



Assessing the relative importance of managed crops and semi-natural grasslands as foraging habitats for breeding lesser kestrels *Falco naumanni* in southeastern Italy

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Farmland habitats host important populations of several threatened bird species. So far, how to reconcile farmland management with the maintenance of viable populations of these taxa is a major challenge for conservation biology. Southeastern Italy hosts ca 7000 pairs of breeding lesser kestrels *Falco naumanni*, representing one of the European strongholds of this small colonial raptor of conservation concern. We firstly assessed the relative importance of managed crops versus semi-natural grasslands in determining the local abundance of lesser kestrels at the landscape scale, and we successively studied the foraging habitat preferences at a smaller spatial scale. Surveys of foraging birds were associated with land-use collection at 191 homogeneous habitat sampling parcels from 14 plots of 16 km² each, uniformly distributed over a 2400 km² area. Each plot was visited six times during the 2017 breeding season (May–July). Land-use markedly changed along the season, unripe cereals being dominant in May, while harvested cereal crops prevailed in July. Land-use did not affect lesser kestrel distribution early in the season while foraging birds were more abundant in plots with a greater proportion of harvested cereal crops and a lower one of semi-natural grassland in the late breeding season. In accordance, the analysis of foraging habitat preferences within plots showed that in May unripe cereal crops and semi-natural grasslands were used proportionally to their availability. In June and July, harvested cereal crops were used more than expected from their availability, while semi-natural grasslands were significantly avoided. Our landscape-scale analysis thus indicates that semi-natural grasslands are much less used in comparison to harvested crops during the mid and late parts of the breeding season, suggesting that lesser kestrel may be able to take advantage of crop management practices more than other farmland birds of conservation priority.

Keywords: agricultural intensification, conservation, farmland management, land use, raptors

In the past centuries, agriculture has radically transformed natural landscapes in several areas across the globe, with dramatic effects on the distribution and the conservation status of wild animal and plant communities (Newbold et al. 2015, Boivin et al. 2016). As a consequence, nowadays many animal species heavily rely on farmland habitats during different portions of their life cycle, to the point that

these habitats may currently host most of the populations of some of these species (Butler et al. 2007, Kleijn et al. 2011). In specific geographic contexts, farmland habitats may provide effective surrogates for natural ones (Arroyo et al. 2002, Morelli et al. 2014, Brambilla 2019). However, the extent to which these man-made habitats can act as surrogates of natural habitats critically depends on management practices, which may rapidly change through time. For instance, the progressive intensification of agricultural practices during the 20th century has eroded the capacity of farmland landscapes to supply key ecosystem services, particularly as a consequence of a marked reduction in the biodiversity of agricultural environments (Tscharrntke et al. 2005, Emmer-

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son et al. 2016). These changes in agricultural practices have significantly impacted populations of those species tied to these man-made habitats, including the diverse guild of farmland birds. This group of species is indeed declining at a steeper rate than any other bird group (Donald et al. 2001, Rosenberg et al. 2019). For the European Union, standardized censuses report a loss of 57% in abundance for the 39 most common farmland bird species since 1980 (PECBMS 2019). To counteract this declining trend at a continental scale, it is urgent to suggest how agricultural management regulations in the framework of the European Union's Common Agricultural Policy (CAP) should be modified to promote biodiversity recovery in intensively managed farmland ecosystems (Kleijn et al. 2011). The major 1992 CAP reform included indeed measures explicitly aimed at promoting environmental-friendly farmland management, the so-called agri-environmental schemes (AES) (Robson 1997). However, subsequent studies found that these interventions could only partially counteract the loss in the proportion of unmanaged patches within the agricultural mosaic (McMahon et al. 2010, Sanz-Pérez et al. 2019, Traba and Morales 2019), eventually having limited efficacy in inverting the negative population trends of most farmland birds (Kleijn et al. 2011, Whittingham 2011, Brambilla 2019). Additionally, inter-population differences in habitat preferences suggest that population-specific conservation measures are more effective than broad-scale measures to counteract the decline of farmland birds (Wilson et al. 2009). Overall, the collection of data about site- and population-specific habitat preferences is a fundamental prerequisite for devising effective conservation actions. Such studies are of special interest when focusing on species of conservation priority or key populations of these species.

In this study, we investigated foraging habitat preferences of the lesser kestrel *Falco naumanni*, a migratory colonial raptor of conservation priority that is tightly linked to cereal (and residual natural) steppe habitats, in the Apulo–Lucanian region (southeastern Italy). This area currently hosts ca 7000 breeding pairs of the species (La Gioia et al. 2018), corresponding to 15% of the current estimated European population size. The Apulo–Lucanian lesser kestrel population should thus be regarded of pivotal importance for the conservation of this species at the European scale (La Gioia et al. 2018). After the widespread collapse of lesser kestrel numbers during the 20th century (Iñigo and Barov 2010), the populations of southern Italy have recently shown signs of recovery and increase (La Gioia et al. 2018), possibly also in response to local conservation measures (i.e. nest-boxes provisioning, Podofilini et al. 2018, Gameiro et al. 2020). However, climate envelope models predict that southern Italy will become less climatically suitable for lesser kestrels the coming decades (Morganti et al. 2017). Furthermore, the close association of this species with agricultural landscapes exposes it to the threats deriving from changes in land-use and farming practices (Iñigo and Barov 2010). Previous studies have suggested that some measures envisaged by AES may conflict with the lesser kestrel conservation needs (Tella et al. 1998, Franco and Sutherland 2004). By characterizing land-use in the area surrounding the colonies (i.e. at the landscape scale), it has been shown that lesser kestrels prefer to settle in low-managed pseudo-steppe environments, where non-irrigated crop

