ORIGINAL RESEARCH

Time series enable the characterization of small-scale vegetation dynamics that influence fine-scale animal behavior – an example from white storks' foraging behavior

Ines Standfuß[1,2] (iD), Christian Geiß[1,2], Ran Nathan[3], Shay Rotics[3], Martina Scacco[4], Grégoire Kerr[5] & Hannes Taubenböck[1,2]

[1]German Aerospace Center (DLR), German Remote Sensing Data Center (DFD), Oberpfaffenhofen, Germany
[2]Institute for Geography and Geology, University of Würzburg, Würzburg, Germany
[3]Movement Ecology Laboratory, Department of Ecology, Evolution and Behaviour, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel
[4]Department Animal Migration, Max Planck Institute of Animal Behavior, Radolfzell/Konstanz, Germany
[5]OHB Systems AG, Oberpfaffenhofen, Germany

Abstract

Agricultural activities and vegetation growth cause rapid small-scale vegetation changes which dynamically alter habitat suitability. Time series enable to track down such variations of vegetation structure and are promising to examine their impact on animals' life. Nevertheless, their potential to characterize vegetation dynamics in ways pertinent to animals' fine-scale habitat use has not been adequately explored and ecologically meaningful proxies are lacking. To address this gap, we exemplary investigated foraging activities of breeding white storks in an agricultural landscape. Reflecting on the understanding that storks require short vegetation to access prey, we examined if good foraging conditions – early growth and post-harvest/mowing periods – are detectable using the points between local minima/maxima in NDVI profiles (half-maximum). We processed 1 year of Landsat imagery to identify half-maximum periods (HM: good prey access) and non-half-maximum periods (non-HM: poor prey access) on field-scale in croplands and grasslands. Additionally, we mapped used/unused fields and retrieved foraging duration/daily visitation rates from GPS tracks of the storks. We then explored habitat use, compared habitat use with habitat availability and tested temporal predictors distinguishing between HM/non-HM in habitat selection models. Examining habitat use, storks revisited croplands and grasslands significantly more often during HM than during non-HM, while foraging duration was only prolonged in croplands during HM. However, comparing habitat use with habitat availability, we observed that storks used croplands and grasslands in significantly higher proportions during HM than during non-HM. Additionally, we found that temporal information affected storks' habitat selection and improved model performance. Our findings emphasize that the half-maximum proxy enables to coarsely distinguish temporal resource variations in storks' foraging habitats, highlighting the potential of time series for characterizing behaviorally-relevant vegetation dynamics. Such information helps to create more species-centered landscape scenarios in habitat models, allowing to unravel effects of small-scale environmental changes on wildlife to ultimately guide conservation and management.

Introduction

Animal habitats are continuously altered by natural and man-made processes (Foley et al., 2005; Newbold et al., 2015; Vitousek, 1997). Remote sensing time series can capture a wide range of these environmental dynamics from small to large spatiotemporal scales (Kerr & Ostrovsky, 2003). Linked to animal behavior, movement and habitat use retrieved from GPS-telemetry, they provide unparalleled means to analyze effects of environmental alterations on animals' lives (Kays et al., 2015; Nathan et al., 2008; Pettorelli et al., 2011). At present, time series-derived proxies remain relatively underused in wildlife studies (He et al., 2015) and are primarily applied to characterize vegetation phenology at large spatial scales (Neumann et al., 2015; Pettorelli et al., 2014). Studies investigating the green wave hypothesis, for example often used the instantaneous rate of green-up to demonstrate that many herbivorous species synchronize their foraging habitat selection with the peak in vegetation green-up during spring migration (Bischof et al., 2012; Merkle et al., 2016; Wang et al., 2019). Fine-scale movements and behaviors of animals are in contrast to migration, much less affected by phenology (Neumann et al., 2015) and rather influenced by short-term changes in vegetation structure, for example through human activities. However, characterization of these small-scale dynamics using temporal proxies is, to our knowledge, not yet established in ecological research.

In addition to phenology, vegetation characteristics in the small-scale landscape mosaic are influenced by agricultural practices (Latus & Kujawa, 2005; Rodríguez et al., 2013). Activities like vegetation removal through mowing/harvest can significantly alter habitat suitability in the short term (Dunning et al., 1995; Johst et al., 2001; Pfeifer & Brandl, 1991). One positive result is a temporary increase in abundance and a restored accessibility of prey for species relying on short vegetation for foraging (Peggie et al., 2011; Vickery et al., 2001). By contrast, negative consequences arise for meadow breeders whose nesting sites and broods often succumb to agricultural practices (Green et al., 1997; Grübler et al., 2008). Gaining a comprehensive understanding of how small-scale environmental drivers influence animals' habitat use, selection and distribution as well as their individual fitness and population demographics is critical for animal ecology and conservation. Consequently, temporal information on small-scale vegetation dynamics are urgently needed to monitor, understand and predict their effects on wildlife to ultimately guide conservation and management (Dunning et al., 1995; Kerr & Ostrovsky, 2003; Pettorelli et al., 2014; Pressey et al., 2007).

