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HUNTING ALTITUDE OF ELEONORA'S FALCON (*FALCO ELEONORAE*) OVER A BREEDING COLONY

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Abstract.—We investigated the flight altitude of hunting Eleonora's Falcons (*Falco eleonorae*) around their colony near the island of Crete (Greece). We used a broadband marine surveillance radar positioned on the coast of Crete and detected the falcons' movements during the breeding period. The birds were monitored using a Java application that enabled us to manually track radar targets directly on the radar screen and transfer the data into a GIS environment. Thirty hours of radar monitoring between 14 September and 22 September 2017 produced 4774 records of the species (1218 over inland and 3556 over the sea). Hunting falcons flew on average at 1292 ± 11 masl (range = 17–3475, median flight altitude 1156 m), though 70% of them were tracked flying between 17 and 1750 m. The range of flight altitude recorded was greater than that previously published, and was consistent with the prey selection during the nestling-rearing period, i.e., migratory passerines. Eleonora's Falcons hunted more frequently over the sea than over the mainland and at a higher altitudes during the morning than at midday or in the afternoon. The daily flight pattern probably reflected the higher intensity of passerine migration in the early morning and late afternoon, as well as an opportunistic prey shift from birds to insects during midday when passerine migration is weak. Compared to other techniques previously used for tracking this species, namely visual observations (1970s), optical range finder (1990s), and satellite telemetry (2000s), broadband marine radar is not limited by small sample size, geolocation error, weather conditions, or poor visibility at high altitudes.

Key Words: *Eleonora's Falcon*; Falco eleonorae; *broadband marine radar*; *Crete*; *flight altitude*; *hunting behavior*.

ALTURA DE CAZA DE *FALCO ELEONORAE* SOBRE UNA COLONIA REPRODUCTIVA

Resumen.—Investigamos la altura de vuelo de individuos de *Falco eleonorae* cazando alrededor de su colonia cerca de la isla de Creta (Grecia). Usamos un radar de banda ancha de vigilancia marina ubicado en la costa de Creta con el cual detectamos los movimientos de los halcones durante el período reproductivo. Las aves fueron monitoreadas usando una aplicación Java que nos permitió seguir manualmente los halcones directamente en la pantalla de radar y transferir los datos a un contexto SIG. Treinta horas de monitoreo de radar entre el 14 de septiembre y el 22 de septiembre 2017 generaron 4774 registros de la especie (1218 sobre tierra y 3556 sobre mar). Los halcones que cazaban volaron en promedio a 1292 ± 69 m snm (rango = 17–3475, altura de vuelo mediana 1156 m), aunque en un 70% fueron registrados volando entre 17 y 1750 m. El rango de altura de vuelo registrado fue mayor que el rango publicado previamente, siendo consistente con la selección de presas durante el periodo de cría de los polluelos, i.e., paseriformes migratorios. *Falco eleonorae* cazó más frecuentemente sobre el mar que sobre la tierra y a alturas más altas durante la mañana que al mediodía o por la tarde. El patrón de vuelo diario probablemente reflejó la mayor intensidad de migración de paseriformes temprano por la mañana y a última hora de la tarde, como también el cambio de presas de aves a insectos durante el mediodía, cuando la migración de paseriformes es débil. En comparación con otras técnicas usadas previamente para seguir a esta especie, tales como las observaciones visuales (1970s), telémetro óptico (1990s), y telemetría satelital (2000s), el radar de banda ancha de vigilancia marina no está

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limitado por un reducido tamaño de muestreo, error de geolocalización, condiciones climáticas o visibilidad reducida a grandes alturas.

[Traducción del equipo editorial]

The Eleonora's Falcon (*Falco eleonorae*) is a long-distance migrant overwintering in Madagascar and breeding colonially in the Mediterranean region and the eastern Atlantic, i.e., the Canary Islands and the Moroccan coast (Walter 1979, Cramp and Simmons 1980). The species' population is considered to be increasing after a moderate decline in the 2000s (BirdLife International 2004, 2018). Its global breeding population numbers approximately 14,500 breeding pairs, with the bulk of them (>85%) distributed on 307 uninhabited islets of the Aegean archipelago in Greece (Dimalexis et al. 2008). This falcon species is peculiar for two unusual behavioral features: its seasonal diet shift from insects outside the breeding season to birds when raising young, and its delayed breeding cycle, which coincides with the peak of the autumn migration of passerines (Walter 1979, Spina et al. 1988, Ferguson-Lees and Christie 2001). Over the past decades, several studies have focused on the movement ecology of the Eleonora's Falcon (Gschweng et al. 2008, 2012, López-López et al. 2010, Kassara et al. 2012, Mellone et al. 2013) mainly due to the species' conservation status and its unusual migration pattern, which was largely unknown until recently. Most Eleonora's Falcons winter in Madagascar after a long crossing of the African continent (López-López et al. 2010, Kassara et al. 2012, 2017, Mellone et al. 2013, during which they fly over the Sahara Desert (Mellone et al. 2011, Agostini et al. 2015). In the breeding colonies, the falcons forage for passerines communally, but adjust their hunting strategy in relation to the local wind conditions (Walter 1979, Alerstam 1990). On windless or weak-wind days (<5 Beaufort scale), Eleonora's Falcons prefer to hunt inland on the nearest land mass, although in the Atlantic colonies they hunt far offshore over the ocean, up to 100 km from the African coast (Ristow et al. 1983, Mellone et al. 2012). Conversely, during windy days (≥5 Beaufort scale), they hunt over their colonies. Their usual hunting technique is hovering against the wind ("standing flight," Walter 1979), forming a "wall" that acts as a barrier for the passing prey. Falcons using this hunting technique fly head-on into the wind at 800–1000 masl more frequently than at lower altitudes (Walter 1979), although this fact does not reveal the extent and intensity of their hunting at higher altitudes.