types dominate, preferably in the presence of grazing cattle (Bustamante 1997, Parr et al. 1997, Tella et al. 1998). At a smaller spatial scale, foraging habitat preferences have been investigated by telemetry studies. These studies showed a clear preference for non-irrigated arable lands as well as for scrubs and herbaceous crops in eastern Spain (Vidal-Mateo et al. 2019) and a preference for dry cereals and grasslands in central Greece, but with significant differences between sexes and stages of the breeding season (i.e. incubation versus nestling-rearing, Vlachos et al. 2015). Lesser kestrels mainly forage on large insects (Di Maggio et al. 2018), opportunistically targeting orthopterans flushed during cereal crop harvesting (Cтры et al. 2014). Behavioural-based models highlighted a dynamic use of resources during the breeding season: at the onset of the season, unmanaged semi-natural grasslands were preferred over cultivated crops, while dry cereal crops became more suitable later in the season, especially while being harvested (Cтры et al. 2012). Overall, these studies suggest that a favourable landscape for the lesser kestrel would consist of a mosaic of semi-natural grasslands and dry cereal crops, with a prevalence of dry cereals. However, previous studies have focused on breeding birds foraging in relatively small areas surrounding breeding colonies, whereas less is known about foraging habitat preferences at broader scales, where observation may include non-breeding individuals (i.e. returning yearlings, that in many cases do not breed; Mihoub et al. 2010). Here, we tackle the study of habitat selection in a breeding area of pivotal importance for the European conservation of the species using randomized surveys of land-use and foraging lesser kestrels at an unprecedented broad spatial scale (ca 2400 km²), accounting for major changes in agricultural habitat structure that occurred during the sampling period. We first described land-use changes through the breeding season and investigated whether the distribution of grasslands or harvested crops determined the abundance of lesser kestrel at a landscape scale. We then modelled at a smaller spatial scale the foraging habitat selection in three different periods of the breeding season, relying on selection ratios (Manly et al. 2010) to characterize habitat preferences in this dynamically changing environment. Our study represents the first habitat preference analysis of the lesser kestrel in this breeding area of European conservation priority for the species. Moreover, it is realized at an unprecedentedly wide spatial scale, also including observations of non-breeding individuals, generally neglected in the literature. Our analysis contributes to disentangling the relative importance of managed and unmanaged crops in defining a favourable landscape for breeding lesser kestrels, possibly contributing to the design of future conservation interventions.

Material and methods

Target species and study area

The lesser kestrel is a small (ca 120 g) colonial raptor of European conservation concern (listed in Annex 1 of European 'Birds Directive' 2009/147/CE; 'SPEC 3' for BirdLife International 2017), even if classified as 'Least concern' by IUCN due to its low risk of extinction at the global scale (BirdLife International 2020). It is a long-distance migrant

that spends part of the non-breeding season in sub-Saharan Africa, and returns to the breeding areas in March–April (Sarà et al. 2019). Between late April and early May, pairs are formed and females lay 3–5 eggs (single brooded). Incubation lasts ca 30 days and nestlings fledge at ca 35–40 days. Egg-laying peaks in late May and juvenile fledging peaks in late June–mid July (Mascara and Sarà 2006, Di Maggio et al. 2013, Podofillini et al. 2019). As of 2017, it was estimated that south-eastern Italy hosts 5900–8000 pairs, distributed over 142 colonies, half of which are located in cities or small villages in the regions of Apulia and Basilicata (the Apulo–Lucanian region) (Morganti et al. 2017, La Gioia et al. 2018). The lesser kestrel has developed a close association with human settlements since at least two thousand years (Negro et al. 2020). In southern Italy, lesser kestrel colonies are settled on buildings in both rural and urban contexts. Rural colonies consist of 2–25 pairs settled on decaying buildings in the countryside, usually far away from cities. Urban colonies are established in urban centres, where kestrels use roofs or wall cavities to breed, normally concentrating in one area of the cities over neighbouring buildings, often creating macro-colonies organized in a series of sub-colonies. Our study area covers a rectangular surface of ~2400 km² located in south-eastern Italy across the Apulia and Basilicata regions, centred on the cities of Gravina (40°49′N, 16°25′E), Altamura (40°49′N, 16°33′E) and Matera (40°39′N, 16°36′E) (Fig. 1). These three small cities (45 000–60 000 inhabitants) host the largest European lesser kestrel colonies, estimated to be ca 1000 pairs for each

city (La Gioia et al. 2018, Supplementary information). All colonies included in our study area are urban, while no rural colonies are known.

The landscape that surrounds these cities is mainly constituted by large extents of pseudo-steppic cereal farmland, with residual patches of Mediterranean unmanaged or little managed semi-natural grasslands belonging to the *Festuco–Brometalia* association (Perrino et al. 2006). These grasslands are composed mainly of gramineous species that can reach a considerable height at the end of the vegetative period (early summer). For instance, two of the most abundant grass taxa in Apulo–Lucanian highlands are *Stipa austroitalica* and *Festuca mediterranea* (Perrino et al. 2006), that grow up to 80 cm in late spring/summer (Pignatti et al. 2017). The study area partially overlaps with the Natura 2000 site ‘Murgia Alta’ (Fig. 1). The Murgia Alta site constitutes one of the most important areas for the conservation of semi-natural dry grassland ecosystems in Europe (Mairota et al. 2013; habitat codes: 6210, 6220 of the EU Habitats Directive 92/43). Moreover, it is a breeding area for other bird species of European conservation priority as the calandra lark *Melanocorypha calandra*, the short-toed lark *Calandrella brachydactyla*, the lesser grey shrike *Lanius minor*, the stone curlew *Burhinus oedicephalus* and the lanner falcon *Falco biarmicus feldeggii* (Liuzzi et al. 2013, Frassanito and Zollo 2020). Cereal production is the main economic activity in the area, while sheep and goat farming are only residual activities. Consequently, grazing is not having a major impact on local habitats, while this activity crucially characterizes the breed-