To date, the dynamics in the small-scale landscape mosaic have often been overlooked (Johst et al., 2001) or the proxies used have not been tailored to the behavioral needs of the studied species (Cord et al., 2013; Roever et al., 2013). One example of such shortcomings are studies exploring foraging activities of breeding white storks; a synanthropic species that benefits from agricultural practices. Due to the growing human footprint, the storks' European breeding territories are increasingly composed of croplands and grasslands (Johst et al., 2001; Olsson & Rogers, 2009). Part of these potential foraging habitats is not available throughout their breeding season (~April–August) because vegetation becomes too tall during summer, making it difficult for storks to access prey (Böhning-Gaese, 1992; Pfeifer, 1989). Mowing and harvest activities, however, re-expose their prey, though often for limited periods (Pfeifer, 1989; Pfeifer & Brandl, 1991). Although well recognized (Alonso et al., 1991; Moritzi et al., 2001; Olsson & Rogers, 2009; Rachel, 2006), these vegetation dynamics received no attention in quantitative research. Earlier studies characterized storks' breeding areas primarily with landcover classifications such as CORINE (Gadenne et al., 2014; Radovic & Tepic, 2009), seldomly supplemented by single-date vegetation indices, typically NDVI from MODIS time series (Zurell et al., 2018). Foraging habitats were therefore either viewed statically or at specific points in time. Additionally, due to the low spatial resolution of MODIS (250 m) and CORINE (10 ha) data, vegetation properties from small fields have likely been blended together frequently (Bischof et al., 2012; Gao et al., 2017). Previous analyses have therefore failed to capture the small-scale vegetation structure and dynamics critical for storks' prey accessibility, which according to Johst et al. (2001), can lead to erroneous conclusions regarding their habitat selection strategy.

Time series from medium-resolution sensors enable to characterize effects of natural and human-induced vegetation dynamics (Kerr & Ostrovsky, 2003; Nagendra et al., 2013) and hold promise for studying fine-scale animal behaviors (Neumann et al., 2015; Pettorelli et al., 2011). The currently active Landsat satellites provide free imagery with 30 m spatial resolution and a default revisit rate of 8 days (Chastain et al., 2019). Using these data, intra-annual vegetation profiles, like daily-resolved NDVI, can be derived for fine-scale habitat features like individual fields (Fig. 1) (Gao et al., 2017; Roy & Yan, 2018). These allow characterizing intra-annual vegetation development (Pettorelli et al., 2005) and can capture effects of harvest/mowing which are known to cause a decline of NDVI (Estel et al., 2015; Gao et al., 2017; Griffiths et al., 2020). As

an established indicator for leaf-unfolding/loss of canopy structure, the so-called half-maximum (Fig. 1) marks the points between local minima/maxima in NDVI profiles (Bradley et al., 2007; Fisher et al., 2006). It has been successfully applied and validated to delineate spring green-up/post-harvest periods in croplands (Estel et al., 2016) and should also be applicable in grasslands where the detection of mowing events underlies similar principles (Estel et al., 2018; Griffiths et al., 2020). Although the Landsat-based half-maximum cannot determine exact harvest/mowing dates, it should allow to roughly identify periods with good prey accessibility – hereafter termed half-maximum periods (HM) (Fig. 1) – for species whose foraging success depends on short vegetation. Nevertheless, the potential of time series for deriving such ecologically relevant dynamic information remains to be tested.

Here, we aim to characterize small-scale vegetation dynamics in an agricultural landscape with time series and explore their potential for studying animals' fine-scale habitat use. As a test case, we focus on landscape-oriented foraging activities of breeding white storks. We use Landsat time series to derive information on intra-annual vegetation dynamics that we assume are related to differences in prey accessibility for storks: the half-maximum proxy on field level. Used and unused fields, foraging duration and daily visitation rates are obtained from GPS-telemetry data of storks breeding in Germany. We first investigate storks' habitat use by comparing foraging duration/daily visitation rates of fields during HM with those of fields during non-half-maximum periods (non-HM) (Fig. 1). Next, we explore whether the observed daily proportions of foraging time in these habitats result from their relative availability or instead are indicative for selection/avoidance. Finally, we contrast foraging habitat selection models fitted with and without temporal predictors that allow discriminating between HM/non-HM. We base our hypotheses on studies showing that breeding storks primarily forage on croplands and grasslands after agricultural activities or during the early growing season when vegetation is short (Alonso et al., 1991; Böhning-Gaese, 1992; Rachel, 2006; Thomsen & Struwe, 1994). Assuming the investigated time series and proxy allow us to identify these favorable conditions, we expect (1) to observe longer foraging duration/higher daily visitation rates on fields during HM compared to non-HM; (2) fields during non-HM to be avoided as these should limit prey accessibility; and (3) that temporal predictors that enable a discrimination between HM/non-HM are associated with foraging habitat selection and improve model performance compared to predictors without such temporal information.
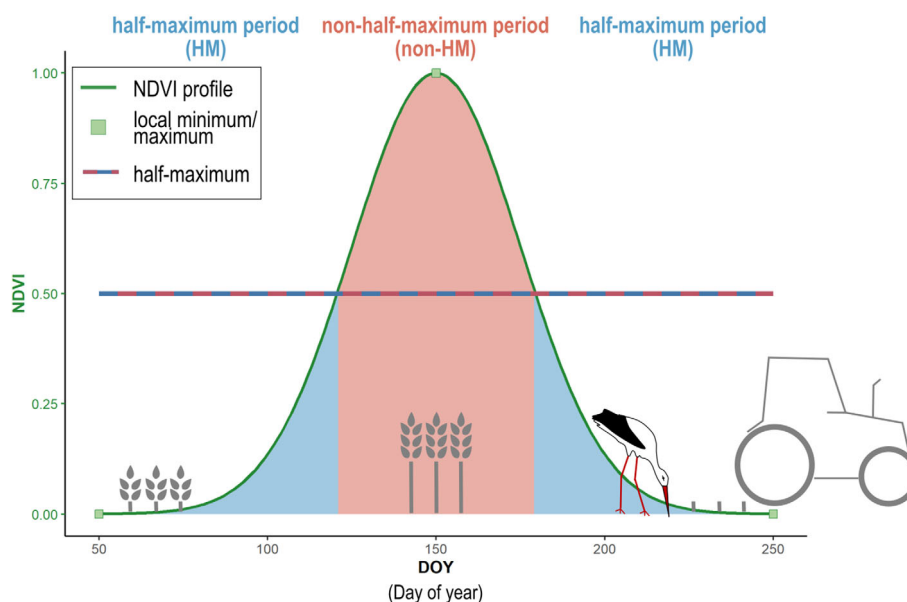