The species' flight performance has been studied during the breeding period by visual observations (Walter 1979), optical range finder (Alerstam and Henderström 1998, Rosén et al. 1999, Rosén and Henderström 2002) and satellite telemetry (Mellone et al. 2012). These techniques have shown that in the morning falcons spent most of their time at sea foraging within 50 km of their colony (Mellone et al. 2012), at a mean altitude of about 1300 m and reaching maximum altitudes of 1650 m (Rosén et al. 1999). However, the limitations of optical equipment (e.g., detection range, poor visibility conditions) hamper efforts to determine the full spectrum of their flight altitude. Marine surveillance (scanning) radars have long been used in the study of bird movements (Casement 1966, Gauthreaux 1970, Harmata et al. 1999), and quite recently for the study of the aerial space use by Eleonora's Falcons at one colony in Cyclades (central Aegean; Fric et al. 2017). The latter study suggested that hunting falcons are mostly active within a 1-km radius of their colony and at altitudes of up to 200–300 m and 700 m above ground level during the day and during the night, respectively (Fric et al. 2017). In the present study, we monitored the flight behavior of the Eleonora's Falcon around a breeding colony in southeast Crete to investigate the species' hunting activity. For the first time in such studies, we tested and used a portable broadband marine radar, i.e., a device continuously transmitting microwaves of different frequency. The study period was selected to cover the species' late breeding season, prior to the fledging of the young, when autumn migration of passerines in the Mediterranean region culminates (Moreau 1972, Bruderer and Liechti 1999) and breeding falcons act as central-place foragers (Walter 1979, Mellone et al. 2012).

Methods

Study Area. The study colony islet (35°1.839′N, 26°14.132′E) is a rock with a perimeter of 620 m and an area of 1.4 ha, located 400 m off the southeasternmost point of the coast of Crete. It hosts 45–50 breeding pairs of Eleonora's Falcons, which have been monitored since 2004 (Dimalexis et al. 2008).

The islet is characterized by steep limestone cliffs all around, from sea level to the top (12 m) and is partly covered by coastal cliff halophile garrigues and Mediterranean shrubs (i.e., *Euphorbia dendroides*). The north and northeast cliff faces are almost vertical, providing many suitable nesting sites for the falcons. The climate of the area is Mediterranean to subtropical, with a mean annual temperature of 20°C and a total annual precipitation of <300 mm; the dry period is relatively prolonged, lasting from early April until mid-November. We collected data between 14–22 September 2017, a period that coincides with the peak activity of Eleonora's Falcons at the Mediterranean colonies, when falcon nestlings are about 3 wk old (Ferguson-Lees and Christie 2001).

Data Collection and Analysis. The radar station was positioned on mainland Crete at an altitude of 5 masl at <50 m from the shore and 850 m northwest of the falcon colony. It consisted of a low-power-consumption (18 watt) Simrad 4G portable broadband marine surveillance radar, with a transmission frequency of 9.3–9.4GHz (X-band), meaning its wavelength was 3.2 cm, i.e., suitable for detecting small targets such as birds (Bruderer 1997). The radar antenna (H × W: 28 × 48.8 cm; weight: 7.4 kg) was positioned vertically on a tetrapod; additional apparatus (power and linking cables, a portable battery for energy source, and radar monitor) were housed in a van parked nearby. Using the radar's upright set-up, the application computed the falcons' altitude above the ground or the sea, in both cases calculated as meters above sea level (masl). The radar monitor was connected by a video cable to image-processing hardware capturing 60 high definition (1080p) frames per second. The received digitized signal was transmitted to a laptop/PC via an HDMI connection. The laptop screen was split into two halves, with the right half encompassing the sea with the study area, and the left half displaying mainland Crete. The radar's ranging ability (0–66 km) was initially tested for falcon detection at range rings of 1 km up to 7 km, but was finally set to 4 km as no tracks attributed to falcons could be identified as such beyond that distance. Birds were monitored continuously using a Java application developed for the purpose—the "Hypatia-TrackRadar"—which allowed the radar operator to manually follow radar targets directly on the laptop screen, and to transfer the data into a GIS environment (Capotosti and Scacco 2017, Pastorino et al. 2017). The software operates like a virtual transparent sheet overlying the radar monitor, allowing the radar operator to store echo data by clicking on them, while concurrently assigning data such as bird species and age gathered via direct observations. We initially looked for "targets" on the radar monitor by searching above the colony and then confirmed them by direct observation. All falcon tracks consisted of single fixes (namely points and not flight trajectories) with X, Y metric coordinates with respect to the radar center. Each falcon track was fixed manually on the laptop screen approximately every 2.5 sec (given the radar's antenna rotation rate), and by inspecting the whole radar screen in every round of it. The default radar pulse was slightly increased to provide larger returned echoes and facilitate the manual fixing of the falcon tracks. Furthermore, we set falcon trails to remain on the radar monitor for approximately 1 min in an effort to avoid tracking the same individual multiple times. Visual validation was regularly carried out with the aid of 10 × 50 binoculars, to confirm that tracks belonged to Eleonora's Falcons. Sunrise and sunset times in the area were 0650 H and 1930 H, respectively, during the study period. However, fieldwork was undertaken from 0720–1920 H, so as to monitor diurnal activity only and avoid tracking nocturnal migrants passing over the study area at dusk or landing at sunrise.

