Sea-crossing behaviour of two migratory eagles in relation to weather conditions

SEA CROSSING BEHAVIOUR OF TWO MIGRATORY EAGLES IN RELATION TO WEATHER CONDITIONS

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Short title: Sea crossing behaviour of migratory eagles

Abstract

During migration, typical soaring species such as eagles and vultures primarily rely on soaring flight to minimize energy expenditure, exploiting thermal currents over land while avoiding prolonged water crossings. This study investigates the flight behaviour of the Booted Eagle (*Hieraaetus pennatus*) and the Short-toed Snake Eagle (*Circaetus gallicus*) as they approach the European coastline of the Strait of Gibraltar, a critical migration bottleneck spanning at least 14 km, during their pre-breeding migration. Visual observations were conducted from two watchpoints on the European side of the Strait to assess migration magnitude and record the birds' flight altitudes upon reaching the coastline. Both species experienced wind drift when flying in crosswinds. Under calm conditions or light easterly winds, they tended to converge at the center of the Strait, whereas westerly winds caused a shift in their migratory flow toward the eastern sector. Short-toed Snake Eagles were observed flying at lower altitudes when facing headwinds or strong crosswinds, increasing their risk of drowning. In contrast, Booted Eagles were less affected, likely due to their lower energetic cost of flapping flight, which helped mitigate drowning risks. Notably, crosswind intensity did not significantly influence the flight altitude of Booted Eagles. These findings highlight interspecific differences in response to challenging wind conditions during water crossings and provide insight into the flight strategies adopted by raptors in the Strait of Gibraltar.

Keywords *Circaetus gallicus*, *Hieraaetus pennatus*, Mediterranean, flight altitude, migration, optimization, transport costs

Statements and declarations

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Competing interests

The authors have no competing interests to declare that are relevant to the content of this article

Data availability

The dataset generated during and/or analyzed during the current study is available from the corresponding author on a reasonable request.

Author contribution

Nicolantonio Agostini, Ugo Mellone and Gianpasquale Chiatante contributed to the study conception and design. Data were collected by Nicolantonio Agostini, Ugo Mellone, Gonzalo Muñoz Arroyo, Andrés De La Cruz, Rafael Benjumea, Marina Guerrero Molina, Blanca Pérez, and Laura Rollán. Analysis were performed by Gianpasquale Chiatante and Jost von Hardenberg. The first draft of the manuscript was written by Nicolantonio Agostini and Gianpasquale Chiatante and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

INTRODUCTION

During migration, soaring raptors take advantage of thermals and deflection updrafts to travel long distances while minimizing energy expenditure. Since vertical currents are typically weaker or absent over water surfaces (especially in temperate zones), birds cannot soar as much, therefore making them reliant on flapping flight, which is costly and risky (Agostini et al. 2015). Although recent research has shown that some facultative soaring raptors, such as the Osprey (*Pandion haliaetus*) and the Red Kite (*Milvus milvus*), can exploit thermals even over the open sea, adopting complex flight strategies that integrate wind support and available vertical uplift over marine surfaces (Duriez et al. 2018; Škrábal et al. 2023), in the case of obliged soaring raptors (e.g. eagles and vultures), landmass distribution clearly shaped their migratory strategies, particularly across the Mediterranean basin (Mellone 2020; Panuccio et al. 2021). Wind conditions play a crucial role in this phase. Favourable winds, such as tailwinds or supportive crosswinds, reduce energy consumption and travel time, facilitating crossings. In contrast, headwinds or adverse crosswinds increase the risks of overwater flights. Several studies indicate that large and medium-sized land birds face higher mortality when crossing water bodies (Zu-Aretz and Leshem 1983; Oppel et al. 2015; Newton 2023; Panuccio et al. 2021). As a result, heavier species with high energetic costs of flapping flight, such as vultures and eagles, typically circumvent the Mediterranean, concentrating their passage through isthmuses and narrow straits (e.g., the Bosphorus and Gibraltar). In contrast, lighter species, such as the European Honey Buzzard (*Pernis apivorus*), the Black Kite (*Milvus migrans*), harriers (*Circus* spp.), and falcons (*Falco* spp.), undertake longer water crossings due to their more efficient flapping flight and lower energy expenditure (Kerlinger 1989; Agostini et al. 2015).

Among European eagles, the Booted Eagle (*Hieraaetus pennatus*) is an exception. This relatively small raptor has a flight morphology associated with lower flapping flight costs, similar to facultative soarers such as the European Honey Buzzard and Black Kite, and lower than that of obligate soarers such as the Short-toed Snake Eagle (*Circaetus gallicus*) and the Lesser Spotted Eagle (*Clanga pomarina*; Agostini et al. 2015; Supplementary Materials, Fig. S1; Agostini et al. 2015). Despite its efficient flight capabilities, the Booted Eagle behaves like a typical obligate soaring species, generally avoiding long water crossings, with rare exceptions (Mellone 2021). Consequently, most Booted Eagles from Europe cross the Mediterranean Sea via the Strait of Gibraltar (14.7 km wide at its narrowest point, Fig. 1) and, to a lesser extent, via the Bosphorus (1–3 km wide; Mellone 2021), a pattern also observed in the Short-toed Snake Eagle (Agostini 2021).