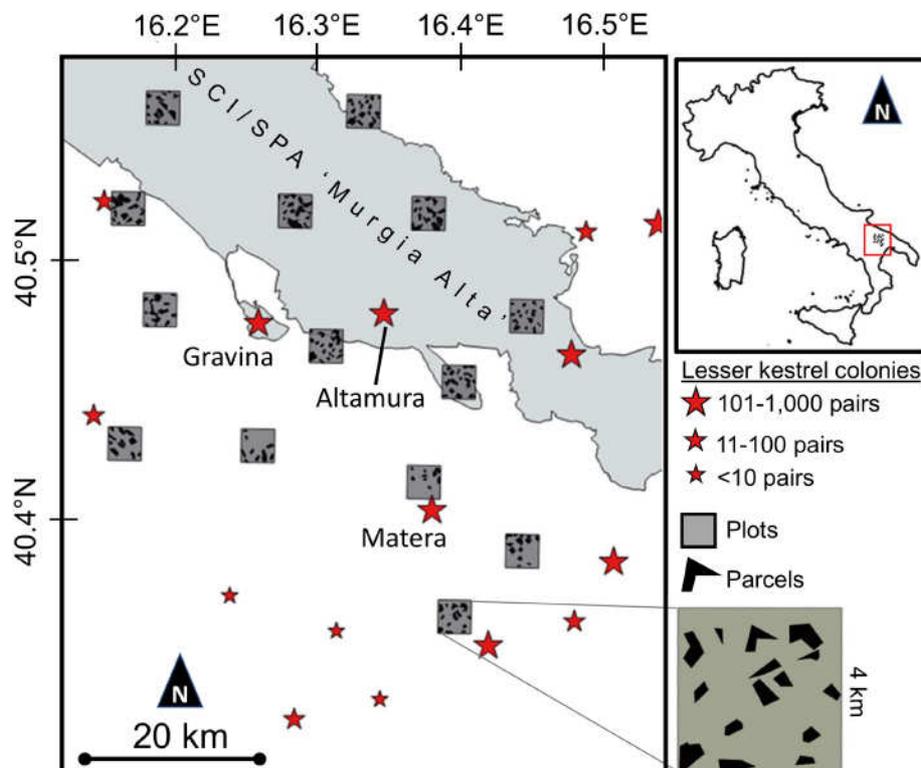


Figure 1. Location of the study area within Italy (upper right box), location of plots and homogeneous habitat sampling parcels within the study area (main box). Land-use and bird surveys were performed within parcels. Stars indicate the location of lesser kestrel colonies, with their size class expressed by the size of the stars. Plots are shaded in grey, while parcels are shaded in black. Borders of the Natura 2000 ‘Murgia Alta’ are also shown.

ing landscape of other lesser kestrel populations (i.e. southern Portugal, Franco and Sutherland 2004). Climatic conditions are 'dry Mediterranean', with a mean \pm SD annual temperature of $13.8 \pm 0.7^\circ\text{C}$ and a mean annual rainfall of 600 ± 20 mm, mainly concentrated in winter (Worldclim2 dataset at 1 km resolution; Fick and Hijmans 2017).

Land-use and bird surveys: sampling design and field data collection

For the establishment of the survey areas, we relied on the approach proposed by Mairota et al. (2015). Specifically, we defined as study area a rectangular landscape of about 40×60 km that included foraging areas of local lesser kestrels (Cecere et al. 2018, 2020). Within this area, we adopted a hierarchical nested sampling strategy at two spatial extents: plots and homogeneous habitat parcels. We selected 14 squares of 4 km side (plots hereafter), uniformly distributed in the area (with the only exception of poorly accessible portions of the study area) (Fig. 1). We then identified sampling parcels within each plot by applying a random sampling as in Mairota et al. (2013, 2015): in GIS, we drew polygons with a homogeneous land-use (i.e. polygons with a same spectral response in all of their extent). These polygons were our sampling parcels. We then relied on photointerpretation of aerial photos and satellite images to assign each of these parcels to a broad land-use type, namely 'grassland', 'cultivated crops', 'trees' (i.e. tree cultivations as olives and fruit orchards together with the few residual wooded areas). Then, we calculated the proportion of each of these three categories in the whole study area and, finally, we randomly selected a number of parcels for each land-use type according to the proportion of each of the three land-use types. Sampling units were thus representative of the actual distribution and proportions of the main land-use types in the whole study area. Parcels were used as survey units for lesser kestrel counts and collection of land-use data (Fig. 1). Overall, each plot eventually comprised on average 13.64 ± 3.81 (mean \pm SD) parcels (min: 6, max: 22). The average extent of surveyed parcels was 8.65 ± 0.76 ha (mean \pm SD) (min: 12.65 ha, max: 57.47 ha, $n = 191$ surveyed parcels). Surveyed parcels covered on average $7.38 \pm 2.33\%$ (mean \pm SD) of the total plot extent. Each parcel was surveyed six times (two surveys per month) at ca 12 day-intervals during May–July 2017, corresponding to the lesser kestrel breeding season (La Gioia et al. 2018). On each survey, for each parcel, were recorded: 1) the land-use type according to six classes: permanent semi-natural grasslands (semi-natural grasslands hereafter), green unripe cereals, dry ripe cereals, harvested cereal crops, ploughed fields, trees (i.e. tree cultivations as olives and fruit orchards together with the few residual wooded areas); 2) foraging lesser kestrels, detected by scan-sampling each parcel using $8\times$ or $10\times$ binoculars for ca 5 min. Lesser kestrel abundance was thus expressed as the total number of foraging birds per parcel observed at each plot by survey combination. Only foraging birds (hunting on the wing, perching or hovering and diving to capture prey) were considered, whereas observations of birds flying over without a clear sign of interaction with the environment were discarded. Depending on the analysis, the six survey sessions were grouped into early (i.e. sessions 1–3) and late (i.e. sessions 4–6) breeding season

or by month (i.e. sessions 1 and 2 grouped into 'May', 3 and 4 into 'June', 5 and 6 into 'July') to increase statistical power (i.e. when sample sizes were too small if not aggregating) and to enhance the biological interpretation of the results.

Statistical analyses

Land-use temporal dynamics

To describe changes in land-use through the sampling period, we compared the land-use composition of the plots in May versus June, and in June versus July surveys. Differences in habitat composition between months were tested by MANOVA (R 'car' package, Fox et al. 2012), with the land-use proportions within each plot as dependent variables. Land-use proportions were computed for each plot and month as the mean extent of each land-use type in each plot across the two monthly surveys, thus obtaining a single value per month. Land-use proportions were log-ratios transformed (Aebischer et al. 1993). Log-ratios were calculated using semi-natural grassland extent as a reference, as this was one of the most abundant land-use types and it was not changing throughout the breeding season (Aebischer et al. 1993).