We checked flight-altitude data for normality using the Shapiro-Wilk test, and inter-daytime and oversea-overland differences in flight altitudes using the Kruskal-Wallis test. We applied a *G*-test in order to test the frequency with which falcons foraged over land and over the sea, or in different wind conditions, and whether they were tracked in the three daytime periods more frequently than expected, based on the proportion of radar work dedicated to each period (Zar 1999). Additionally, we used a generalized linear model (GLM; McCullagh and Nelder 1989, Dobson 1990) to investigate the factors that might influence the species' flight altitude in the study area. Flight altitude was set as the dependent variable (count data) and explanatory variables were: (1) time (morning [0730–1129 H], midday [1130–1529 H] or afternoon [1530–1900 H]), which was selected at random each day, (2) location (position of the bird track over the sea or over the land), and (3) wind speed (categorical data: weak [0–10 knots], moderate [11–21 knots] or strong [≥22 knots]). Archived data of three wind-speed observations corresponding to the daily observation times (i.e., 1000 H, 1400 H, 1800 H) were downloaded from the online database of the National Center for Environmental Information (https://www.esrl.noaa.gov/psd/). In addition (based on the air pressure), wind data were attributed to five altitudinal classes (masl; 0–100, 101–1000, 1001–2000, 2001–3000, 3001–4000) to correspond with the radar (1-km) range rings. A Poisson error distribution was applied in the GLM, and the fitness of the model was evaluated by visually inspecting the distribution of the residuals. The computer-generated NOAA weather data files were decoded and read by using the zyGrib 8.0.1 software (http://www.zygrib.org), and all statistical analyses were made using R (R Core Development Team 2015). Descriptive statistics are presented as averages with standard errors. We considered $P < 0.05$ as significant.

RESULTS

Weather conditions in the study area were stable and typical for Crete during early autumn. The mean daily temperature was 24.9°C ± 0.8 (range = 23.7–26), though at midday it sometimes reached 29°C. The prevailing winds were northwest (297° ± 0.39°), with an average speed of 24.4 ± 0.3 km/hr (range = 1.3–103.6). During fieldwork, weak and moderate winds dominated, with the weakest wind conditions observed in midday (*G*-test, $\chi^2 = 20.59$, $P < 0.001$). Overall, approximately 30 hr of radar monitoring was accomplished (4.8 ± 1.2 hr/d, range = 4–7), with 27%, 40%, and 33% of the hours allocated to the morning, midday, and afternoon periods, respectively. The spatial distribution of birds was heterogeneous. Fewer falcons were tracked over the land ($n = 1218$) than over the sea ($n = 3556$; *G*-test, $\chi^2 = 1195$, $P < 0.001$; Fig. 1) and this difference occurred during all wind conditions (*G*-test, $\chi^2 = 117.10$, $P = 0.001$; Fig. 2). Overall, the number of falcon flights varied considerably relative to wind speed, peaking during moderate winds (*G*-test, $\chi^2 = 1744.70$, $P < 0.001$). The species tended to be more active during the afternoon than during the rest of the day (*G*-test, $\chi^2 = 5.89$, df = 2, $P = 0.052$). Falcons flew on average at 1292 ± 11 masl (range = 17–3475, median = 1156 masl), though 70% of them were tracked flying between 17 and 1750 m. Flight altitude did not differ between individuals foraging over mainland Crete (1298 ± 20 masl, range = 107–3475) and those foraging off the coast over the sea (1289 ± 13 masl, range = 173–3427; Table 1, Kruskal-Wallis $H_1 = 0.46$, $P = 0.49$). However, falcons hunted at higher altitude during the morning (1641 ± 26 m) than during the midday (1058 ± 17 m) or afternoon (1295 ± 14 masl; multiple comparison post Kruskal-Wallis test $H_2 = 297.76$, $P < 0.001$; Fig. 3). Flight altitude was positively associated with wind speed (Spearman's correlation coefficient $r_s = 0.40$, $P < 0.001$), with falcons flying higher during windy weather (weak winds: 1277 ± 17 masl, range = 17–2998; moderate winds: 1236 ± 13 masl, range = 101–3475; strong winds: 2560 ± 26 masl, range = 2014–3152, multiple comparison post Kruskal-Wallis test $H_2 = 308.42$, $P < 0.001$; Fig. 4), and more frequently higher than 2000 masl during calm days (*G*-test, $\chi^2 = 79.29$, $P < 0.001$; Fig. 4). Likewise, the GLM revealed a strong interaction between wind and time of day on flight altitude (Table 2); falcons selected high altitudes during strong or weak wind conditions and flew lower as the day progressed. The latter was most likely to occur during poor wind conditions.

DISCUSSION

Average flight altitude for hunting Eleonora's Falcons was 1292 ± 11 masl, and the maximum was approximately 3500 masl. Nevertheless, 70% of recorded flights were from 17 to 1750 masl and the species' typical hunting technique (of flying against the prevailing wind) was documented at a mean altitude of approximately 1300 masl. The median flight was approximately 1100 masl, suggesting that the "wall" formed by "standing" individuals covers a vertical surface of 100–300 masl in the air space at approximately 1000 masl above the colony. The lowest-flying falcon we documented (17 masl) likely represented one advantage of the applied tracking technique, which eliminated the sea clutter and improved bird-track detection on the radar screen (sidelobe suppression). Anecdotally, we also witnessed falcons in hunting pursuits after passerines close the sea surface, with their wing tips occasionally touching the water. The flight altitude of foraging falcons recorded in the present study closely matches that reported for passing passerines at Mediterranean migration watch-sites. Most migratory passerines have been found flying up to 3000 masl, reaching a maximum altitude of 4500 masl (Bruderer and Liechti 1998). The bulk of trans-Saharan migrants travel during the night, flying at higher average altitudes than during the daytime (daytime range = 900–1500 masl; Casement 1966, Walter 1979, Alerstam 1990, Bruderer and Liechti 1998).

