Crop phenology reshapes the food-safety landscape for roe deer in an agroecosystem

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Abstract

1. Understanding the behavioural adjustments of wildlife in anthropized landscapes is key for promoting sustainable human-wildlife coexistence. Little is known, however, about how synanthropic species navigate spatio-temporal variation in the availability of food and cover that are shaped by human practices such as agriculture.

2. Animal habitat use is predominantly driven by spatial and temporal variations in food and cover, as individuals respond to fluctuations in the trade-off between food acquisition and risk avoidance. In agroecosystems, the availability of high-quality forage and cover are dependent on agricultural practices (e.g., harvesting) and crop phenology, providing an ideal opportunity to evaluate how wildlife adjust their behaviour in a heterogeneous human-dominated landscape.

3. We investigated the influence of crop phenology on the behaviour of European roe deer (*Capreolus capreolus*) to infer the functional roles of crop types in the food-cover landscape. We analysed the habitat use and activity patterns of 105 GPS-collared female roe deer using a unique dataset combining field-specific land cover data, region-specific estimates of crop phenology and weekly harvesting data for three common crops in a French agroecosystem.

4. We found very distinct habitat use and activity patterns according to crop type, phenological stage and time of day. Wheat and artificial meadows were strongly selected at night-time during the early and post-harvest stages only, when roe deer were highly active, suggestive of feeding activity. On the contrary, roe deer strongly selected maize during the day when it was high enough to provide cover, when they were less active, indicating that it was primarily used for refuge. These patterns depended on the availability of more ‘natural’ cover, suggesting that mature maize may substitute for ‘natural’ cover when the latter is scarce.

5. *Synthesis and application*. Our work highlights the importance of behavioural plasticity and habitat complementation in the persistence of this synanthropic species in agroecosystems. This behavioural adjustment may buffer the consequences of the reduction in natural habitats that accompanies intensification of agricultural production and has implications for understanding how agricultural practices shape the food-safety trade-off of wildlife living in these highly modified landscapes.

Keywords: Agricultural landscape, behavioural plasticity, cover, forage, habitat use, phenology, ungulate

Introduction

Plant phenology is a key driver of the distribution of resources across landscapes, so that animals must move accordingly, trying to track these changes in space and time (Armstrong et al., 2016). Indeed, plant phenology drives predictable changes in forage quantity and quality during plant growth and senescence. In response, many herbivores modify their use of space at scales ranging from weeks to seasons (Abrahms et al., 2021). For example, sequential green-up across landscapes promotes the migration of large herbivore populations that surf the green wave of high-quality forage during spring (Aikens et al., 2017). At a finer spatial scale, plant phenology may also influence animal space use by providing pulses of high-quality forage. For example, mast fruiting by trees and grasses is known to strongly influence the habitat use of birds, small mammals and European ungulates (Bogdziewicz et al., 2016).

Human activities can also alter patterns of resource distribution and phenology for wild animals across many ecosystems (Plummer et al., 2015). This is especially true in human-dominated landscapes, such as agroecosystems, where resource availability and quality are driven by both natural and anthropogenic factors (Barker et al., 2019). Agroecosystems are, by definition, spatially heterogeneous as they combine both semi-natural habitats and agricultural crops (Fahrig et al., 2011). Agricultural landscapes are also characterized by strong temporal variation in resource distribution for wildlife. The quantity, quality, and availability of resources for a given species varies across crop types and depends both on phenological changes in plant development (Doorenbos & Kassam, 1979) and agricultural activities (e.g., harvesting, mowing, or irrigation). Crops are known to attract wildlife as they generally have a high sugar and fat content, with low levels of toxins and fibres (Abbas et al., 2011), and are concentrated in large dense patches that require less search time (Simon & Fortin, 2020). Phenological changes in crop nutrient content are, thus, key in determining the crop foraging behaviour of herbivores. For example, African elephants (*Loxodonta Africana*) increased their selection for crops during the brown-down stages, resulting in diets with higher levels of crude protein and energy (Branco et al., 2019) and higher body mass (Chiyo et al., 2011) compared to individuals that fed solely on natural forage.

