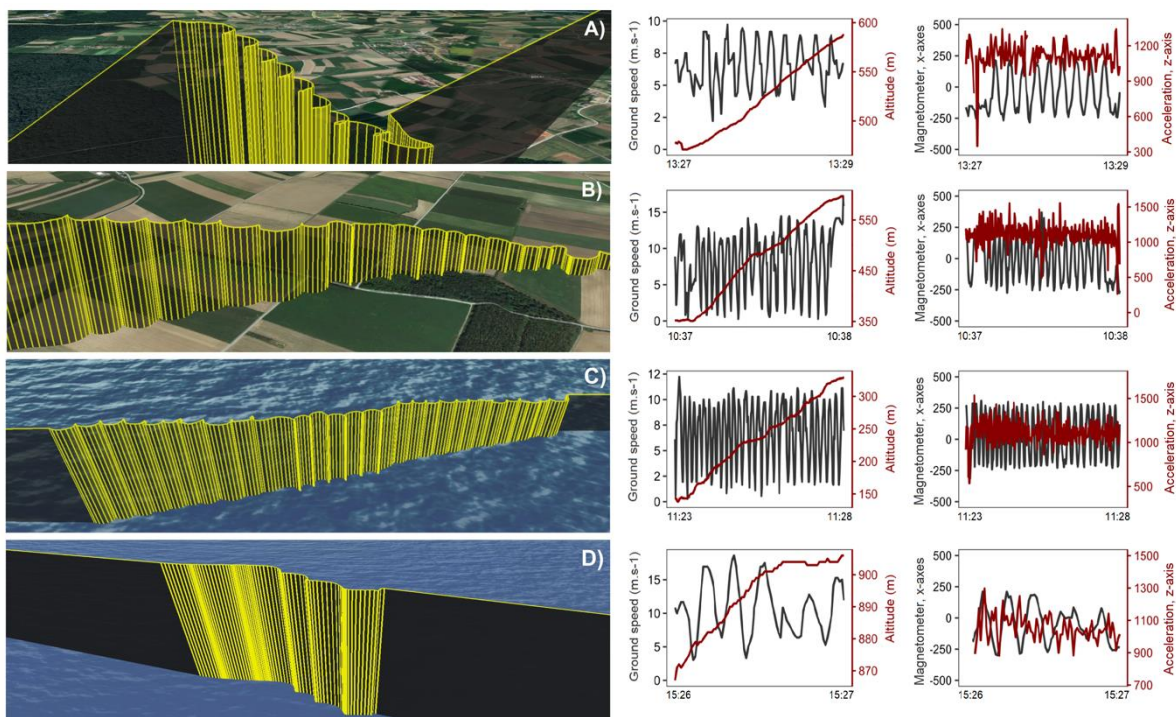


584

585 **Figure 2** – Predicted effect of a wind support on the probability of departure over Adriatic Sea
586 with confident interval 95 % of our best GLMM (Generalized linear mixed) model.