In this study, we analysed the factors affecting migratory flow and flight altitude in these two eagle species as they reached the eastern and western European coasts of the Strait of Gibraltar during pre-breeding migration. Our goal was to investigate potential species-specific flight strategies shaped by differences in transport costs. We expected both species to exhibit site-specific differences in migratory flow based on wind direction. Specifically, we predicted that more individuals would be observed at the western watchsite (Cazalla) under easterly winds and at the eastern watchsite (Punta Carnero) under westerly winds due to wind-driven drift patterns. We also predicted that stronger crosswinds and headwinds would force Short-toed Snake Eagles (the larger species) to fly at lower altitudes upon reaching the European coastline, thereby increasing their risk of drowning. Conversely, Booted Eagles, owing to their lower flapping flight costs, would be less affected by wind intensity in terms of flight altitude.

Finally, we expected both species to reach the European coastline at higher altitudes under favourable thermal conditions. Under poor thermal conditions (e.g., high cloud cover and weak thermals), we predicted that individuals would compensate by increasing their flapping effort, leading to species-specific differences in crossing strategies. In particular, Booted Eagles, benefiting from a lower energetic cost of flapping flight, were expected to adopt a more risk-averse strategy by maintaining higher flight altitudes in adverse conditions (e.g., headwinds and strong crosswinds), whereas Short-toed Snake Eagles were likely to be more susceptible to altitude loss.

MATERIALS AND METHODS

Study area and data collection

The Strait of Gibraltar is the main bottleneck for soaring raptors breeding in Western Europe and wintering in Sub-Saharan Africa, funnelling them across the Mediterranean Sea during migration (De la Cruz et al. 2011a; Panuccio et al. 2021). Here, crosswinds prevail during both spring and autumn: westerly winds in spring, and easterly winds in autumn (Finlayson 2010; Hidalgo and Gallego 2019). We used a dual approach, taking advantage of two different dataset: (1) magnitude of migratory flow (from the watchsites with optimal visibility) and (2) birds' flight altitude (recorded from watchsites closer to the sea). Therefore, to quantify the magnitude of the migratory flow, we carried out systematic counts of Booted and Short-toed Snake Eagles crossing the Strait in spring. Observations were carried out daily from 11:00 to 17:00 local time between 1 March and 15 April in 2022 and 2023, using binoculars and telescopes. Data were collected from two watchpoints: Punta Carnero (-5.429 °E, 36.076 °N, elevation = 41 m a.s.l.) and Cazalla (-5.577 °E, 36.033 °N, elevation = 158 m a.s.l.) (Fig. 1).

Previous spring surveys in 2008 and 2009, covering six watchpoints between Bolonia and Punta Carnero (Fig. 1), revealed that these two locations accounted for more than 70% of migrating raptors (De la Cruz et al. 2011b). Moreover, to determine flight altitude over the sea, we used two observation posts along the coastline, approximately 15 km apart: Trafico (-5.587 °E, 36.014 °N; elevation = 52 m a.s.l.), located two km south of Cazalla, and Punta Carnero (Fig. 1). We recorded flight altitude measurements as soon as the raptors became visible upon reaching the coastline, while they were still flying over the sea and not yet over land, between 09:00 and 19:00 local time, from 1 to 31 March in 2011, 2017, and 2022. This period coincides with the peak overlap of the spring migration of these species at the Strait of Gibraltar (Finlayson 2010).

We used a Leica Rangemaster 1600-R optical range finder to determine bird altitude relative to the observer, accounting for non-overhead or lower-altitude passes. Using a trigonometric formula for a right triangle, we calculated bird altitude based on the acute angle and distance from the observer. Finally, we derived the bird's altitude above the sea was by incorporating the watchpoint's altitude (SM, Fig. S2).

Weather data

We analysed the effect of five weather variables on both species flow and flight altitude, interpolated for the exact date and time of observations. These data were obtained from Movebank (www.movebank.org), a free online database of animal tracking and related environmental data, which compiles information from the most relevant gridded global datasets (Dodge et al. 2013; Wikelski and Kays 2018). Thereby, from the Movebank ECMWF ERA5 weather dataset, we obtained cloud cover (% coverage) and temperature (°C), whereas from the Movebank ECMWF ERA-Interim weather dataset, we extracted horizontal wind components, namely the eastward (U) and the northward (V) wind speeds (m/s). Positive U values indicate flow toward the east (westerly wind), while positive V values indicate flow toward the north (southerly wind) (Wallace and Hobbs 2006).

For species flow analysis, weather data were extracted for a pressure level corresponding to 110 m, approximately the mean flight altitude observed (see *Results*). To explore flight altitude, data were bilinearly interpolated by Movebank for each watchsite at the exact measured flight altitude. To describe wind conditions during the study period, we obtained daily horizontal wind data (extracted at 12:00 AM at 100 m above ground) from the Movebank ECMWF ERA5 SL dataset. Additionally, we retrieved hourly ERA5 horizontal wind components from the ECMWF Climate Data Store (Hersbach et al. 2023) at a 950 hPa pressure level (corresponding to approximately 500 m altitude), for the observation days, matching the presumed average flight altitude of raptors crossing of the Strait of Gibraltar (see Santos et al. 2020). Wind maps for the Gibraltar region were computed by averaging daily mean values, weighted between 9:00 UTC and 17:00 UTC based on the number of observations of each species at Punta Carnero and Cazalla.