Foraging strategies, and more generally space use, are, however, strongly constrained by risk perception, as individuals must navigate between habitats that rarely provide both high-quality forage and sufficient cover simultaneously (Brown, 1992). As a result, the use of a given crop type by wildlife should also depend on the amount of cover it provides at a particular phenological stage. Many ungulates are known to leave more 'natural' habitats that provide cover to use agricultural areas at night, probably because crop fields are perceived as riskier during daytime due to the presence of humans and lack of vegetation cover (Bonnot et al., 2013; Branco et al., 2019; Mysterud & Østbye, 1999). In agricultural landscapes, the spatial distribution of food and cover thus depends on the type and phenological stage of each crop in relation to the species' feeding and risk management strategy, defining a dynamic food-fear landscape for wildlife. This aspect has been largely neglected in the past, with agricultural land often being considered as a single static 'open' habitat, potentially providing forage, but little or no cover. Recent studies have shed some light on the effects of spatio-temporal variations in crop availability and quality on animal space use at fine temporal scales (Branco et al., 2019; Paolini et al., 2018; Wilber et al., 2020), but none formally considered the role of crops as potential cover, nor how this balance between food and cover availability varies across time. There is an increasingly urgent need to understand how agricultural practices shape the trade-off between resource acquisition and exposure to risk for wildlife as future predictions concerning land conversion and severe climatic events suggest that the scope for human-wildlife coexistence will be reduced (Abrahms et al., 2021).

Here, we investigated the influence of human-driven changes in crop phenology on European roe deer (*Capreolus capreolus*) behaviour to identify the functional role of various crop types across phenological stages in the food-cover landscape. To do so, we used a unique dataset combining detailed annual land cover data, weekly estimates of crop phenology for three crop types and tracking data from 105 GPS-monitored animals living in an agroecosystem. This enabled us to map the availability of cover across the landscape at a fine spatio-temporal scale and disentangle the influence of plant phenology and harvesting events on crop use. The roe deer is a particularly appropriate species for this investigation as it thrives in agricultural landscapes (Hewison et al., 2009) due to its high ecological and behavioural plasticity (Andersen et al., 1998). Little is known, however, about how roe deer navigate spatio-temporal variations in the availability of food and cover that are shaped by human practices in agroecosystems, nor how changes in these practices might modify the species' food-safety trade-off. We aimed to: (1) determine the influence of crop type, phenology and time of day (night/day) on crop use to understand how roe deer adjust their behaviour to the spatio-temporal cycles of an agroecosystem, (2) contrast use and associated activity levels between day and night for the various crop types to identify potential functional roles in terms of food or cover across phenological stages (3) determine how the availability of crops or woodland/hedgerows, that provide alternative, more 'natural', habitats, modifies the use of a given crop type, providing insight on how landscape composition determines the reliance of roe deer on cultivated land for food or cover subsidies.

Materials and methods

Study site and population

The study was conducted on a roe deer population located in a 19 000-ha rural region in southern France (N43°17, E0°53). The area is a heterogeneous agricultural landscape consisting of woodlands (18.9%, two large forests and fragmented woodland patches), hedgerows (3.5%), natural meadows (28.7%) and arable land (38.9%). Arable crops include artificial meadows (11.0%), cereals (wheat 13.2%, maize 2.9%, barley 2.0%, sorghum 1.2%) and oilseed (sunflower 6.0%, soybean 1.7%, rapeseed 0.9%). A network of roads link isolated houses, farms, and small villages. Drive hunting represents the most lethal human activity for roe deer in the area, occurring regularly between mid-September to February. Trophy hunting occurs from June to September, likely maintaining a high perception of risk for roe deer during most of the year. The density for this roe deer population was estimated around eight individuals per 100 ha using capture-mark-recapture re-sighting (Hewison et al., 2021).

Landscape composition

Areas of homogeneous habitat patches were manually digitized as polygons (in ArcView GIS 3.3, Esri, Redlands, CA, U.S.A.) based on aerial photographs of the study site (from the IGN’s BD Ortho, http://professionnels.ign.fr/bdortho-50cm). We considered 6 habitats in our analyses (**Figure S1,** details in **Appendix S1.1**): woodland, hedgerows, maize, *Zea mays,* wheat, *Triticum* sp., artificial meadows (including lucerne, *Medicago sativa,* ray-grass, *Lolium perenne,* clover, *Trifolium sp.,* alfafa, *Medicago sativa*), other (all other land cover types, mainly composed of natural meadows). We focused on these three crop types for which we had the widest coverage (present in most individual home ranges) and which are known to provide potential cover and/or forage for roe deer (Abbas et al., 2011; Putman, 1986). This allowed us to compare crops with contrasting temporal patterns of availability (e.g., maize in spring-autumn, wheat in winter-summer, see **Figure S2**) and different phenological characteristics (e.g., mature maize offers cover, emerging wheat offers palatable food).

