Context-dependent foraging habitat selection in a farmland raptor along an agricultural intensification gradient

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ABSTRACT

Gradients of agricultural intensification in agroecosystems may determine uneven resource availability for predators relying on these man-made habitats. In turn, these variations in resource availability may affect predators' habitat selection patterns, resulting in context-dependent habitat selection. We assessed the effects of gradients of landscape composition and configuration on habitat selection of a colonial farmland bird of prey, the lesser kestrel (*Falco naumanni*), relying on 76 GPS-tracked nestling-rearing individuals from 10 populations scattered along an agricultural intensification gradient. Analyses were conducted considering two ecological levels of aggregation (the population and the individual) and two spatial scales of habitat availability (the colony surroundings and the individual home-range). Overall, non-irrigated croplands and semi-natural grasslands were the most preferred habitats at both spatial scales. At the colony scale, lesser kestrels showed a preference for grassland compared to non-irrigated crops, whereas the opposite was the case within individual home-ranges. Conversely, croplands were positively selected with comparable intensity at both spatial scales. Strong selection for grassland at the colony scale highlights the importance of this semi-natural habitat for the species. The weaker preference for grassland at the home-range scale is likely due to the phenology and structure of the vegetation in the late breeding season. Spatial scale differences in selection patterns may thus derive from spatio-temporal changes in resource availability through the breeding season. The strength of selection for the two most used habitats varied markedly among individuals. At the spatial scale of the colony, individual selection strength for grasslands increased with decreasing compositional diversity of the surrounding landscape, suggesting that agroecosystem heterogeneity may at least partly buffer the loss of semi-natural habitats. At the within home-range scale, higher cropland availability reduced the strength of individual preference for this habitat, suggesting a negative functional response possibly related to density-dependent processes acting on foraging movements. Our study provides evidence that farmland species show context-dependent habitat selection patterns in response to landscape gradients shaped by agricultural intensification as well as by intrinsic characteristics and habitat availability. Our findings highlight the importance of addressing both individual and population-level variability and considering multiple spatial scales in studies of habitat selection to inform species' management and conservation.

1. Introduction

Human-driven natural and semi-natural habitat loss and fragmentation are the main causes of the global biodiversity crisis (Chase et al., 2020; Fahrig, 2003; Hanski, 2011). In this context, agricultural expansion and intensification have been playing a central role, determining dramatic landscape transformations during the past centuries (Ramankutty and Foley, 1999; Tscharntke et al., 2005). Agricultural activity shapes the landscape modifying both its composition (i.e., amount of different habitat within the landscape) and configuration (i.e., shape, size, and spatial configuration of habitat patches) (Martin et al., 2019; Proulx and Fahrig, 2010). This can lead to habitat gradients that may affect organisms' distribution patterns and resource selection (Duflot et al., 2017; Médiène et al., 2011; Tscharntke et al., 2012). Most animal species are negatively affected by the loss of semi-natural habitats within the cultivated matrix (Feber et al., 2015; Petit and Firbank, 2006) and/or by the reduction of landscape compositional heterogeneity due to agricultural intensification (Benton et al., 2003; Reynolds et al., 2018). Responses to changes in landscape configuration (e.g., fragmentation) are instead difficult to predict and generally species-specific (Fletcher et al., 2018; Krauss et al., 2010).

Animals can use a given habitat disproportionately compared to its availability, resulting in habitat selection, by for example favouring habitats rich in beneficial resources or avoiding those in which predation risk is higher, thus improving fitness and survival (Manly et al., 1972; Manly et al., 2002; Morris, 2003a). Habitat selection is a hierarchical process that acts at multiple spatial scales (e.g., the landscape used by a population vs. the home-range of an individual belonging to that population) (Johnson, 1980; Meyer and Thuiller, 2006). Specific habitats can be preferred at a scale but not at another, with studies conducted at different scales often leading to conflicting evidence. Studies conducted at multiple spatial scales indeed provide a better characterization of habitat selection patterns (Mayor et al., 2009).

Since landscape patterns drive resource distribution, often determining uneven resource availability (Boyce et al., 2003; Mayor et al., 2007), habitat selection may be influenced by landscape composition and configuration (Paolini et al., 2019; Sánchez-Clavijo et al., 2016). For instance, landscape composition at a wider scale could heavily affect fine-scale habitat selection (e.g., the selection of foraging habitat within the individual home-range) by shaping food availability and accessibility (Beatty et al., 2014; Chambers et al., 2016).

Habitat selection studies generally focus on populations, describing general patterns of species–habitat relationships (Leclerc et al., 2016; Lesmerises and St-Laurent, 2017). However, natural selection acts on individuals. Understanding the drivers of individual variability in habitat selection is therefore pivotal to answer fundamental eco-evolutionary questions (Leclerc et al., 2016; Mitchell et al., 2020; Muff and Fieberg, 2019). Despite its potential significance, such inter-individual variation in habitat selection patterns has been little explored (Avgar et al., 2020). Sex, age, and social status have been suggested as potential intrinsic drivers of inter-individual differences in habitat selection (Lesmerises and St-Laurent, 2017; Nilsen et al., 2009; Ofstad et al., 2019). In parallel, climatic conditions, ecological interactions (e.g., predation, competition), anthropogenic impacts, and local availability of different habitats may play an important role as extrinsic factors (Herfindal et al., 2009; Mysterud and Ims, 1998; Raynor et al., 2017; Treinys et al., 2016; van Beest et al., 2016). Moreover, animals often exhibit context-dependent habitat selection, occurring when selection varies across individuals as a function of variation in local environmental conditions. Whenever the individual use/selection of specific habitats varies as a function of the availability of this habitat within the frequented area, a so-called 'functional response' in habitat use/selection occurs (Mysterud and Ims, 1998; Holbrook et al., 2019). Functional responses are relevant to characterize behavioural plasticity, the relative advantages or disadvantages of exploiting different habitats, and the potential for a species or population to respond to spatial and temporal landscape changes (Mitchell et al., 2020).