Spatial variation in abundance of foraging birds

As the following step, we explored whether the variability in counts of foraging lesser kestrels between plots (i.e. at a landscape scale) was explained by land-use or proximity to the breeding colonies. The main aim of this analysis was to verify whether lesser kestrel distribution was related to those of unmanaged (i.e. grassland) or managed (i.e. harvested cereal crops) habitats across the landscape. We preliminarily checked the occurrence of any scaling effect due to variation in the extent of surveyed parcels per plot, potentially biasing the results. We thus tested the correlation between the number of lesser kestrels counted in each plot (mean among sessions) and the percentage of surveyed plot surface. The two variables were weakly correlated ($r_s = 0.22$, $n = 14$ plots), which points to negligible scaling effects on count data.

We fitted negative binomial generalized linear mixed models (GLMMs) with the number of lesser kestrels observed in each plot at each session as the dependent variable and the log-number of surveyed parcels within each plot as an offset (to account for variation in the number of surveyed parcels per plot and for potential scaling effects), while the percentage cover of the two main land-use types (cereal crops and semi-natural grasslands) per plot and a distance-to-colony index for each plot were included as predictors. Negative binomial GLMMs are appropriate for the modelling of overdispersed count data (Zuur et al. 2009). Since the likelihood to observe a foraging lesser kestrel in a plot was expected to increase proportionally to both the proximity of the plot to the surrounding colonies and their size (Cecere et al. 2018), we assigned to each plot a 'proximity-to-colony' index. Proximity-to-colony was calculated for each plot according to the following formula (modified from Cecere et al. 2015):

$$\text{proximity-to-colony} = \sum_b S_b / d_b^2$$

where S is the size of the colony b (number of pairs) and d is the distance in km between the colony b and the centre of the plot. The distance d was raised to the second power to account for the fact that the probability for a lesser kestrel to reach a given plot was expected to decrease non-linearly with distance (Cecere et al. 2015). For each plot, proximity-to-colony index was calculated using data for the five nearest colonies to the centre of the plot (see the Supplementary information for the exact colony sizes, positions and data sources). Due to the progressive seasonal change in habitat composition, we could not fit a single model to the entire dataset (harvested crops were absent in May and early June) because of the strong collinearity between sampling session and harvested crop cover percentage ($r=0.76$). We, therefore, fitted two separate models: the first one with data collected during the first three surveys, when harvested crop extent was almost negligible (mean=3.8%) (early season model), and a second one on data for the last three surveys (mean harvested crop extent=43.0%) (late season model). We could not use the same temporal aggregation (three monthly periods, i.e. May, June, July) used in the habitat selection analysis because of insufficient sample size. Plot identity was included as a random effect to account for repeated surveys of the same plots. Negative binomial GLMMs were fitted with the 'glmmTMB' R package (Brooks et al. 2017).

Land-use preference analysis

As the last step, foraging habitat preferences were assessed by multinomial goodness-of-fit tests followed by the calculation of selection ratios (i.e. use/availability) for specific land-use types (Manly et al. 2010). Our study fits into the Manly et al. (2010) categorization 'Design I and Sampling protocol A with estimated proportions', whereby there is no unique identification of different animals, and availability is estimated from sample proportions when a random sample of used resource units is taken.

To account for temporal changes in land-use as well as for potential seasonal changes in habitat preferences, multinomial tests and selection ratios were computed for each of the three monthly periods (May, June, July) by summing up observations of the two sessions carried out in each period (grouping session data by month was required because of the small sample size of observed birds in each session).

Habitat use was estimated as the proportion of lesser kestrels observed in each of the six different land-use types in a given month. Habitat availability was estimated by simulation, assuming that foraging lesser kestrels within each plot would scatter at random within surveyed habitat parcels. Basically, for each survey/plot combination ($n=84$; 6 surveys \times 14 plots), we: 1) calculated the overall extent of each available land-use (maximum of six land-use types per survey/plot); 2) computed the total number of observed foraging lesser kestrels in that plot in that survey session; 3) generated a simulated landscape including all land-use types in the exact proportions recorded; 4) randomly distributed a number of points equal to the number of foraging lesser kestrels observed across the simulated landscape, and recorded the number that occurred in each land-use, repeating this process 10 000 times; 5) calculated the expected number of foraging lesser kestrels as the mean number of points occurring in each land-use across the 10 000 simulations, divided

by 10 000. Estimated availability was eventually calculated as the proportion of the expected number of foraging lesser kestrels in each land-use (for each monthly period).

Multinomial goodness-of-fit tests were used to evaluate the significance of the difference between the observed and expected number of birds among land-use types and were run using the 'xmult' function of the 'XNomial' R package (Engels 2015). Confidence intervals (CI) for selection ratios were estimated using the Koopman's score method, as recommended by Aho and Bowyer (2014). Selection ratios larger than 1 indicate a preference for a given land-use, whereas values below 1 indicate avoidance (Manly et al. 2010). All the analyses were run in R 4.0.2 (<www.r-project.org>).

Results

Land-use temporal dynamics

Land-use within plots, representing habitat availability, significantly differed between May and June (Pillai's trace test: $F_{5,22}=15.74$, $p < 0.001$) and June and July surveys ($F_{5,22}=8.37$, $p < 0.001$) (Fig. 2a). Land-use changes were mainly due to dry cereal crops ripening and harvesting (Fig. 2a). Specifically, green unripe cereals represented 56.5% of the available land-use in May, strongly decreasing to 10.8% and 2.2% in June and July surveys, respectively (Fig. 2a). At the same time, the percentage of available dry ripe cereals peaked in June (33.7%), while it was negligible in May and July (2.6% and 5.1% respectively). The ripe cereal harvesting began in June (14.2% of the available habitats) and increased in July, when 51.9% of the surveyed crops were harvested fields. In July, a small but non-negligible proportion of fields (including those with cereal stubbles) was ploughed after harvesting. Semi-natural grassland cover was 29.4% in May and slightly decreased in June and July, due to the mowing of some grassland parcels (Fig. 2a).