Roe deer biologging data

We measured roe deer habitat use using GPS data collected on 105 adult female roe deer from 2011 to 2021 with a 6h fix rate (details in **Appendix S1.2**). As we wished to compare diurnal versus nocturnal habitat use, we only considered locations recorded at 12:00 (day) and at 00:00 (night). This also ensured that we focused mainly on foraging and/or resting behaviour as roe deer are known to concentrate their inter-patch movements during crepuscular phases (Benoit et al., 2023). All GPS collars integrated an activity sensor which indexed intensity of movement on the x (forward-backward) and y (sideways) axes (details in **Appendix S1.2**). We measured total activity as the sum of activity values for both axes (range 0-510). We then extracted total activity values for each GPS location as the mean of activity values taken within <5 min of the GPS location.

Estimating crop phenological stages and monitoring agricultural practices

Information on annual crop phenological stages (from sowing to harvest) is scarce and often recorded in crop-specific monitoring programs for parasite and disease surveillance (e.g., Vigicultures ®). For this study, we combined data from different monitoring programs to produce weekly estimations of phenological stage for each crop type and year (**Table S1**, see **Appendix S1.3** for a detailed description). We also assessed median harvest date for each year and crop type in our study area using annual field observations. We then combined the estimated phenological stages and median harvest dates to create weekly estimations of emergence, growth, maturity, harvest and post-harvest periods for each crop type and year.

Estimating roe deer crop use across phenological stages

We first tested the influence of phenology and time of day on the use of each crop type (coded as 0/1 for each location). We extracted habitat type from the year-specific habitat map and attributed a phenological stage to each location by cross-referencing the date of the GPS location with the weekly crop phenology estimates. As habitat availability was constant for a given individual over the year (all polygons contained a single habitat type in each year), comparing the distribution of 'used' locations across phenological stages for a given crop was equivalent to estimating relative selection among stages. For these analyses, we only considered individuals that had at least one location in the focal crop during their monitoring period as we wished to compare patterns of use among phenological stages within a given crop type.

For each crop type, we fitted a binomial generalized linear mixed model (GLMM) with a logit link function, considering use as the response variable (focal crop type vs. other habitats) and phenological stage and time of day as fixed effects. As we were interested in the interplay between crop phenology and time of day, we included this interaction in our models. We set individual identity as a random intercept to account for repeated measures.

Identifying potential functional roles for crops

We wished to investigate whether different crop types played different functional roles depending on their phenological stage. Roe deer have distinct nychthemeral activity patterns, with low activity levels when resting in refuge habitat during the day, but higher activity levels when they forage, mostly during the night (Bonnot et al., 2020; Pagon et al., 2013). In the absence of direct behavioural observations, we used this nychthemeral pattern of activity to infer potential functional roles for each crop type across phenological stages. For these analyses, we considered three phenological stages that were common to all crop types and represented contrasting characteristics in terms of cover and food resources: emergence (no cover, potential forage), maturity (cover, little forage for cereals, potential forage in certain meadows) and post-harvest (no cover, potential forage in wheat and maize). We contrasted patterns of use during night and day for each crop type and phenological stage by performing post-hoc contrast analyses on our previous model predictions for crop use and adjusting for multiple comparisons using the Dunnett adjustment method (Dunnett, 1964).

We classified activity sensor data into active versus inactive behaviour by using the thresholds of activity level specified by Bonnot et al. (2020) who worked on the same dataset. Since we considered phenological stages that were common to all crop types, we fitted a single binomial GLMM with a logit link function to analyse variation in activity in relation to crop type, phenological stage (emergence/maturity/post-harvest) and time of day (night/day), including a random intercept for individual identity to control for repeated observations. We included the three-way interaction between crop type, phenological stage and time of day as we wished to test whether activity differed between night and day in relation to crop height (‘tall’, for mature maize and wheat vs. ‘low’ for all other crops and stages), indicating different functional roles for different crop types and phenological stages. We accounted for seasonal variation in activity levels linked to female reproductive phenology (Pagon et al., 2013) by including a circular spline on the Julian date. We also included collar type as a fixed effect as using activity level thresholds that were specific to each collar brand did not completely account for variation due to collar type (LRT test, dAIC=20, Chisq= 21.95, $P<0.001$).

Does landscape composition influence crop use across phenological stages?

