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LOCAL AND REGIONAL WIND PATTERNS AFFECT SPRING MIGRATION MAGNITUDE, FLYWAYS AND FLOCKING OF EUROPEAN HONEY-BUZZARDS *PERNIS APIVORUS* AT THE STRAIT OF MESSINA

LOS PATRONES DE VIENTO LOCAL Y REGIONAL AFECTAN A LA MAGNITUD DE LA MIGRACIÓN PRIMAVERAL, LAS RUTAS DE VUELO Y LA AGREGACIÓN EN BANDOS DE LOS ABEJEROS EUROPEOS *PERNIS APIVORUS* EN EL ESTRECHO DE MESINA

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Summary.—During spring migration, a few tens of thousands of European Honey-buzzards wintering in sub-Saharan Africa cross the central Mediterranean to reach their breeding grounds in central-eastern Europe. In so doing they concentrate passage through the Sicilian Channel but choose different flyways in response to different wind conditions. This study investigated the influence of local and regional wind conditions on the movement patterns of this species along the Strait of Messina, a migration bottleneck located between eastern Sicily and southern continental Italy where some raptors fall victim to illegal shooting by poachers each spring. Simultaneous observations occurred at four watchpoints, three on the Sicilian side and one on the continental boundary (Calabrian side). Although northwesterly winds prevailed at the Strait during peak migration days, slightly different local patterns of both horizontal and vertical winds at each observation site affected flocking and shaped the passage of raptors through this bottleneck, broadening the migration front. The results confirm that the magnitude

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of Honey-buzzard spring migration at the Strait is strongly affected by wind patterns in the Sicilian Channel. In particular, migrants concentrate at this bottleneck after crossing the Channel in northwesterly winds the previous day. In conclusion, by interpreting migratory behaviour both at local and regional scales, this work can help to plan more efficient monitoring of Honey-buzzards through the Strait and improving the siting of conservationist efforts. —Agostini, N., Chiatante, G., Gustin, M., Cento, M., von Hardenberg, J., Dell'Omo, G. & Panuccio, M. (2021). Local and regional wind patterns affect spring migration magnitude, flyways and flocking of European Honey-buzzards *Pernis apivorus* at the Strait of Messina. *Ardeola*, 68: 373-390.

Key words: horizontal wind, flocking, migration, pathways, *Pernis apivorus*, vertical wind, water crossing.

RESUMEN.—Durante la migración de primavera, algunas decenas de miles de abejeros europeos que invernan en el África subsahariana cruzan el Mediterráneo central para llegar a sus zonas de reproducción en Europa central y oriental. Al hacerlo, concentran el paso a través del canal de Sicilia, pero eligen diferentes rutas migratorias en respuesta a las diferentes condiciones del viento. Este estudio investigó la influencia de las condiciones del viento local y regional en los patrones de movimiento de esta especie a lo largo del estrecho de Mesina, un cuello de botella migratorio ubicado entre el este de Sicilia y el sur de Italia continental, donde algunas aves rapaces son víctimas de la caza furtiva cada primavera. Se realizaron observaciones simultáneas en cuatro puntos de observación, tres en el lado siciliano y uno en el límite continental (lado calabrés). Los vientos del noroeste prevalecieron en el Estrecho durante los días con pico de migración. No obstante, los patrones locales levemente diferentes de vientos horizontales y verticales en cada sitio de observación afectaron la formación de bandadas y dieron forma al paso de las aves rapaces a través de este cuello de botella, ampliando el frente de migración. Los resultados confirman que la magnitud de la migración primaveral del abejero europeo en el Estrecho se ve fuertemente afectada por los patrones de viento en el canal de Sicilia. En particular, los migrantes se concentran en este cuello de botella después de cruzar el Canal con vientos del noroeste el día anterior. En conclusión, al interpretar el comportamiento migratorio tanto a escala local como regional, este trabajo puede ayudar a planificar un seguimiento más eficiente de los abejeros europeos a través del Estrecho y mejorar la ubicación de las acciones de conservación. —Agostini, N., Chiatante, G., Gustin, M., Cento, M., von Hardenberg, J., Dell'Omo, G. y Panuccio, M. (2021). Los patrones de viento local y regional afectan a la magnitud de la migración primaveral, las rutas de vuelo y la agregación en bandos de los abejeros europeos *Pernis apivorus* en el estrecho de Mesina. *Ardeola*, 68: 373-390.

Palabras clave: congregación, cruce de agua, migración, *Pernis apivorus*, rutas, viento horizontal, viento vertical.

INTRODUCTION

During migration long-distance migrants adopt flight strategies to minimise energy and/or the time they spend travelling (Newton, 2008). Wind patterns strongly affect birds en route and several nocturnal migrants actively select their flight altitude to take advantage of favourable horizontal winds, thus minimising both time and energy (Bruderer *et al*., 1995; Liechti *et al*., 2000; Schmaljohann *et al*., 2009). Among diurnal migrants, soaring birds exploit vertical winds (thermals and deflection updrafts) over land to minimise energetic costs and they avoid crossing large water bodies as part of a conservative strategy (Alerstam, 2001; Newton, 2008). Indeed, vertical winds are very weak over water, especially in temperate zones, and birds are thus forced to use flapping flight during water crossings, incurring a high energy cost. Moreover, for species unable to

rest at sea, falling into the water means death (Kerlinger, 1989). Among raptors, heavier and rounded winged species are obligate soarers and avoid long water crossings (Kerlinger, 1989; Agostini *et al*., 2015a). They sometimes follow extremely detoured flyways over land, as is the case with Short-toed Snake-eagles *Circaetus gallicus* breeding in Italy and Greece (Panuccio *et al*., 2012). Most of these species show a strong tendency to migrate in flocks, sometimes of hundreds of individuals, with flock position a clue for the location of thermal currents: migrating raptors tend to join other individuals that are already soaring (Kerlinger, 1989). In contrast, some medium-sized species with higher aspect ratio wings, such as Ospreys *Pandion haliaetus* and harriers *Circus* spp., are readily able to cross large water surfaces since this morphological feature reduces induced drag and thus the energetic cost of flapping flight (Kerlinger, 1989; Agostini *et al*., 2015a). Moreover, unlike typical soarers, they mostly migrate singly or in small loose flocks (Kerlinger, 1989).