According to other studies, Eleonora's Falcons' flight altitudes vary depending on the local condi-

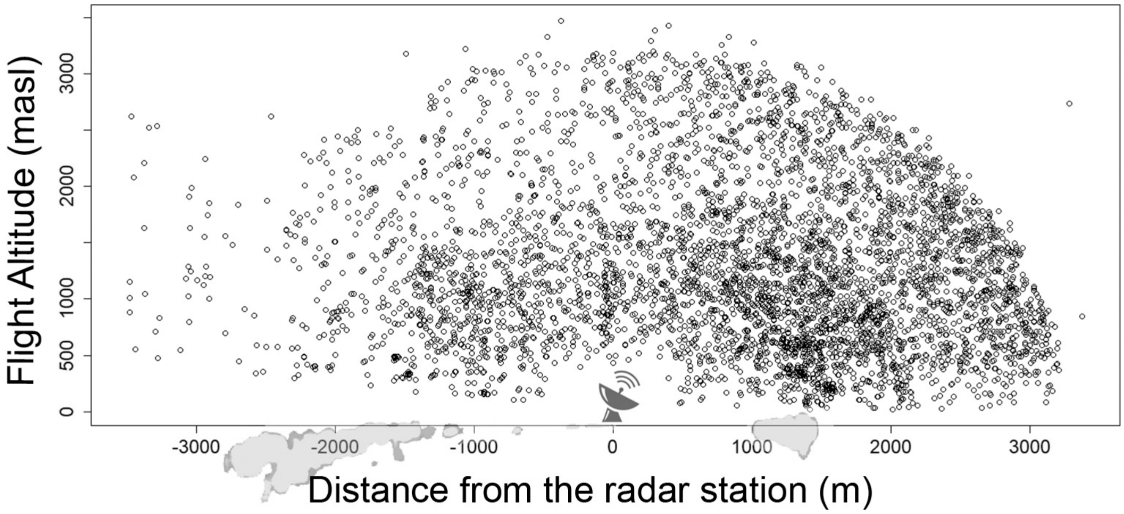

Figure 1. Distribution of the variation of Eleonora's Falcon fixes in the radar range. The irregular shapes at the bottom of the graph indicate the island of Crete (left) and the colony islet (right) as they were picked up on radar. The radar station is shown in the center. Negative values on the X-axis indicate land, positive values indicate sea.

tions and the technique used. By direct observations, hunting falcons were mostly sighted above 800 masl (Walter 1979), whereas use of optical range finders yielded an approximate flight altitude of 1300 m (max. 1649 m; Rosén et al. 1999), and marine surveillance radars 300 m during daytime and up to 800 m during the night (Fric et al. 2017). However, visual techniques (e.g., direct observations by binoculars or range finders) only allow researchers to follow one falcon at a time, and birds can only be monitored for a limited distance, as they soon get too far away and disappear from view (Henderström et al. 1999). Likewise, altitude calculations by GPS radio-tags might be inaccurate due to short satellite-acquisition times aimed at saving battery life, or the incorrect alignment of satellites, which impedes exact vertical measurements (Hansen and Riggs 2008). Furthermore, budgetary constraints restrict satellite tracking to a handful of birds rather than the entire population of a colony. In contrast marine surveillance radars can overcome these problems and have been widely used in ornithological research (Gauthreaux and Belser 2003).

Traditional pulse radars transmit microwaves in blasts, and the distance (range) of birds is calculated

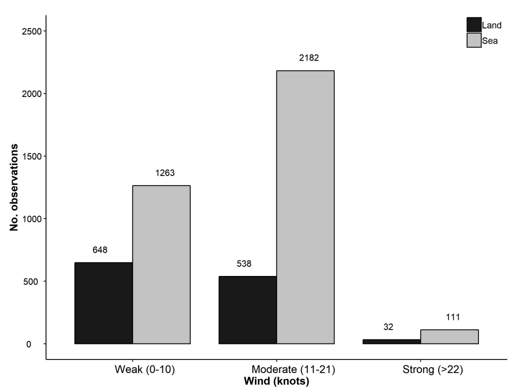

Figure 2. Number of hunting Eleonora's Falcon flights over the sea and land in relation to wind conditions.

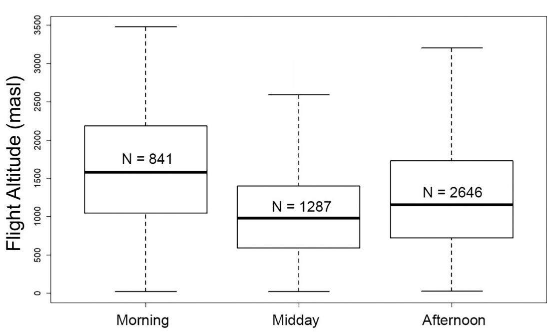

Figure 3. Variation of the Eleonora's Falcon flight altitude throughout the day in a breeding colony. The thick bar in boxes represents the mean flight altitude, the top and bottom of the box is the standard error, and the ranges are at the extremes of the dashed lines.

Table 1. Flight altitude of hunting Eleonora's Falcons from a Crete islet colony (Greece) during the fledging period. Data presented in masl, as mean ± SE (range).

