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Gone with the wind: Seasonal trends in foraging movement directions for a central-place forager

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Abstract Lesser kestrels *Falco naumanni* are migratory central-place foragers that breed in dynamic arable landscapes. After arriving from migration, kestrels have no knowledge of the distribution of crops, and consequently prey, around their colony. The energy demand of pairs increases as breeding season progresses, but at the same time prey abundance, and their knowledge on prey distribution, also increases. Wind can have a strong influence on flight cost and kestrels should try to reduce energy expenditure when possible. When prey abundance is low, kestrels have little knowledge of prey distribution, and pairs have no chicks, they could reduce foraging flight cost by leaving the colony with tailwinds. When prey is abundant, knowledge on prey distribution has increased, and chick demand is high, kestrels should fly to the most favorable foraging patches. We analyzed foraging trips directions in a lesser kestrel colony along the breeding season and in relation to wind speed and direction. We recorded 664 foraging trips from 19 individuals using GPS-dataloggers. We found that outward flights direction changed from uniform to a concentrated distribution along the season, as prey abundance and individual experience increased. We also found a temporal trend in the angular difference between outward flights and wind directions, with low values early in the season and then increasing as expected, but again low values at the end, contrary to expectation. Results suggest changes in kestrels foraging strategy along the season in relation to wind. Kestrels depart more with tailwinds in exploratory flights early in the season, while there is a spurious coincidence in direction to preferred foraging patches and dominant wind direction at the end [*Current Zoology* 60 () : − , 2014].

Keywords *Falco naumanni*, Movement ecology, Foraging behavior, Wind effect, GPS-dataloggers

Movement reflects an individual response to optimize its fitness within a heterogeneous environment. But movement transcends individual fitness and influences the dynamics of higher levels of organization, like populations or communities (Turchin, 1998). It arises from the interplay of four components: the individual internal state, its motion capacity, orientation ability, and external factors (Nathan et al., 2008). Individuals constantly experience changes, endogenous and exogenous, along their life influencing their movements (Martin et al., 2013).

Wind is one of the most important external factors affecting the movement of animals that fly (Alerstam, 1979; Liechti, 2006). It can be the only way of displacement for some animals, as is the case in spiders dispersal by ballooning (Bell et al., 2005). For other animals, flying with or against wind may cause great differences in flight cost, for that reason different strategies have evolved in animals to increase the efficiency of movement when affected by wind (Chapman et al., 2011). Numerous studies have assessed the effect of wind on bird migratory movements. Birds actively choose to compensate or to be drifted by wind depending on endogenous and exogenous factors (Thorup et al., 2003; Klaassen et al., 2011) and that determines flight speed or altitude during migration (Kemp et al., 2010; Mateos-Rodriguez and Liechti 2012). However, there has been very little research on the effect of wind in dispersal or foraging movements of birds and most studies have been conducted in seabirds (Weimerskirch et al., 2000; Wakefield et al., 2009). For example, wandering albatrosses *Diomedea exulans* increase the flight speed and reduce the duration of their foraging movements by flying with wind support, and consequently they obtain lower hatching failure by increasing the incubating time (Weimerskirch et al., 2012).

The lesser kestrel is a small migratory falcon associated to agricultural landscapes. It breeds in colonies and behaves as central-place forager during the breeding season. The central-place foraging strategy predicts that the species would maximize the energy intake in their central place (Schoener, 1971; Orians and Pearson, 1979), so individuals should decide which prey to catch and the time or energy spent on it, balancing the trade-offs between costs and benefits to optimize the foraging behavior (MacArthur and Pianka, 1966). Each individual decision emerges from a dynamic interaction between endogenous and exogenous factors that change with time. Lesser kestrel breeders experience an increasing energy demand for reproduction along the breeding season, in the same way as other species (Masman et al., 1988). Early in the season, when they arrive to a colony, they would not strictly behave as central-place foragers because they have no chicks to be fed and there are no important reasons to return to the colony frequently. As the breeding season progresses, energy demand increases and breeders should maximize the feeding rate of their chicks at the colony. Then they would behave as "true" central-place foragers. Such change could have a strong influence in individual foraging movements through the breeding season. Agricultural arable landscapes can be highly dynamic ecosystems and the spatial distribution of arable crops can change from year to year. In our study area the arable crops planted on a field alternates between sunflower and wheat in consecutive years with the occasional legume or fallow (see www.juntadeandalucia.es/agriculturaypesca). Lesser kestrels must update their knowledge on the spatial distribution of arable crops around the colony after they arrive from migration. Prey distribution and availability is determined by different factors ranging from crop type or degree of vegetation cover to agricultural activities (Rodríguez et al., 2013). High-quality foraging patches would be determined by prey size and abundance and both factors increase as the breeding season progresses (Rodríguez, 2004; Rodríguez et al., 2010). At the same time as optimal prey become more available, kestrel knowledge of prey distribution refines, potentially influencing kestrels foraging movements.