Figure 1. Hypothetical (Gaussian) representation of an intra-annual NDVI profile of a single field with half-maximum (HM) and non-half-maximum periods (non-HM). The half-maximum marks the point between local minima and maxima in NDVI profiles and has been applied to discriminate early vegetation growth and harvest phases (Bradley et al., 2007; Estel et al., 2016; Fisher et al., 2006). The index might therefore be useful for identifying periods of potentially good or poor conditions of prey accessibility for species whose foraging success depends on short vegetation.

Materials and Methods

Study areas

The breeding areas of the studied storks are located in north-eastern Germany between Berlin, Hanover and Hamburg (Fig. 2A). The considered sites are dominated by agricultural land use with high shares of croplands (47–56%) and low to medium amounts of cultivated grasslands (6–32%) (Supplementary Material of Zurell et al. (2018)). We delimited the extent of our study areas using a radius of 3.3 km around the nest of each stork. This distance corresponds to the 95th percentile of the measured nest distances of all foraging locations recorded during the considered breeding season (see next section).

Telemetry: derivation of foraging locations, duration and visitation rates

To retrieve storks foraging locations, foraging duration and daily visitation rates we utilized e-obs telemetry data

of 18 breeding individuals from 2014, with a 5-min temporal resolution and a movement behavioral class provided for every location (Rotics et al., 2016) (Fig. 2B). Initially, we excluded the migration periods, i.e. days with covered distances larger than 100 km (Flack et al., 2016), to limit the observations to the breeding season. The latter was bounded by the days between the first stork arriving at (27 March 2014) and the last stork leaving the breeding territory (18 August 2014). Since storks forage while walking and stop only for short resting periods (Carrascal et al., 1990), we sampled locations classified as walking/resting. We allocated the samples to individual foraging bouts which were subdivided when a stork had returned to its nest or the distance covered between two locations exceeded 500 m (Alonso et al., 1991) and excluded resting periods lasting longer than 10 min. Continuous movement trajectories provide more reliable estimates of habitat use than individual locations (Fleming et al., 2016). Hence, we applied continuous-time movement modeling (using the R package *ctmm* (Fleming &
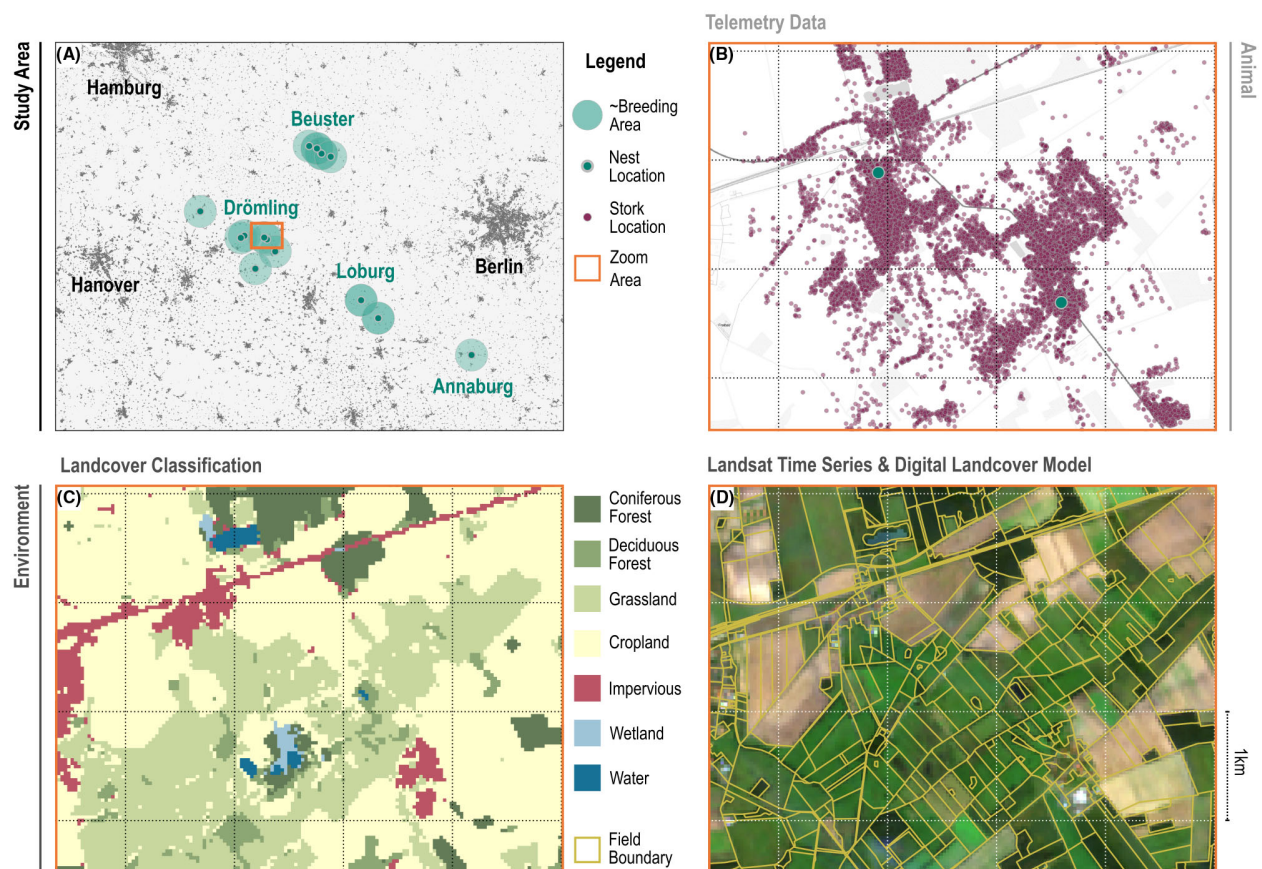