By exploiting state-of-the-art GPS tracking technologies, we aimed at shedding light on the drivers of habitat selection in a colonial farmland bird of prey of European conservation priority, the lesser kestrel (*Falco naumanni*). European lesser kestrels largely rely on traditional agricultural landscapes, including semi-natural grasslands and dry cereal pseudo-steppe habitats, for acquiring food resources (BirdLife International, 2021; Bustamante, 1997; Morganti et al., 2021). For this reason, it was argued that this species could serve as an indicator/flagship species in different types of agroecosystems (Santana et al., 2014). We relied on GPS data from 76 nestling-rearing adult lesser kestrels belonging to 10 populations scattered throughout Italy (hereafter we refer to the term 'population' to define a group of individuals breeding in the same colony site and frequenting the same environments surrounding the colony site). We aimed at assessing how landscape composition and configuration of key foraging habitats affected population- and individual-level foraging habitat selection. Habitat availability was assessed at two different spatial scales, the area surrounding the colony site (colony scale) and the individual home-range (home-range scale). On the one hand, results from the colony scale analysis are expected to provide information on the effects of the landscape surrounding the colony site on habitat selection patterns, testing the idea that birds from populations settled in different landscape contexts may show different habitat preferences. Hence, this analysis should reflect the general experience/knowledge of the area surrounding the colony that individuals obtain during the entire breeding season (including the period before tracking started, i.e. before hatching). On the other hand, results from the home-range scale analysis will allow an assessment of how individuals respond to the different habitats they actually encounter during their foraging activity, reflecting a short-term response to habitat availability. Specifically, by calculating individual metrics of habitat selection within home-ranges, we tested for the occurrence of functional responses in habitat selection, focusing on whether foraging individuals differently selected semi-natural grasslands and non-irrigated crops (the main foraging habitats in our study; see also Morganti et al., 2021) as a function of their availability within the home-range. The study populations were located along a gradient of agricultural intensification, where semi-natural grassland progressively decreased up to be entirely replaced by intensive cropland. This allowed us to investigate the role of landscape composition and configuration as drivers of foraging habitat selection patterns during the highly energy-demanding nestling-rearing period while accounting for sex-specific differences in offspring care (i.e., males taking most of the share of offspring provisioning; Hernández-Pliego et al., 2017, Soravia et al., 2021).

2. Material and methods

2.1. Target species and study area

The lesser kestrel breeds in open and flat landscapes (natural steppes, pseudo-steppes, farmland), where it relies on natural cliffs or rural and urban buildings as nesting sites (Negro et al., 2020), and forages on small prey (insects and small rodents) (Di Maggio et al., 2018; Negro, 1997). In the second half of the 20th century, European lesser kestrel populations have experienced a dramatic range contraction and decline, likely due to agricultural intensification (BirdLife International, 2004; Iñigo and Barov, 2010). Intensification may have reduced the quality of foraging areas, leading to low breeding success and population contraction (BirdLife International, 2021; Donazar et al., 1993). European populations are now partly recovering, although they are far from reaching pre-decline levels (Gameiro et al., 2020).

The study was conducted at 10 colony sites (i.e., populations) encompassing the entire Italian breeding range (La Gioia et al., 2017) (Fig. 1a-b). Colony sites were located on buildings either in urban (Altamura, Gravina, and Matera; these cities harbour large colonies of
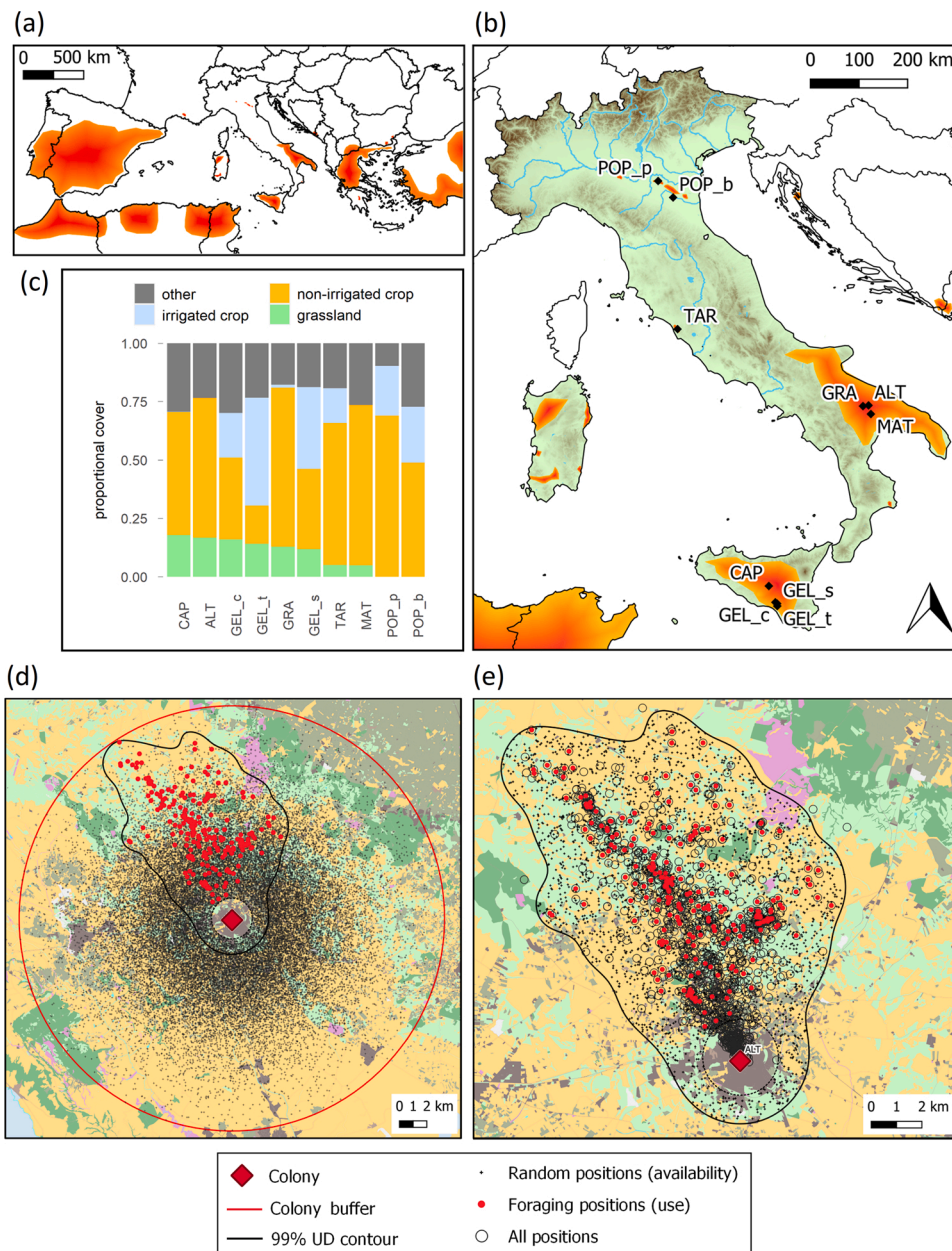
Fig. 1. a) Distribution (red-orange shade) of the lesser kestrel in the Mediterranean basin [Modified from BirdLife International (2020)]. b) Location of the 10 Italian colonies considered in this study. c) Proportional composition of the three main land use categories (non-irrigated crop, irrigated crop, and grassland) for each colony; the proportional cover is calculated within a circle with a radius equal to the 99th percentile of the distribution of all the positions (colony buffer). Colonies are ordered left to right along a gradient of decreasing semi-natural grassland cover. d) Colony scale habitat selection: example of a colony buffer (Altamura colony); used (foraging positions) and available (random) positions on which the colony scale selection analysis is based are shown. e) Home-range scale habitat selection: home-range of an individual from the Altamura colony, with the GPS positions used to define the home-range (all positions in the legend), the foraging positions, and the random positions on which the home-range scale habitat selection analysis is based. In d) and e), the 1.5 km inner buffer around the colony on which the *tripSplit* analysis is based is additionally represented with a dotted circle; positions within this buffer were excluded from habitat selection analyses (see Methods and Supporting information). Population abbreviations: CAP (Capodarso), ALT (Altamura), GEL_c (Gela – Canalotto), GEL_t (Gela – Torre Vecchia), GRA (Gravina), GEL_s (Gela – San Gregorio), TAR (Tarquinia), MAT (Matera), POP_p (Po Plain – Poggio Rusco), POP_b (Po Plain – Baricella).