Due to intermediate morphology between obligate soaring species and harriers, the European Honey-buzzard *Pernis apivorus*, a medium-sized raptor, shows an intermediate migration behaviour, being a versatile soarer with a strong tendency to migrate in flocks. As a result, Honey-buzzards adopt flexible flight strategies under changing atmospheric conditions. They choose to glide at near time-optimal airspeeds when thermals are strong and abundant (e.g. when crossing the desert), are able to exploit the weaker updrafts near the top of thermals and are capable of extended periods of flapping flight over water, especially when exploiting tailwinds (for a review see Vansteelant & Agostini, 2021). During both spring and autumn migration, a few tens of thousands of Honey-buzzards breeding in central-eastern Europe and wintering in west-central Africa cross the central Mediterranean region, concentrating at the Sicilian Channel, between the Cap Bon Peninsula (Tunisia) and western Sicily. During spring, when passing through this area, Honey-buzzards choose among alternative flyways over water en route to continental Italy in response to different wind conditions and, in so doing, substantial numbers use several small circum-Sicilian islands as 'stepping stones' (Figure 1; Agostini *et al*., 2016, 2019; Panuccio *et al*., 2019). In particular, when leaving the Cap Bon Peninsula during northwesterly winds, they move along the southern side of the Sicilian Channel in larger flocks and typically concentrate at the Strait of Messina, between eastern Sicily and southern continental Italy, the following day (Agostini *et al*., 2016). In contrast, with southerly winds blowing both over the Sicilian Channel and the Tyrrhenian Sea, they move along more direct flyways towards the Italian Peninsula, taking advantage of tailwinds to make long water crossings over the Tyrrhenian Sea, bypassing the Strait (Agostini *et al*., 2016; Panuccio *et al*., 2019). As a result, the migratory flow at the Strait is characterised by a few peak days (Agostini, 1992), each involving at least 1,000 individuals recorded from a single watchpoint (maximum 5,465 on 30 April 2010; Agostini *et al*., 2016). Each spring several raptors fall victim to shooting while passing through this bottleneck, especially during peak days, but thanks to the effort of international volunteers and wardens this illegal activity has decreased in recent years (Vansteelant & Agostini, 2021).

Our objective for this study was to investigate the spring migration of Honey-buzzards at the Strait of Messina in relation to wind patterns, to improve data collection and to help conservation efforts by interpreting migratory behaviour at both local and regional scales. In particular, the effect of local wind conditions on the migratory flow was studied at a fine scale during peak days by making simultaneous observations at four watch-

points, three located on the Sicilian side and one on the continental side of the Strait. We further investigated the hypothesis that concentrations of Honey-buzzards at the Strait of Messina mostly occur after northwesterly winds between the Cap Bon Peninsula and western Sicily the previous day.

Study area and methods

Fieldwork

Observations, using binoculars and spotting scopes, were made simultaneously from four watchpoints, three on the Sicilian side of the Strait (Serro, Dinnammare, Mount Ciccia) and one on the continental side (Solano) (Figure 1). Data were collected between 09:00 and 19:00 (local time) from 20 April to 20 May 2014-2018, during the Honey-buzzard spring migration peak in the Mediterranean basin (Agostini *et al.*, 2016). At Serro, data were not collected in 2015. One observer counted migrants at each watchpoint. The watchpoint at Dinnammare (Lat. 38.159°N; Long. 15.465°E; 1,115m a.s.l.) was about 11km SSW of that on Mount Ciccia (Lat. 38.240°N; Long. 15.537°E; 550m a.s.l.), both located along the ridge of the Peloritani

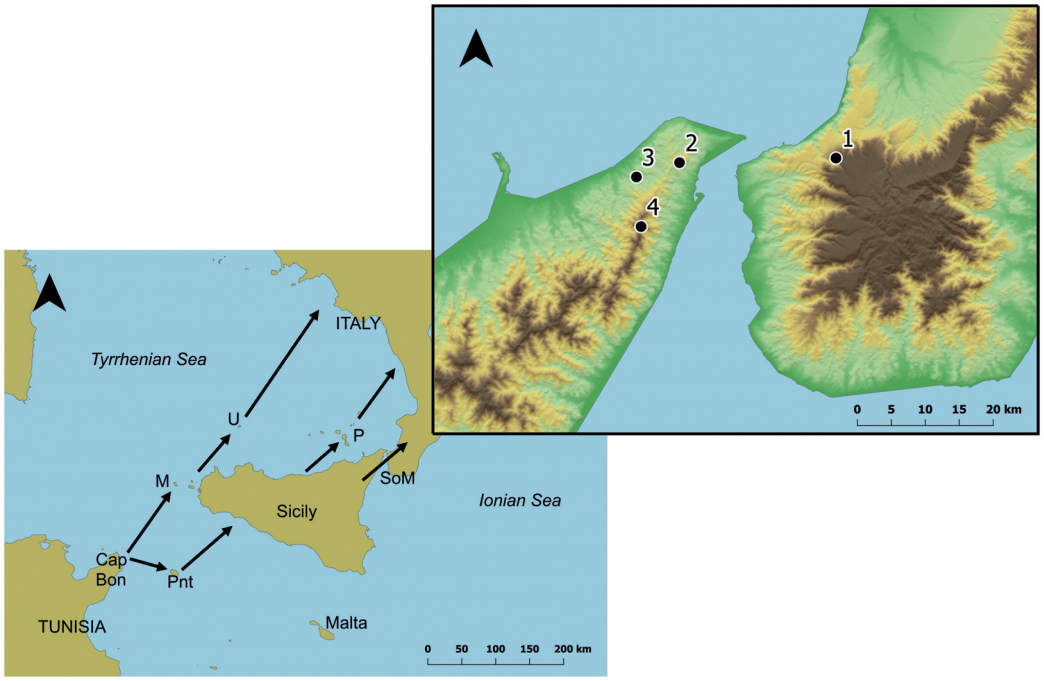

FIG. 1.—The Central Mediterranean area. Arrows show approximate routes used by Honey-buzzards using some circum-Sicilian islands used as stepping stones (Pnt = Pantelleria; M = Marettimo; U = Ustica; P = Panarea) and across the Strait of Messina (SoM). Watchpoint locations at the Strait of Messina are shown (1 Solano, 2 M. Ciccia, 3 Serro, 4 Dinnammare).
[La región mediterránea central. Las flechas muestran las rutas aproximadas usadas por los abejeros europeos que emplean las islas en torno a Sicilia como pasos en su migración (Pnt = Pantelleria; M = Marettimo; U = Ustica; P = Panarea) y a través del estrecho de Mesina (SoM). Se señalan los puntos de observación en el estrecho de Mesina (1 Solano, 2 M. Ciccia, 3 Serro, 4 Dinnammare).]

Mountains, a coastal chain overlooking the 3-35km-wide Strait. The Serro watchpoint (Lat. 38.225°N; Long. 15.463°E; 240m a.s.l.) was located in a hilly area about 7km north of Dinnammare and 6.5km WSW of Mount Ciccia. The watchpoint on the continental side of the Strait was located near the edge of a plateau in the Aspromonte Mountains (Calabria; Lat. 38.231°N; Long. 15.800°E; 1,030m a.s.l.), about 7km from the Tyrrhenian coast, 23km E of Mount Ciccia and 30km ENE of Dinnammare (Figure 1).

Weather data

The large data set recorded in this study allowed us to investigate the variation in migratory flow in relation to both regional and local wind patterns. At a regional scale horizontal wind data were obtained using ERA5 (C3S, 2017) a global atmospheric reanalysis product produced by the European Centre for Medium-Range Weather Forecasts (ECMWF), downloaded from the Copernicus Climate Change Service Data Store (C3S, 2017) (Supplementary Material, Appendix A1). Gridded fields of relevant atmospheric variables were interpolated to a regular lon/lat grid at 0.25° spatial resolution and on pressure levels representative of the average winds in approximately the first 1,000m of altitude above sea level, encompassing the range of altitudes covered by migrating raptors over water (Kerlinger, 1989; Agostini *et al*., 2012). Winds were averaged between 5:00 UTC and 17:00 UTC to obtain daily average values in the flight period.