Figure 2. Overview of the locations of the breeding areas of the studied white storks in north-eastern Germany (A) and the data utilized for the analyses (B–D). The latter comprise e-obs telemetry data of 18 white storks of 2014 (Rotics et al., 2016) (B), time series of Landsat 7 and Landsat 8 data from 2014 (D), a digital landcover model with field geometries from 2012 (BKG, 2016) (D) and a landcover classification from 2014 (Mack et al., 2016) (C). Map data basis in (A): Global Urban Footprint (GUF) (Esch et al., 2017).

Calabrese, 2020)) to simulate up to 1000 – until convergence – movement paths per foraging bout. To detect foraging locations and quantify habitat use, we spatially linked the simulation sets with field geometries retrieved from the Digital Landcover Model of Germany (BKG, 2016); a vector database of environmental objects from 2012 (Fig. 2D). The foraging duration in a field per foraging bout and stork corresponds to the median drawn from one simulation set. The daily visitation rate per field equals the number of daily foraging bouts in which the storks used a given field divided by the number of storks that visited that field on that day. See Text_S1 for methodological details.

Remote sensing: derivation of vegetation dynamics on field-level

To characterize small-scale vegetation dynamics, we used time series of Landsat 7 Enhanced Thematic Mapper+ (ETM+) and Landsat 8 Operational Land Imager (OLI) data (Fig. 2D). We acquired all available ETM+ and OLI scenes (Level 1 – Tier 1) with cloud coverage below 100% for the year 2014, covering the storks' breeding areas. In total, we used 128 scenes (ETM+: 55 and OLI: 73) distributed among five spatial tiles with the number of scenes per tile ranging from 20 to 31 (Fig. 3A and B). We pre-processed each scene (see Text_S2) and computed the NDVI. Next, we linked the time series with the field geometries (Digital Landcover Model of Germany (BKG, 2016)) and derived the spatial median of NDVI for every field and time step. To ensure temporal representativity of vegetation dynamics over the breeding season, we only retained fields with at least six valid acquisitions during that time (Fig. 3C–F), as suggested in Franke et al. (2012). We used a pre-existing Landsat-based landcover classification from 2014 (Mack et al., 2016) to sample cropland and grassland fields and eliminated objects with different landcover type (Fig. 2C). Next, we generated interpolated NDVI profiles with 1-day temporal resolution for every field through thin-plate spline curve fitting (Duchon, 1977), using the R package *fields* (Nychka et al., 2017). Aggregated NDVI profiles retrieved from the individual cropland and grassland fields are displayed in Figure 3G and H. We extracted the half-maximum to delimit the periods that we assumed to be related to differences in storks' prey accessibility. Unlike previous studies (Bradley et al., 2007; Estel et al., 2016; Fisher et al., 2006), we did not determine a global half-maximum for the whole year (Fig. 1), but instead derived local half-maxima between successive minima and maxima from the NDVI profiles of each field. We labelled days with NDVI below the local half-maximum day NDVI as HM and those above as non-

HM. We expected these periods to represent good (HM) and poor (non-HM) foraging conditions for storks, respectively.

Habitat use related to vegetation dynamics

We examined habitat use in croplands and grasslands based on the individual foraging duration and daily visitation rate per field. Storks are known to forage longer in fields with favorable foraging conditions and/or to visit them more often (Alonso et al., 1991; Johst et al., 2001). To explore if the foraging duration/daily visitation rate per field are higher in fields during HM than during non-HM, we compared the distributions of these measures against each other. The significance of the differences (HM > non-HM) was determined using the Wilcoxon signed-rank test. Storks' foraging duration increases naturally as the breeding season progresses, because adults can spend longer times away from the nest when the offspring reaches a certain age (Böhning-Gaese, 1992; Moritzi et al., 2001). We therefore analyzed habitat use on a monthly basis. Foraging duration and daily visitation rates from March and April were combined as the breeding season started at the end of March (27 March 2014).

Comparison of habitat use versus habitat availability

Next, we explored if storks' use of the four studied habitat types – croplands and grasslands during HM and non-HM – reflects their relative availability or instead resulted from selection/avoidance. We compared use/availability on a daily basis, focusing on the entire stork population (18 individuals) but incorporating use/availability shares of each individual separately (design III following (Thomas & Taylor, 1990)). We derived population-level selection ratios using the Manly Selectivity Index (Manly, 2002). This index can be computed for each habitat with the following equation:

$$\hat{w}_i = u_{i+} / \sum_{j=1}^{n} \pi_{ij}\, u_{+j}$$

where u_{i+} is the proportion of foraging time on habitat i of all storks, u_{+j} is the total foraging time of the j_{th} stork and π_{ij} is the available proportion of habitat i to stork j. For each stork, we defined the proportion of available habitat as the number of fields of habitat type i compared to the total number of cropland and grassland fields within its breeding area. $\hat{w}_i$ can range from zero to infinity and values close to one suggest that use is proportional to the availability. Values that are significantly below or above one are indicative for avoidance or
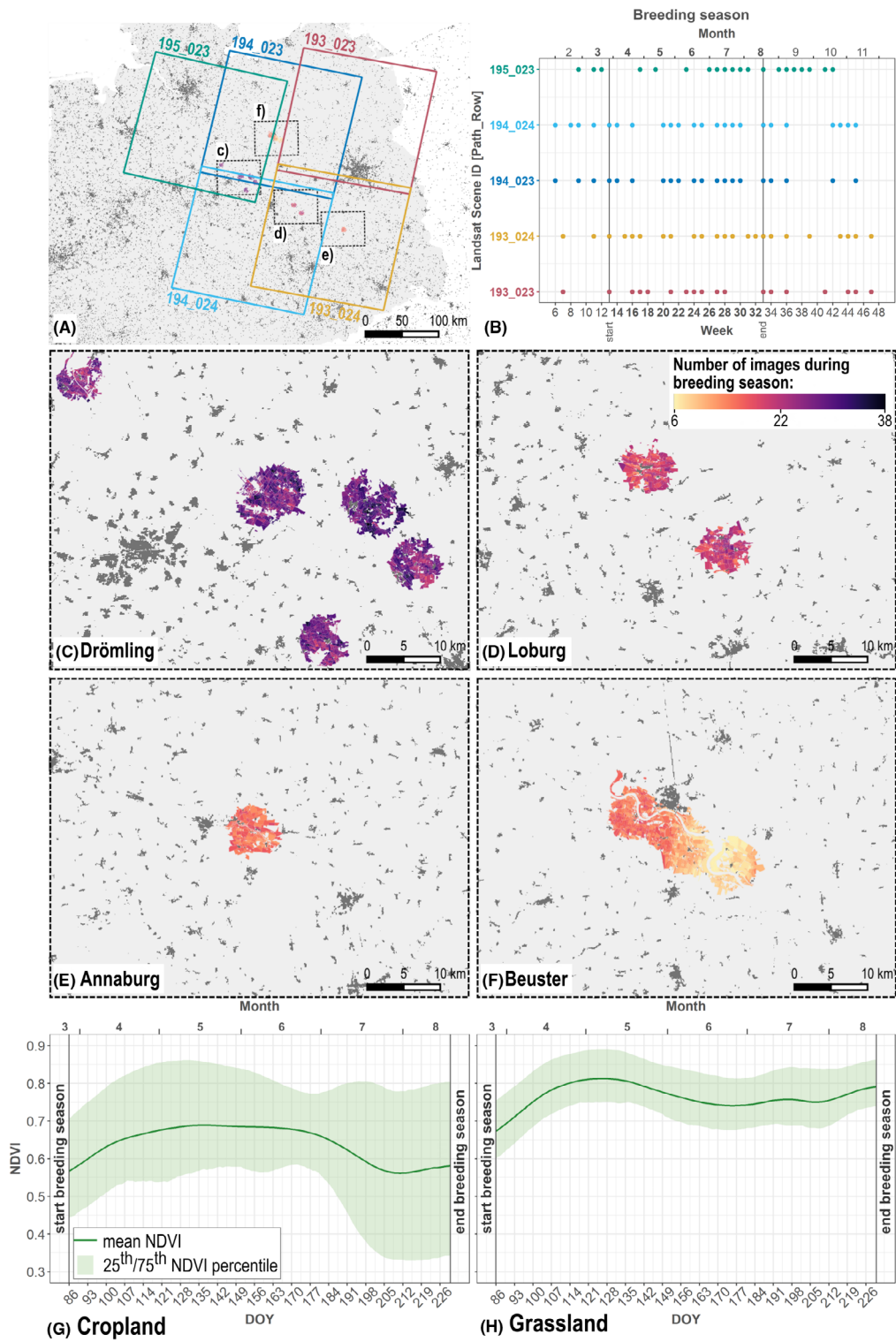
(A)

(B) Breeding season

(C) Drömling

(D) Loburg

Number of images during breeding season: 6 22 38

(E) Annaburg

(F) Beuster

(G) Cropland

(H) Grassland

mean NDVI
25th/75th NDVI percentile

Figure 3. Overview of the temporal coverage of the study area with Landsat 7 (ETM+) and 8 (OLI) imagery and the resulting NDVI profiles of the fields under consideration. (A) A map with the location of the four study regions and breeding areas as well as their spatial coverage by Landsat tiles. (B) A weekly breakdown of Landsat data availability for each Landsat tile in 2014. (C–F) The cropland and grassland fields considered within this study together with information on the number of valid images that were available for each field during the breeding season 2014. Aggregated NDVI profiles of the studied cropland and grassland fields including their variance (mean and 25th–75th percentile) are displayed in (G and H), respectively. Mean, 25th and 75th percentile were derived for each day (DOY 86–230) using the interpolated NDVI values from all fields (separately for croplands (2855 fields) and grasslands (2908 fields)) in the storks' breeding areas. Map data basis: Global Urban Footprint (GUF) (Esch et al., 2017). ETM+, Enhanced Thematic Mapper+; OLI, Operational Land Imager.

selection, respectively. We tested the significance of $\hat{w}_i$ by estimating its standard error SE $(\hat{w}_i)$, calculating the following statistic:

$$\{(\hat{w}_i-1)/SE(\hat{w}_i)\}^2$$

and comparing it with critical values for the chi-squared distribution with one degree of freedom (Manly, 2002). The computation of $\hat{w}_i$, their statistical significance and 95% confidence intervals with Bonferroni correction (Manly, 2002) were performed using the R package *adehabitatHS* (Calenge, 2006). Lastly, we examined which habitat type – HM or non-HM – was used at higher proportions relative to its availability in croplands and grasslands. Thus, we compared the daily distributions of $\hat{w}_{\mathrm{HM}j}$ and $\hat{w}_{\mathrm{non\text{-}HM}j}$ values (single-stork selectivity indices) per landcover type and used the Wilcoxon signed-rank test to determine if either of them had significantly higher values than the other. See Text_S3 for methodological details.