LOCATION/ TIME OF DAY	LAND	*n*	SEA	*n*	OVERALL	*n*
Morning	1670 ± 63.1 (303–3475)	163	1634 ± 29.2 (17–3427)	678	1641 ± 26.5 (17–3475)	841
Midday	1068 ± 26.2 (107–3031)	470	1053 ± 22.5 (21–3099)	817	1058 ± 17.2 (21–3099)	1287
Afternoon	1379 ± 29.7 (149–3190)	585	1271 ± 16.4 (28–3200)	2061	1295 ± 14.3 (28–3200)	2646
Overall	1298 ± 20.3 (107–3475)	1218	1289 ± 12.6 (17–3427)	3556	1292 ± 10.7 (17–3475)	4774

by the time interval elapsing between signal transmission and the returning echo from them. Broadband radars receive and transmit at the same time, sending out a continuous signal at a variable frequency to determine the range of the birds by the change in that frequency when reflected back. Pulse technology generally offers greater range than broadband through its ability to transmit more power, but at the expense of energy consumption and increased microwave hazards. By contrast, broadband units do not need to switch between transmit and receive modes and as range discrimination depends on the pulse length (Johnson 2009), their high resolution at short range makes their target detection far superior to that of pulse units. Meanwhile, by operating at much lower power (watts rather than kilowatts), they are safer for personnel. To our knowledge, broadband radars have not been used or tested for aeroecological studies prior to this study, despite their good performance in target

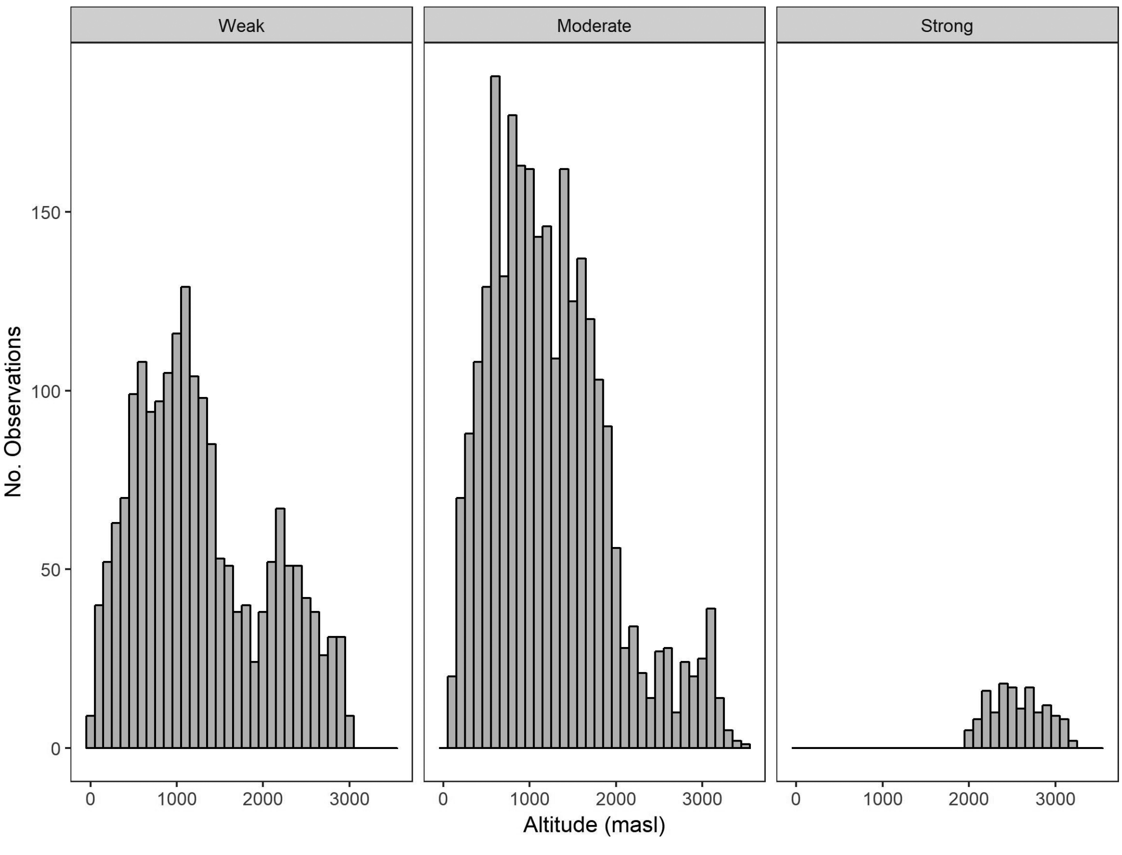

Figure 4. Frequency of the Eleonora's Falcon flight altitudes (100-m increments) relative to wind speed conditions.

Table 2. Results of the GLM model investigating the variation of the Eleonora's Falcon flight altitude (masl).

VARIABLES	ESTIMATES	STD. ERROR	Z-VALUE	P
Intercept	6.939	0.012	571.833	<0.001
Midday	0.489	0.109	4.486	<0.001
Morning	0.559	0.023	23.394	<0.001
Strong wind	0.907	0.046	19.338	<0.001
Weak wind	0.650	0.027	24.017	<0.001
Midday: weak wind	−1.127	0.112	−9.987	<0.001
Morning: weak wind	−1.389	0.056	−24.705	<0.001

discrimination and clarity at short ranges (Kerlinger and Gauthreaux 1985a, 1985b, Panuccio et al. 2016a). The broadband radar allowed us to use a sharp target resolution to accurately distinguish Eleonora's Falcons moving within short detection ranges (<5 km), and to store appropriate data in an effective way. However, given that radars do not produce species-specific tracks or allow identification of individuals, some of the data acquired must be viewed with caution. For example, some radar tracks of falcons flying high at dusk were beyond the possibility of validation by binoculars or spotting scope, and might actually represent large migratory passerines. In addition, some bias due to double-counting the same individuals cannot be ruled out, despite our effort to minimize this by retaining target trails on the radar screen for 1 min.