Statistical analysis

First, we used the χ^2 test and the Kruskal-Wallis test to verify the presence of significant differences in wind direction, wind speed, and the number of days with slow winds (< 2 m/s) between the three watchsites (Trafico, Cazalla, Punta Carnero). In addition, we compared flight altitudes between species with the non-parametric Mann-

Whitney *U* test. Then, we investigated the flow and flight altitude of both species in relation to the weather variables through regression analysis, using daily counts with ≥ 1 individual observed. First, we ran an exploratory analysis showing the importance of quadratic effects of the variables (i.e., $y \sim x + x^2$) through a pair-wise comparison of the second-order Akaike information criterion (AICc; Akaike 1973) of two linear models: one with the linear terms ($y \sim x$) and the other with the quadratic term ($y \sim x + x^2$) (Burnham et al. 2011). When the AICc value of the model with the quadratic effect was lower than the model with the linear term, with a difference of at least two (ΔAICc ≤ 2), the quadratic effect was retained, otherwise, we retained the linear term (Burnham and Anderson 2002) (SM, Tables S1-S2). In the same way, we defined the importance of interaction terms between each variable and the watchsite (SM, Tables S1-S2).

Then, using the covariates retained in the exploratory analysis, we built four multiple linear regressions, (which could have different variable combinations), one for each species and one for each response variable (flight altitude, species flow). Because the response variables were not normally distributed, we log-transformed them, reaching normality (SM, Table S4). Correlation matrices showed that covariates were not highly correlated (r_S <|0.60|) (SM, Table S3). Considering the different units of measurements used in the analysis, the covariates were standardized by normalization (Quinn and Keough 2002). For all the models, we performed model selection using the Akaike Information Criterion (AIC) on all possible combinations of the covariates, with the function *dredge* of the package “MuMIn” (Bartoń 2018) for R 4.1.1 (R Core Team 2021). We selected models within the ‘95% confidence set’ based on cumulative Akaike weights; these models were averaged and the importance of each variable in the set *sw* was calculated (Burnham and Anderson 2002). The goodness-of-fit of the model obtained was assessed by correlating expected and observed values with Spearman's rank correlation test, while the variance explained was measured with the coefficient of determination R^2. Statistical analyses were computed with R software version 4.1.1 (R Core Team 2021) and the packages "MuMIn" (Bartoń 2018) and "car" (Fox and Weisberg 2011).

RESULTS

Wind pattern

During the study period, wind direction did not differ between watchsites (χ^2 = 0.348, df = 6, P = 1.00), with easterly and westerly winds prevailing (92.7%). The average wind speed was 7.9 m/s ± 4.04 (SD), with no significant differences between watchsites (Kruskal-Wallis test, χ^2 = 0.05, df = 2, P = 0.976). Calm days (wind speed < 2 m/s) were rare, accounting for only 7.4% of the total.

Species flow

Short-toed Snake Eagle

A total of 13,360 Short-toed Snake Eagles (Cazalla, N = 2,890; Punta Carnero, N = 10,470) were observed in 2022, and 13,497 (Cazalla, N = 2,058; Punta Carnero, N = 11,439) in 2023. The analysis showed that three models were considered in the set of best models, including all the weather variables (SM, Table S5). The strength of the eastward component of the wind had a negative effect at Cazalla, while positive at Punta Carnero. This means that at Cazalla more birds were seen with easterly winds than westerly; at Punta Carnero, contrarily, more eagles were seen with westerly winds (Table 1; Fig. 2). The temperature and the strength of the northward component of the wind had very weak effects, negative and positive respectively. Moreover, watchsite was important too, with a positive effect on Punta Carnero. The variance explained by the model R^2 is equal to 30.2% and expected values are correlated with observed ones (r_s = 0.535, P < 0.001). Averaged wind maps weighted by counts are reported in Fig. 3: they show that Short-toed Snake Eagles crossed the Strait with weak average winds when observed at Cazalla and a strong westerly component when observed at Punta Carnero, with no relevant average meridional component.

Booted Eagle

A total of 8,209 Booted Eagles (Cazalla, N = 5,075; Punta Carnero, N = 3,134) were observed in 2022, and 9,460 (Cazalla, N = 2,367; Punta Carnero, N = 7,093) in 2023. The analysis showed that only one model was considered as the best one, including all the weather variables (Table 1). As regards horizontal winds, the strength of the eastward component had a negative effect at Cazalla, while positive at Punta Carnero. This means that, similarly to the Short-toed Snake Eagle, at Cazalla more birds were seen with easterly winds, whereas at Punta Carnero with strong westerly winds (Fig. 2). In relation to the northward component, the flow showed a non-linear effect, with more Booted eagles passing with no wind; this effect is stronger at Punta Carnero than at Cazalla. In addition, the temperature had a positive effect on the species flow. The variance explained by the model R^2 is equal to 44.6% and expected values are correlated with observed ones (r_s = 0.668, P < 0.001). In this case, the analysis is confirmed by the averaged wind maps at about 500 m, weighted by counts, reported in Fig. 3: Booted Eagles were seen crossing the Strait with weak average easterly winds when observed at Cazalla and a stronger westerly component when observed at Punta

Carnero. A moderate northerly meridional component was present for passages at Punta Carnero.