Habitat selection modeling

Finally, we investigated if the probability of fields being used as foraging habitats by storks can be associated with temporal proxies that enable to discriminate HM/non-HM, and if these can improve model performance compared to common predictors. We employed a binary response variable that distinguishes visited and non-visited fields throughout the breeding season. As no true absences (non-visited fields) were known, we followed the approach suggested by Zurell et al. (2018): for each cropland/grassland field that the storks' visited during a foraging bout (presences), we randomly sampled three fields (pseudo-absences) of the same landcover type within 1 km distance, making sure the three selected were not used within 4 weeks around the visit. For every presence/pseudo-absence field, we derived a set of five predictor variables (Fig. 4): Distance (1) and NDVI (2) are common proxies in studies addressing storks foraging habitat selection. They characterize the decrease in habitat quality for central place foragers – like breeding storks – with increasing distance from their nest (Olsson & Bolin, 2014) and the vegetation status of the fields at the visiting day (Zurell et al., 2018), respectively. We further introduced two proxies that enable to differentiate between HM/non-HM: The half-maximum amplitude (HM_Amp) (3) measures

the relative difference between NDVI during a visiting day and NDVI at the closest local half-maximum day(s) (Fig. 4). It is positive during HM and negative during non-HM. The half-maximum distance HM_Dist (4) measures the absolute distance (days) of a visiting day to the nearest local half-maximum day on the fields (Fig. 4). Additionally, NDVI_Range (5) quantifies the absolute difference between the absolute minimum/maximum of an NDVI profile and thus indirectly captures information on vegetation management (Esch et al., 2014; Franke et al., 2012). We modeled habitat selection using all presence/pseudo-absence fields together (croplands and grasslands = combined LC) as well as separately for each landcover type (croplands or grasslands = single LC) with generalized linear mixed models (GLMMs). For every combination (combined and single LC), we fitted seven GLMMs (binomial distribution; maximum-likelihood-estimation) with varying degrees of temporal information (Table 1). Stork identity was included as random effect on the predictors' intercepts/slopes (Muff et al., 2019) and the normalized field-size was considered as offset. Additionally, we added the landcover type in the combined LC models. Prior to modeling, we checked for collinearity between the predictors and did not consider NDVI and HM_Amp together in one model because they were correlated (Pearson's $r > 0.5$). We used the R package *lme4* (Bates et al., 2015) for model fitting and assessed the proportion of total variance explained by the fixed model terms and hence, model performance, with the marginal R^2 (Nakagawa & Schielzeth, 2012).

Results

Throughout their breeding season in 2014, the studied storks spent 3290 ± 405 h (total $\pm$ standard deviation (SD) of simulated movement paths) (~27.5%) of their foraging time in croplands and 8668 ± 994 h (~72.5%) in grasslands. This time was distributed among 7980 and 20 133 field visits, respectively.

Habitat use related to vegetation dynamics

In croplands, we found that foraging duration was longer in fields during HM and that storks tended to visit these fields more frequently than those during non-HM (Fig. 5:
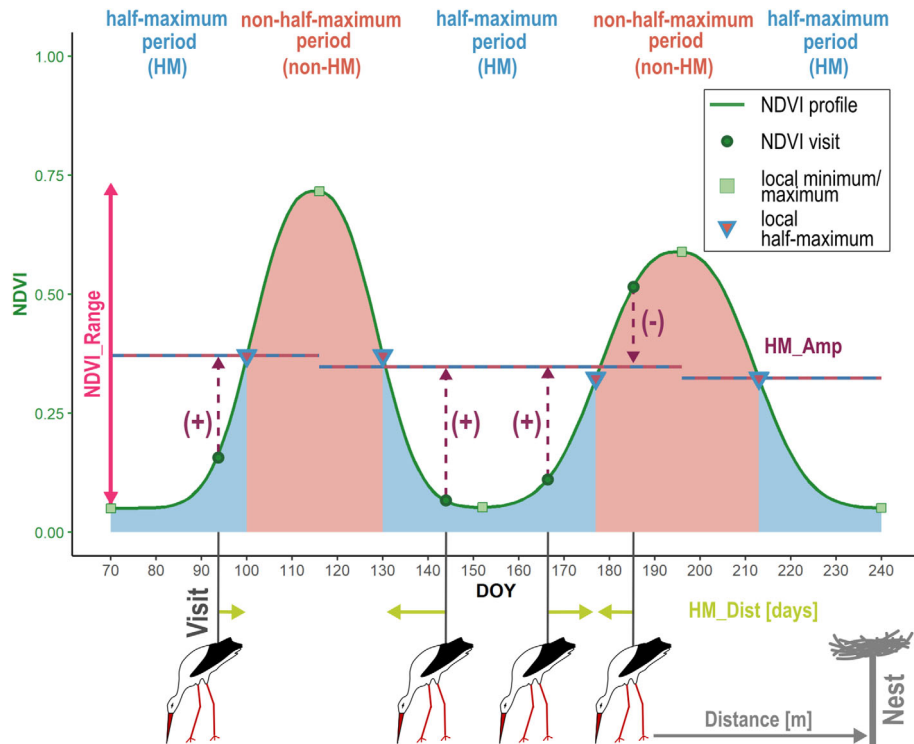
Figure 4. Hypothetical (Gaussian-mixture) representation of an intra-annual NDVI profile of a single field and the proxies we considered for foraging habitat selection modeling within this study. NDVI on a visiting day and distance to the nest have been frequently used to study white storks foraging habitat selection but do not or only indirectly contain information on vegetation development. Half-maximum amplitude (HM_Amp) and half-maximum distance (HM_Dist) are proxies that use temporal information and enable to relate foraging visits relative to HM and non-HM of a field. We assume those periods to be associated with good and poor conditions for prey accessibility of storks, respectively. The NDVI_Range measures the difference between the absolute minimum/maximum of a field and does therefore indirectly capture information on its vegetation management.