ca. 1000 pairs each) or rural habitats (all other colonies, ranging between 10 and 32 pairs) (Cecere et al., 2018; La Gioia et al., 2017). In all cases, colony surroundings were dominated by cropland and semi-natural grassland, the latter ranging from 0% (Po Plain) to 17.3% (Capodarso, Fig. 1c).

2.2. Breeding stage assessment, GPS deployment and tracking data

The breeding stage was assessed by regularly checking nest sites for egg-laying, hatching and presence of nestlings (Podofillini et al., 2019, 2018; Soravia et al., 2021). Lesser kestrels were captured by hand within nest-boxes/cavities and equipped with GPS tags, usually a few days before egg hatching, during 2015–2020. We deployed solar-driven, remote-downloading GPS-UHF tags (< 5% of body mass; see Cecere et al., 2020; Sarà et al., 2019 and Supporting information), with an actual mean (± SD) sampling rate of 1 GPS position every 23 ± 10 min (see Cecere et al., 2018 and Supporting information). We discarded night roosting positions, data from malfunctioning devices, those

referred to egg-laying/incubation phase and those from birds that failed reproduction (see Supporting information). Our final dataset consisted of data from 76 nestling-rearing individuals (38 males, 38 females; 7.6 ± 7 SD individuals per study population; range 2–22) that were tracked over 27 ± 5 days (range 10–31) (Table S1).

2.3. Colony buffer, home-range definition, and identification of foraging locations

We tackled habitat selection at two different spatial scales of habitat availability, reflecting two different degrees of spatio-temporal interaction of birds with their habitats (see Introduction), the colony scale (comparing habitats used to those available in the surrounding of the colony; Fig. 1d) and the individual home-range scale (comparing habitats used to those available within each individual home-range; Fig. 1e). The colony scale was approximated by a colony buffer, defined for each colony as a circle with a radius equal to the 99th percentile of the distribution of the distances between the colony sites and the GPS positions

of tracked individuals at that colony (see Cecere et al., 2015 for a similar approach). Individual home-ranges were estimated for each bird as the 99% Utilization Distribution (UD) using the fixed kernel density estimation (KDE) with reference bandwidth (href) using the R package *adehabitatHR* (Calenge, 2006).

To assess habitat use, we focused on the potential foraging sites of the tracked individuals. However, the temporal resolution of GPS devices was unsuitable to identify actual foraging sites. We thus relied on two different methods to assess habitat use, one suited for the largest populations and the second for the smallest ones. Briefly, for the largest populations, where birds usually perform long-lasting/ranging foraging trips (Cecere et al., 2018, 2020), we could reliably estimate the actual foraging areas and the associated positions using the furthest point for each foraging trip (see details in Supporting information). For smaller populations, where foraging occurs even in the immediate colony surroundings, we instead assumed that most GPS positions could reflect foraging sites, and only performed a temporal subsampling to reduce temporal autocorrelation (see details in Supporting information). The analysis of habitat selection was eventually based on 160 ± 60 SD positions/individual on average, ranging between 32 and 331.

2.4. Land use data and landscape composition and configuration variables

We obtained a comprehensive land cover map for all the study areas by merging different regional land-use maps derived from comparable methodologies (based on aerial photographs and with a mapping scale below 1:10000; details in Supporting information). We identified 10 habitat categories (largely based on a simplified CORINE classification): permanent grassland (including semi-natural grassland and pastures); non-irrigated crop (mainly cereals, but also including hayfields at some study sites); irrigated crop (mostly vegetable crops and maize), heterogeneous crop (areas of traditional and low intensive agriculture with both annual and permanent crops intermixed), permanent crop (mostly orchards and vineyards); bare ground (mainly rocky areas, gravel pits, sparsely vegetated areas), shrubland, forest, urban area/infrastructure, and water bodies/courses. The original data were rasterized at a resolution of 40 m (*st_rasterize* function in *stars* R package; Pebesma, 2020), which represents the actual median accuracy of GPS loggers according to a pre-deployment test.

At the colony scale, we assessed the proportional cover of each land use category within the colony buffer and computed the Shannon landscape compositional diversity index (Shannon index hereafter). This is a landscape diversity metric that quantifies the ecosystem diversity within a given landscape. Formally, it is the same index widely used in community ecology (Shannon, 1948) but applied to the proportional amount of different habitat types within the landscape. The metric can span from zero to infinite; the higher its value, the greater the landscape diversity is (McGarigal, 2014). Additionally, at both colony and home-range scales, we used the clumpiness index as a metric of landscape fragmentation (McGarigal, 2014). We calculated the clumpiness index for each of the two most used habitats (non-irrigated cropland and semi-natural grasslands, together representing > 85% of the used locations). The index can range from − 1–1, being negative when the land use type is disaggregated and positive when it is aggregated; it was previously shown to efficiently isolate the configurational component from the compositional component (McGarigal, 2014). All landscape metrics were calculated with the R package *landscapemetrics* (Hesselbarth et al., 2019).

2.5. Foraging habitat selection analysis

Habitat selection analysis was conducted according to a used-available design (Manly et al., 2002) with each individual lesser kestrel as the sampling unit. At the colony scale, availability was estimated by generating 10 random positions for each used (foraging)

position within the colony buffer. Colony-scale availability was assumed to be the same for all the individuals of a given colony. As breeding lesser kestrels are central place foragers, we expected the distance distribution of the positions from the colony not to be uniform (their frequency is expected to decrease with distance). Following Cecere et al. (2015), we assessed for each colony the distance distribution parameters based on all the positions and generated available positions at random within the colony buffer using the same distance distribution parameters and a random angle to ensure no bias in the directionality of generated positions (details in Appendix S2).

At the home-range scale, availability was estimated by generating 10 random positions for each foraging position within each home-range (command *spsample* in R package *sp*; Bivand et al., 2013). This approach allowed us to explore the third order of habitat selection, i.e. the use of different habitat patches within the home.range (Johnson, 1980; Meyer and Thuiller, 2006). At both scales, the area within the colony site (defined as the distances below the threshold defined in Table S2) was excluded when creating random positions. For both scales, habitat use was estimated with the positions likely representing foraging events (see above). A use to availability ratio of 1:10 is considered a good compromise between an adequate representation of true availability to animals and computing time (Muff and Fieberg, 2019; Northrup et al., 2013).