At a local scale, the study considered both horizontal and vertical winds from Movebank (http://www.movebank.org; Dodge *et al*., 2013; Wikelski & Kays, 2018). Wind data for horizontal winds were extracted for a pressure level corresponding to an altitude between 445 and 1,145m (Schmaljohann *et al*., 2012) which is considered the best approximation of the cruising altitude of birds (Klaassen *et al*., 2011; Mellone *et al*., 2012; Vidal-Mateo *et al*., 2016; Agostini *et al*., 2019). Wind data for vertical winds were extracted for thermal and orographic uplift (deflection updrafts; see Supplementary Material, Appendix A1, for details).

Analysis

For the analyses, we only considered data from the peak flight days (see also Agostini *et al*., 2016), i.e., when at least at one watchpoint recorded the passage of at least 1,000 Honey-buzzards. First, we analyzed the migratory flow of Honey-buzzards by comparing the four watchpoints excluding solitary birds and all data recorded in 2015, when observations were not made at Serro. In particular, we compared the magnitude of the flow (number of European Honey-buzzards counted per day) using a Kruskal-Wallis rank test and a Dunn test for post-hoc nonparametric multiple comparisons with unequal sample sizes.

Then, for each watchpoint separately, we modelled the flock size of Honey-buzzards (i.e., groups with at least two individuals, as a *proxy* of intensity of migratory flow) in relation to the weather at local scale using a Generalized Linear Model (GLZ) with Negative-binomial distribution (link = log) (Lindén & Mäntyniemi, 2011). We used as covariates the speed of the east-west (U) component of the wind, the speed of the north-south (V) component of the wind and the speed of both thermal and orographic uplifts. For the analysis, all the variables considered were standardised by normalisation; that is, each variable had a mean of zero and a standard deviation of one. We tested for multicollinearity among them through the Variance Inflation Factor (VIF) and using a threshold of three (Zuur *et al*., 2010). Preliminary graphic analyses showed that some

covariates might affect Honey-buzzards non-linearly; therefore, we first ran two models for each covariate independently, one with the linear effect ($y \sim x$) and one with the nonlinear effect ($y \sim x + x^2$) (Supplementary Material, Table A2). In order to identify the best effect we compared them with the second-order Akaike Information Criterion (AIC_c, Akaike, 1973), with the best model evaluated as the model with the lowest AIC_c value (Burnham & Anderson, 2002). In this way, we selected for each variable either linear or nonlinear terms to be included in the next modelling procedure. We then built a set of 16 models *a priori* defined for each station as hypotheses on the effects of winds on migration flow (see Supplementary Material, Table A3) and compared them with the AIC_c value as previously described, selecting the most plausible. However, as the best model sometimes lacks less important variables (i.e., those comprised in models with $\Delta AIC_c < 2$ respect the one with the lowest AIC_c; Burnham & Anderson, 2002), we also described and argued those variables that affected the flock size to a lesser extent (Fieberg & Johnson, 2015). The *goodness-of-fit* of the model obtained was assessed by Pearson's χ^2 test (Agresti, 2007) and the VIF was calculated to prevent covariate collinearity with a threshold of three.

We used Spearman's correlation analysis to investigate the relationships among the Honey-buzzard numbers observed at each watchpoint. In particular, the total of birds observed on each peak day was related to the number observed on the same day at the other watchpoints. Finally, we compared the flock size on the peak days using a Kruskal-Wallis rank test and a Dunn test for post-hoc nonparametric multiple comparisons with unequal sample sizes. In order to have a better overview of the migratory flow, we also compared the number of solitary Honey-buzzards at each watchpoint with Pearson's χ^2 test.

Results

We found no significant difference in the magnitude of the migratory flow between the four watchpoints (Serro: 87.5 ± 337.8 (median ± IQR), Dinnammare: 55.5 ± 398.0, M. Ciccia: 61.52 ± 333.8, Solano: 129.5 ± 532.3; Kruskal-Wallis, $\chi^2 = 2.123$, $P = 0.547$; Supplementary Material, Figure A4). On the other hand, a marked variation in yearly migration counts was recorded, with the lowest number at all watchpoints in 2016 (Supplementary Material, Table A5).

At Serro, the westernmost watchpoint located at a relatively low altitude between the Peloritani Mountains and the Tyrrhenian coast, on average 12,588 ± 934 (SE; maximum: 13,956 in 2014; minimum: 9,827 in 2016) birds were counted each year (N = 4), with 14 peak days reported. During these peak days, on average 1,746 ± 181 birds were detected (maximum: 3,037 on 2 May 2016) with the migratory flow intensity increasing during weak-moderate northwesterly winds, although passage of large flocks was also reported during weak easterly and stronger westerly winds (Table 1). Flock size was negatively affected by the strength of orographic uplift and unaffected by the strength of thermals and by the N-S component of the wind; nonetheless, the last entered in the second best model ($\Delta AIC_c < 2$) (Table 1; Figures 2-5). The *goodness-of-fit* of the model was good ($\chi^2 = 87377$, $P = 0.706$) and no collinearity was observed (Table 1).

At Dinnammare, the southernmost and highest watchpoint on the Peloritani Mountains, on average 14,583 ± 1,883 (maximum: 19,007 in 2015; minimum: 8,045 in 2016) birds were counted yearly (N = 5) and 18 peak days were reported (maximum: 5 days in 2018; minimum: 1 day in 2016). During each peak day, an average 2,095 ± 223 birds were counted (maximum: 4,248 on 7 May 2014). Migrants were seen mostly during winds with weak northerly and slightly

TABLE 1

Parameters of the best GLZ explaining the migration flow of Honey-buzzards at the Strait of Messina. Table shows variable estimates, standard errors (SE), 95% confidence intervals (LCI lower confidence interval, UCI upper confidence interval) and the variance inflation factor (VIF).
[Parámetros del mejor GLZ que explican el flujo de migración de los abejeros europeos en el estrecho de Messina. La tabla muestra estimaciones de variables, errores estándar (SE), intervalos de confianza del 95% (intervalo de confianza inferior LCI, intervalo de confianza superior UCI) y el factor de inflación de la varianza (VIF).]