1A/B). In grasslands, we also observed higher daily visitation rates of fields during HM than during non-HM in most months (Fig. 5: 2B). However, in terms of foraging duration, no lasting pattern of preference for grassland fields during HM became apparent (Fig. 5: 2A).

Comparison of habitat use versus habitat availability

Throughout most parts of the breeding season, storks significantly avoided croplands during non-HM ($\hat{w}_i < 1$, $P < 0.05$: 80.1% of all days) (Fig. 6: 1). Significant selection over a longer period mainly occurred in grasslands during HM in the middle of the breeding season (~May until mid-July) ($\hat{w}_i > 1$, $P < 0.05$: 46.4% of the breeding season) (Fig. 6: 2). In contrast, storks' use of croplands during HM and of grasslands during non-HM was mostly proportional to the availability of those habitats ($\hat{w}_i \sim 1$, $P \geq 0.05$: cropland 63.6%; grassland 82.1% of the breeding season) (Fig. 6: 1/2).

In both landcover types, the individual storks' field use during HM occurred throughout large parts of the breeding season in higher proportions than field use during non-HM, compared to the relative availability of those habitats ($\hat{w}_{HMj}\sim > \hat{w}_{non-HMj}\sim$) (Table 2: a/c) (Fig. 6: 1/2). For grasslands, however, this difference was significant primarily from mid-May to mid-July, whereas throughout April, storks even used grassland fields during non-HM in significantly higher proportions than fields during HM ($\hat{w}_{non-HMj}\sim > \hat{w}_{HMj}\sim$) (Fig. 6: 2).

Habitat selection modeling

We found that the best-performing habitat selection models – combined and single LC – were the ones fitted with temporal predictors (see detailed model outputs Table 3 [combined LC] and Table_S2 [single LC]). Among those, the models with HM_Amp instead of NDVI could explain a higher share of the overall variance (marginal_R^2 (combined LC): M2 = 0.256 vs. M3 = 0.270).

Table 1. Overview of foraging habitat selection model parameters and their degree of temporal information.

Model	Fixed effect(s) combined LC	Fixed effect(s) single LC	Temporal information	Random effect(s)
Response: presence/pseudo-absence (visit)				
M1	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
				and Slopes)
M2	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	NDVI	NDVI	Partial	and Slopes)
M3	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	HM_Amp	HM_Amp	Yes	and Slopes)
M4	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	NDVI	NDVI	Partial	and Slopes)
	HM_Dist	HM_Dist	Yes	
M5	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	HM_Amp	HM_Amp	Yes	and Slopes)
	HM_Dist)	HM_Dist	Yes	
M6	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	NDVI	NDVI	Partial	and Slopes)
	HM_Dist	HM_Dist	Yes	
	NDVI_Range	NDVI_Range	Yes	
M7	Landcover type		No	Stork_ID
	Distance	Distance	No	(Intercepts
	HM_Amp	HM_Amp	Yes	and Slopes)
	HM_Dist	HM_Dist	Yes	
	NDVI_Range	NDVI_Range	Yes	

Distance and HM_Amp were always – in the combined and single LC models – significant model terms (M3/M5/M7). In particular, our results suggest that storks' habitat selection is negatively influenced by the distance from the nest (combined LC M5: -5.86 ± 1.06 [estimate±SE]) and positively affected by the HM_Amp (combined LC M5: 4.23 ± 0.58) (Fig. 7A/C). HM_Dist (M5) showed a negative, yet only slight effect on habitat selection (combined LC M5: -1.08 ± 0.29) (Fig. 7D), though was not a significant term in all single LC models. Adding the NDVI_Range (M7) positively affected habitat selection in the single LC cropland model but worsened model performance and was not significant in the combined LC and single LC grassland model. Despite its poorer performance relative to HM_Amp, including NDVI in the combined LC and single LC cropland model (M2) improved performance compared to the model considering only non-temporal predictors (M1) (marginal_R^2 (combined LC): M1 = 0.234 vs. M2 = 0.256). Here, we identified a significant negative effect of NDVI on storks' habitat selection (combined LC M2: -1.53 ± 0.29). Interestingly, NDVI had no significant effect in grasslands. Finally, the combined LC models showed that storks tended to select grasslands over croplands (combined LC M5: Landcover [Grassland] 0.50 ± 0.02) (Fig. 7B).

Discussion

Phenology and agricultural activities alter the small-scale vegetation structure of the landscape mosaic, thereby affecting prey accessibility and availability for species such as the white stork (Johst et al., 2001; Pfeifer & Brandl, 1991; Tryjanowski et al., 2005). Since the landscape-oriented foraging behavior of storks is well studied, we used this species to explore the potential of time series for characterizing behaviorally-relevant vegetation dynamics. Reflecting the understanding that storks generally prefer short vegetation for foraging (Moritzi et al., 2001; Sackl, 1989; Struwe & Thomsen, 1991), we attempted to identify early vegetation growth and post-harvest/mowing periods (HM = good conditions) with the half-maximum proxy. Although not all our findings were significant, we found that storks tended to favor foraging during HM (=poor conditions) in croplands and grasslands throughout large parts of their breeding season. Hence, we propose that time series are indeed suitable for deriving ecologically relevant information on small-scale vegetation dynamics.