For each of the 10 habitat categories and each individual at both scales, we computed the selection ratio as a metric of selection strength (Manly et al., 2002). Selection ratios are particularly suited for categorical variables, are easy to compute and interpret, and were recently shown to be a unifying metric in habitat selection (Chamaillé-Jammes, 2019). Following Manly et al. (2002), we defined a selection ratio for a given habitat *i* as follows:

$$SR_i = \frac{Nu_i/Nu}{Na_i/Na}$$

were Nu_i is the number of used locations in habitat *i*, Nu is the overall number of used locations, Na_i is the number of available locations in habitat *i*, and Na is the overall number of available locations.

Selection ratios were calculated using the R package *asbio* (function *ci.prat*, Aho, 2020), and their confidence intervals were estimated according to the Koopman method (Aho and Bowyer, 2015).

2.6. Statistical analyses

2.6.1. Overview and rationale of the analyses

Our analyses were split into three parts. We first conducted an analysis of habitat selection aimed at disentangling the overall pattern of habitat selection for all the populations considered (paragraph 2.6.2). Secondly, we performed a population-level analysis aimed at investigating variation in patterns of habitat selection among populations for the two most used habitats (paragraph 2.6.2). Both these analyses were performed separately at both spatial scales of habitat availability (colony and home-range). Finally, we performed an individual-level analysis aimed at disentangling the drivers of between-individual differences in habitat selection for the two most used habitats, both at the colony scale (paragraphs 2.6.3) and home-range scale (2.6.4).

2.6.2. Overall and population-specific patterns of habitat selection

Differences in overall habitat selection patterns among the 10 habitat categories were investigated by fitting two separate (colony- and home-range scale) Generalized Linear Mixed Models (GLMMs) (see paragraph 2.6.5 for details of fitting procedures) with individual selection ratios as the response variable, habitat category as the unique predictor, and individual and population identities as random intercept effects.

Differences among populations in patterns of habitat selection were tested by focusing on non-irrigated crops and semi-natural grasslands, as they are the two most used habitats. To this end, we fitted two separate

(colony- and home-range scale) Generalized Linear Models (GLMs) (see paragraph 2.6.5 for details of fitting procedures) with individual selection ratios for each of these two habitats as response variables and population identity as a fixed effect.

2.6.3. Drivers of individual patterns of habitat selection at the colony scale

At the colony scale, we tested for the effect of the gradient of agricultural intensification on individual habitat selection for grassland and non-irrigated crop. We expressed this gradient with three proxies measured within the colony buffer: the proportional cover of grassland, the grassland clumpiness index and the Shannon landscape compositional diversity index (McGarigal, 2014). We fitted separate GLMMs for each habitat including individual selection ratios as a response, the above described three landscape variables and sex as fixed predictors, and population identity as a random intercept effect.

2.6.4. Drivers of individual patterns of habitat selection at the home-range scale

At the home-range scale, we tested whether habitat availability and habitat configuration (clumpiness) affected grassland and non-irrigated crop individual selection ratios while controlling for individual home-range size and sex. Separate models were fitted for each habitat and each of them included habitat availability and clumpiness of the corresponding habitat type within the home-range. Assessing the effect of habitat availability on an individual metric of selection (here, the selection ratio) is a direct method to assess the occurrence of a functional response (Holbrook et al., 2019). To disentangle within-population (individual) from between-population effects, we adopted the within-group centering approach suggested by Van de Pol and Wright (2009). To this aim, continuous predictors (i.e., habitat availability, habitat clumpiness and home-range size) were split into two components. The "between" component expresses the between-population variation, calculated as the mean value of the variable at the population level, whereas the "within" component expresses the within-population variation, calculated as the centered value (individual value - mean population value) for each individual of a given population (van de Pol and Wright, 2009). The within-population component of habitat availability was interpreted as representing the functional response of individuals to different amounts of available habitats within their home-range.

Eventually, the full models (one for each of the two habitats) contained sex, within- and between-population home-range size ($\log_{10}$-transformed to reduce skewness), within- and between-population habitat availability, and within-and between-population clumpiness index. We additionally included in GLMMs the two-way interaction of the three pairs of between- and within-population terms, aiming at assessing whether the within-population effect depended on the local environmental context (expressed by the between-population term). Home-range size was included as a covariate to investigate whether inter-individual variation in home-range size affected the selection of a specific habitat while accounting for the huge inter-population variation in home-range size (Cecere et al., 2018). Population identity was included as a random intercept effect.

2.6.5. Details of GLMM and GLM fitting and sample size

In all models, continuous covariates were standardized before analysis (Cade, 2015) and selection ratios were weighted according to their uncertainty by including the reciprocal of the confidence interval length as a weight variable (Fieberg et al., 2010; Murtaugh, 2007). GLMMs and GLMs of selection ratios were fitted with a gamma error distribution and log-link function, as selection ratios are strictly positive (Zuur et al., 2013). GLMMs were fitted by means of the *glmer* function of the *lme4* R package (Bates et al., 2015). Non-significant interactions were removed at once (Bolker et al., 2009). Before fitting models, we conducted exploratory analysis following Zuur, Ieno, and Elphick (2010) to avoid common statistical issues. Models' assumptions were validated using R

package *performance* (function *check_model*) (Lüdecke et al., 2020). Analyses were performed with R 3.6.1 (R Core Team, 2019).

Colony-scale analyses were based on 76 individuals from 10 populations for non-irrigated cropland and 70 individuals for grassland, as we excluded data from the two Po Plain populations where no grassland is present (and hence selection ratios could not be calculated). Home-range-scale analyses were based on data from 68 individuals, excluding data from three populations that were located in distinct landscapes compared to the other populations, specifically the two Po Plain populations in which grassland is absent and the Gela-Torre Vecchia population which is surrounded by irrigated crops (Fig. 1c). To facilitate comparisons, we used the same sample also for non-irrigated crop analysis (results were similar when including all the individuals; details not shown for brevity).

3. Results

3.1. Overall and population-specific patterns of habitat selection

Regarding the overall patterns of habitat selection, we found large variation in the strength of selection among habitats available in the colony surroundings (colony scale GLMM: $\chi^2 = 203.93$, df = 9, P < 0.001), grassland being the most preferred habitat, followed by non-irrigated crops. Irrigated crops and bare ground were used according to their availability, while all other habitats (heterogeneous crop, permanent crop, bare ground, shrubland, forest, urban area/infrastructure, and water bodies/courses) were avoided. A large variation emerged also within home-ranges (home-range scale GLMM: $\chi^2 = 183.39$, df = 9, P < 0.001), with non-irrigated crops being the most preferred habitat, while grassland, irrigated crops and bare ground were used according to availability and all other habitats were avoided (Fig. 2a).