In this paper, we study the influence of wind on foraging behavior of the lesser kestrel along the breeding season. The single paper we know (Limiñana et al., 2013), shows that lesser kestrels are strongly affected by crosswinds during their migratory movements. During the nestling period each member of a lesser kestrel pair feeds the chicks on average once per hour (Rodríguez et al., 2006) performing foraging trips 11 km long. As mean day length at this time is 15 hours, breeding kestrels may end up performing 165 km per day (J. Hernández-Pliego et al. unpublished data). For this reason, the potential wind effect on foraging cost should not be underestimated. Wind is an exogenous factor that can influence bird movement decisions along the breeding season but there are also other endogenous factors likely influencing movement that also change along that period like energy demand and knowledge on prey distribution and

availability. We expected that early in the breeding season, when prey abundance is low, kestrels have little knowledge about arable crop distribution and potential prey availability, and they have no temporal constraint for returning frequently to the colony, individuals would have no special preference for any area to forage and they could leave the colony flying more with tailwinds to reduce movement cost and in random directions to explore the wider area possible. If foraging flights are long and kestrels delay their return they could wait until wind direction and speed is more favorable. On the other hand, at the end of the breeding season when prey abundance is high, kestrels have chicks to be fed and they have accumulated knowledge on crop distribution and prey availability, we expected that kestrels would concentrate departure directions to the most favorable foraging patches. As they cannot wait for a favorable wind direction, foraging flights would leave independent of wind direction. Consequently, we hypothesized that: in a scenario of random wind directions (1) the departure direction of foraging flights would change from a random to a more concentrated distribution as the breeding season progresses. (2) The angular difference between foraging flight departure and wind directions would be small at the beginning of the breeding season but would increase towards the end. (3) Returning flights would show no temporal pattern in the angle between flight and wind direction because kestrels cannot choose the direction to return to the colony. And finally, (4) if wind is a limiting factor to kestrel foraging activity, individuals should reduce foraging activity, stay at the colony or perch somewhere when they are out of the colony, when strong winds are blowing.

1 Material and Methods

1.1 Study species and area

The lesser kestrel is one of the smallest raptor in the Palearctic (wingspan 58–72 cm, body mass 120–140 g). This insectivorous hole-nesting falcon breeds in colonies associated with urban areas and non-irrigated arable crops across the Mediterranean basin and Central Asia, and has its wintering quarters in Africa. Lesser kestrel populations in Europe suffered a strong decline during the second half of the twentieth century (Serrano and Delgado, 2004) presumably due to changes in land-use derived from agricultural intensification (Tella et al., 1998, Franco and Sutherland 2004). However, the world population has apparently levelled in the last decades and the species has recently been cataloged as 'Least Concern' (IUCN, 2013).

The study colony is situated at a building holding a grain elevator in La Palma del Condado (Huelva, Southwestern Spain). It is located in the Guadalquivir river basin, which is predominantly flat (elevation range 20–240 m above sea level) and dominated by arable crops (Fernandez et al., 1992). Primary crops are wheat and sunflowers, although cotton and legume crops, olive groves and vineyards are also present in the area. Kestrels nest in nest-boxes installed at the windowsills or directly on the windowsills.

1.2 Field procedure

In 2012, we monitored all breeding pairs at the colony (18 breeding pairs, 10 of them nesting in nest-boxes) throughout the whole breeding season, from February to July. We attached GPS-dataloggers (GiPSy-2 model, 1.8 g, 27×15×6 mm with whip antenna, TechnoSmart, Rome, Italy) with small-sized batteries (100 mA, 2.4 g, 30x15x4 mm) to individual kestrels using the nest-boxes. The devices were fixed to their backs using a micro-size harness from Marshall Radio Telemetry (North Salt Lake, Utah, U.S.A.) or a hand-made harness formed by a carbon fiber plate and a 4 mm width teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). The teflon ribbon crossed just over the breastbone, passed under the wings and was fixed to the plate situated on the back following the attachment procedure recommended by Marshall Radio Telemetry. The GPS devices were covered by a thermoretractable case. The total mass of the equipment including harness was about 6 g, representing 4%–5 % of mean body mass, the generally

accepted recommended limits for birds (Barron et al., 2010).

At the beginning of the breeding season, we initiated the equipment fitting protocol. First, birds were captured and fitted a harness. One week later birds were recaptured and a dummy GPS-datalogger with the same weight was fixed on the harness. Another week later the bird was recaptured and the dummy was replaced by the GPS-datalogger. This protocol was designed to get the birds used to the harness and the weight of the device before recording movement data. The lesser kestrel body mass limits the battery weight we could use and so the battery life, which limits data collection frequency and duration. We configured the GPS devices to collect spatial locations at four different sampling frequencies: (1) one fix per second (mean battery life ± standard deviation = 2.57 hours ± 0.60, n = 14), or five consecutive fixes (one per second) (2) every minute (17.00 hours ± 6.31, n = 11), (3) every three minutes (45.39 hours ± 10.76, n = 14) or (4) every five minutes (49.24 hours ± 24.13, n = 21). All the GPS, but those configured at five-minutes intervals, were programmed to start operating with a 24-hours delay to avoid monitoring abnormal behavior due to the capture stress. We recaptured kestrels to download the data stored in the logger and to recharge the GPS batteries to continue tracking the same individuals. Kestrels were recaptured when they entered the nest-boxes. They were recaptured a mean 7.28 ± 2.14 times during the study period (range 4–11, n = 19). Data collection ranged from 10th April to 8th July 2012. It is possible to view the tracking data in the study "Lesser Kestrels EBD" at Movebank (www.movebank.org).