Finally, we investigated whether crop use depended on its availability and/or the availability of 'natural' cover, that is, woodlands and hedgerows, in the local landscape. Indeed, woodlands and hedgerows are known to provide key 'cover' habitats for roe deer in agricultural landscapes (Morellet et al., 2011; Mysterud & Østbye, 1999; Padié et al., 2015). We tested for functional responses in crop use within the home-range (third order selection, Johnson, 1980). We defined availability as the proportion of a given habitat type within each individual's annual home range, using the fixed kernel method at 95% with an ad hoc approach to select the optimal smoothing parameter *h* for each home range estimate (Worton, 1989). We defined crop use as the proportion of locations in a given crop type within an individual's home range. Following Mysterud and Ims (1998) and previous work on this system (Morellet et al., 2011), we regressed proportional use against proportional availability for each crop type, logit-transforming both response and predictor variables to maintain linearity on the logit scale. For each crop type, we fitted a binomial GLMM with a logit link function, including phenological stage (emergence/maturity/post-harvest), time of day, crop availability and 'natural' cover availability as fixed effects, with a random intercept for individual identity to control for repeated observations. We included the four-way interaction to test whether the degree of use of a given crop as forage (mainly night) or cover (mainly day) during certain phenological stages was influenced by its availability and/or the availability of woodlands and hedgerows within the home range.

Analyses were performed in R version 4.0.2 (R Core Team, 2020); the R package 'amt' (Signer et al., 2019) was used for computing home ranges, 'glmmTMB' (Brooks et al., 2017) and 'gamm4' (Wood & Scheipl, 2020) were used to fit GLMM models and 'ggeffects' (Lüdecke, 2018) was used for model predictions.

Results

Crop use in relation to phenological stage

Patterns of use by roe deer varied markedly among crop types (**Figure 1**) and were influenced by both time of day and phenological stage (**Table S2**). For maize, use increased during the late phenological stages (**Figure 1a**, flowering, maturity and post-harvest) and was significantly higher during the day than during the night when it was tall enough to provide cover (flowering and maturity stages, **Table S3**, contrast day/night: odds ratio>2.98, t ratio>7.42, P<0.001). For wheat, use was highest during the night for the emergence and post-harvest stages (day/night: both odds ratios<0.24, t ratios< -9.77, P<0.001), as well as during both day and night for the mature stage (**Figure 1b**). For artificial meadows, use was higher during the night across all phenological stages (day/night: all odds ratios<0.45, t ratios< -5.50, P<0.001) and highest during the early stages (**Figure 1c**).

Potential functional roles of crops

There was a strong day/night contrast in patterns of activity (**Tables S3, S5**) and crop use across crop types and phenological stages (**Figure 2**). Roe deer used mature maize significantly more during the day than during the night (**Figure 2a**, **Table S4**, contrast use day/night: odds ratio=2.99, t ratio=7.42, P<0.001) and exhibited lower activity during the day when doing so (**Table S5**, contrast activity day/night: odds ratio=0.43, t ratio= -3.03, P=0.002). On the contrary, they exhibited a somewhat higher level of use at night (day/night: odds ratio=0.73, t ratios= -1.78, P=0.074) and a higher activity level when using maize during post-harvest (odds ratio=0.26, t ratio= -3.81, P<0.001). Similarly, wheat and artificial meadows were almost systematically used only at night (**Figure 2bc,** day/night: all odds ratios<0.81, all t ratios< -4.1, all P<0.001), except when wheat was mature. Furthermore, roe deer were highly active when using wheat during the emergence and post-harvest stages at night, but significantly more so only during post-harvest (odds ratio=0.35, t ratio= -3.35, P<0.001), and across all stages when using artificial meadows at night (**Figure 2c** all lower CI bounds>0.5 at night).

Influence of landscape composition on crop use across phenological stages

Availability of the crop itself and the availability of ‘natural’ cover (woodland and hedgerows) influenced crop use only for certain crop types, phenological stages and times of day. Roe deer strongly avoided maize irrespective of its availability or of the availability of ‘natural’ cover during emergence (use < availability, **Figure 3a.**). When maize availability was higher than a certain threshold (15-20%) and ‘natural’ cover more abundant (≥24%), roe deer selected maize at night during the post-harvest stage (use > availability, **Figure 3c.**). In contrast, mature maize was selected during daytime only if ‘natural’ cover was less available (≤14%, **Figure 3b.**). In both cases, selection for maize increased with increasing availability, but this relationship depended on the availability of ‘natural’ cover. On the contrary, use patterns for wheat and artificial meadows did not depend on ‘natural’ cover availability (**Figure S3, Figure S4**). Wheat was strongly avoided during daytime during the emergence and post-harvest stages, and was used proportionately to its availability at night, irrespective of its availability (**Figure S3**). Artificial meadows were avoided during daytime across all phenological stages and availabilities and were used proportionately to their availability at night during maturity (**Figure S4**). Roe deer strongly selected artificial meadows during the night and did so progressively more with increasing availability during the emergence stage (**Figure S4**).