Selection ratios for the two main used habitats significantly varied among populations at both scales (grassland, colony scale GLM: $\chi^2 = 25$, df = 7, P < 0.001; home-range scale GLM: $\chi^2 = 53.67$, df = 7, P < 0.001; Fig. 2b; non-irrigated crops, colony scale GLM: $\chi^2 = 54.46$, df = 9, P < 0.001; home-range scale GLM: $\chi^2 = 114.12$, df = 9, P < 0.001; Fig. 2c). Selection for grassland was generally stronger at the colony scale compared to the home-range scale in most populations, whereas the pattern for non-irrigated crops was more heterogeneous.

Selection ratios for grassland and non-irrigated crops showed large inter-individual variability within the same population, both at the colony and the home-range scale (Fig. S2).

3.2. Drivers of individual habitat selection at the colony scale

At the colony scale, variation in individual selection ratios was explained by landscape compositional diversity (Shannon index, Table 1). Specifically, semi-natural grasslands were more intensely selected in less diverse landscapes, whereas this habitat was largely used in proportion to its availability (or even slightly under selected) in more heterogeneous landscapes (Fig. 3a). Additionally, females tended to avoid non-irrigated crops, whereas this was not the case for males (Table 1; Fig. 3b). Grassland cover and clumpiness index did not significantly affect habitat selection of both habitats at this spatial scale (Table 1).

3.3. Drivers of individual habitat selection at the home-range scale

Nestling-rearing lesser kestrel used semi-natural grasslands according to their availability, irrespective of their extent within the home-range (Table 2). Selection strength for non-irrigated crops increased with increasing mean non-irrigated crop availability (between-population effect) (Fig. 4b). When accounting for between-population effects, birds showed a negative functional response to non-irrigated crops within-populations, meaning that selection strength, which was positive in contexts of low crop availability, decreased with increasing crop
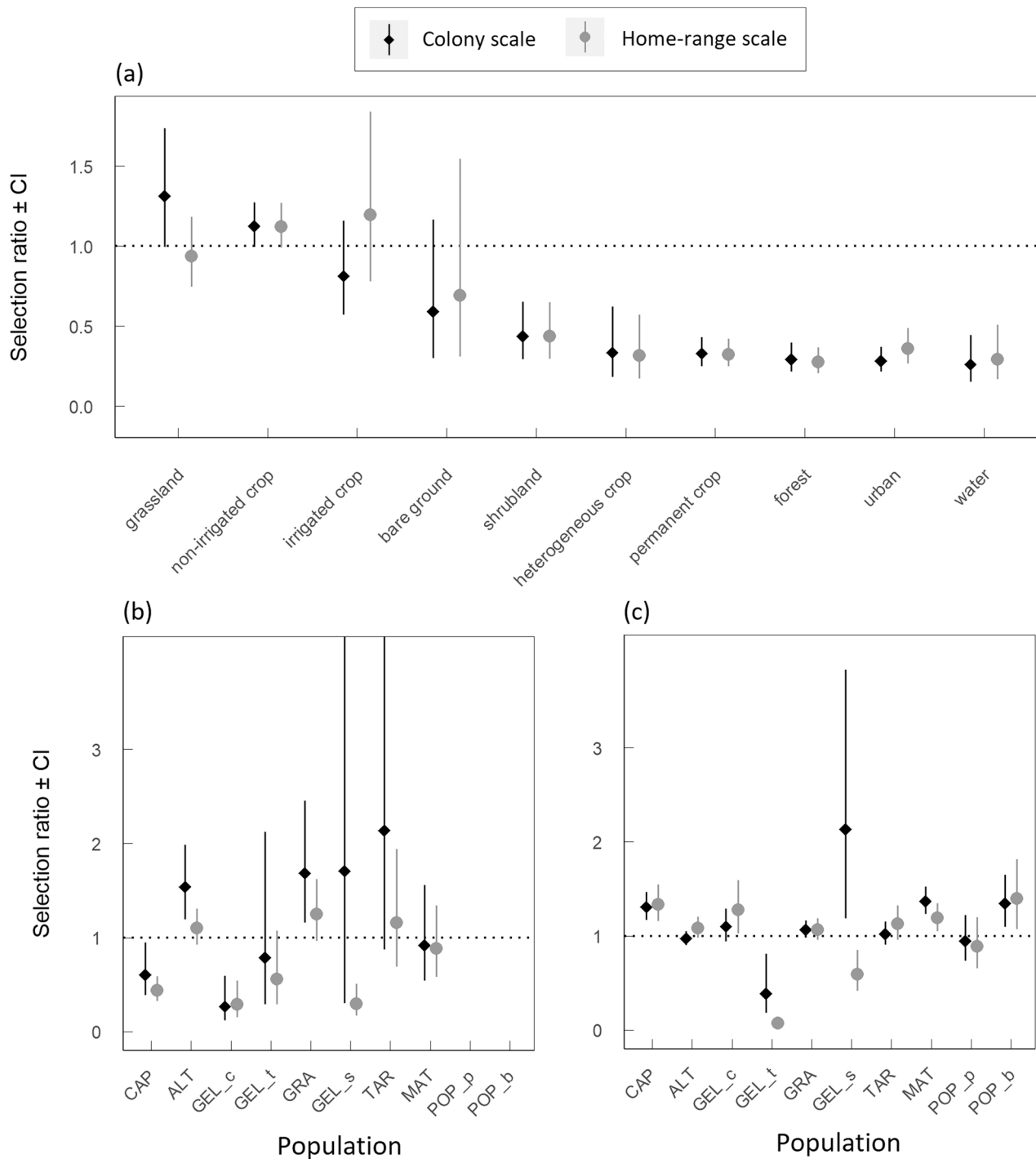
Fig. 2. (a) General pattern of habitat selection for 10 habitat categories by Italian lesser kestrels, with availability assessed at both the colony and the home-range scale; (b) and (c) population-specific patterns of habitat selection for the two most widely used habitat types (grassland and non-irrigated crop, respectively). Marginal means (with 95% confidence intervals) derived from a gamma GLMM (top) and GLM (bottom) were calculated by means of R package *emmeans* (Lenth, 2020). Selection ratios (SR) > 1 (with confidence intervals not encompassing one) denote positive selection, SR < 1 (with confidence intervals not encompassing one) denote avoidance, SR ≈ 1 (with confidence intervals encompassing one) indicate habitat use in proportion to availability. Colonies are ordered left to right along a gradient of decreasing semi-natural grassland cover around the colony site. Population abbreviations: CAP (Capodarso), ALT (Altamura), GEL_c (Gela – Canalotto), GEL_t (Gela – Torre Vecchia), GRA (Gravina), GEL_s (Gela – San Gregorio), TAR (Tarquinia), MAT (Matera), POP_p (Po Plain – Poggio Rusco), POP_b (Po Plain – Baricella).

availability, approaching a use proportional to availability (Fig. 4c).