Station	Variable	estimate	SE	LCI	UCI	VIF
Serro	Intercept	3.302	0.044	—	—	—
	Wind U	−1.922	2.815	−7.807	3.638	1.606
	Wind U^2	7.509	2.366	3.130	12.162	
	Orographic uplift	−0.229	0.114	−0.460	−0.006	2.579
Dinnammare	Intercept	3.350	0.039	—	—	—
	Wind V	4.959	2.220	0.549	9.436	1.389
	Wind V^2	−4.680	1.965	−8.426	−0.872	
	Wind U	0.107	0.056	0.0001	0.212	1.414
	Thermal uplift	−0.893	1.448	−3.817	1.991	1.037
	Thermal $uplift^2$	5.766	1.390	2.908	8.717	
	Orographic uplift	−1.718	2.828	−7.138	3.743	1.492
	Orographic $uplift^2$	−6.844	1.492	−9.760	−3.920	
M. Ciccia	Intercept	3.071	0.036	—	—	—
	Wind V	8.138	1.773	4.530	11.767	1.122
	Wind V^2	4.314	1.473	1.596	7.221	
	Wind U	−0.096	0.045	−0.191	−0.002	1.264
	Thermal uplift	−0.061	0.037	−0.134	0.012	1.025
	Orographic uplift	−7.927	2.053	−11.951	−3.788	1.218
	Orographic $uplift^2$	−3.492	1.538	−6.430	−0.354	
Solano	Intercept	3.012	0.034	—	—	—
	Wind V	0.317	0.043	0.230	0.407	1.282
	Wind U	−10.021	2.764	−15.562	−4.446	1.603
	Wind U^2	−8.019	1.715	−11.529	−4.413	
	Thermal uplift	−8.819	1.691	−12.137	−5.505	1.137
	Thermal $uplift^2$	3.262	1.416	0.417	6.148	
	Orographic uplift	15.133	3.374	8.359	21.872	1.763
	Orographic $uplift^2$	0.545	1.702	−2.916	4.087	

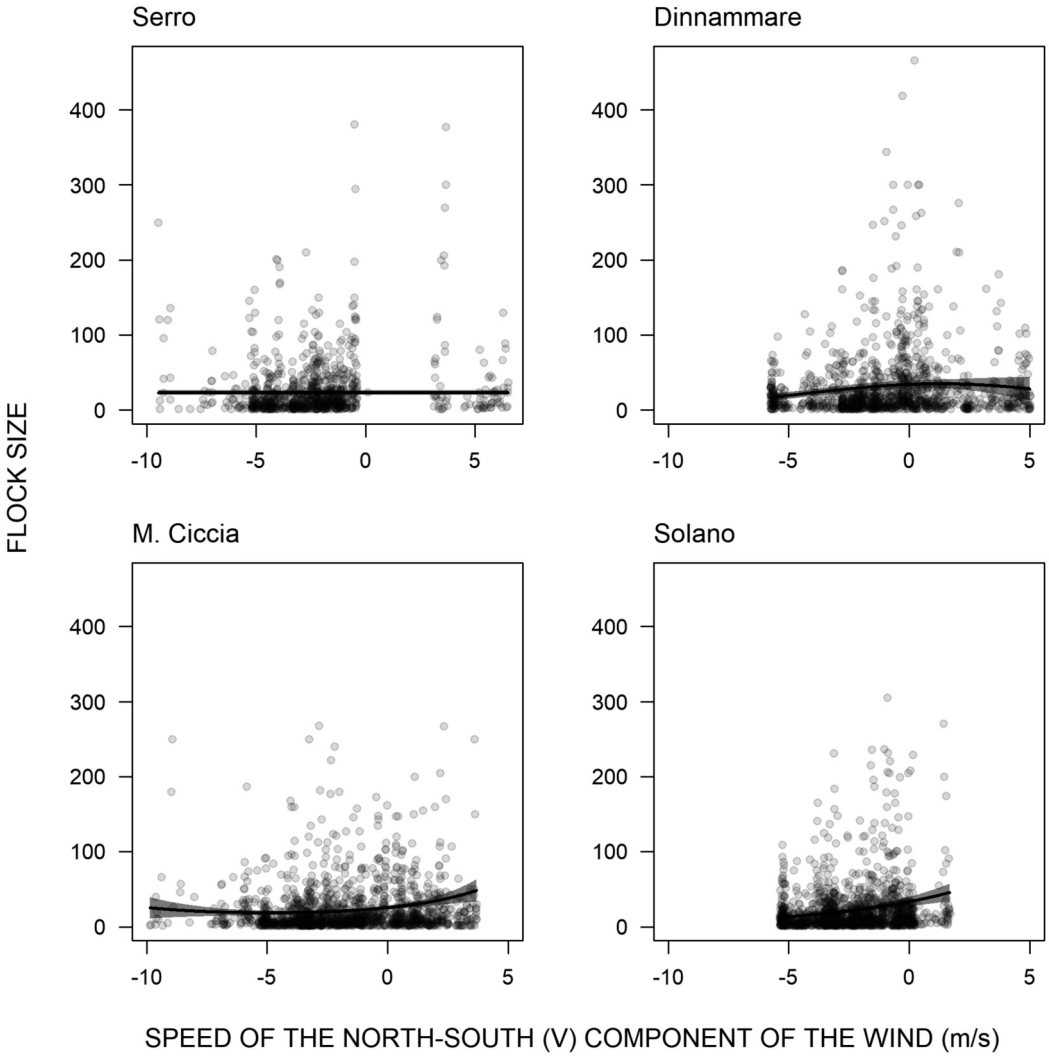

FIG. 2.—Spring passage of Honey-buzzards in relation to local north-south wind at Serro, Dinnammare, M. Ciccia and Solano (Strait of Messina).
[Paso primaveral de abejeros europeos según el régimen local de vientos norte-sur en Serro, Dinnammare, M. Ciccia y Solano (estrecho de Mesina).]

stronger westerly components (Figures 2, 3). This was the only watchpoint from which the number of birds reported during westerly winds was higher than during northwesterly winds (Supplementary Material, Figure A6). Larger flocks were seen with stronger westerly and weaker northerly and southerly winds. Regarding the influence of vertical winds, flock size increased during both weaker and stronger thermal conditions such as during moderate orographic uplifts (Table 1; Figures 4, 5). The *goodness-of-fit* of the model was good ($\chi^2 = 175450$, $P = 0.403$) and no collinearity was observed (Table 1).