Overall, across all surveys, we observed 187 foraging kestrels, with an average abundance across all surveys and plots equal to 2.22 foraging birds/parcel ($n=84$, range 0–23 birds/parcel). In May, most birds were observed foraging on unripe cereals, but a considerable number of birds were also observed over semi-natural grasslands (Fig. 2b). In June and July, most birds were instead observed foraging on harvested fields, while ripe cereals and grasslands were used much less frequently (Fig. 2b).

Spatial variation in abundance of foraging birds

The number of foraging lesser kestrels varied among plots with different habitat composition only in the late breeding season (Table 1), when plots with lower grassland and greater harvested crops extent hosted a larger number of foraging individuals (Table 1). The proximity to breeding colonies did not affect the number of foraging lesser kestrels (Table 1).

Land-use preference analysis

The multinomial goodness-of-fit test was not significant in May ($p=0.35$) while it was highly significant in both June and July ($p < 0.001$ in both cases) in May, lesser kes-

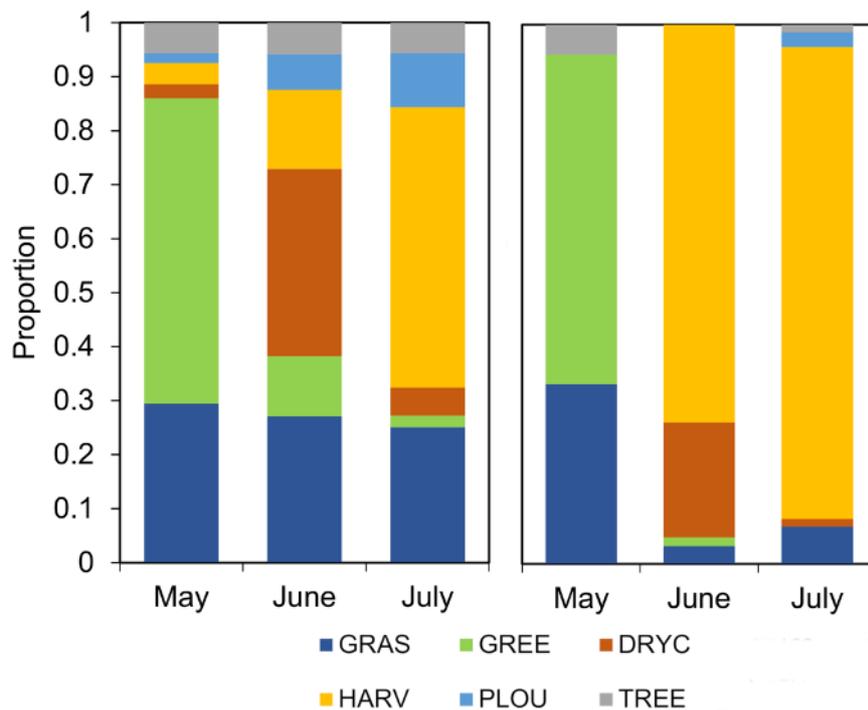


Figure 2. Changes in land-use throughout the sampling period, corresponding to the lesser kestrel breeding season (May–July) (left box) and proportions of observed foraging lesser kestrels over different land-use types (sample size: May = 54 birds; June = 61; July = 72) (right box). GRAS: semi-natural grasslands, GREE: green unripe cereals; DRYC: dry ripe cereals; HARV: harvested cereal crops; PLOU: ploughed fields, TREE: tree-dominated areas.

trels foraged in different land-use types according to their availability, whereas this was not the case in June and July. Specifically, semi-natural grasslands and green cereals crops were used in proportion to their availability in May (Fig. 3), whereas grasslands were strongly avoided in June and July. In the latter two months, a strong preference for harvested fields emerged (Fig. 3). Dry ripe cereals were used proportionally to their availability in June, and the same was true for ploughed crops in July, when this land-use type became frequent. The confidence interval of the selection ratios for tree-dominated patches (i.e. ‘trees’ land-use type) could not

be reliably estimated due to the low sample size, in terms of both observed and expected birds.

Discussion

Through a landscape-scale randomized survey, we showed that lesser kestrels of the Apulo–Lucanian region (southeastern Italy), hosting 15% of the European population of this species, evenly distributed among patches at the beginning of the breeding season while later on they tended to concentrate where the proportion of harvested cereal crops prevailed over semi-natural grasslands. Accordingly, the preference for semi-natural grasslands versus managed crops as feeding grounds changed in the course of the breeding season: at the beginning of the season, semi-natural grasslands and unripe cereal crops were used in proportion to their availability, while later in the season the birds preferred to forage on harvested cereal crops and actively avoided semi-natural grasslands. The remaining habitat types were exploited in proportion to their availability. Hence, in the second half of the breeding season, lesser kestrels appeared to re-distribute over a landscape scale, concentrating in areas with a higher proportion of harvested crops. Once in these areas, they actively selected harvested crops above any other land-use, including semi-natural grasslands that were even avoided in June and July. By contrast, grasslands and cereal crops were used proportionally to their availability in May.

Our findings are based on data collected over a single breeding season. Yearly oscillations in prey abundance (Badenhausser et al. 2009) or other parameters affecting habitat suitability (Rodríguez and Bustamante 2008, Catry et al.

Table 1. Negative binomial mixed models exploring whether the proximity to a breeding colony and the extent of semi-natural grasslands or harvested cereal crops affected the distribution of lesser kestrels within the 2400 km² of the study area (i.e. between-plots comparison). Separate models were fitted to data from the first three (early breeding season model, May to mid-June) or the last three surveys (late breeding season model, mid-June to July), respectively. Sample size: 42 plot/survey combinations for each model.