Overall 74.5% of the observations of falcons were made above the sea (including the colony islet) and all these were attributed to foraging falcons. Although some low altitude flights (<300 masl) might have been territorial disputes or adult individuals landing on the islet to feed their young or to cast a pellet (S. Xirouchakis unpubl. data), these accounted for 4.6% of the observations; thus any resulting bias would be small. This tendency of falcons to hunt near their breeding colony has been cited as support of the species' preference for migrating passerines, which have higher biomass than insect prey (Walter 1979). It could also be viewed as a strategy employed by parent birds to both optimize their foraging and to maximize reproductive success. Prey capture may be enhanced in the air space between the foraging falcons and the sea surface, as escape opportunities for passerines are limited (Walter 1979). In other raptor species, the individuals moving across larger home ranges are those with poorer breeding performance, probably due to low food availability in the vicinity of nest sites and higher energy expenditures during foraging sorties (Newton 1986, Pfeiffer and Meyburg 2015). Falcons were more frequently tracked over the sea than over the land irrespective of the wind conditions, which suggests that foraging on the nearest land mass might take place far inland or only during windless days (Walter 1979).

Eleonora's Falcons' time-energy budgets indicate that falcons spend most of their time at sea during the morning, stay inland during the afternoon, and rest in their colony during the night (Mellone et al. 2012). However, this pattern depends on the local conditions, as Eleonora's Falcons sometimes hunt birds and insects throughout the night when suitable (artificial lights or moon) light conditions exist (Ristow 1999, Buij and Gschweng 2017). In general, the passerine migration pulse starts to build up prior to sunset, peaks after midnight, and levels off during the morning (Bruderer and Liechti 1995, 1998, Newton 2008). Nevertheless, in autumn, the dominant wind pattern favors a migratory strategy described as "sit-and-wait-for-favorable-winds," which might produce irregular migration pulses (Gauthreaux et al. 2005). This may be reflected in our study by the variable amount of time the falcons dedicated to foraging. Falcon flights peaked during periods of moderate winds in the afternoon, indicating that the falcons hunted intensively around sunset when nocturnal migrants resume their migration.

The daily temporal dynamics of the passerine migration seem also to affect the falcons' flight altitude. The falcons flew high during the morning, probably trying to effectively exploit the early arrivals of migratory passerines before they descend and retreat to safe cover on mainland Crete. In contrast, the falcons' lower flights in the afternoon may be attributed to attempts to capture passerines ascending rapidly after take-off to the maximum altitude of their nocturnal trips (Able 1970). The lowest flights, observed during the midday, suggest that the falcons were probably searching for insects over the olive groves and scrubland of mainland Crete, as passerine migration is much less intense during the daytime period (Schmaljohann et al. 2007).

Our study showed that the falcons' flight altitude was positively related to the wind intensity, although a larger proportion of falcons hunting above 2000 masl was observed during poor wind conditions (Fig. 4). Wind speed may change considerably with altitude ("thermal wind"; Holton 2004) and migratory birds can control the atmospheric conditions they experience by selecting specific flight altitudes (Kemp et al. 2012). At temperate latitudes, "wind assistance" has been identified as a key factor fostering high-altitude migration when surface winds are unsuitable (Dokter et al. 2013). In the present study, the main wind direction observed was north-northwest, and thus represented a suitable wind (i.e., tailwind) for migrating birds heading to Africa (Panuccio et al. 2016b). Therefore, one might propose that the falcons flying high during calm periods were most likely targeting a high-altitude migration layer. However, throughout our fieldwork, air speed values beneficial for migratory passerines (Bloch and Bruderer 1982, Bruderer and Boldt 2001, Karlsson et al. 2011) were common in the range of 2000–3000 masl, but Eleonora's Falcons were rarely tracked above 2000 masl (18.5% of the overall observations). Plausible explanations for this discrepancy might include (1) low bird densities in the upper elevations because favorable conditions for high-altitude migration are relatively uncommon in autumn compared to spring (Klaasen and Biebach 2000, Zehnder et al. 2001, Schmaljohann et al. 2009); (2) migratory landbirds selecting flight altitudes with weak winds and avoiding strong wind profiles because of the potential danger of displacement (Able 1970, Cochran and Kjos 1985, Schaub et al. 2004); and (3) if hunting falcons opt to perform long ascents to high elevation in pursuit of passerines, their climb rates would gradually decay as the air density declines with increasing altitude (Pennycuick 1978). In that case, possible benefits from foraging above 2000 masl might be outweighed by increased flight costs. In conclusion, the factors that influence the falcons' hunting altitude should to be explored more thoroughly in the future, particularly at colonies located at various distances from the mainland. This could be achieved by monitoring vertical atmospheric conditions and simultaneous radar tracking of migratory birds and insects. In this way, we would substantially improve our understanding of the Eleonora's Falcons' flight behavior at their breeding grounds.

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Literature Cited

Able, K. (1970). A radar study of the altitude of nocturnal passerine migration. Bird Band 41:282–290.

Agostini, N., M. Panuccio, and C. Pasquaretta (2015). Morphology, flight performance, and water crossing tendencies of Afro-Palearctic raptors during migration. Current Zoology 61:951–958.

Alerstam, T. (1990). Bird Migration. Cambridge University Press, Cambridge, UK.

Alerstam, T., and A. Hedenström (1998). The development of bird migration theory. Journal of Avian Biology 29:343–369.