1.3 Wind data

Wind data were obtained from a meteorological station located at ground level (192 m a.s.l.), less than 3 km away from the colony. It belongs to the agroclimatic stations network from the Agriculture Department of the Junta de Andalucía (IFAPA) (www.juntadeandalucia.es/agriculturaypesca/ifapa/ria). Wind speed and direction were registered by a windmill anemometer with a temporal resolution of 30 minutes. We use the term "wind direction" to indicate the direction the wind blows to and in the same way we use the term "track direction" as the direction the individual moves to.

1.4 Analytical procedure

The foraging trips were split into three parts: (1) the "outward flight", i.e. the movement from the colony to the hunting area; (2) the "foraging event", i.e. the movements within the hunting area; and (3) the "inward flight", i.e. the return movement from the hunting area to the colony. Outward and inward flights are also called commuting flights. We were able to distinguish these parts of the trips according to the spatiotemporal distribution of the GPS locations (mostly straight between the colony and the hunting area during the commuting flights vs. winding and grouped within a discrete area during the foraging event) and the instantaneous speed and altitude measurements provided by the GPS (lower altitude and more variable speed during the foraging events). We only considered as foraging trips those that went further than 300 m from the colony and in which we were able to identify the foraging event (a 300 m radius from the colony mostly includes urban area). GPS locations were graphically explored using ArcGIS 10 (ESRI, Redlands, California, U.S.A.) to identify the foraging trip parts. To carry out the analysis, we discarded incomplete foraging trips, i.e. those foraging trips that had not recorded the departure or the return to the colony. Moreover, GPS locations collected by less than four satellites were removed to reduce spatial accuracy errors.

Visualizing the foraging trips recorded at one-second frequency, we observed that individuals started the commuting flights (outward and inward flights) with non-directional flights, soaring up using thermals to gain altitude. In addition, during the final part of the commuting flights individuals also made non-directional flights before reaching their goal. We calculated the distances from the departure site and to the arrival place at which the mean direction of commuting

flights stabilized, i.e. oscillated <10º from the mean heading (n = 19). We used the values that corresponded with the 75 percentile of those distances to split the commuting flights into three sections: initial (< 600 m from departure site), middle, and final (< 775 m from arrival site) sections. We discarded those commuting flights in which the initial and final sections overlapped. To calculate the track direction of a commuting flight we discarded the GPS positions of the initial and final section of the flight (Fig. 1).

Every commuting flight was assigned to one of the four phenology stages we divided the breeding season of each individual using the laying and hatching date at its nest: establishment (since the beginning of the study period until courtship), courtship (21 days from laying the first egg), incubation (between laying and hatching of the first egg), and nestling (from hatching of the first egg until the end of the study period). We calculated the mean track direction of every outward flight and analyzed their angular distribution throughout the breeding period.

To explore the possible limitation to flight due to strong winds, for each half hour of tracking data, each individual was classified as "at the colony" or "out of the colony". If more than half of the GPS locations of the individual were within a 50 m-radius from the colony the individual was considered "at the colony" and if not as "out of the colony". Individuals "out of the colony" were classified as "perched" or "flying", according to the altitude and speed registered by the GPS device. A bird was considered "perched" if more than half of the total GPS locations had flight speed below 1 km/h and altitudes below 150 m a.s.l.; on the contrary, the bird was considered "flying". For each half hour we had a wind speed measurement registered by the weather station.

For every commuting flight we had a mean track direction and a mean wind direction, which was obtained rounding the track time-date to the nearest half hour. We also calculated the Track-Wind-Angle (hereafter TWA) as the angular difference between the track and the wind direction per commuting flight. The TWA ranges from 0º (purely tailwind) to 180º (purely headwind). A TWA of 90º for a single commuting flights indicates flying with crosswind, while a mean TWA of 90º could also indicate no influence of wind in mean track direction of the commuting flights as 0º and 180º TWA values of flights get averaged.

1.5 Statistical analysis

We conducted circular statistics tests to analyze the track direction of outward flights and wind direction patterns (Jammalamadaka and SenGupta 2001). The Watson's test assesses the homogeneity of two angular data samples and we used it to compare the outward flight direction distributions among phenological stages. The Rayleigh's test evaluates the significance of the mean resultant length (ρ), i.e. the length of the mean of random direction vectors. It is a measure of angular dispersion that ranges between 0 (uniform distribution of directions) and 1 (maximum concentration of directions). The temporal correlation of daily mean wind direction along the study period was tested by a circular version of the Pearson's correlation. Those tests were computed using the 'circular' package (Agostinelli and Lund 2011) for R-software 3.0.2 (R Core Team 2013). The temporal trend of the wind speed throughout the study period was tested with linear models and graphically explored for non-linearity using smoothing splines.

We fitted generalized linear mixed-effect models (GLMMs) to a binary response variable (0="at the colony" or 1="out of the colony") to model the probability of staying away of the colony and also to model the probability of being flying (0="perched" or 1="flying"), in relation to wind speed. We used a binomial distribution of errors and a logit link. The individual was included as a random factor to avoid pseudoreplication and the mean wind speed included as a continuous predictor. We also introduced the day-of-year as a continuous predictor to reduce the temporal autocorrelation of the response. We expected that the probability of staying out of the colony and the probability of being flying would decrease with the increasing wind speed if there was any limitation to flight due to strong winds. The significance of the wind speed was tested comparing models with and without wind speed using likelihood ratio

tests.