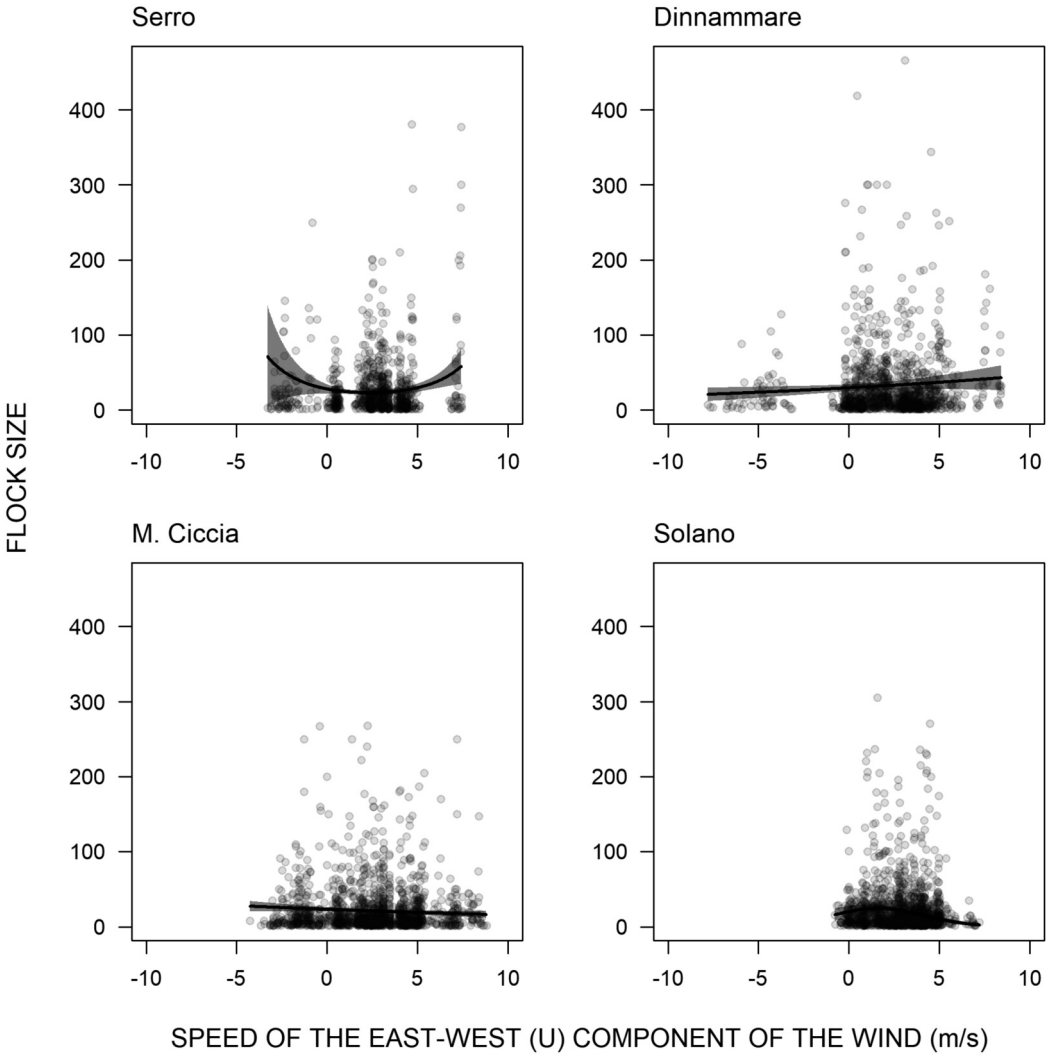

FIG. 3.—Spring passage of Honey-buzzards in relation to local east-west wind at Serro, Dinnammare, Mount Ciccia and Solano (Strait of Messina).
[Paso primaveral de abejeros europeos según el régimen local de vientos este-oeste en Serro, Dinnammare, M. Ciccia y Solano (estrecho de Mesina).]

At Mount Ciccia, the other watchpoint located on the Peloritani Mountains, we counted on average 13,473 ± 1,522 (maximum: 17,680 in 2018; minimum: 8,928 in 2016) birds per year (N = 5) and reported a total of 22 peak days in which, on average, 1,719 ± 110 birds were counted (maximum: 2,288 on 8 May 2018). At this watchpoint, the intensity of the migratory flow was higher during northwesterly winds (Supplementary Material, Figure A6) with a weak-moderate northerly and slightly weaker westerly component, but with flock size increasing during weak southerly and easterly winds (Table 1;

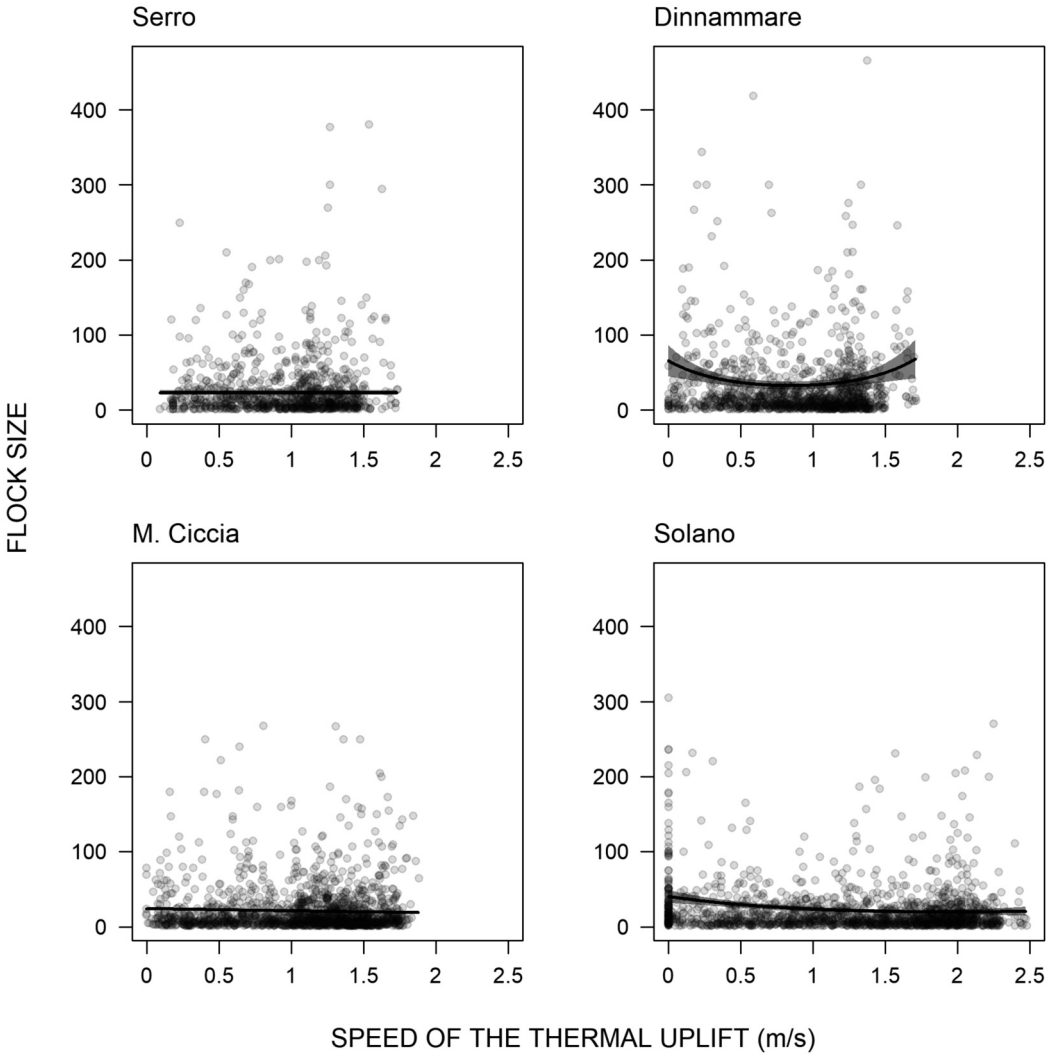

FIG. 4.—Spring passage of Honey-buzzards in relation to the strength of thermal uplift at Serro, Dinnammare, M. Ciccia and Solano (Strait of Messina).
[Paso primaveral de abejeros europeos según la fuerza de las corrientes térmicas ascendentes en Serro, Dinnammare, M. Ciccia y Solano (estrecho de Mesina).]