Discussion

There is a growing need to better understand how human-driven resource dynamics influence wildlife behaviour in shared areas to promote sustainable coexistence (Abrahms et al., 2021). In this context, our study provides insight on how synanthropic species that are successful in heavily human-impacted landscapes can cope with rapid and sudden modifications of their environment (e.g., cultivation) through behavioural plasticity. We found strong evidence that roe deer adjust their behaviour to spatio-temporal variations in crop phenology within a heterogeneous agroecosystem. Past work on fine-scale responses to crop phenology, mainly on wild ungulates (Branco et al., 2019; Paolini et al., 2018), focused solely on the role of crops as food subsidies. Our unique dataset enabled us to evaluate the potential role of crops as alternative cover habitat for roe deer and to explore how crop phenology and landscape composition influence the trade-off between resource acquisition and risk avoidance, especially when access to ‘natural’ cover is limited. Our results strongly suggest that the functional role of crops for roe deer varied across crop types in relation to their phenological stage, with each type providing contrasting feeding and refuge potential. We demonstrated that certain crops at certain phenological stages, notably mature maize, provide an alternative source of cover in a system where more ‘natural’ refuge habitat is limited. Overall, our study highlights the importance of agricultural practices and landscape composition in determining the reliance of roe deer on cultivated land for food or cover subsidies, potentially shaping the food-risk landscape for this ungulate that has widely adapted to Europe’s agroecosystems.

In agroecosystems, agricultural land is intertwined with more ‘natural’ habitats to form a complex matrix shaped by both natural and anthropogenic factors (Fahrig et al., 2011). Many species thrive in these highly heterogenous agricultural landscapes (Linnell et al., 2020; Smith et al., 2020), but little is known about how they navigate among crop types that provide very different resources in terms of food and cover at specific times of the year. In the predominantly cultivated landscape of our study area, maize, wheat, and artificial meadows each appear to provide alternative food resources for roe deer, but only during specific phenological stages. We found that roe deer used these three crops mostly at night and during phenological stages when the crops were either more palatable (emerging wheat, early stages for meadows, Abbas et al., 2013), or provided a high energetic content (post-harvest maize and wheat, Abbas et al., 2011). Indeed, when using these crops at night, roe deer exhibited high activity levels that were indicative of foraging (Bonnot et al., 2020). These observations, thus, suggest that roe deer used maize, wheat, and artificial meadows as complementary resources, selectively foraging in different crop types in relation to the timing of agricultural interventions (e.g., sowing, harvesting). Seasonal variations in diet composition have previously been documented in cervids across a wide range of environments (Spitzer et al., 2020). Specifically, in this agroecosystem, crops, notably maize and wheat, represented a high proportion of their diet during summer and autumn (Abbas et al., 2011, 2013), which is when crop harvesting occurs (**Figure S2**).

Similarly, these authors showed that grasses and forbs could constitute a substantial part of the roe deer's diet during spring, corresponding to the early phenological stages of meadows in our study area (**Figure S2**). This plasticity in feeding behaviour presumably plays an important role for determining individual performance and population dynamics in agroecosystems, as opportunistically switching between crops and 'natural' vegetation likely leads to faster body growth of new-born fawns during spring/summer and higher reproductive success by weaning (Hata et al., 2021), during autumn. Note, however, that we did not account for phenological changes in resource availability in more 'natural' habitats, such as woodlands and hedgerows. To better understand how the interplay between 'natural' and agricultural forage availability defines the foodscape for wild herbivores living in agroecosystems, future studies should investigate whether they substitute crops for woodlands in relation to woodland plant phenology (Morellet et al., 2011), especially when resources are scarce or when energetic demands are high, such as during gestation and lactation.