Flight altitude

We analysed the effect of the weather on 996 and 222 flight altitude records, for the Short-toed Snake Eagle and Booted Eagle, respectively. In general, Short-toed Snake Eagles were detected at higher altitude than Booted Eagles and higher at Punta Carnero than at Trafico (Short-toed Snake Eagle: 150 m ± 139.12 (SD), range 1-670 m; Booted Eagle: 100 m ± 90.32, range 18-465; Mann-Whitney *U* test, $P < 0.001$) and both species arrived higher at Punta Carnero than at Trafico (Punta Carnero: 154 m ± 147.62; Trafico: 107 m ± 76.82; Mann-Whitney *U* test, $P < 0.001$). This was true even considering species separately (Short-toed Snake Eagle: Punta Carnero, 148 m ± 119.34, Trafico, 118 m ± 72.61, $P = 0.039$; Booted Eagle: Punta Carnero, 121 m ± 106.97, Trafico, 94 m ± 80.36; $P = 0.004$).

Short-toed Snake Eagle

Only one model was considered in the set of best ones, including all the weather variables (Table 2). In particular, the cloud cover had a positive effect on the flight altitude, especially at Punta Carnero; conversely, the temperature and the strength of the thermal uplift had a weak negative effect (Fig. 4). Flight height at Punta Carnero tended to be higher with easterly winds, while at Trafico birds reached higher altitudes with winds blowing from the west (Fig. 4). The strength of the northward component had a marked quadratic effect, with opposite patterns between watchpoints, even though this species tended to fly higher with northerly winds than with strong southerly winds (Fig.

4). The variance explained by the model R^2 is equal to 30.8% and expected values are correlated with observed ones ($r_s = 0.522$, $P < 0.001$).

Booted Eagle

The analysis showed that three best models explained the flight altitude of the Booted Eagle (Table S6), and the average model included all the variables with the exclusion of the cloud cover (Table 3). In particular, the strength of the northward component of the wind showed a strong quadratic effect on the flight altitude, with a different pattern between watchsites, whereas the thermal uplift had a weak negative effect (Fig. 5). Indeed, at Punta Carnero the altitude was higher with strong winds, both northerly and southerly, whereas at Trafico Booted Eagles flew higher with strong northerly winds than with southerly winds (Fig. 5). The temperature and the strength of the eastward component of the wind had very little importance. The variance explained R^2 is equal to 26.3% and the expected values are correlated with the observed ones (r_s = 0.471, $P < 0.001$).

DISCUSSION

Among the factors affecting the sea-crossing performance of soaring migrants, wind conditions, starting altitude, and the bird's physiological state are crucial to success (Kerlinger 1989; Bildstein 2006; Santos et al. 2020; Panuccio et al. 2021). Strong crosswinds during a sea crossing force birds to extend their flapping flight and/or lengthen their flight path over water, whereas a higher starting altitude allows a soaring bird to glide for longer before resorting to flapping flight (Kerlinger 1989). In our study, Short-toed Snake Eagles reached the Spanish coast at higher altitudes than Booted

Eagles, likely because they attained much greater starting altitudes along the Moroccan coast, as expected for an obligate soaring species. However, we cannot rule out the possibility that these findings were influenced by size differences between the two eagle species: the Short-toed Snake Eagle typically weighs around 1.5–2.3 kg with a wingspan of 160–190 cm, whereas the Booted Eagle is smaller, weighing approximately 0.8–1.0 kg with a wingspan of 110–135 cm (Ferguson-Lees & Christie 2001).

Our results confirm the prediction regarding the influence of wind direction on migratory flow. Both eagle species were clearly affected by drift when flying in crosswinds. Their migratory flow was concentrated at Cazalla under weak wind conditions or light easterly winds, while more individuals reached Punta Carnero when winds had a westerly component. A substantial number of birds were observed even farther eastward as westerly winds increased in strength. Conversely, under stronger easterly winds, birds were seen west of Tarifa (see also Finlayson 2010). Wind maps indicate that migration at Punta Carnero typically occurs under a relevant westerly wind component, whereas the conditions at Cazalla are characterized by only weak easterly winds. Our findings align with those of De la Cruz et al. (2011b), who reported a very low passage of both Booted and Short-toed Snake Eagles at western observatories of the Strait under easterly winds. Therefore, our results suggest that under strong easterly winds, most individuals of both species either delay or abort the crossing to avoid being drifted on a longer route over water. On the Atlantic side the risk of being drifted towards the open sea is much higher than in the Mediterranean due to the geography of the coastline, heading more abruptly towards the north-west.

The strength of crosswinds negatively affected the flight altitude of the larger species, supporting our hypothesis: Short-toed Snake Eagles were detected at lower altitudes when crosswinds were stronger, likely because they were forced to cover longer distances over water, leading to altitude loss. However, under such conditions, we cannot exclude the possibility that they deliberately flew closer to the sea surface where winds were weaker, thereby reducing energy costs but increasing the risk of drowning. Similarly, Black Kites, a facultative soaring species, have been shown to experience drift when flying in crosswinds through the Strait of Gibraltar during autumn migration, often reaching the Moroccan coast at 20–100 m a.s.l. (Santos et al. 2020). Black Kites also lower their flight altitude over water and increase flapping effort when flying in strong crosswinds (Santos et al. 2020). Conversely, the few Short-toed Snake Eagles that reached the two watchpoints while compensating for drift were observed at higher altitudes, likely because they relied more on flapping rather than gliding during the crossing. This strategy was probably adopted by individuals in better physical condition, who reduced their risk by maintaining a more direct route at a higher altitude, albeit at the cost of increased energy expenditure. Since birds are expected to adopt a time-minimization strategy during spring migration, they may continue flying even in suboptimal weather conditions (Duerr et al. 2014).