We also fitted GLMMs using a Gaussian distribution of errors and identity link to model the variables that influenced the angle between wind and track directions: (1) the TWA of outward flights; (2) the TWA of inward flights; and (3) the TWA of outward flights performed with strong winds (when wind speed was higher than 9.98 km/h, 70 percentile of wind speeds associated with outward flights). In these models, the individual was included as a random factor. The day-of-year was included as a continuous predictor to test for the existence of a linear temporal trend of mean TWA. We expected a negative influence of wind speed and flight altitude on TWA, so these variables were included as predictors. We also introduced the gender of individual as a fixed factor and the GPS frequency at which the foraging trip was tracked as a correction factor, given that the different temporal resolution could influence the variables measured. We hypothesized that the mean TWA of outward flights would increase its value throughout the breeding season (from tailwinds to crosswinds) as the need to return frequently with prey to the colony increases and kestrels fly to the more favorable foraging patches. Meanwhile the mean TWA of inward flights is not expected to follow a particular pattern during the breeding season because kestrels cannot choose a direction when flying back to the colony. However, the true impact of wind on bird movements could be blurred by the relative weak winds observed in the area; for that reason we also analyzed mean TWA of outward flights considering only the strongest wind conditions (the upper 30% of wind speed distribution). The p-values for the fixed effects were calculated by Markov Chain Monte Carlo (MCMC) sampling (Baayen et al., 2008). Once the random effect was accounted for, non-significant variables were removed one by one using a backward stepwise procedure until all the variables remaining in the model were significant. Statistical assumptions of GLMMs (residual homocedasticity, collinearity of predictors, influential cases) were checked for all models. We also analyzed graphically the variation of TWA of outward flights, outward flights performed with strong winds, and inward flights by adjusting smoothing splines to the mean daily values per individual, as an alternative to the linear relationship fitted by the GLMMs. GLMMs and MCMC sampling were computed using the 'lme4' (Bates et al., 2013) and 'languageR' (Baayen 2011) packages, respectively, for R-software.

2 Results

We tracked 19 individuals (10 females and 9 males) throughout the study period. We recorded 664 foraging trips, most of them complete ($n = 582$). We discarded the trips of three individuals that did not breed, and remained 570 complete foraging trips. A mean 35.62 ± 31.07 foraging trips per individual (range 5–103 trips). The mean distance per foraging trip was 11.58 ± 9.24 km (range 1.09 –57.50 km). Kestrels flew an average distance per day of 82.53 ± 35.22 km (range 34.25–238.99 km, $n = 82$) at a mean ground speed of 27.99 ± 11.39 km/h. After considering the buffers from the colony and from the foraging area to discard initial and final sections of the foraging trip, a total of 520 commuting flights, 240 outward and 280 inward flights, could be analyzed (Table 1).

2.1 Departure direction pattern of outward flights

We found significant differences in mean outward flight directions (Table 2). Individuals headed more to the East during the establishment stage (mean direction: 125.85º, $n = 48$), to the West during courtship stage (290.25º, $n = 66$),

and to the North during incubation (349.08º, *n* = 36) and nestling stages (28.83º, *n* = 90). A Rayleigh's test indicated a variation in outward flights direction pattern going from a uniform angular distribution during the establishment stage (Rayleigh's test ρ = 0.20, *P*>0.1) toward a more concentrated distributions in later stages (courtship: ρ = 0.26, *P* = 0.01; incubation: ρ = 0.71, *P* = 0.001; nestling: ρ = 0.51, *P* = 0.001), as expected (Fig. 2).

2.2 Wind speed and direction

Wind speed and direction were recorded during the whole period the individuals were tracked (*n* = 4,317). The median wind speed was 5.93 km/h (percentile 25 = 3.85 km/h, percentile 75 = 8.69 km/h) ranged 0 to 23.68 km/h. Intraday mean variation of wind speed was 2.76 ± 0.74 km/h (*n* = 90). Wind had a prevalent direction, was non-uniformly distributed and blew dominantly to the East, both along the study period and in all phenological stages: overall: 105.02º, Rayleigh's test ρ = 0.55, *P* <0.001; establishment: 111.14º, ρ = 0.85, *P* <0.001, *n* = 816; courtship: 71.47º, ρ = 0.24, *P* <0.001, *n* = 1008; incubation: 113.27º, ρ = 0.61, *P* <0.001, *n* = 1488; and nestling: 96.11º, ρ = 0.58, *P* <0.001, *n* = 1005 (Fig. 3). Intraday mean dispersion of wind direction was ρ = 0.73 ± 0.26 (*n* = 90).

A significant and negative seasonal trend appeared in the daily mean wind speed (y = -0.03x + 10.12, Pearson's r = -0.33, *P* = 0.001, *n* = 90), indicating that the wind blew stronger in the earlier stages of the breeding season than in the later ones (Fig. 4). There was no evidence of any seasonal trend in daily mean wind direction (Pearson's r = -0.04, *P* = 0.63, *n* = 90).

2.3 Wind limitation models

We had a sample of 3,355 half-hour x individual observations in which individual location was classified as 0 ("at the colony", *n* = 766) or 1 ("out of the colony", *n* = 2,589). The model showed a significant and positive effect of the wind speed on the probability of staying out of the colony (χ^2 = 58.61, *P* <0.001). "Out of the colony" locations were classified as 0 ("perched", *n* =849) or 1 ("flying", *n* = 1,740). This model indicated that the wind speed did not affect the probability of being perched or flying (χ^2 = 2.58, *P* =0.12). Both models suggested the absence of any limitation to flight for kestrels due to strong winds at our study site.