BirdLife International (2004). Birds in Europe: Population Estimates, Trends and Conservation Status. BirdLife Conservation Series No. 12. BirdLife International, Cambridge, UK.

BirdLife International (2018). Species factsheet: *Falco eleonorae*. http://www.birdlife.org.

Bloch, R., and B. Bruderer (1982). The air speed of migrating birds and its relationship to the wind. Behavioral Ecology and Sociobiology 11:19–24.

Bruderer, B., and A. Boldt (2001). Flight characteristics of birds: I. Radar measurements of speeds. Ibis 143:178–204.

Bruderer, B., and F. Liechti (1995). Variation in density and height distribution of nocturnal migration in the south of Israel. Israel Journal of Zoology 76:1106–1118.

Bruderer, B. (1997). The study of bird migration by radar - Part 1: The technical basis. Naturewissenschaften 84:1–8.

Bruderer, B., and F. Liechti (1998). Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting? Journal of Avian Biology 29:499–507.

Bruderer, B., and F. Liechti (1999). Bird migration across the Mediterranean. In Proceedings of the International Ornithological Congress, Durban (N. Adams and R. Slowtow, Editors). BirdLife South Africa, Johannesburg, South Africa. pp. 1983–1999.

Buij, R., and M. Gschweng (2017). Nocturnal hunting by Eleonora's Falcons *Falco eleonorae* on their breeding and non-breeding grounds. Acta Ornithologica 52:35–49.

Capotosti, S., and M. Scacco (2017). Combined manual and automatic video tracking of bird movements with a surveillance radar. In Proceedings I International Conference: Radar Aeroecology, Applications and

Perspectives (G. Dell'Omo and Ornis Italica, Editors). Ornis Italica, Rome, Italy. p. 61.

Casement, M. B. (1966). Migration across the Mediterranean observed by radar. Ibis 108:461–491.

Cochran, W. W., and C. G. Kjos (1985). Wind drift and migration of thrushes: a telemetry study. Illinois Natural History Survey Bulletin 33:297–330.

Cramp, S., and K. E. L. Simmons (1980). The Birds of the Western Palearctic, Vol. II. Oxford University Press, Oxford, UK.

Dimalexis, A., S. Xirouchakis, D. Portolou, P. Latsoudis, G. Karris, J. Fric, P. Georgiakakis, C. Barboutis, S. Bourdakis, M. Ivovic, T. Kominos et al. (2008). The status of Eleonora's Falcon (*Falco eleonorae*) in Greece. Journal of Ornithology 149:23–30.

Dobson, A. J. (1990). An introduction to generalized linear models. Chapman and Hall, London, UK.

Dokter, A. M., J. Shamoun-Baranes, M. U. Kemp, S. Tijm, and I. Holleman (2013). High altitude bird migration at temperate latitudes: A synoptic perspective on wind assistance. PLoS ONE 8:e52300. doi:10.1371/journal.pone.0052300.

Ferguson-Lees, J., and D. A. Christie (2001). Raptors of the World. Helm, Hastings, UK.

Fric, J., T. Dimalexis, and M. Tzali (2017). Radar technology applied to the study of Eleonora's Falcon foraging. In Proceedings I International Conference: Radar Aeroecology, Applications and Perspectives (G. Dell'Omo and Ornis Italica, Editors). Ornis Italica, Rome, Italy. p. 65.

Gauthreaux, S. A., Jr. (1970). Weather radar quantification of bird migration. BioScience 20:17–20.

Gauthreaux, S. A., Jr., and C. G. Belser (2003). Radar ornithology and biological conservation. The Auk 120:266–277.

Gauthreaux, S. A., Jr., J. E. Michi, and C. G. Belser (2005). The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). The Johns Hopkins University Press, Baltimore, MD, USA. pp. 182–193.

Gschweng, M., E. K. V. Kalko, P. Berthold, W. Fielder, and J. Fahr (2012). Multi-temporal distribution modelling with satellite tracking data: predicting responses of a long-distance migrant to changing environmental conditions. Journal of Applied Ecology 49:803–813.

Gschweng, M., E. K. V. Kalko, U. Querner, W. Fielder, and P. Berthold (2008). All across Africa: highly individual migration routes of Eleonora's Falcon. Proceedings of the Royal Society of London Series B 275:2887–2897.

Hansen, M. C., and R. A. Riggs (2008). Accuracy, precision, and observation rates of global positioning system telemetry collars. Journal of Wildlife Management 72:518–526.

Harmata, A. R., K. M. Podruzny, J. R. Zelenak, and M. L. Morrison (1999). Using marine surveillance radar to study bird movements and impact assessment. Wildlife Society Bulletin 27:44–52.

Hedenström, A, M. Rosén, S. Åkesson, and F. Spina (1999). Flight performance during hunting excursions in Eleonora's Falcon *Falco eleonorae*. Journal of Experimental Biology 202:2029–2039.

Holton, J. R. (2004). An Introduction to Dynamic Meteorology, Fourth Ed. Academic Press, Aalborg, Denmark.

Johnson, B. (2009). Essential Boat Radar. John Wiley and Sons, Hoboken, NJ, USA.

Karlsson, H., C. Nilsson, J. Bäckman, and T. Alerstam (2011). Nocturnal passerines migration without tailwind assistance. Ibis 153:485–493.

Kassara, C., J. Fric, M. Gshweng, and S. Sfenthourakis (2012). Complementing the puzzle of Eleonora's Falcon (*Falco eleonorae*) migration: new evidence from an eastern colony in the Aegean Sea. Journal of Ornithology 153:839–848.