Figures 2, 3). Finally, the flock size was negatively affected both by the strength of thermal and orographic uplift (Table 1; Figures 4, 5). The *goodness-of-fit* of the model was good (χ^2 = 196870, P = 1.00) and no collinearity was observed. No significant relationship was reported between counts recorded during the peak days at the three Sicilian watchpoints (Table 2; Figure 6).

At Solano, on average 14,814 ± 2,014 (N = 5) birds were detected each year (maximum: 19,875 in 2018; minimum: 8,554 in 2016) with 19 peak days, during which on average 1,849 ± 205 birds were counted

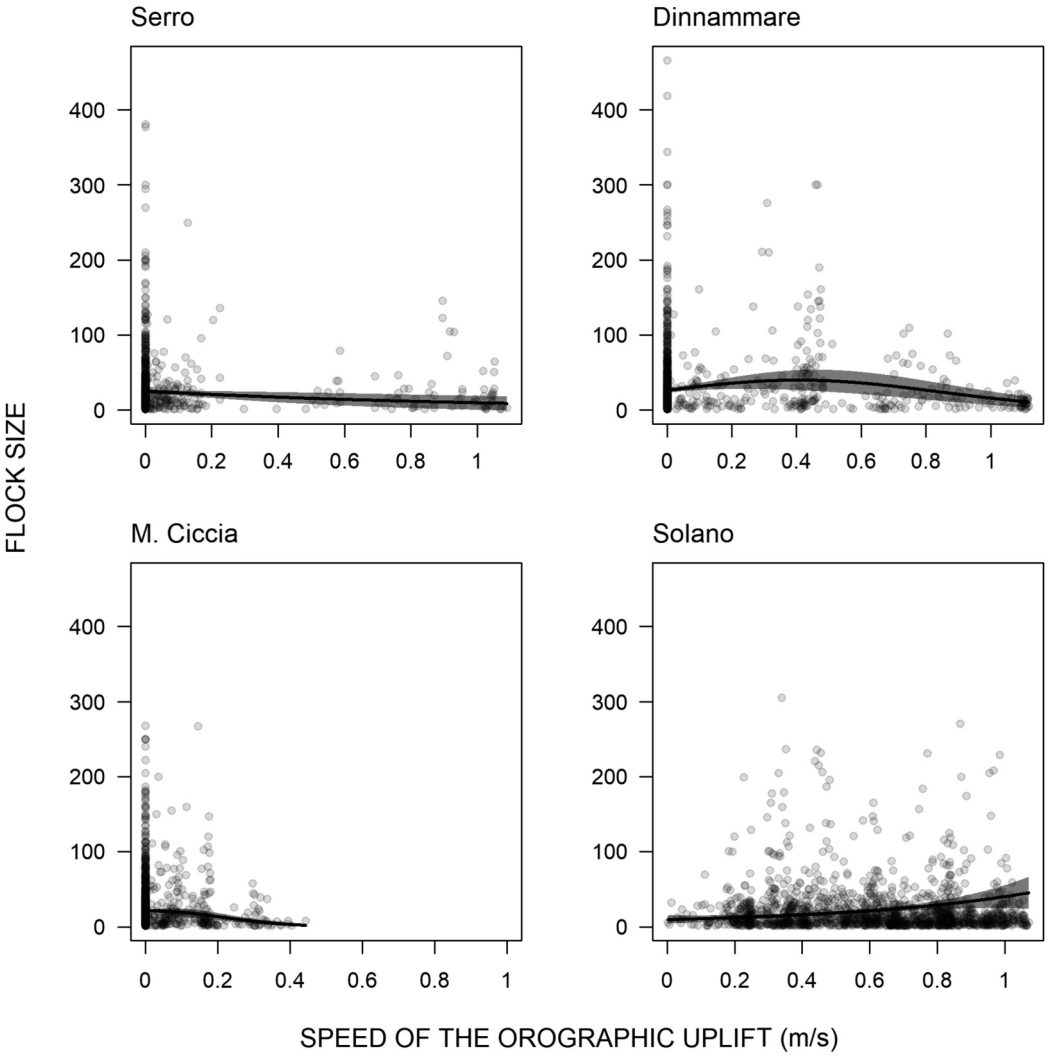

FIG. 5.—Spring passage of Honey-buzzards in relation to the strength of orographic uplift at Serro, Dinnammare, M. Ciccia and Solano (Strait of Messina).
[Paso primaveral de abejeros europeos según la intensidad de las corrientes orográficas ascendentes en Serro, Dinnammare, M. Ciccia y Solano (estrecho de Mesina).]

(maximum: 4,491 on 7 May 2014). At a local scale, the migratory flow and flock size increased during weak northwesterly winds and during weak southerly winds (Table 1; Supplementary Material, Figure A6, Figures 2d, 3d); flock size was negatively affected by the strength of thermals and positively affected by the strength of orographic uplift (Table 1; Figures 4d, 5d). The *goodness-of-fit* of the model was good (χ^2 = 207900, P = 0.996) and no collinearity was observed. Counts during the peak days at this watchpoint were positively correlated with those reported at Dinnammare (Table 2; Figure 6).