2.4 GLMM models for TWA

We fitted a model to the variable TWA based on the information of the 240 outward flights. Values of TWA close to 0º indicate kestrels flying with tailwinds while values close to 180º indicate kestrels flying with headwinds. Sex and GPS frequency had non-significant effects on the TWA. However, the model showed that the TWA decreased with increasing median flight altitude and mean wind speed, as expected, indicating that when flying higher and with stronger winds, kestrels flew more with tailwinds. There was a significant negative trend with the day-of-year indicating that TWA declined as the season progressed, contrary to our predictions. When only the data from outward flights performed with strong winds were analyzed (*n* = 71), the day-of-year showed a non-significant negative trend. We repeated the same model fitting procedure with the data from the 280 inward flights. The mean wind speed showed a significant positive effect on TWA, contrary to what could expect, as it indicates that kestrels prefer to fly with headwinds when winds are stronger. But, there was no significant trend in TWA with day-of-year, as predicted (Table 3).

We adjusted a smoothing spline with four degrees of freedom to TWA of outward flights, outward flights performed with strong winds and inward flights. The TWA of outward flights partially satisfied our hypothesis with values below 90º at the beginning of the season and then values above 90º during the intermediate stages (courtship and incubation) as we expected, but again values below 90º at the end, contrary to our expectation. The TWA of outward flights

performed with strong winds showed a similar temporal trend but it was always below 90º. The TWA of inward flights first decreased with day-of-year and then increased toward the end of the breeding season (Fig. 5).

3 Discussion

Lesser kestrels showed a temporal pattern in the distribution of foraging trips departure direction from a uniform to a concentrated distribution along the breeding season in agreement with the hypothesis that during establishment they devote more time exploring the surroundings of the colony and during the nestling period they concentrate exploiting the areas with higher prey availability. Wind speed did not cause any limitation to kestrel flight. With stronger winds kestrels did not stay at the colony nor remained perched when they were away, indicating they could fly with all winds speeds we registered during our study period. We found some small influence of wind direction in foraging trips departure directions, especially at the beginning of the breeding season when individuals tended to leave the colony with tailwinds, in agreement with the hypothesis that during the initial exploratory phase kestrels could take advantage of tailwinds to leave the colony.

This is first study, up to our knowledge, that evaluates the effect of wind speed and direction on foraging movements on a terrestrial bird, and also the first one to study foraging trip departure direction patterns along the whole breeding season. Wind influence in foraging movements has only been assessed in colonial seabirds, and almost exclusively during the nestling period. Due to the absence of studies in terrestrial birds we can only compare our results to those published for seabirds even though the ecological conditions experience by kestrels can be very different.

Departure directions of lesser kestrels foraging trips changed from a uniform angular distribution in the establishment stage to a concentrated distribution in later stages, as we predicted. The uniform angular distribution of departure directions resulted from leaving the colony in random directions at the beginning of the season. We consider that kestrels have little knowledge on the distribution of arable crops surrounding the colony when they arrive from migration and so they have no preference for any direction to move. Kestrels would leave the colony in random directions to explore the possible largest area around the colony at that time when they are not forced to return to the colony frequently. Individuals could locate the potential most favorable foraging patches at the beginning of the breeding season. In the process of learning and remembering the spatial distribution of prey in relation to crop type and phenological stage, individual memory has a paramount role, which is acquired through individual experience as the breeding season progresses (Fagan et al., 2013). Thus, later in the season when they are feeding their chicks individuals would already know where the most favorable patches are and they would concentrate the departure direction of their foraging trips towards them, as suggested by our results. Kestrels would satisfy more efficiently the higher energy demand of the nestling stage by following this strategy.

Our results concerning departure direction patterns are consistent with the findings of previous studies on seabirds. Several seabirds species (Northern gannets *Morus bassanus* and Peruvian boobies *Sula variegate*) concentrate the departures from the colony in the same directions repeatedly during the nestling stage to exploit the same foraging areas (Hamer et al., 2001; Weimerskirch et al., 2010). Pettex et al. (2010) suggest that it could be the consequence of bird spatial knowledge about profitable foraging areas distribution that individuals acquired during previous breeding seasons and/or refined during the earlier stages of the same season. However, those studies did not cover the complete breeding period to confirm the hypothesis that knowledge was acquired or refined in a previous exploratory phase.

At the beginning of the breeding season, kestrels forage on a wide range of small prey, whereas at the end of the season when optimal prey (bush-crickets, Tettigoniidae) are abundant, individuals feed almost exclusively on them (Rodríguez, 2004; Rodríguez et al., 2010). This change in diet is presumably caused by a synchronization of the lesser

kestrel breeding phenology so that the maximum of energy demand, i.e. nestling period, is coincident with optimal prey availability (Masman et al., 1988). Thus, the more generalist and varied diet of the kestrels early in the season (Rodríguez et al., 2010) could be partially a consequence of the random distribution of the departure directions of foraging trips at the beginning of the season when kestrels do not know how prey are distributed and are exploring the territory. On the other hand, the more specialized diet of kestrel at the end of the season (Rodríguez et al., 2010) could be caused by the greater availability of optimal prey, and this would cause a concentration of departure directions towards the patches where individuals would already know that optimal prey are more available. However, it may be difficult to distinguish between causes and consequences in this relationship between lesser kestrel diet and departure direction of foraging trips.