Unexpectedly, both eagle species reached the European coast at lower altitudes under atmospheric conditions ideal for the formation of strong thermals over land (e.g., high temperatures and weak winds). A likely explanation is that, under such conditions, they were able to gain higher starting altitudes (see also Panuccio et al. 2019) but extensively used gliding flight during the crossing to minimize energy expenditure by reducing flapping effort. Similarly, during rare occurrences of southerly winds at the Strait of Gibraltar, both species reached the European coast at lower altitudes, particularly at Trafico, and were detected in lower numbers at the two watchpoints. In contrast with our expectations, Short-toed Snake Eagles were observed at higher altitudes when flying under high cloud cover, despite such conditions being unfavourable for strong thermal formation. Under these circumstances, they may have compensated by increasing flapping flight effort during the crossing. Finally, in agreement with our predictions, the few Booted Eagles crossing in strong headwinds preferred to fly at higher altitudes, minimizing the risk of drowning. Their ability to maintain altitude was likely facilitated by their ability to sustain flapping flight at a lower energetic cost. For the same reason, crosswind intensity did not significantly influence their flight altitude. As mentioned above, recent studies have revealed that thermal uplift can also occur over water, challenging the traditional assumption that soaring flight is largely unsupported over marine surfaces (Duriez et al. 2018; Nourani et al. 2021; Škrábal et al. 2023). Although our analyses did not include uplift potential over the sea, such findings suggest that thermals over water could occasionally aid even obliged soaring raptors at least during short sea-crossings. This phenomenon may partially explain some of the observed variability in flight altitude at the Strait of Gibraltar, particularly in individuals maintaining relatively high altitudes in suboptimal conditions.

In conclusion, this study demonstrates that the two eagle species adopt distinct strategies when facing adverse conditions during sea crossings, with the Short-toed Snake Eagle being more susceptible to altitude loss than the Booted Eagle. These findings enhance our understanding of the role of morphological and flight performance differences in shaping migratory behaviour under variable wind conditions. By providing ground-based observational evidence on non-tagged individuals, this study fills a gap in the existing literature concerning overwater flight strategies in soaring raptors. Future research integrating ground observations with high-resolution weather models and GPS tracking will be essential to explore individual variability, physiological condition, and the influence of localized uplift on sea-crossing performance.

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TABLES

Table 1. The average model obtained by the linear regression investigating the migration flow of both the Short-toed Snake Eagle and the Booted Eagle during the spring migration at the Strait of Gibraltar (SE = standard error; LCI = 95% lower confidence interval; UCI = 95% upper confidence interval; *sw* = relative importance). When the watchsite is indicated, then the covariate is the interaction term with the variable. For the watchsite the reference level is Cazalla.

Variable	Watchsite	Estimate	SE	LCI	UCI	*sw*
Short-toed snake-eagle						
Intercept		3.627	1.298	-	-	-
Watchsite	*P. Carnero*	0.644	0.547	-0.428	1.715	1.00
Temperature		-0.112	0.070	-0.249	0.025	0.63
Eastward wind	*P. Carnero*	0.225	0.072	0.083	0.366	1.00
	Cazalla	-0.152	0.049	-0.248	-0.057	
Northward wind		0.0001	0.141	-0.276	0.276	0.15
Booted eagle						
Intercept		0.479	0.991	-	-	-
Watchsite	*P. Carnero*	-0.089	0.408	-0.897	0.719	1.00
Temperature		0.141	0.059	0.024	0.258	1.00
Eastward wind	*P. Carnero*	-0.205	0.038	0.058	0.271	1.00
	Cazalla	0.165	0.054	-0.281	-0.129	
Northward wind	*P. Carnero*	-9.571	2.803	-15.127	-4.015	1.00
	Cazalla	1.827	2.474	-3.077	6.732	
Northward wind^2	*P. Carnero*	-6.814	2.606	-11.979	-1.648	
	Cazalla	-1.986	2.617	-7.173	3.200	

Table 2. The best model obtained by the linear regression investigating the effect of the weather on the flight altitude of the Short-toed Snake Eagles during the spring migration at the Strait of Gibraltar (SE = standard error; LCI = 95% lower confidence interval; UCI = 95% upper confidence interval). When the watchsite is indicated, then the covariate is the interaction term with the variable.

Variable	Watchsite	Estimate	SE	LCI	UCI
Intercept		2.094	0.020	-	-
Cloud cover	*P. Carnero*	0.056	0.012	0.033	0.079
	Trafico	0.022	0.022	-0.020	0.065
Temperature		-2.036	0.417	-2.854	-1.219
Temperature^2		0.330	0.341	-0.338	0.999
Thermal uplift		-0.051	0.012	-0.074	-0.028
Eastward wind	*P. Carnero*	-6.395	1.532	-9.402	-3.389
	Trafico	2.687	0.761	1.193	4.180
Eastward wind^2	*P. Carnero*	0.994	1.110	-1.184	3.173
	Trafico	-0.074	0.587	-1.225	1.077
Northward wind	*P. Carnero*	-5.037	0.372	-5.768	-4.306
	Trafico	-7.169	1.261	-9.645	-4.694
Northward wind^2	*P. Carnero*	3.109	0.409	2.306	3.911
	Trafico	-2.939	0.898	-4.701	-1.177

Table 3. The average model obtained by the linear regression investigating the effect of the weather on the flight altitude of the Booted Eagles during the spring migration at the Strait of Gibraltar (SE = standard error; LCI = 95% lower confidence interval; UCI = 95% upper confidence interval; *sw* = relative importance). When the watchsite is indicated, then the covariate is the interaction term with the variable.