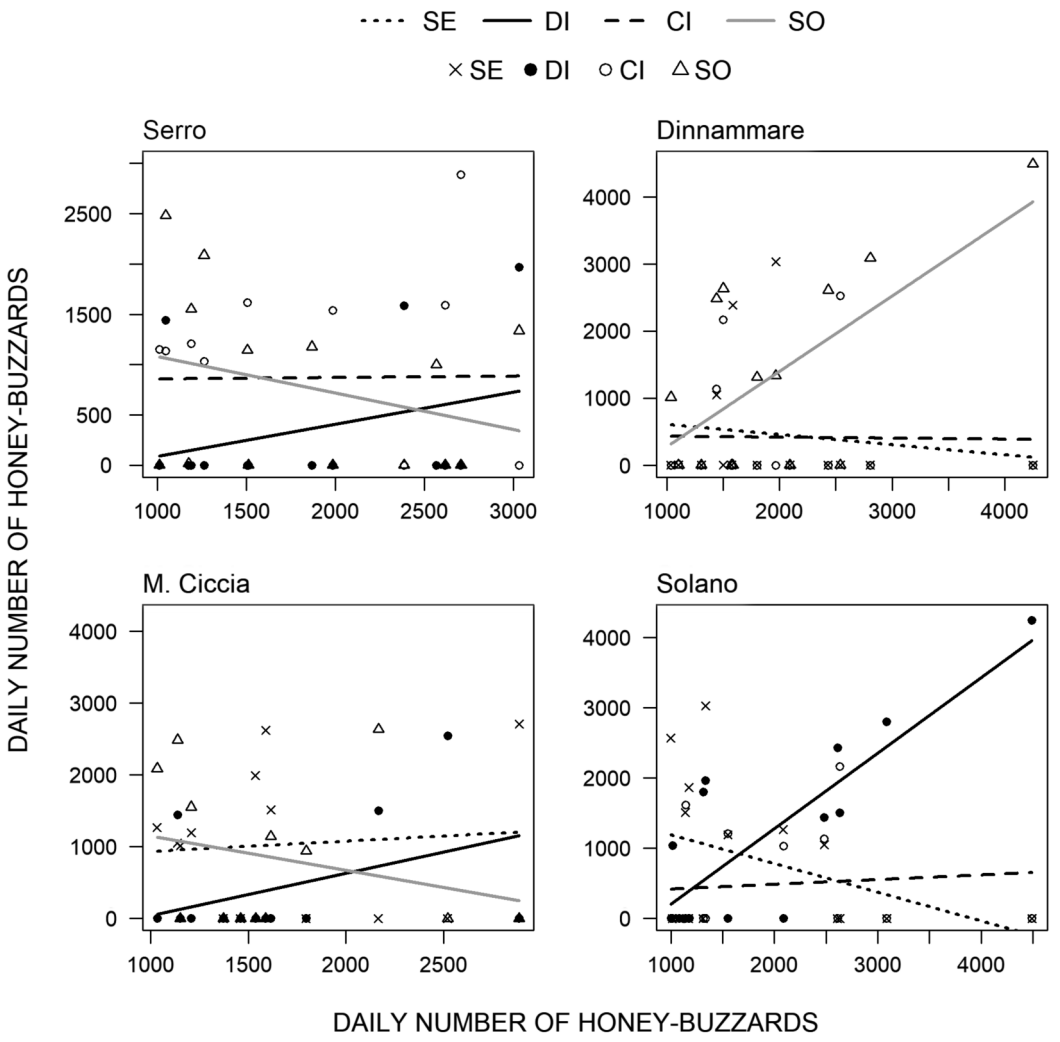

FIG. 6.—Correlations between the numbers of Honey-buzzards recorded during the peak days at Serro, Dinnammare, M. Ciccia and Solano and the relative numbers migrated at Serro (SE), Dinnammare (DI), M. Ciccia (CI) and Solano (SO).

[Correlaciones entre el número de abejeros europeos registrados durante días pico de migración en Serro, Dinnammare, M. Ciccia y Solano, y el número registrado en el resto de puntos de observación: Serro (SE), Dinnammare (DI), M. Ciccia (CI) y Solano (SO).]

We found significant differences in terms of the median flock size between Serro (14.0 ± 26 [IQR]) and M. Ciccia (11.09 ± 22; Dunn Test, P = 0.002), Dinnammare (14.0 ± 28) and M. Ciccia (Dunn Test, P < 0.001), and Dinnammare and Solano (12.5 ± 22; Dunn Test, P = 0.043). As expected, some Honey-buzzards migrated alone (Serro: N = 114 individuals vs 910 flocks, 11.1%; Dinnammare: N = 129 vs 859 flocks, 13.1%; M. Ciccia: N = 210 vs 1256 flocks, 14.3%; Solano: N = 170 vs 1152 flocks, 12.9%).

TABLE 2

Correlation matrix (Spearman's rank correlation) between the numbers of Honey-buzzards observed on each peak day (by rows) and the numbers observed on the same day at the other watchpoints (by columns). Significant correlations shown in bold.
[Matriz de correlación (correlación de rango de Spearman) entre los números de abejeros europeos observados en cada día pico (por filas) y los números observados el mismo día en los otros puntos de observación (por columnas). Las correlaciones significativas se muestran en negrita.]

	Serro	Dinnammare	M. Ciccia	Solano
Serro	—	0.223 (P = 0.443)	0.005 (P = 0.988)	−0.309 (P = 0.283)
Dinnammare	−0.076 (P = 0.795)	—	−0.184 (P = 0.528)	0.414 (P = 0.141)
M. Ciccia	0.081 (P = 0.793)	0.268 (P = 0.377)	—	−0.313 (P = 0.408)
Solano	−0.316 (P = 0.252)	**0.704 (P = 0.003)**	0.219 (P = 0.433)	—

Their frequency was significantly different among the watchpoints (Serro: 18.3%, Dinnammare: 20.7%, M. Ciccia: 33.7%, Solano: 27.3%; ($\chi^2 = 35.986$, $P < 0.001$), being significantly higher at M. Ciccia and Solano.

Finally, wind conditions at a regional scale the day before and during peak days generally consisted of moderate northwesterly winds between the Cap Bon Peninsula and western Sicily and slightly weaker northwesterly winds between eastern Sicily and southern continental Italy, respectively (Supplementary Material, Figure A7).

DISCUSSION

Although northwesterly winds prevailed at the Strait of Messina on peak days, slightly different local wind conditions affected migration patterns at each of the four watchpoints and shaped at least two distinct pathways through this bottleneck. In particular, European Honey-buzzards were recorded at Dinnammare, the southernmost and highest watchpoint on the Peloritani Mountains, mostly when flying in winds with a stronger westerly component. Apparently, during these wind conditions they tend to follow the ridge of the mountain chain, aligned along the axis of migration (SW-NE), probably exploiting both thermals and deflection (orographic) updrafts. Both vertical winds form at the site because of the topographical features, but during different wind strengths; unlike orographic uplift, thermals are stronger with weaker winds (Kerlinger, 1989). The phenomenon explains why at Dinnammare large flocks were also observed with weaker thermals, when birds probably soared, exploiting a stronger ridge uplift (Bildstein, 2006; Duerr *et al*., 2012; Agostini *et al*., 2015b).

Our study suggests that a considerable number of the birds recorded at Dinnammare exploited soaring flight to undertake a water crossing immediately thereafter, probably heading eastwards for about seven kilometres over land and eight kilometres over water to reach the continental coast of the Strait by exploiting tailwinds, especially when migrating in larger flocks. This is not unexpected, since in Honey-buzzards flock size is positively related to flight altitude, and both flock size and flight altitude are posi-

tively related to the water crossing tendency (Agostini *et al.*, 1994; Panuccio & Agostini, 2010; Panuccio *et al.*, 2017, 2019). In addition, during the crossing, flocking can improve flight efficiency as a larger flock size will lead to a lower flapping rate (Bildstein, 2006), while birds starting at higher altitudes are likely to reach the opposite coast with less flapping effort (Santos *et al.*, 2020). This pattern of migration would explain why the flock size recorded at Dinnammare was greater than that at Mount Ciccia, the northernmost and lower station along the ridge of the mountain chain, and why the migratory flow at Dinnammare was significantly correlated with that recorded at Solano, located about 30km ENE and at nearly at the same altitude, near the edge of a plateau on the continental slope inland of the Strait.