In populations with small home-ranges, kestrels tended to avoid grassland, while the opposite was the case for those with larger home-ranges (Fig. 4a). Additionally, within-population, individuals that strongly selected non-irrigated crops had also larger home-ranges,

although this relationship was weak and only marginally significant (Fig. 4d). No sex differences in the preference for grassland habitats emerged whereas males showed a stronger preference for non-irrigated crops compared to females (Fig. 4e). We found no significant effects of within- or between-population components of the landscape clumpiness

Table 1

Gamma GLMMs assessing colony and home-range scale drivers of lesser kestrel individual foraging habitat selection for grassland and non-irrigated crop for 10 populations in Italy. Significance was assessed through Wald's χ^2 tests (Fox and Weisberg, 2011). Marginal and conditional r-squared values for mixed models were calculated based on Nakagawa et al. (2017). Important effects (i.e., with 95% CI of estimates not including zero) are shown in bold. For grassland, the variance of the random effect was null in both models. Home-range area was $\log_{10}$ transformed. F: female; M: male. Subscript B: "between" component (between-population variation); subscript W: "within" component (within-population variation).

Colony scale	Grassland selection				Non-irrigated crop selection			
	Estimate ± CI	χ^2	df	p	Estimate ± CI	χ^2	df	p
Sex	F: 0.42 [0.08, 0.76]M: 0.07 [− 0.24, 0.38]	2.36	1	0.12	**F: − 0.20 [− 0.85, 0.42]M: 0.92 [− 0.70, 0.55]**	**29.37**	**1**	**< 0.001**
Grassland cover	0.23 [− 0.32, 0.80]	0.67	1	0.40	-0.34 [− 1.03, 0.35]	0.93	1	0.34
Grassland clumpiness	0.71 [− 1.27, 2.70]	0.49	1	0.48	0.10 [− 0.34, 0.56]	0.22	1	0.63
Shannon landscape diversity	**-0.35 [− 0.65, − 0.04]**	**5.18**	**1**	**0.02**	0.08 [− 0.25, 0.43]	0.25	1	0.61
	Marginal R^2 = 0.355; conditional R^2 = -				Marginal R^2 = 0.276; conditional R^2 = 0.682			

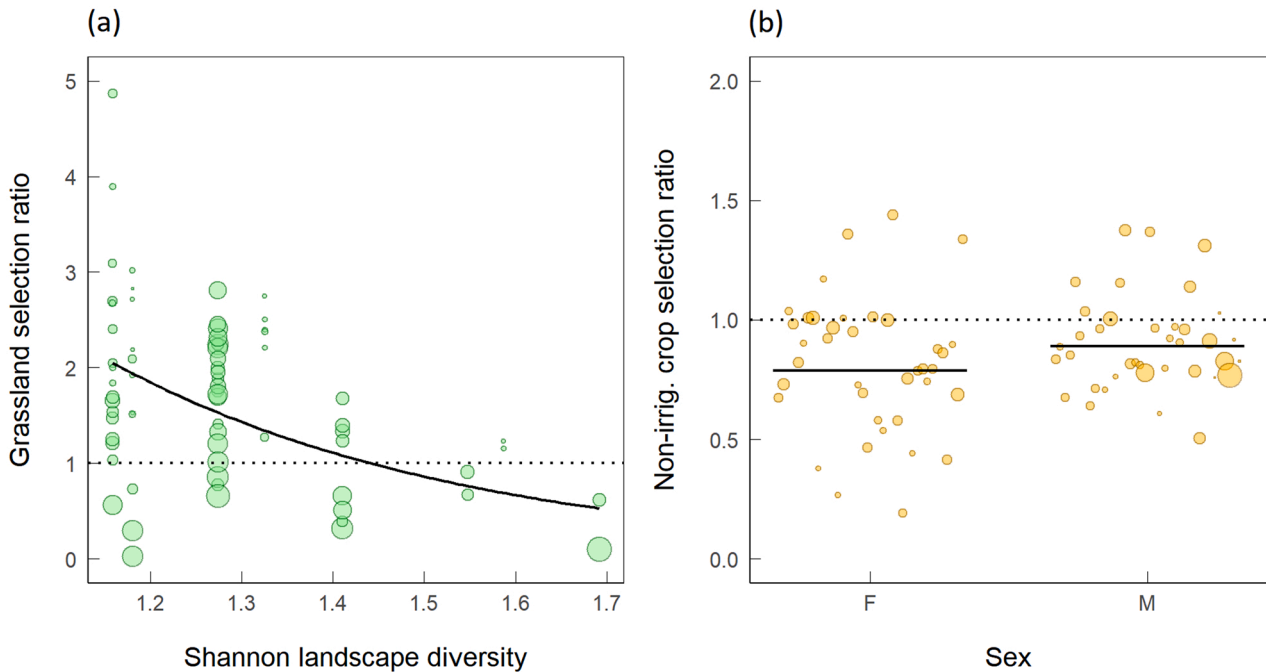| Home-range scale	Grassland selection				Non-irrigated crop selection			
	Estimate ± CI	χ^2	df	p	Estimate ± CI	χ^2	df	p
Sex	F: − 0.02 [− 0.25, 0.20]M: − 0.13 [− 0.35, 0.08]	0.47	1	0.49	**F: 0.01 [− 0.15, 0.17]M: 0.11 [− 0.04, 0.28]**	**20.29**	**1**	**< 0.001**
Home-range area$_B$	**0.36 [0.15, 0.57]**	**12.02**	**1**	**< 0.001**	-0.01 [− 0.14, 0.11]	0.08	1	0.77
Home-range area$_W$	-0.01 [− 0.16, 0.14]	0.01	1	0.90	**0.02 [0.01, 0.05]**	**5.13**	**1**	**0.02**
Clumpiness$_B$	-0.05 [− 0.29, 0.17]	0.53	1	0.46	-0.03 [− 019, 0.11]	0.23	1	0.63
Clumpiness$_W$	0.07 [0.75, 1.19]	0.23	1	0.63	0.01 [− 0.01, 0.04]	2.34	1	0.12
Availability$_B$	0.03 [− 0.14, 0.22]	0.15	1	0.69	**0.26 [0.13, 0.40]**	**15.67**	**1**	**< 0.001**
Availability$_W$	-0.01 [− 0.27, 0.18]	0.01	1	0.92	**-0.03 [− 0.05, − 0.01]**	**7.11**	**1**	**0.007**
	Marginal R^2 = 0.401; conditional R^2 = -				Marginal R^2 = 0.196; conditional R^2 = 0.304			

Fig. 3. Drivers of lesser kestrel selection for grassland and non-irrigated crops with availability assessed at the colony scale. a) Effect of Shannon index of landscape diversity on grassland selection ratios; b) effect of sex (F: female; M: male) on non-irrigated crop selection ratios. Dots represent the partial residuals of the gamma GLMM reported in Table 1 and their size is proportional to the weight applied in the linear model (see Methods). Other variables in the model were kept at their mean value.

index on selection ratios of both habitats (Table 2). All interaction terms were non-significant (P > 0.34) and were removed from the models in a single step.