Lesser kestrels concentrated their foraging trip departure directions towards the North at the end of the breeding season. The Northern and Eastern parts of the study area are mostly dominated by wheat crops which are usually harvested during June, coincident with the incubation and nestling stages. Thus, individuals would be heading to forage towards wheat crops, at a time they are started to be harvested, consistent with the described foraging habitat selection in the lesser kestrel (Donázar et al., 1993; Tella et al., 1998; Rodríguez et al., 2013).

Wind had some effect on the direction of outward foraging flights. The model fitted to TWA of outward flights suggests that stronger winds and flying at higher altitudes made kestrels fly more with tailwinds. It could be that kestrels choose to fly higher when wind direction is in the direction they want to depart, or that they are drifted as a consequence of flying higher with stronger winds. This model also showed a decreasing linear trend along the breeding season, indicating that kestrels leave the colony flying more with tailwinds as the season progresses, contrary to our expectation. The low values of TWA of outward flights at the end of the season seemed to result from the non-random distribution of wind directions and a spurious coincidence between wind direction and the location of the most favorable foraging patches in our study area. Kestrels headed towards the most favorable foraging patches independent of wind direction, but wind blows dominantly to the East and wheat crops are located predominantly to the North and East of the study colony. The graphical exploration of TWA of outward flights also shows an initial increase at the beginning of the breeding season and then a decreasing trend towards the end. This suggests the existence of some wind effect and that individuals would also be leaving the colony flying more with tailwinds early in the season as we predicted, but it was blurred in linear models by the stronger coincidence of foraging trip departure and wind direction at the end of the season. When we limited our analyses to outward flights performed with strong winds, the fitted model did not show any linear temporal trend of TWA; but the graphical exploration showed a similar result that obtained with all outward flights. However, in this case the temporal trend was shifted to values below 90º, suggesting that weak winds did not blur the true wind effect on kestrel foraging trips, although individuals tended to depart more with tailwinds when winds were strong. The model fitted to TWA of inward flights did not show any temporal trend, as predicted. But its graphical exploration showed a decreasing trend at the beginning of the breeding season and then increasing towards the end in a mirror image to TWA of outward flights. This pattern probably arises as consequence of leaving the colony in a certain direction and returning following usually the opposite one within a scenario of winds relatively constant in direction through the day, as occurred in our study area during the year of our study. That would also explain the positive relationship of TWA of inward flights and mean wind speed showed by the model, contrary to that showed by the model fitted to TWA of outward flights.

Wind effect has been evaluated in foraging movements of colonial seabirds. However, there are no common patterns across the studies and seabirds can leave the colony flying both with tailwinds or headwinds towards the foraging areas. Cory's shearwaters *Calonectris diomedea* and common murres *Uria algae* leave the colony flying with

tailwinds in their foraging trips (Paiva et al., 2010; Evans et al., 2013). Wandering albatrosses leave the colony flying with headwinds and return flying with tailwinds, or they perform a loop to take advantage of tailwinds both in outward and inward flights with strong winds blowing in the area (Weimerskirch et al., 2000; Wakefield et al., 2009). Wind is usually variable in speed and direction through the day and seabirds could adjust their long lasting foraging movements to wind conditions to reduce flight cost daily. Grémillet et al. (2004) demonstrated that Cape gannets *Morus capensis* leave the colony flying with light headwinds in the morning and return flying with strong tailwinds in the evening. Wind was weak and constant in direction through day in our study site, so leaving the colony flying with tailwinds would not reduce flight cost because individuals would have to return to the colony most probably with headwinds, and vice versa.

We found that the probability of lesser kestrels being away from the colony was positive affected by the wind speed, probably because winds tend to be stronger at midday when kestrels are foraging far from the colony, but the probability of being flying or perched when individuals were outside the colony was independent of wind speed. Both results suggested an absence of a limitation to flight caused by wind speed, probably explained by the relative weak winds blowing during the study period, with the upper 25 percentile in approximately 9 km/h (light breeze according to Beaufort scale, and around 30% of recorded mean ground speed of lesser kestrel). While some studies have evaluated the limitation caused by wind on migratory flights, showing that birds tend to depart only under favorable wind conditions (Liechti, 2006), this has been overlooked in relation to foraging movements. Åkesson and Hedenström (2000) found several passerines species departed in days with stronger tailwinds component in their migratory route direction. Bar-tailed godwits *Limosa lapponica baueri* even start migration as soon as favorable winds blow in the area, although birds have not reached the optimal fuel load to cope with the journey (Conklin and Battley, 2011).

Future studies should focus on the effect of wind conditions on foraging movement of terrestrial birds. This aspect has received very little attention and wind effects could have important consequences at population level, especially for species foraging over large areas and for populations inhabiting areas with strong winds.