A radar study, made along the continental coast of the Strait of Messina during spring migration, monitored the flight altitude and direction of migrants over the sea using a station located about nine kilometres east of Mount Ciccia. It revealed that migrants crossed heading eastwards and below the optimal flight altitude with respect to tailwind assistance, reaching the coastline at a relatively low altitude (450m a.s.l.) after a flight over water of at least six kilometres (Bächler *et al.*, 2006; Mateos-Rodríguez & Liechti, 2012). This probably takes place because the birds would have to invest too much energy to stay at, or climb to, the high altitudes required to maximise wind support whilst over the sea (Vansteelant & Agostini, 2021). As a result, when facing the Strait, they reach an adequate starting altitude to glide over this relatively short water crossing, lowering the energetic cost by limiting flapping flight as much as possible. Assuming no wind, a bird with an 8:1 glide ratio needs a starting altitude of 800m to glide 6-7km before resorting to flapping flight (Kerlinger, 1989). Moreover, since migrating European Honey-buzzards readily reduce gliding airspeed with tailwind support where soaring conditions are poor (e.g., when crossing a water surface), they extend their gliding range, further reducing the need for flapping flight (Vansteelant *et al.*, 2017).

Once inland, radar studies made at the Solano station showed that Honey-buzzards change their direction, heading NE and modulating the response to wind drift in relation to the exploitation of the vertical wind (Panuccio *et al.*, 2016). In line with predictions of optimal migration flight theory (Pennycuick, 1978; Alerstam, 1979, 1991), they decrease airspeed under increasing tailwind speed, presumably to lower the energetic cost of the flight over land (Becciu *et al.*, 2018). Our observations are in agreement with these results, highlighting that Honey-buzzards detected from the Solano watchpoint probably modulate their behaviour allowing partial wind drift at a local scale when flying in northwesterly winds, and mostly exploiting the orographic updrafts generated by the deflection of such winds on the edge of the plateau and flying in smaller flocks than at Dinnammare.

We cannot exclude the possibility that a substantial number of birds approaching the Strait passed undetected in this survey, by leaving Sicily even further south of Dinnammare and undertaking a longer water crossing, perhaps when they could exploit a stronger talilwind support in westerly winds. Conversely, when birds approaching the Strait fly in winds with a weaker westerly component they probably tend to follow the Sicilian mainland reaching Serro and Mount Ciccia, the northernmost Sicilian watchpoint along the mountain ridge, where larger flocks were observed during weak southerly winds. Since migration counts were not significantly correlated between the three Sicilian watchpoints during the peak days, this further confirms that birds crossed this bottleneck on a broader front, with those using the northernmost flyway near the northern end of the

Strait passing undetected from the Solano station, probably concentrating along the continental coast. As a result, it is reasonable to speculate that the minimum number of birds passing through the study area each season could be obtained by adding up birds counted at Serro and Solano, on average approximately 28,000 birds each season during the study period.

Finally, this study confirms that the magnitude of the spring migration of the Honey-buzzard at the Strait of Messina is strongly affected by the regional pattern of horizontal winds. In agreement with the previous study carried out in the Central Mediterranean region, with a single watchpoint at the Strait, these raptors concentrated at this bottleneck after crossing the Sicilian Channel during northwesterly winds, which blew both the day before and during the day of peak counts at the Strait of Messina (Agostini *et al*., 2016). During such wind conditions they are expected to drift to a variable extent during the sea crossing between the Cap Bon Peninsula and Sicily, reaching the southwestern coast of the Sicilian mainland. Conversely, as mentioned above, during southerly winds they tend to choose more direct flyways towards the Italian Peninsula bypassing the Strait, where fewer birds are observed (Agostini, 1992; Panuccio, 2011; Agostini *et al*., 2016; Becciu *et al*., 2018). Further confirmation of these migration patterns has been recently given by an adult male, breeding in Hungary and wintering in Cameroon, tracked by satellite telemetry. This bird crossed the central Mediterranean area in springs 2016, 2017 and 2018 using the Tyrrhenian flyway in 2016 in southwesterly winds, but using the Strait of Messina in 2017 and 2018, after crossing the Sicilian Channel in northwesterly winds the day before (Agostini *et al*., 2019). It is interesting that 2016 was also the year in which the lowest counts were recorded at all the watchpoints used in this study, perhaps because large numbers of Honey-buzzards crossed the Tyrrhenian Sea, like the Hungarian bird.

In conclusion, this study highlights a flexibility in flight strategies adopted by Honey-buzzards passing through the Strait of Messina in relation to horizontal and vertical winds at a local scale. In this scenario, future monitoring at this bottleneck could be carried out using two watchpoints, Solano and another located along the continental coast overlooking the northern end of the Strait. It would allow the possibility of double counting migrants to be limited as much as possible by detecting those following the two distinct flyways. Finally, it confirms that wind conditions through the Sicilian Channel the previous day strongly affect the magnitude of the spring migration of Honey-buzzards at the Strait, thus causing great variation in numbers recorded in different years. This flexibility in route choice through the central Mediterranean region may restrict our ability to infer population trends of this species at this bottleneck. Also, the interpretation of migration behaviour in relation to wind patterns at both regional and local scales can help conservationists to protect migrants from poachers by predicting the routes taken by the birds.

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AUTHOR CONTRIBUTIONS.—NA made bird observations, prepared data for analysis and wrote the first draft of the manuscript. MP and MC coordinated the fieldwork and made bird observations. GC did all the statistical analyses. MG and GD helped with the study design. JvH provided the analysis of wind patterns at a regional scale. Except for Michele Panuccio, who passed away before the preparation of the manuscript, all authors read and approved this final version.

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Supplementary Electronic Material

Additional supporting information may be found in the online version of this article. See the volume 68(2) on www.ardeola.org

Appendix A1. Description of methods used to obtain weather data.
[Descripción de los métodos para obtener la información meteorológica.]

Table A2. AIC_c comparison between Generalized Linear Models (GLZ) with linear effect ($y \sim x$) and GLZ with nonlinear effect ($y \sim x + x^2$).
[Comparación mediante AIC_c de modelos lineares generalizados (GLZ) con efecto linear ($y \sim x$) y con efecto no linear ($y \sim x + x^2$).]

Table A3. Generalized Linear Models investigating the flock size of Honey-buzzards during spring migration at Strait of Messina.
[Modelo linear generalizado para el tamaño de bando de los abejeros europeos durante la migración primaveral en el estrecho de Mesina.]

Figure A4. Daily totals of Honey-buzzards passing during spring migration at the four watchpoints at the Strait of Messina during 20 April-20 May, 2014-2018.
[Número de abejeros europeos totales por día en paso durante la migración primaveral en cuatro puntos de observación en el estrecho de Mesina (del 20 de abril al 20 de mayo, 2014-2018).]

Table A5. Annual totals of Honey-buzzards at the four watchpoints at the Strait of Messina during 20 April-20 May, 2014-2018.
[Número de abejeros europeos totales por año en los cuatro puntos de observación en el estrecho de Mesina del 20 de abril al 20 de mayo, 2014-2018.]

Figure A6. Numbers of Honey-buzzards counted at Strait of Messina during the peak days at the four watchpoints during different wind directions.
[Número de abejeros europeos contados en el estrecho de Mesina en los días pico de migración en cuatro puntos de observación con diferentes direcciones del viento.]

Figure A7. Strength and direction of the winds in the Central Mediterranean region on peak days and on the days before a peak.
[Fuerza y dirección de los vientos en la región mediterránea central, en los días pico de migración y para los días previos.]

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