Predictors	Estimate (SE)	z	p
Early breeding season			
Semi-natural grassland extent	−0.037 (0.023)	1.61	0.11
Harvested cereal crop extent	0.032 (0.052)	0.61	0.54
Proximity to colony	0.444 (1.336)	0.33	0.74
Late breeding season			
Semi-natural grassland extent	−0.029 (0.012)	2.39	0.017
Harvested cereal crop extent	0.028 (0.012)	2.28	0.023
Proximity to colony	0.418 (0.674)	0.62	0.53

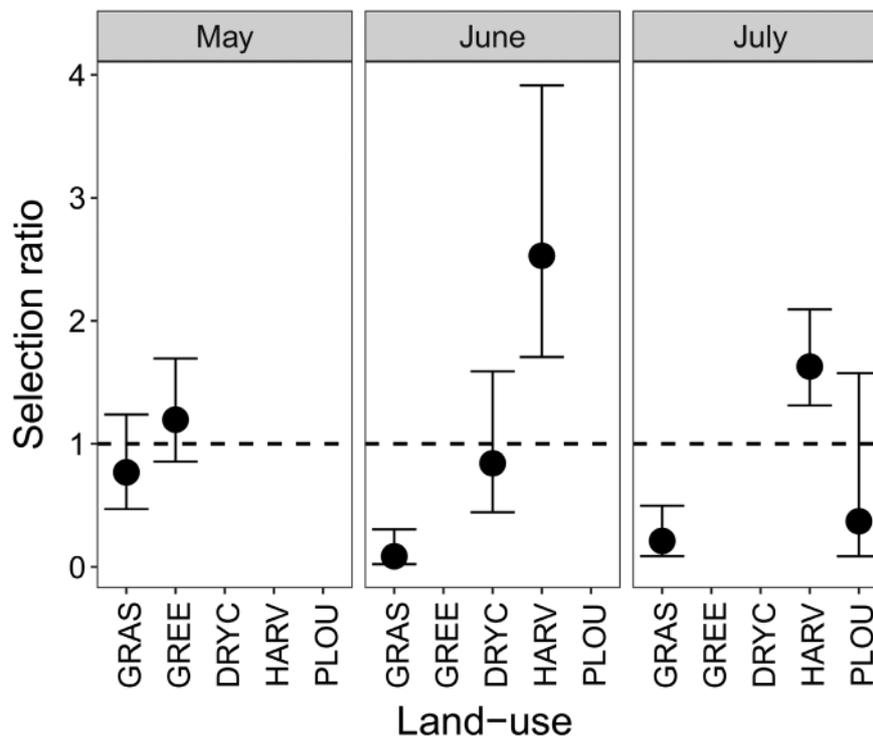


Figure 3. Selection ratios for different land-use types by foraging lesser kestrels through the breeding season. Whiskers represent 95% CI (Koopman's method, Aho and Bowyer 2014), indicating no significant preference/avoidance for a given land-use type when including 1 (i.e. whiskers crossing the dashed line). Missing dots indicate that a land-use type was unavailable in that period or had an expected sample size < 5 individuals, preventing a reliable estimation of CIs. Land-use type abbreviations: GRAS: semi-natural grasslands, GREE: green unripe cereals; DRYC: dry ripe cereals; HARV: harvested cereal crops; PLOU: ploughed fields.

2012) may determine yearly changes in habitat selection by foraging lesser kestrels. The replication of our sampling over multiple years would certainly be advisable to better support our conclusions. A further potential limitation of our study may be the small overall number of observed birds if compared with the size of the local population of lesser kestrels. However, we emphasize that our sampling protocol was focused on obtaining a representative sample of the land-use types of the study area and, consequently, sampling plots were randomly distributed at the landscape level.

Semi-natural grasslands, including fallow-fields and unmanaged crops, are widely regarded as key habitat elements to foster biodiversity conservation in agricultural landscapes (Kleijn and Sutherland 2003). For instance, semi-natural grassland patches within broad cereal crop areas are essential for those ground-nesting species that characterize the guild of steppe-dwelling birds of European conservation priority, such as the short-toed lark *Calandrella brachydactyla*, the little bustard *Tetrax tetrax* (Traba and Morales 2019) and the Montagu's harrier *Circus pygargus* (Arroyo et al. 2002, Limiñana et al. 2006). The maintenance of natural elements in the agricultural landscape for these and other species can exert both direct (i.e. offering land patches with no management where nesting is safe, Moreira 1999) or indirect effects (i.e. offering refugia to their prey species, Vickery et al. 2009) on their populations, in both cases, grassland patches should increase habitat quality. It was therefore surprising that semi-natural grasslands were not clearly and positively selected during the entire breeding period.

In the study area, lesser kestrels are secondary cavity nesters that mostly breed on rural or urban buildings and only visit agricultural landscapes to forage (Cecere et al. 2018, La Gioia et al. 2018). Hence, unlike other cereal steppe species, lesser kestrels do not breed on the ground and opportunistically use steppe-like crops and semi-natural grasslands for foraging purposes only. At the same time, it must be noticed that it is essential that those residual grasslands are of high vegetation quality (i.e. hosting a wide plant diversity) to effectively represent a valid invertebrate reservoir (Vickery et al. 2009) and eventually exert a relevant ecological role in the agricultural landscape. Our data did not enter into this detail and we could not discern between grassland patches of good or poor quality, so we can not exclude that we may have found a more important role of high-quality grasslands if these have been treated as a distinct category. Vegetation structure of the grassland patches is also crucial for determining their suitability as nesting areas for species of high conservation concern (Moreira 1999). Semi-natural grasslands of our study area are characterised by herbaceous vegetation belonging to the *Festuco-Brometalia* (Perrino et al. 2006), whose characterizing species normally reach 80 cm at their full development. The vegetation height of these grasslands has a similar dynamic to the main cereal crop types cultivated in the study area. Indeed, in April both semi-natural grasslands and unripe cereal crops are used proportionally to their availability, and lesser kestrels do not show any preference for specific foraging habitats. However, foraging lesser kestrels are known to strongly prefer short vegetation