In highly modified landscapes such as agroecosystems, where natural habitats are scarce and the risk of human disturbance is high (Bonnot et al., 2013; Padié et al., 2015), the fact that certain crops, at certain phenological stages, could provide an alternative source of refuge for wildlife has been largely overlooked (but see Bonnot et al., 2013; Llaneza et al., 2016). A key finding of our study is that common crops, such as maize and wheat, also provided refuge habitat for roe deer at certain phenological stages. Roe deer used maize more during the day than at night solely when it was mature, and were less active when doing so, suggesting that they exploited maize primarily for resting when it was tall enough to provide cover. Similarly, a previous study observed that wolves living in human-dominated landscapes occasionally used maize and grasslands for resting during the day, with 5.8% of their long-term diurnal bed sites found in croplands (64.5% grasslands and 32.3% corn, Llaneza et al., 2016). In contrast, roe deer were active during both night and day when using mature wheat, irrespective of woodland and hedgerow availability, but avoided wheat during daytime during all other phenological stages. Therefore, we hypothesize that roe deer used this habitat for both cover and food during summer, as mature wheat can conceal a standing roe deer (pers. obs., **Figure S6**). Although resting (vs. not resting) behaviour is robustly identified using activity levels (Augustine & Derner, 2013), future work should combine detailed analyses of diet composition with behavioural predictions derived from accelerometer data (Brown et al., 2013) to determine if, when and how various crop types contribute to the roe deer's food and cover landscape within agroecosystems.

Animals may satisfy their resource needs by moving between different habitat types offering similar, substitutable, resources (Dunning et al., 1992). For example, roe deer in this same agricultural landscape used hedgerows as a substitutable habitat for woodlands to provide cover when the latter was rare (Morellet et al., 2011). Similarly, here we showed that roe deer substituted mature maize for woodlands and hedgerows during the day, as selection for maize increased when 'natural' cover availability decreased (≤24%). Most of the roe deer in our study occupied home ranges with little woodland/hedgerows (mean proportion 28% ± 0.21 s.d., **Figure S5**), underlining that plasticity in habitat use is likely a key factor in determining the persistence of wildlife populations in human-dominated agricultural areas. Indeed, the habitat selection decisions of roe deer concerning maize depended on its local availability, as well as the availability of more 'natural' cover in the home range. Specifically, mature maize was not selected during the day and post-harvest maize was avoided at night when it made up <20% of the home range, suggesting what Holling (1959) termed as a type IV functional response. Functional responses were initially conceptualized to describe how the intake rate of a consumer varies with resource availability (or density) but can be transposed to habitat selection to understand how habitat preference is conditional on availability in the local landscape (Mysterud & Ims, 1998). Holling considered that type IV responses implied a "threshold of security" below which the strength of stimuli linked to a resource is low, but above which it is high. In this context, we interpret this threshold as indicative of the costs associated with using maize relative to a roe deer's perception of risk, particularly when risk is high due to intense hunting during summer and autumn. We suggest that mature maize was only selected for when it was sufficiently abundant, and when levels of 'natural' cover were low, as exploiting these crops as refuge habitats may be perceived as too risky when 'natural' cover is easily accessed. Similarly, post-harvest maize was used disproportionately to its availability when it was sufficiently abundant, and when the availability of refuge habitat in the surrounding landscape was high, implying that maize may be perceived as a highly rewarding, but high-risk, foraging habitat (Bonnot et al., 2013; Bonnot et al., 2018). Despite these general patterns, there was pronounced inter-individual variation in observed responses to crops and their phenology. We speculate that this may result from individual differences in risk perception, with ‘bold’ individuals more inclined to forage in riskier habitats (spider: Steinhoff et al., 2020), such as autumn crops (roe deer: Bonnot et al., 2018). Linking individual variation in patterns of crop use with survival and reproduction would help to further understand how resource variability, risk perception and human interventions shape individual performance in a human-dominated landscape (Simon & Fortin, 2020).

Author contributions

Noa Rigoudy, Simon Chamaillé-Jammes, Nicolas Morellet and A.J. Mark Hewison conceived the ideas and designed the study; all authors collected the data and discussed the analytical approach; Noa Rigoudy, Simon Chamaillé-Jammes and Nicolas Morellet designed the methodology and Noa Rigoudy analysed the data with the help of Simon Chamaillé-Jammes and Nicolas Morellet; Noa Rigoudy wrote the first draft of the manuscript and all authors contributed critically to revision.

Statement on inclusion

Our study involved scientists based in the country where the study was carried out as well as local stakeholders who work within or close to the study area. These stakeholders participated in providing data and expertise on estimating crop phenology. Each stakeholder was sent a summary of the findings of this study and was able to provide feedback on this work.