Variable	**Watchsite**	**Estimate**	**SE**	**LCI**	**UCI**	***sw***
Intercept		1.878	0.018	-	-	-
Temperature		-0.038	0.044	-0.125	0.049	0.26
Thermal uplift		-0.973	0.368	-1.699	-0.248	1.00
Thermal uplift^2		0.564	0.306	-0.039	1.167	
Eastward wind		0.015	0.020	-0.025	0.055	0.23
Northward wind	*P. Carnero*	0.221	0.599	-0.960	1.401	1.00
	Trafico	-1.625	0.467	-2.546	-0.705	
Northward wind^2	*P. Carnero*	2.154	0.590	0.992	3.316	
	Trafico	-0.117	0.518	-1.137	0.904	

FIGURES

Figure 1 The watchsites used at the Strait of Gibraltar (Spain) to investigate daily counts (Cazalla and Punta Carnero) and the flight altitude (Trafico and Punta Carnero) of Short-toed Snake Eagles and Booted Eagles during the pre-breeding migration

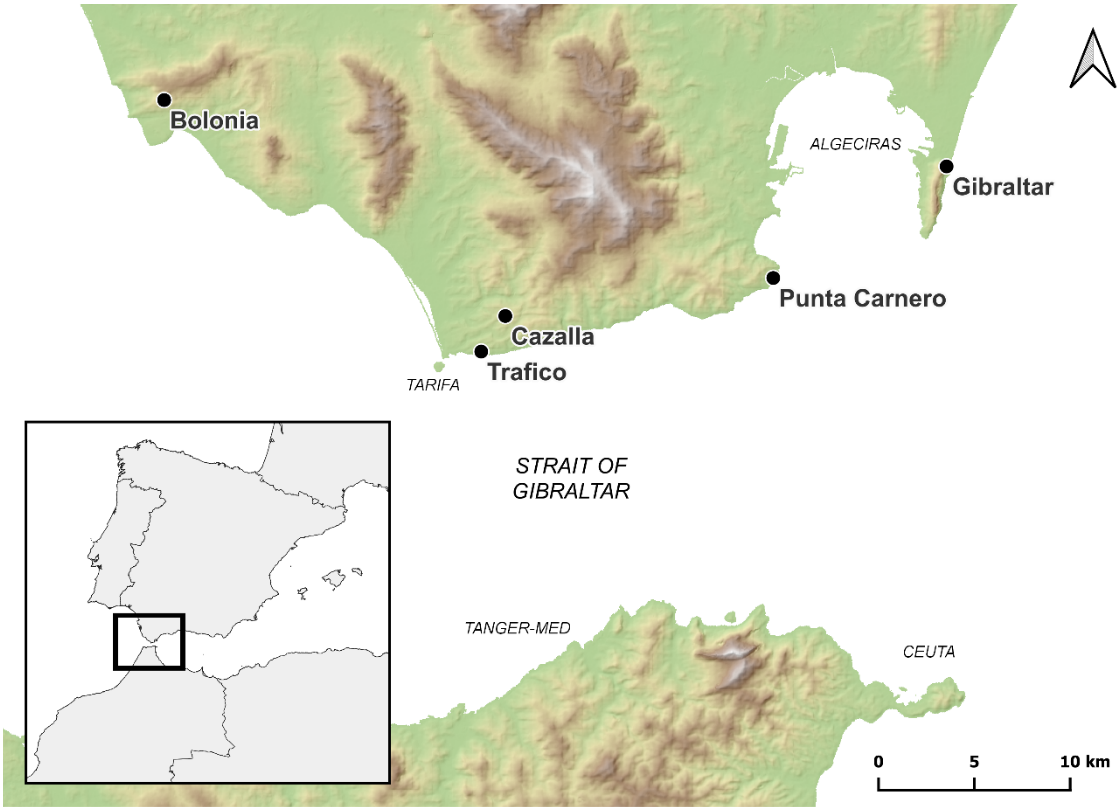

Figure 2 Response curves of the variables with higher relative importance (*sw* = 1.00) selected by the linear regression investigating the migration flow of both the Short-toed Snake Eagle (a) and the Booted Eagles (b-d) during the spring migration at the Strait of Gibraltar. For the temperature (d) the effect includes both watchsites