patches, which favour detectability and capture of preferred prey (large orthopterans and small mammals) (Catry et al. 2012, 2014, Rodríguez et al. 2014, Cioccarelli et al. 2019). Hence, as soon as cereal crops grew ripe and began to be harvested, typically around mid-June, lesser kestrels in our study area shifted to harvested crops, where they could more easily spot and catch their main prey, at the same time avoiding semi-natural grasslands. These patterns resemble those previously documented in Portugal, where lesser kestrels foraging around breeding colonies were found to shift from grasslands to harvested crops, aiming to take readily available insects flushed during harvesting operations (Catry et al. 2014). The profitability of these habitats for lesser kestrels is suggested to rapidly decline after harvesting since the orthopterans quickly move to safer areas with tall vegetation (Catry et al. 2014). However, our findings indicate that cereal stubbles in the Apulo–Lucanian area probably remain profitable for a longer time, as they are still preferred compared to semi-natural grasslands even in July, when harvesting operations have ceased completely. Such differences may be related to differences in habitat structure and/or differences in orthopteran communities and behaviour between study areas. A preference for short vegetation has been documented also in Spain, where lesser kestrels were shown to prefer foraging in grazed versus ungrazed grasslands (Bustamante 1997, Tella et al. 1998). Grazing is an occasional activity in the study area and thus its impact is too limited to contribute to creating favourable feeding grounds for lesser kestrels. As comparative studies confirm, it is hard to identify specific environmental and habitat features that would unequivocally favour all the species of a guild, eventually generating simple and clear management indications. A valid example is provided by a case study by Barry et al. (2010) on a guild of steppic birds breeding in set-aside crops in Catalonia. They found that two out of four studied species (calandra lark and stone curlew) occurred in all census patches, while the other two (short-toed lark, little bustard) were only found in half of these patches, with specific vegetation height and shape of the crops (Barry et al. 2010). So far, even if the rule-of-thumb that ‘the most natural elements are included in a landscape the better it is’ (Moreira 1999) holds certainly true in our study area, we suggest that species-specific needs may be site-specific and conservation measures that could be well suited for a species may not result in a safe environment for others. Nevertheless, the early season use of grassland patches suggests that promoting their maintenance could be important for preserving viable lesser kestrel populations over the long-term.

Semi-natural grasslands may represent insect refugia (Vickery et al. 2009), sustaining cereal crop invertebrate communities that are largely destroyed during harvesting operations (Catry et al. 2014). However, in the late breeding season, foraging lesser kestrels were more abundant in plots where most of the land was dedicated to cereal crops and less abundant in plots dominated by semi-natural grasslands. Hence, large extents of cereal crops seem the main essential component of valuable foraging habitat for breeding lesser kestrels, at least during part of the breeding period. The relative importance of grasslands may increase in other parts of the lesser kestrel life cycle. Lesser kestrels are indeed known to abandon cereal crops and concentrate mostly on

grasslands-dominated areas after the breeding season and before migration (Sarà et al. 2014), where they also perform a partial moult of the plumage (Bounas 2019).

Our findings, together with previous evidences, indicate a tight link between lesser kestrel distribution, foraging habitat preferences and timing of harvesting operations. We argue that future conservation efforts targeting pseudo-steppe avian guilds in the Apulo–Lucanian area should focus on: 1) the maintenance or restoration of a heterogeneous landscape including both semi-natural grasslands and cereal crops, and 2) crop management schemes that promote spatially and temporally asynchronous harvesting, by e.g. promoting the use of mosaics of crop varieties that ripe at different times of the season. This may become of special importance in a near future, as southern Italian lesser kestrel populations (and likely other bird species in the area) may be threatened by ongoing climate changes due to the predicted reduction in spring rainfall abundance (Morganti et al. 2017). Moreover, harvested fields are expected to yield habitat patches of high food availability not only for the lesser kestrel but also for other species preferentially feeding on stubbles and short-vegetation crops (Johst et al. 2001). Increased availability of crop patches that are repeatedly harvested during spring–summer, such as leguminous fodder (i.e. alfalfa *Medicago sativa*), that have largely replaced irrigated crops normally avoided by lesser kestrels (Ursúa et al. 2005), may have indeed favoured the expansion of the species in recently colonized areas (i.e. northern Italy, Morganti and Grattini 2018). We thus argue that the spread of alfalfa cultivation and other small-sized and poorly irrigated crops should be promoted in pseudo-steppic agricultural areas suitable for hosting bird communities of conservation concern.

Overall, our study goes a step forward in confirming that European lesser kestrel populations critically depend on human activities: not only the foraging opportunities for the species are favoured by harvesting operations as previously observed, but also the distribution of foraging birds at a landscape scale is tied to vast extents of cereal crops. Hence, it appears that this species can thrive even in landscape contexts that are not completely favourable for other steppe-dwelling birds of European conservation interest. However, the maintenance of patches of semi-natural grasslands still emerges as a valuable management option because this land-use is anyway used by lesser kestrels, and of course it remains crucial for the maintenance of most of the other farmlands bird species. Eventually, we suggest that future conservation efforts should consider also the timing of crop harvesting as a major factor affecting habitat suitability for pseudo-steppe dwelling birds during the breeding season, with likely cascading consequences for the reproductive success and population dynamics of these species.

Acknowledgements – We thank S. Podofillini, D. Menard, C. Soravia and all the students that contributed to field data collection.

Funding – The study was partly funded by the European Commission through the LIFE project ‘Un Falco per Amico’ (LIFE11 NAT/IT/000068) and by the POR Puglia FESR-FSE 2014-2020 INNONETWORK-COHECO Project (Cod. 8Q2LH28) ‘Sistema Integrato di Monitoraggio, Allerta e Prevenzione dello stato di conservazione di Habitat ed ECOSistemi in aree interne e costiere protette e da proteggere’. CT and PNB were funded by

the H2020 E-SHAPE project – EuroGEO Showcases: Applications Powered by Europe (<www.e-shape.eu>), Grant Agreement: 820852.

Author contributions – DR, JGC, MG, CT and PNB conceived the study. MM, JGC and DR wrote the first draft of the manuscript. SQ, JGC and DR realized the field samplings. RA, MM and DR analysed data. All the authors contributed in significantly improve the text and the analyses.

Conflicts of interest – No conflicts to be declared.

Permit(s) – No special permits were required to realize the fieldwork.

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Supplementary information (available online as Appendix wlb-00800 at <www.wildlifebiology.org/appendix/wlb-00800>).