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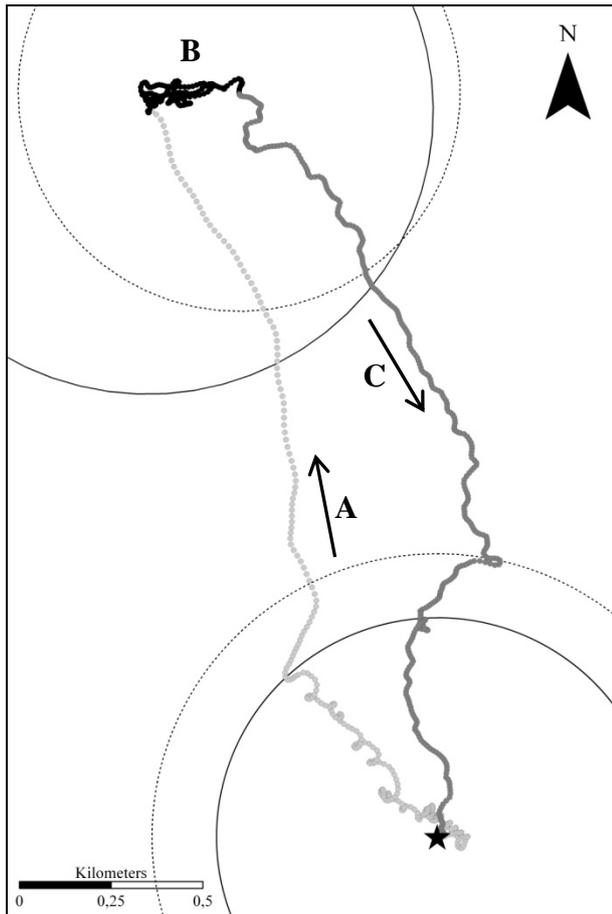
Fig. 1 Example of foraging trip recorded at one-second frequency, in which we defined three parts: (A) outward flight in pale grey, (B) foraging area in black and (C) inward flight in dark grey

Arrows indicate the direction of movement and the black star indicate the location of the colony. Continuous circles for the outward flights and dotted circles for the inward flights show the distance buffers from the colony and the foraging area applied to define the three sections of commuting flights (initial, middle, and final).
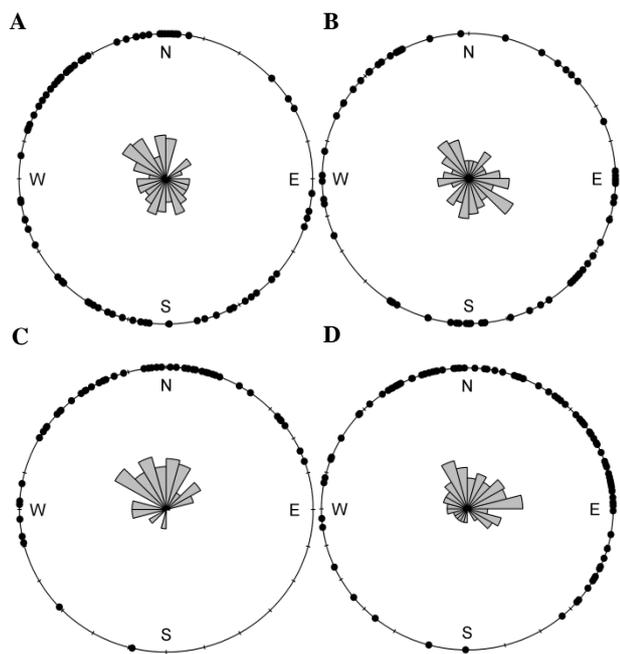
Fig. 2 Angular distribution of mean directions of outward flights in: (A) establishment, (B) courtship, (C) incubation and (D) nestling stages
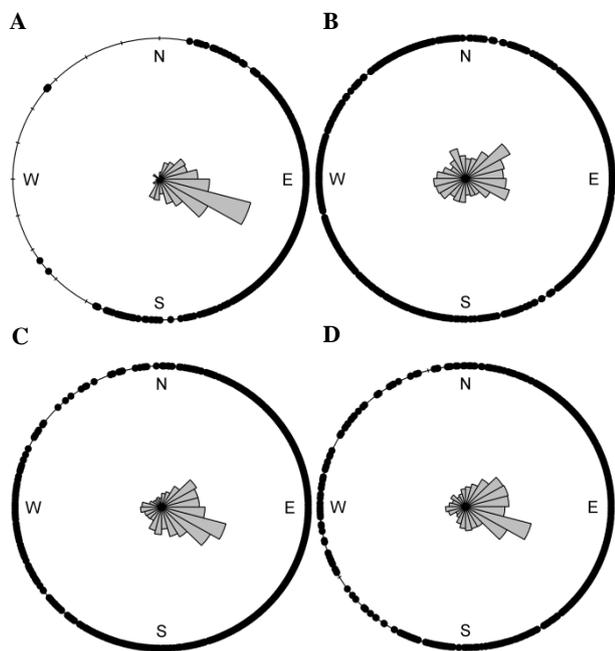
Fig. 3 Angular distribution of wind directions in: (A) establishment, (B) courtship, (C) incubation and (D) nestling stages
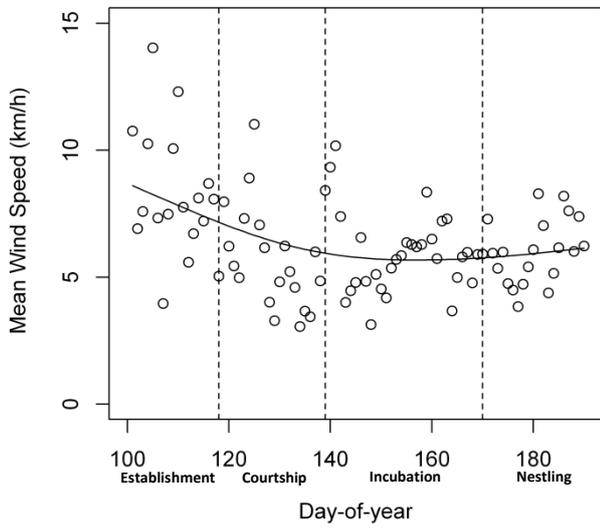
Fig. 4 Temporal trend of daily mean wind speed obtained by adjusting a smoothing spline with three degrees of freedom