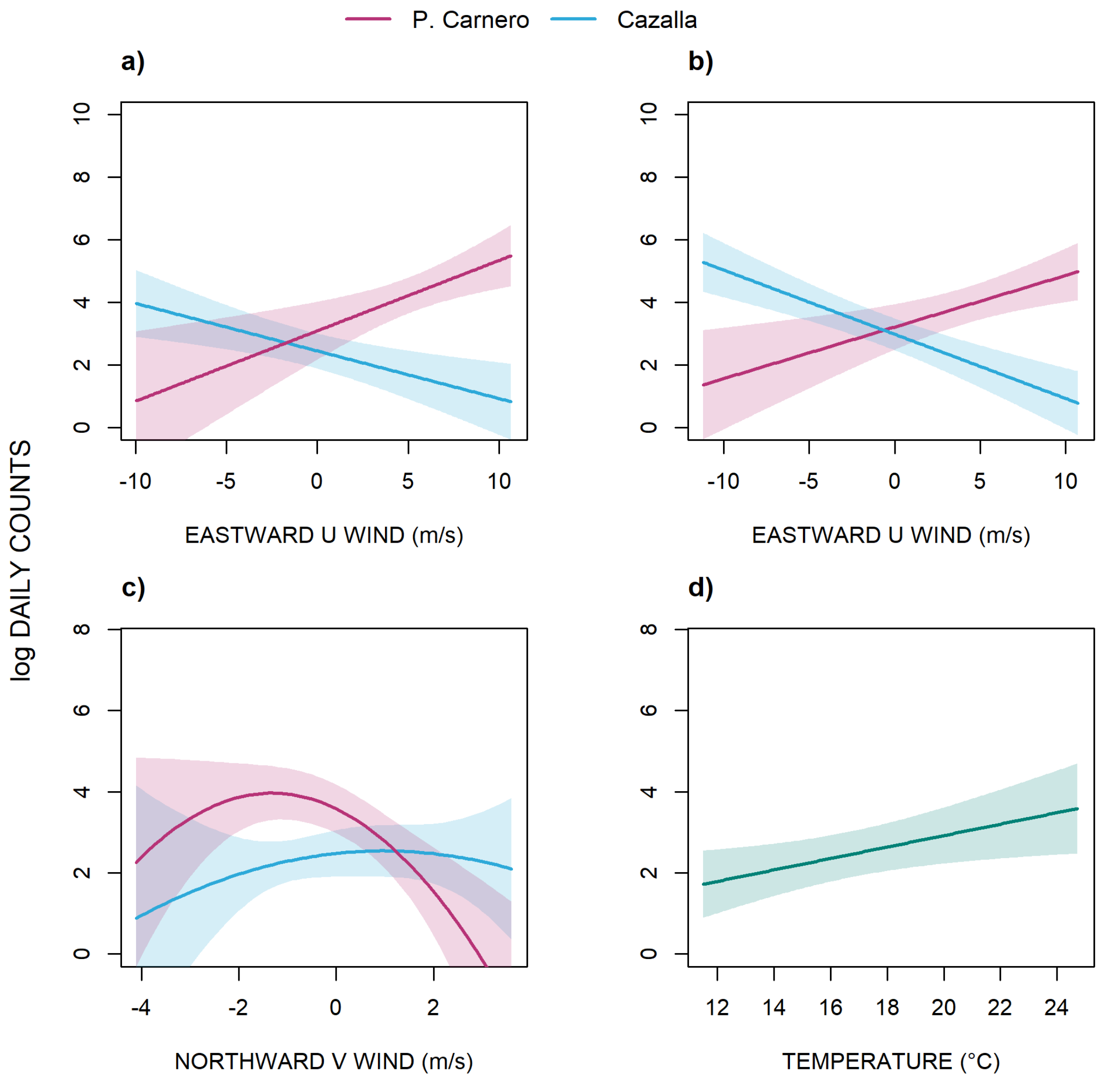

Figure 3 Average wind vectors obtained by daily averaging ERA5 wind between 09:00 UTC and 17:00 UTC and weighting by the number of counts on observation days, for each species and observation site. The background colour reports the strength of the horizontal wind component (positive is westerly)