Wildlife Biology

WLB-00800

Morganti, M., Cecere, J. G., Quilici, S., Tarantino, C., Blonda, P. N., Griggio, M., Ambrosini, R. and Rubolini, D. 2020. Assessing the relative importance of managed crops and semi-natural grasslands as foraging habitats for breeding lesser kestrels *Falco naumanni* in southeastern Italy. – Wildlife Biology 2020: wlb.00800

Appendix 1

Data on colony size used to calculate the proximity-to-colony index

Figure A1. Distribution of the colonies used in the calculation of the proximity-to-colony index. Stars represent colony position and star size indicate colony class size. Numbers correspond to colony ID values reported in Table A2. For each plot, the index was calculated taking into account the distance and the size of the five nearest colonies. For this reason, some of the colonies lay outside the border of our study area.

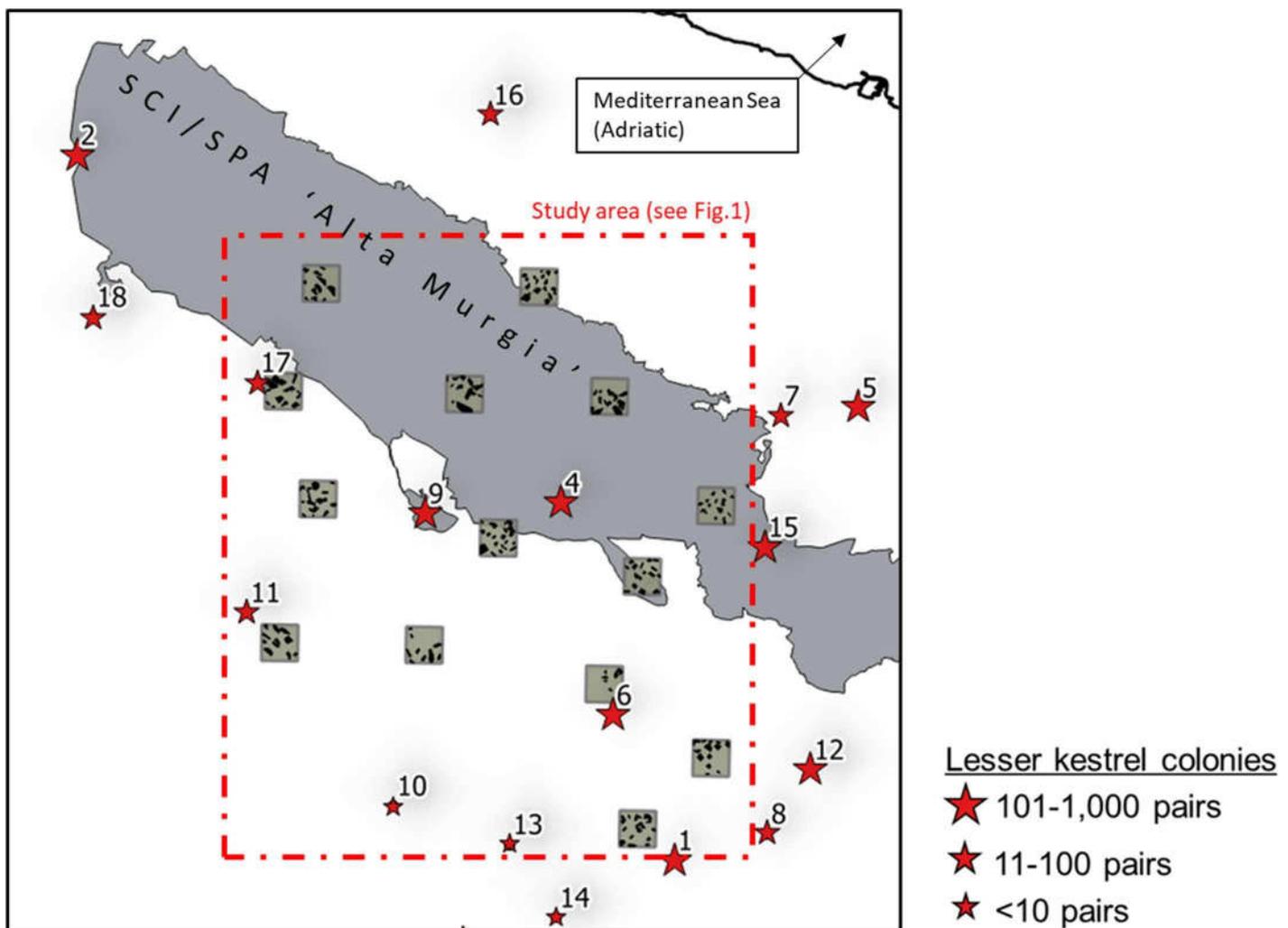


Table A2. Data on colony size (number of pairs) of the lesser kestrel colonies neighbouring the plots of our study area and used to calculate the proximity-to-colony index. Colony ID values correspond to those used in Fig. A1.

ID	Colony name (city)	Latitude	Longitude	Number of pairs	Reference year	Source
1	Montescaglioso	40.557	16.664	140	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
2	Minervino	41.086	16.077	366.5	mean 2015-2016	La Gioia et al. 2018
3	Andria	41.227	16.297	12	2013	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
4	Altamura	40.825	16.553	766.5	mean 2015-2016	La Gioia et al. 2018
5	Acquaviva delle fonti	40.897	16.845	179	mean 2015-2016	La Gioia et al. 2018
6	Matera	40.666	16.604	925	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
7	Cassano delle murge	40.891	16.769	185.5	mean 2015-2016	La Gioia et al. 2018
8	Ginosa	40.577	16.756	111	mean 2015-2016	La Gioia et al. 2018
9	Gravina	40.817	16.419	1128.5	mean 2015-2016	La Gioia et al. 2018
10	Grottole	40.598	16.388	1	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
11	Irsina	40.743	16.244	12	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
12	Laterza	40.625	16.798	106	mean 2015-2016	La Gioia et al. 2018
13	Miglionico	40.569	16.502	2	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
14	Pomarico	40.514	16.548	7	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
15	Santeramo	40.792	16.753	567.5	mean 2015-2016	La Gioia et al. 2018
16	Ruvo di Puglia	41.116	16.483	10	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
17	Poggiorsini	40.916	16.254	10	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)
18	Spinazzola	40.965	16.093	10	2014	G. Giglio, G. Palumbo, M. Visceglie, M. Bux, V. Cripezzi (data published in Morganti et al. 2017)