4. Discussion

Agroecosystems are characterized by landscape gradients that are expected to influence the availability of resources to consumers (Clavero and Brotons, 2010; Vallecillo et al., 2008), which can respond by

showing context-dependent patterns of habitat selection. This latter phenomenon is probably widespread, although understudied (Avgar et al., 2020). To shed light on context-dependent patterns of habitat selection, including functional responses, we exploited a large dataset of GPS-tagged breeding lesser kestrel, a farmland bird of prey of European conservation priority.

Previous work on habitat selection in this species (e.g., Morganti et al., 2021; Rodríguez et al., 2014; Ursúa et al., 2005) was conducted at the population level, and thus did not focus on the drivers of
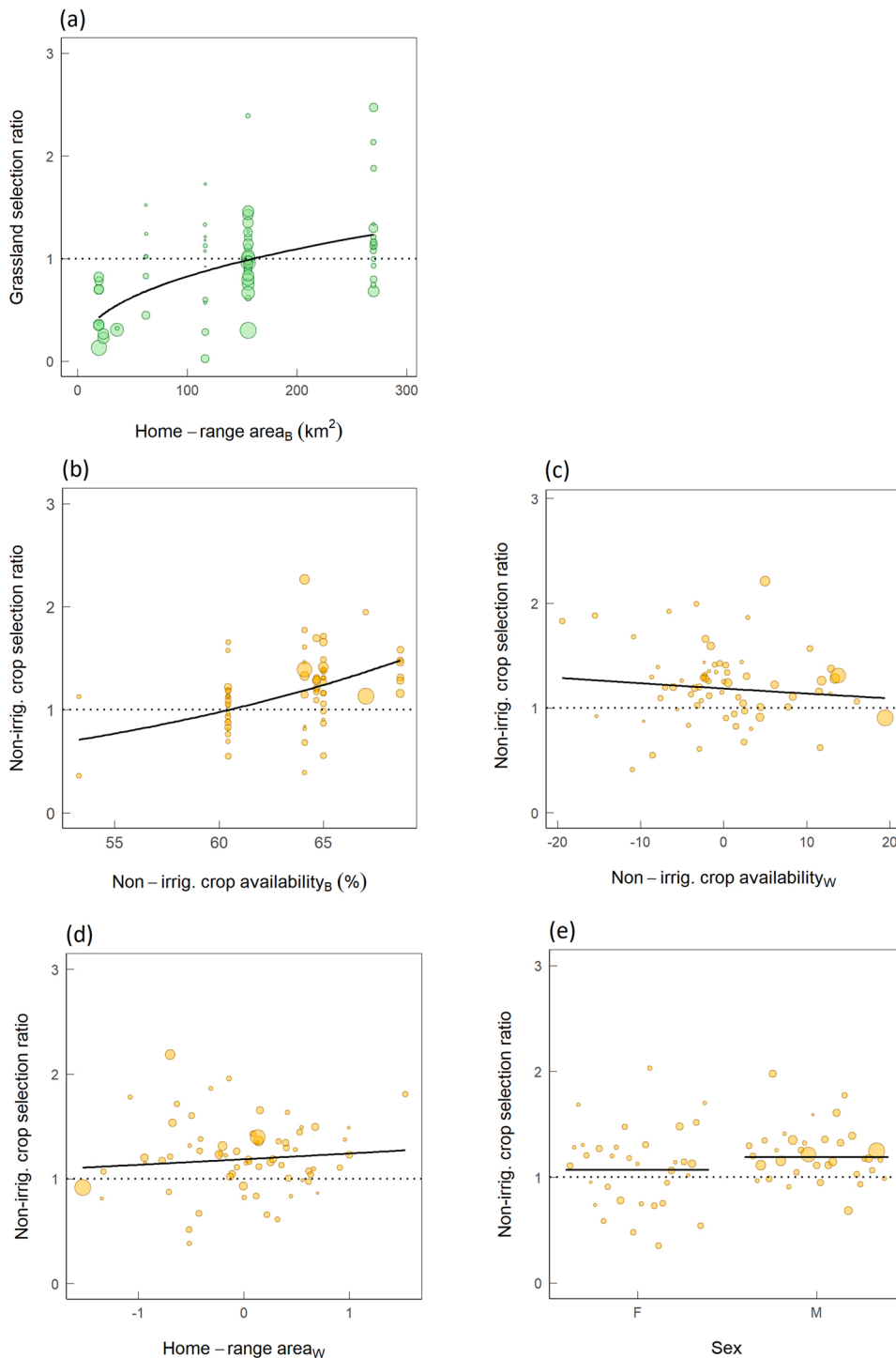
Fig. 4. Drivers of lesser kestrel selection for grassland and non-irrigated crop with availability assessed at the home-range scale. a) Effect of between home-range area on grassland selection ratios; b-e) effect of non-irrigated crop availability (both between and within), within home-range area, and sex on non-irrigated crop selection ratios. Dots represent the partial residuals of the gamma GLMM reported in Table 1 and their size is proportional to the weight applied in the weighted regression (see Methods). Other variables in the model were kept at their mean value.

inter-individual variability, despite their potential overarching eco-evolutionary consequences (Leclerc et al., 2016; Mitchell et al., 2020). Here we filled this gap of knowledge by exploring the role of intrinsic and extrinsic drivers affecting inter-individual variability in habitat selection.

When comparing overall foraging habitat selection patterns at different spatial scales, we detected substantial differences between the two main used habitats. At the colony scale, grasslands were more strongly selected than non-irrigated crops, whereas the opposite was true at the home-range scale. For grassland, this was consistent also when separately considering different populations, whereas for non-

irrigated crops the pattern was more variable. The strong selection for grassland at the colony scale by birds breeding in all study populations highlights the importance of this semi-natural habitat for lesser kestrels (Catry et al., 2012; Donazar et al., 1993; Franco et al., 2004). The weaker preference for this habitat at the home-range scale by nestling-rearing birds is likely due to the phenology and structure of the vegetation in the late breeding season (Morganti et al., 2021). In early spring, during the pre-breeding and egg-laying and incubation period, vegetation is low, and grassland is highly suitable for foraging lesser kestrels, while cultivated fields are largely bare ground with little vegetation. In late spring and summer, during nestling rearing, vegetation growth turns

grassland into a sub-optimal foraging habitat, with birds switching to more suitable harvested non-irrigated crops (Morganti et al., 2021), in which prey accessibility is also higher (Catry et al., 2014). Yet, our result showing that foraging grounds around the colony are located in landscapes that have a higher semi-natural grassland cover than expected by chance suggests that the presence of grassland is a key element determining lesser kestrels' overall habitat suitability during the breeding season.