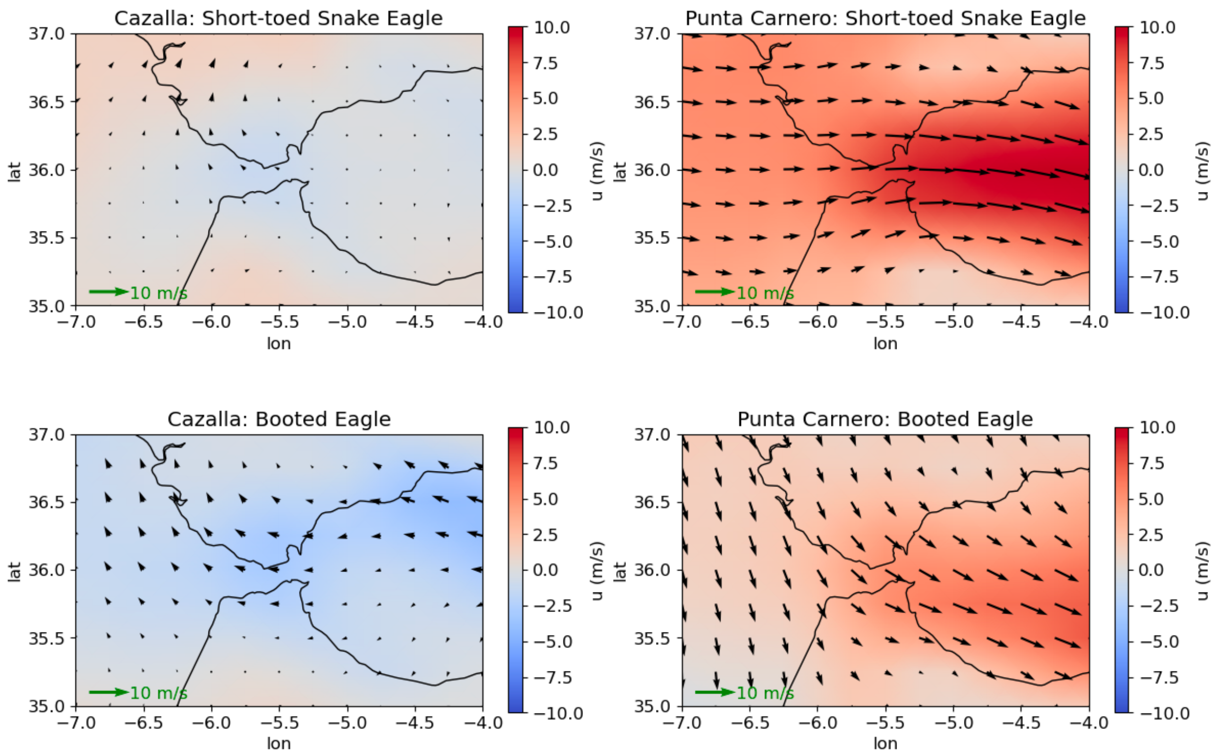

Figure 4 Response curves obtained by the linear regression investigating the effect of the weather on the flight altitude of the Short-toed Snake Eagles during the spring migration at the Strait of Gibraltar

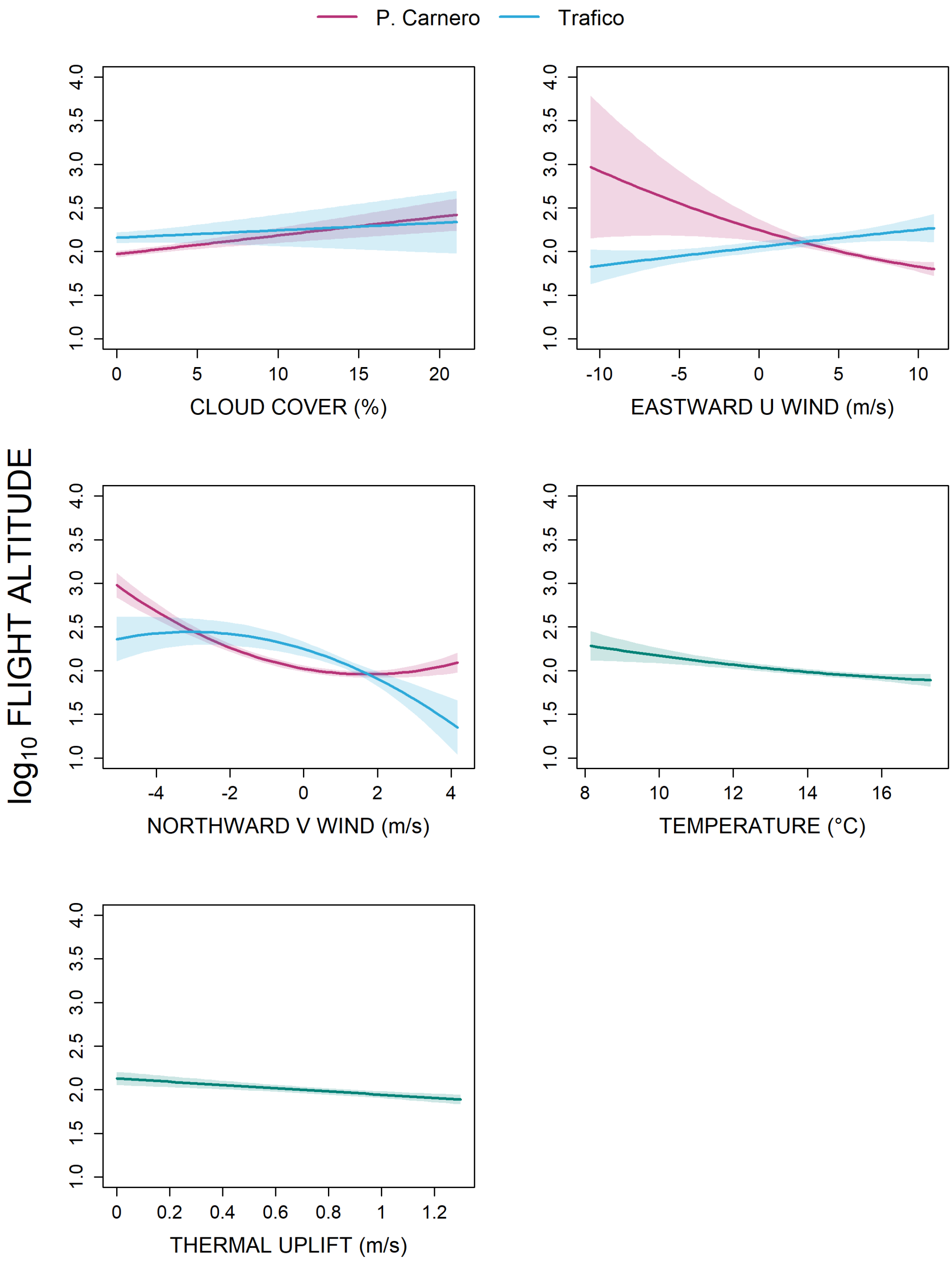

Figure 5 Response curves of the variables with higher relative importance (*sw* = 1.00) selected by the linear regression investigating the effect of the weather on the flight altitude of the Booted Eagles during the spring migration at the Strait of Gibraltar