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Data availability statement

We confirm that, should the manuscript be accepted, the data supporting the results will be archived in Zenodo.

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Figure 1. Predicted probability of crop use according to phenological stage and time of day for three crop types: (a) maize, (b) wheat, (c) artificial meadow based on, respectively, (a) 54, (b) 90 and (c) 98 individuals. Points are predicted marginal means estimated using binomial GLMMs with associated 95% confidence intervals (mean +/- CI).

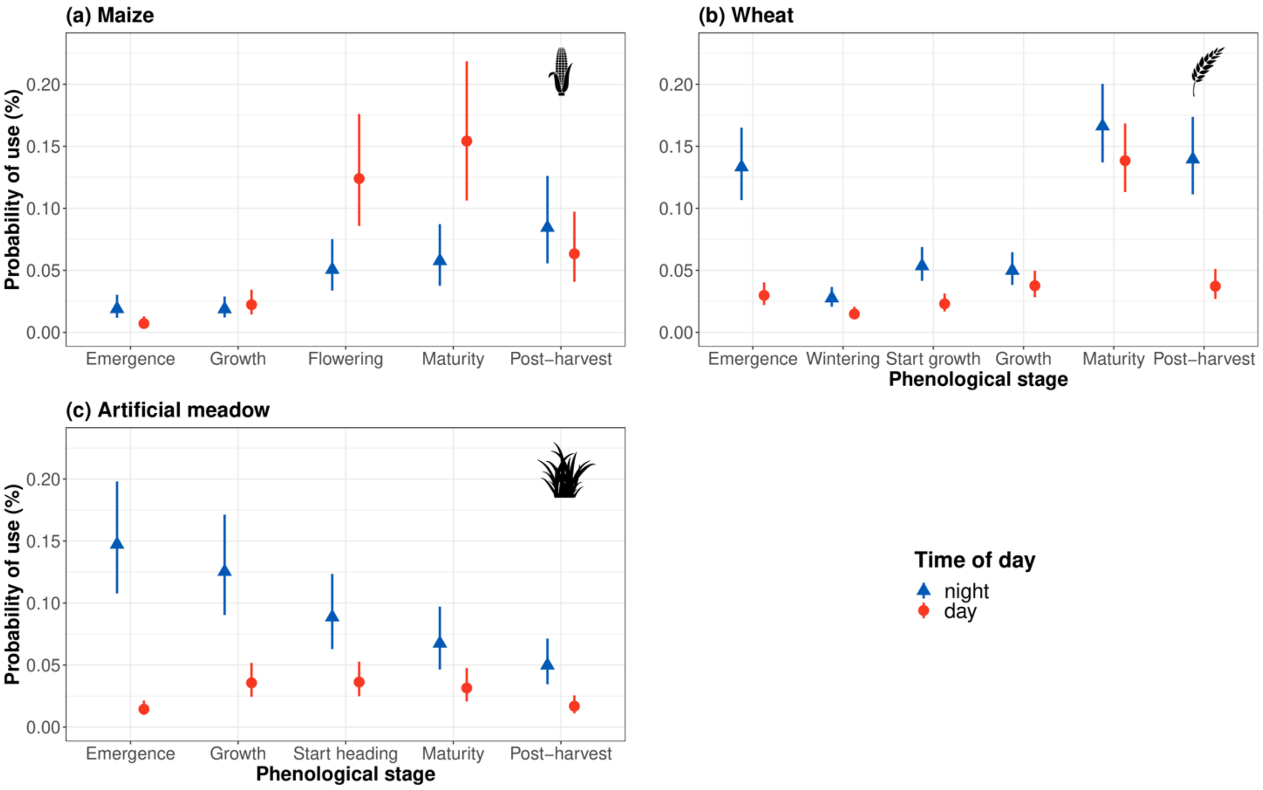

Figure 2. Log odds ratios of use during the day versus night plotted against predicted probability of activity for the emergence, maturity and post-harvest stages of three crop types: (a) maize, (b) wheat and (c) artificial meadow. Odds ratios were calculated using contrast analyses on predictions from models of crop use; activity level was estimated using binomial GLMMs. Points represent predicted marginal means and log odds ratios with associated 95% confidence intervals. Vertical and horizontal grey lines represent 50% activity level and an odds ratio of 1 for day to night use.