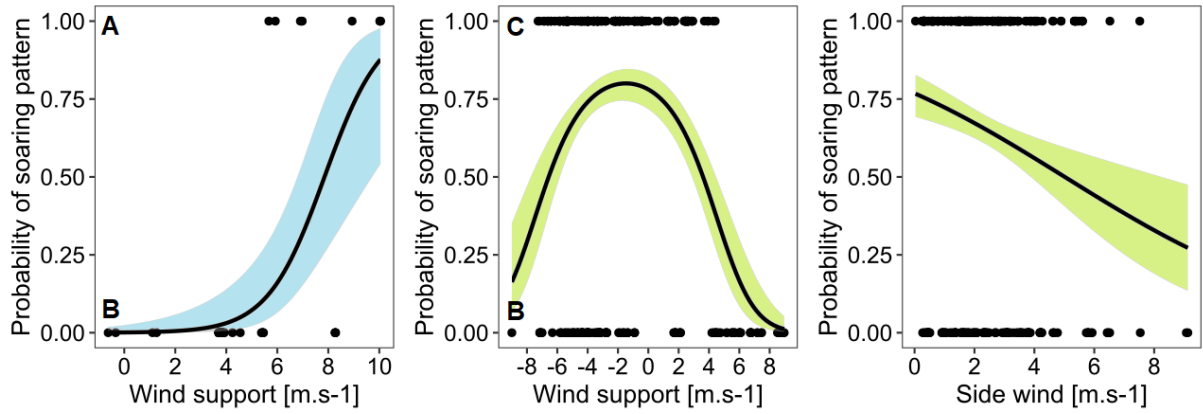


588 **Figure 3** – Three-dimensional view of soaring movement employed by Red Kites over the land
 589 (A, B) and Adriatic Sea (C, D). The GPS position was obtained in 5-minute bursts of frequency,
 590 one location per second, followed by a 10-minute break. Yellow vertical lines show the
 591 projection of the 3D track over the 2D surface. The panels in the middle show the differences
 592 in oscillation of birds' speed ($\text{m}\cdot\text{s}^{-1}$) and gain in altitude. The panels on the right show the
 593 acceleration (z -axis, in black, mG) and the magnetometer (x -axis, in red, mGauss) signals.
 594 Oscillation on birds' speed and magnetometer reflect the circular movement.

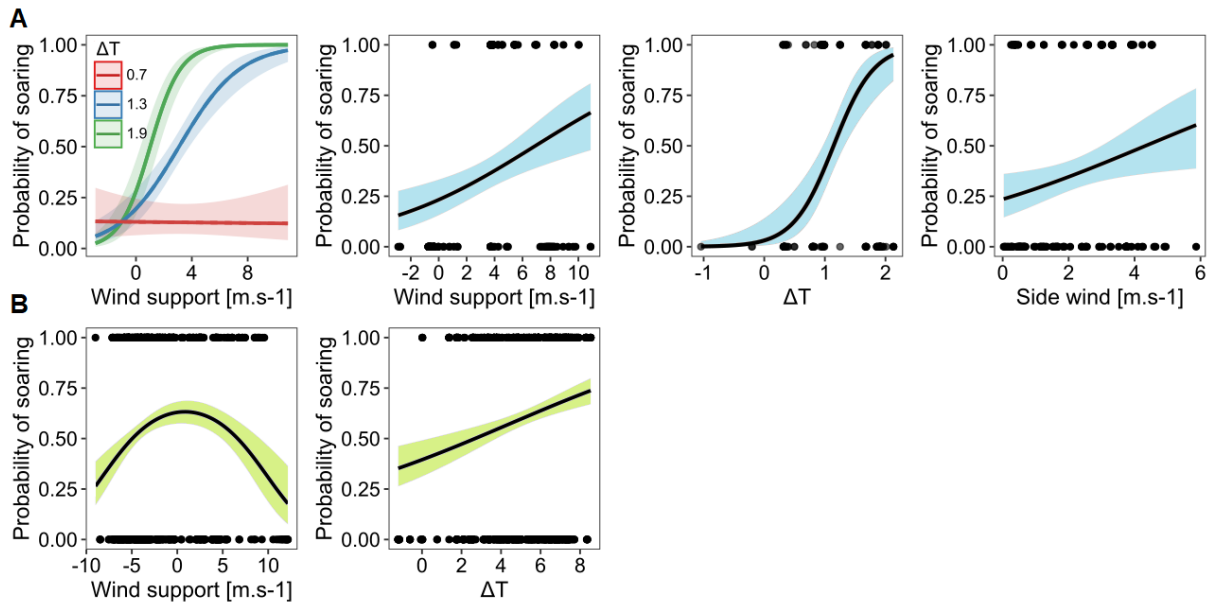


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596 **Figure 4** - Predicted effects statistically significant variables with confident interval 95 % of
597 our best GLMM (Generalized linear mixed) models. Predicted effects of wind support on
598 observed soaring patterns over sea (blue) and land (green). A – S shaped pattern, B – spring
599 pattern, C – staircase pattern.



601 **Figure 5** – Predicted effects statistically significant variables with confident interval 95 % of
 602 our best GLMM (Generalized linear mixed) models. Predicted effects of wind support, side
 603 wind, ΔT and interaction between wind support and ΔT on the probability of soaring behaviour
 604 over the sea (A, blue) and over land (B, green). Negative values of wind support represent
 605 headwind and positive tailwind.



606