The dashed lines show the mean starting days of courtship, incubation and nestling stages.
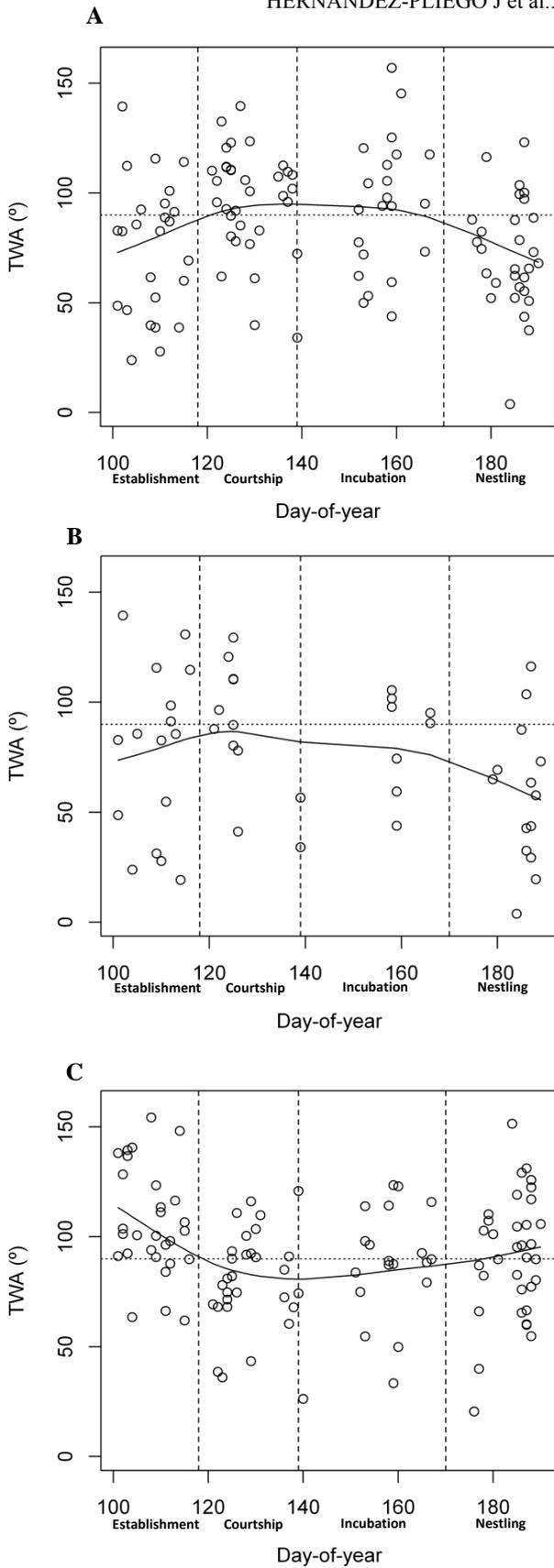
Fig. 5 Temporal trends of daily mean TWA of (A) outward flights, (B) outward flights performed with strong winds, and (C) inward flights

The dashed lines show the mean starting days of courtship, incubation and nestling stages in both panels. The dotted line indicates a TWA of 90° (crosswind) in both panels.

Table 1 Distribution of complete foraging trips as function of phenological stages and sex

Stage\Sex	Females	Males	Total
Establishment	67 (27/32)	76 (21/26)	143 (48/58)
Courtship	15 (7/5)	112 (59/56)	127 (66/61)
Incubation	24 (12/12)	61 (24/20)	85 (36/32)
Nestling	119 (46/68	96 (44/61)	215 (90/129)
Total	225 (92/117)	345 (148/163)	570 (240/280)

The values that appear within parentheses are the numbers of outward and inward flights respectively used in the statistical analysis. The difference in the total number of outward and inward flights is due to the different locations considered as first and last points of the foraging event to calculate the distances buffers.

Table 2 Paired comparisons of mean outward flight directions at each phenological stage (*P<0.01, *** P<0.001)**

	Watson's Test		
Phenological Stage	Courtship	Incubation	Nestling
Establishment	0.29**	0.75***	0.62***
Courtship		0.34**	0.81***
Incubation			0.27**

Table 3 Estimates of GLMMs parameters

A) On the mean TWA of outward flights (explained deviance = 0.69%)

Predictors	β	Standard Error	P-value
Intercept	131.07	14.19	<0.001
Altitude	-0.05	0.02	<0.01
Wind speed	-1.26	0.64	0.05
Day-of-year	-0.18	0.07	0.01

B) On the mean TWA of outward flights performed with strong winds (explained deviance = 0.47%)

Predictors	β	Standard Error	P-value
Intercept	104.91	17.37	<0.001
Day of year	-0.22	0.12	0.08

C) On the mean TWA of inward flights (explained deviance = 0.18%)

Predictors	β	Standard Error	P-value
Intercept	77.20	6.71	<0.001
Wind speed	1.48	0.65	0.03