Kassara, C., L. Gangoso, U. Mellone, G. Piasevoli, T. G. Hadjikyriakou, N. Tsiopelas, S. Giokas, P. López-López, V. Urios, J. Figuerola, R. Silva, et al. (2017). Current and future suitability of wintering grounds for a long-distance migratory raptor. Scientific Reports 7:8798.

Kemp, M. U., J. Shamoun-Baranes, E. E. van Loon, J. D. McLaren, A. M. Dokter, and W. Bouten (2012). Quantifying flow-assistance and implications for movement research. Journal of Theoretical Biology 308:56–67.

Kerlinger, P., and S. Gauthreaux (1985a). Seasonal timing, geographic distribution, and flight behavior of Broad-winged Hawks during spring migration in south Texas: A radar and direct visual study. The Auk 102:735–743.

Kerlinger, P., and S. Gauthreaux (1985b). Flight behavior of raptors during spring migration in South Texas studied with radar and visual observations. Journal of Field Ornithology 56:394–402.

Klaassen, M., and H. Biebach (2000). Flight altitude of trans-Sahara migrants in autumn: a comparison of radar observations with predictions from meteorological conditions and water and energy balance models. Journal Avian Biology 31:47–55.

López-López, P., R. Limiñana, U. Mellone, and V. Urios (2010). From the Mediterranean Sea to Madagascar: are there ecological barriers for the long-distance migrant Eleonora's Falcon? Landscape Ecology 25:803–813.

McCullagh, P., and J. A. Nelder (1989). Generalized Linear Models. Chapman and Hall, London, UK.

Mellone, U., P. López-López, R. Limiñana, G. Piasevoli, and V. Urios (2013). The trans-equatorial loop migration system of Eleonora's Falcon: differences in migration patterns between age classes, regions and seasons. Journal of Avian Biology 44:417–426.

Mellone, U., P. López-López, R. Limiñana, and V. Urios (2011). Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor. International Journal of Biometeorology 55:463–468.

Mellone, U., V. Urios, H. Rguibi-Idrisi, R. Limiñana, A. Benhoussa, and P. López-López (2012). Ranging behaviour of Eleonora's Falcons *Falco eleonorae* during chick-rearing. Acta Ornithologica 47:195–198.

Moreau, R. E. (1972). The Palearctic-African Migration System. Academic Press, London, UK.

Newton, I. (1986). The Sparrowhawk. T. and A. D. Poyser, Calton, UK.

Newton, I. (2008). The Migration Ecology of Birds. Academic Press, London, UK.

Panuccio, M., C. Barboutis, G. Chiatante, A. Evangelidis, and N. Agostini (2016b). Pushed by increasing air temperature and tailwind speed: weather selectivity of raptors migrating across the Aegean Sea. Ornis Fennica 93:159–171.

Panuccio, M., V. Stanzione, C. Catoni, M. Santini, and G. Dell'Omo (2016a). Radar tracking reveals influence of crosswinds and topography on migratory behavior of European Honey Buzzards. Journal of Ethology 34:73–77.

Pastorino, A., J. R. Ramirez, N. Agostini, G. Dell'Omo, and M. Panuccio (2017). Fog and rain lead migrating White Storks *Ciconia ciconia* to perform reverse migration and to land. Avocetta 41:5–12.

Pennycuick, C. J. (1978). Fifteen testable predictions about bird flight. Oikos 30:165–176.

Pfeiffer, T., and B.-U. Meyburg (2015). GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. Journal of Ornithology 156:963–975.

R Development Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ristow, D. (1999). International Species Action Plan: Eleonora's Falcon, *Falco eleonorae*. BirdLife International, Cambridge. http://ec.europa.eu/environment/nature/conservation/wildbirds/-action_plans/docs/falco_eleonorae.pdf.

Ristow, D., C. Wink, and M. Wink (1983). Biologie des Eleonorenfalken (*Falco eleonorae*): die Anpassung des Jagdverhaltens an die vom Wind abhängigen Zugvogelhäufigkeiten. Die Vogelwarte 32:7–13.

Rosén, M., and A. Hedenström (2002). Soaring flight in the Eleonora's Falcon (*Falco eleonorae*). The Auk 119:835–840.

Rosén, M., A. Hedenström, A. Badami, F. Spina, and S. Åkesson (1999). Hunting flight behaviour of the Eleonora's Falcon *Falco eleonorae*. Journal of Avian Biology 30:342–350.

Schaub, M., F. Liechti, and L. Jenni (2004). Departure of migrating European Robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Animal Behaviour 67:229–237.

Schmaljohann, H., F. Liechti, and B. Bruderer (2007). Daytime passerine migrants over the Sahara – are these diurnal migrants or prolonged flights of nocturnal migrants? Ostrich 78:357–362.

Schmaljohann, H., F. Liechti, and B. Bruderer (2009). Trans-Sahara migrants select flight altitudes to minimize energy costs rather than water loss. Behavioural Ecology and Sociobiology 63:1609–1619.

Spina, F., S. Focard, P. Magagnoli, and A. Scappi (1988). Autumn migration through the Mediterranean and the hunting activity of Eleonora's Falcon *Falco Eleonorae* (Gené) (Aves Falconidae): A comparison between two methods of data collection. Italian Journal of Zoology 22:307–313.

Walter, H. (1979). Eleonora's Falcon: Adaptations to Prey and Habitat in a Social Raptor. University of Chicago Press, Chicago, IL, USA.

Zar, J. H. (1999). Biostatistical Analysis. Prentice Hall, NJ, USA.

Zehnder, S., S. Åkesson, F. Liechti, and B. Bruderer (2001). Nocturnal autumn bird migration at Falsterbo, South Sweden. Journal of Avian Biology 32:239–248.

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