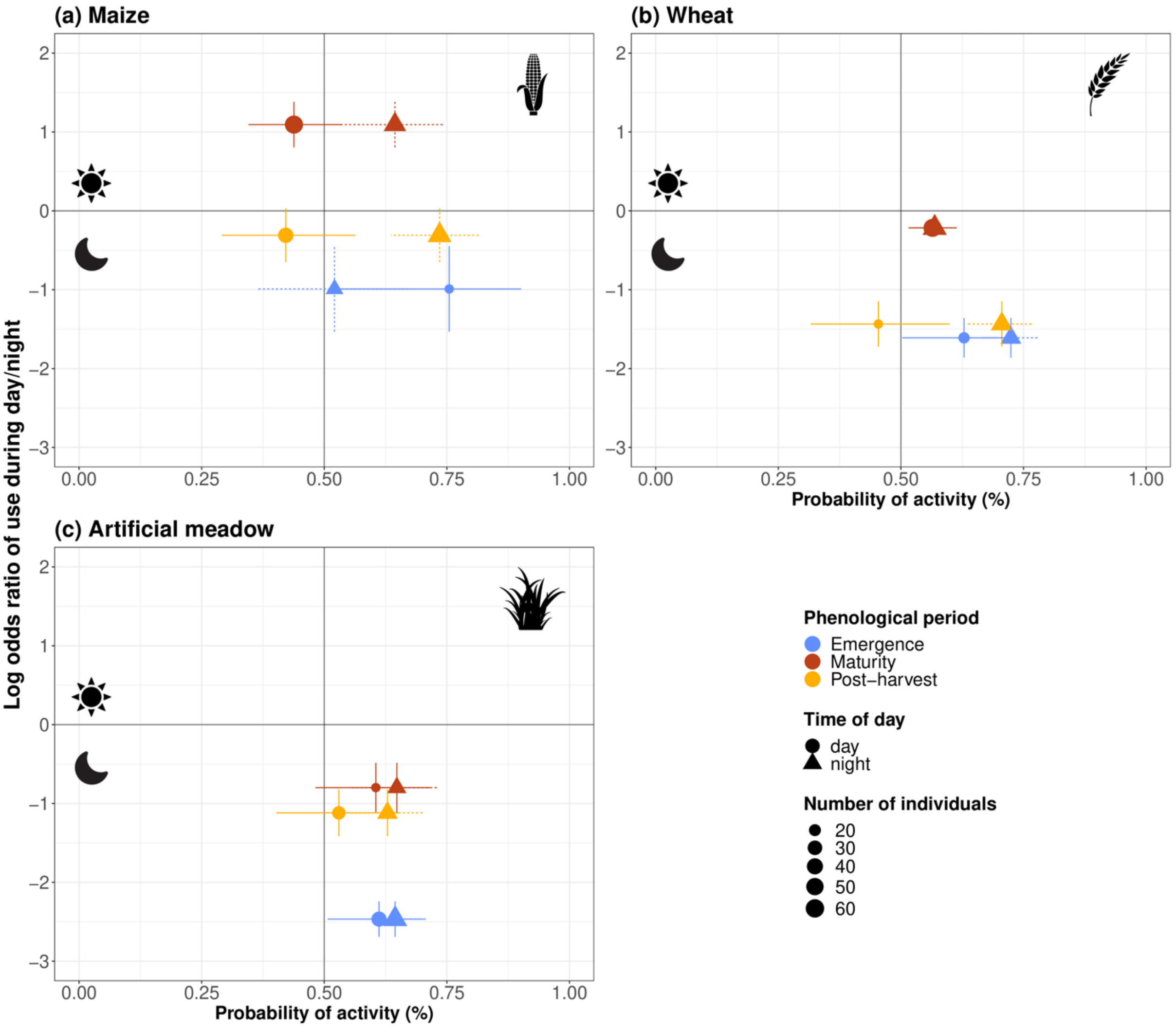

Figure 3. Predicted probability of use of maize during (a) emergence, (b) maturity, (c) post-harvest plotted against its availability in the home range (HR) during the day and night for different proportions of 'natural' cover (woodlands and hedgerows) in the HR (14%, 24%, 35%, illustrated by the black tree icons). Coloured lines represent mean predicted probabilities with associated 95% confidence intervals estimated using logistic regressions. Points represent the observed proportion of used and available maize within the HR for each roe deer. Predictions are not represented beyond the values of availability present in the data. The diagonal black line represents the (1:1) ratio where use is equal to availability.