Our individual-level habitat selection analysis highlighted a negative functional response of lesser kestrels to non-irrigated cropland availability at the home-range scale, whereby the use of this habitat tended to become proportional to availability as its availability increased within the individual home-range (the within-population effect, see Results). Conversely, individual selection for cropland increased when the average availability of this habitat around the colony increased (the between-population effect, see Results). These two apparently contrasting patterns can possibly be reconciled by invoking density-dependent processes acting on foraging movements. Increasing strength of selection with increasing cropland cover around the colony site may in fact trigger a higher density of birds foraging in croplands, with prey becoming limiting due to overexploitation (see Bonal and Aparicio, 2008), making predators less selective for this habitat within individual home-ranges. Indeed, the functional response may be affected by intraspecific competition in those species, like the lesser kestrel, which are non-territorial and use non-exclusive foraging areas. Similar density-dependent processes may explain the decrease in non-irrigated crop selection strength within smaller home-ranges. Birds with smaller home-ranges may indeed forage in overexploited cropland close to the colony site, which may become prey-depleted during the nestling-rearing period and may thus be avoided (or less strongly positively selected). Finally, the positive association between semi-natural grassland selection strength and the between-population home-range size effect may be a side-effect of inter-population differences in colony size. Birds breeding in large colonies (with broader home-ranges) may show a stronger preference for semi-natural grasslands than those from small colonies (with small home-ranges) because of a combination of complex density-dependent and habitat quality effects resulting from the high density of foraging birds in the proximity of large colonies. Future studies assessing prey availability/accessibility and density of conspecifics in different habitats within individual home-ranges across colonies differing in size may allow a better understanding of the ecological processes driving such associations.

Males were more strongly tied to cropland than females. Sex-dependent habitat selection is quite widespread within vertebrates and may be related to sex differences in offspring provisioning (Bergan and Smith, 1989; Laforge et al., 2021; Ofstad et al., 2019; van Toor et al., 2011). On the one hand, in Greek intensive agricultural landscapes, Vlachos et al. (2015) reported that male lesser kestrels positively selected cereals and field margins while females preferred grasslands and cotton fields. On the other hand, Tella et al. (1998) and Hernandez-Pliego et al. (2017) found no sex differences in habitat selection in Spain. The latter study however reported spatial segregation between the sexes, with females roaming over larger areas than males. We hypothesize that foraging males, which take most of the share of offspring provisioning (Hernández-Pliego et al., 2017), favoured crops because this is likely the optimal foraging habitat during the energy-demanding nestling-rearing period, whereas females, to minimize competition and food depletion would favour suboptimal foraging habitats (i.e., grassland). Alternatively, the two sexes, which differ in morphology and may differ in foraging mode (perch-hunting vs. foraging in-flight; Hernández-Pliego et al., 2017, but see Cecere et al., 2020), may have different prey capture optima in different environmental contexts, leading to differential habitat selection.

All individual habitat selection models had good explanatory power (Table 1), suggesting that the extrinsic and intrinsic variables we selected have an important role in explaining inter-individual variability

in habitat selection. Additional factors that may contribute to explain inter-individual variability (but could not be considered in this study) include age/experience, personality, or body condition (e.g. Harris et al., 2020; Lesmerises and St-Laurent, 2017; Nilsen et al., 2009; Ofstad et al., 2019).

We showed distinct patterns of habitat selection at different spatial scales, in accordance with previous multi-scale habitat selection studies (Mayor et al., 2009; McGarigal et al., 2016). We suggest that this result likely depends on trade-offs arising when the resources provided by a given habitat change throughout the breeding cycle. This is likely the case in highly dynamic farmland environments, characterized by rapid structural changes of the vegetation and continuous anthropogenic disturbance. Indeed, farmland-dwelling species need to cope with the double challenge of retrieving their resources in habitats regulated by both natural cycles and anthropogenic activities (Longoni et al., 2011; Paolini et al., 2018; Rodríguez et al., 2014). This can contribute to explaining why habitat heterogeneity at multiple spatial scales often results as a key determinant of biodiversity in farmed landscape (Batáry et al., 2011; Benton et al., 2003; Vickery and Arlettaz, 2012). Heterogeneous agroecosystems are, in fact, more likely to fulfil the ecological needs of farmland species throughout different phases of their life cycle (Santana et al., 2017). Additionally, the intensity of selection for semi-natural habitat remnants decreased with increasing landscape compositional diversity, irrespective of the extent of the semi-natural habitat. In agroecosystems, the reduction of landscape compositional diversity is often related to agricultural mechanization/intensification, which in turn determines the loss of semi-natural and marginal habitats that host rich animal and plant communities, and a reduction of crop diversity, which may lead to lower foraging habitat quality for predators (Benton et al., 2003; Reynolds et al., 2018). Therefore, this finding suggests that reliance on a key semi-natural habitat for such a farmland-dependent species is likely reduced wherever the compositional diversity of the agricultural landscape (and hence the quality of the foraging habitats) is high. Indeed, agroecosystem diversification may at least partly offset the loss of key semi-natural habitats, supporting the idea that the maintenance of a diverse agricultural landscape will increase the conservation value of the agroecosystems (Tscharntke et al., 2021; Vickery and Arlettaz, 2012).

Agricultural expansion and intensification are among the main drivers of global biodiversity loss (Gonthier et al., 2014; Kehoe et al., 2017). Effective actions for the conservation of species and their supporting ecosystems require a sound knowledge of the ecology of the target organisms (Segan et al., 2011; Sutherland et al., 2004). The study of habitat selection, a cornerstone of evidence-based conservation, is crucial for proper habitat management and for boosting the effectiveness of species' conservation efforts (Morris, 2003b). Our study provides evidence for context-dependent habitat selection patterns (including functional responses) in a farmland bird of prey of conservation priority. Individual habitat selection was in fact modulated by a landscape compositional gradient shaped by agricultural intensification as well as by intrinsic characteristics (sex) and habitat availability. We suggest that comprehensive approaches addressing habitat selection at multiple spatial scales and considering both population and individual levels of selection, and their drivers, may be important in tackling emerging challenges in the conservation and management of farmland biodiversity.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Ethical statements

The study was conducted following relevant guidelines and regulations. Capture and tagging were carried out by Istituto Nazionale per la Protezione e la Ricerca Ambientale (ISPRA) under the authorization of Law 157/1992 [Art.4 (1) and Art. 7 (5)], except for Sicily, where they were carried out by the University of Palermo under authorization n. 1616/2014 issued by Regione Sicilia.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107782.

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