Storks generally prefer grasslands over croplands (Gadenne et al., 2014; Pfeifer & Brandl, 1991; Radovic & Tepic, 2009). Accordingly, the birds spent more foraging time in grassland fields and were more likely to select grasslands instead of croplands, as indicated by the habitat selection models. However, given the dynamics in agricultural landscapes, both habitat types vary in importance throughout their breeding season (Moritzi et al., 2001). Storks can achieve the largest foraging success during harvest/mowing activities (Thomsen & Struwe, 1994) when prey gets disturbed or killed by agricultural machinery (Peggie et al., 2011).

In croplands, vegetation is removed during harvests and prey retreats quickly after (Catry et al., 2014; Peggie et al., 2011; Sackl, 1989). Although the habitat is known to be visited not only around harvests, foraging conditions beyond this time are unfavorable due to vegetation height and limited prey availability (Alonso et al., 1991; Böhning-Gaese, 1992; Rachel, 2006). Correspondingly, our results showed long foraging duration/high visitation rates in fields during HM and a significant avoidance of fields during non-HM throughout the breeding season. Although the birds' use of croplands during HM was mostly proportional to its availability, we sporadically identified selective use in early May/August. An explanation is given by Rachel (2006), who observed a
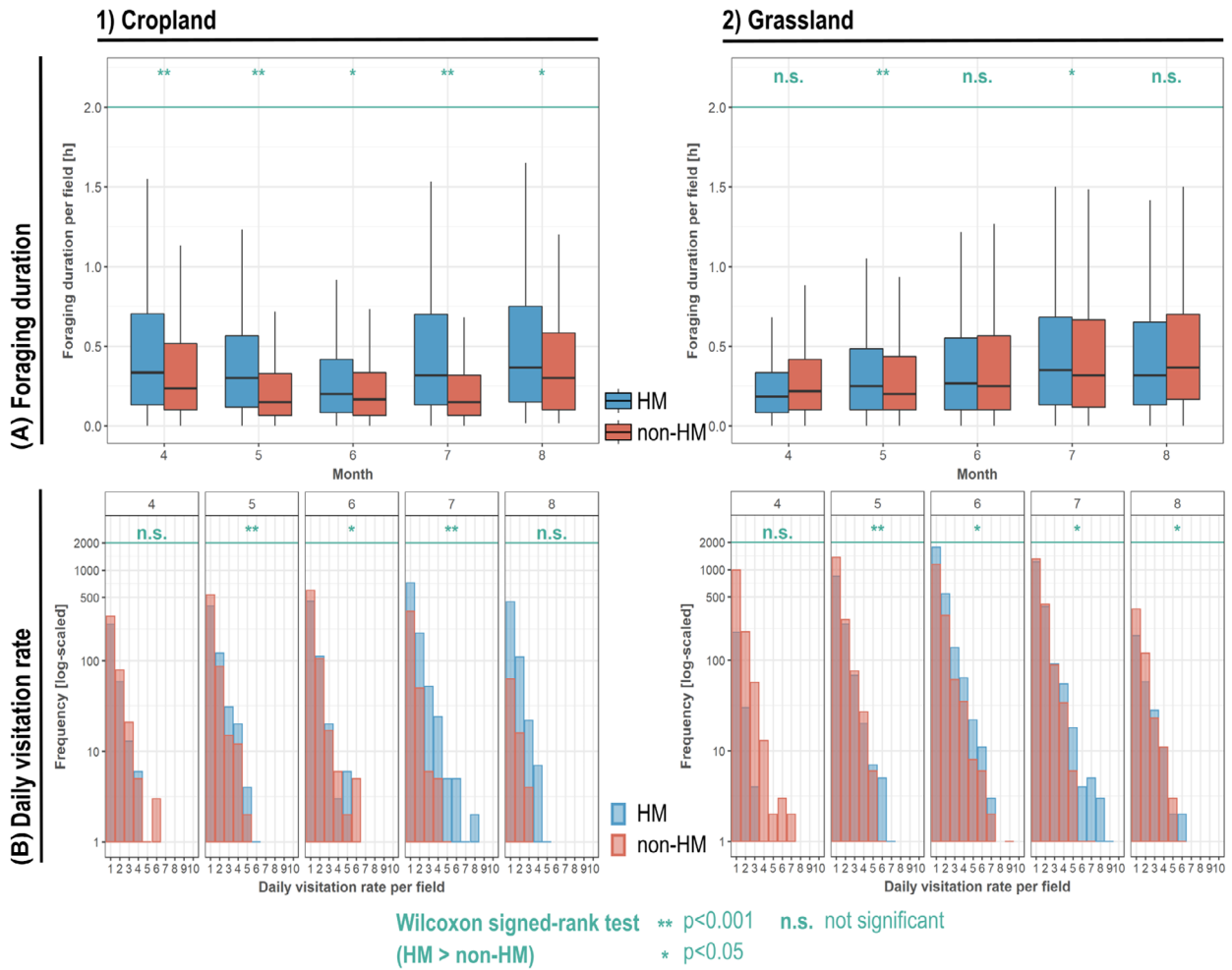
Figure 5. Distribution of the storks' (A) foraging durations and (B) daily visitation rates in fields during half-maximum (HM) and non-half-maximum (non-HM) periods for croplands (1) and grasslands (2) (measured on a monthly basis during the breeding season of 2014). In cropland fields, storks foraged significantly longer during HM than during non-HM throughout the whole breeding season (1A). Additionally, the birds seemed to revisit cropland fields during HM significantly more frequently from May to July (1B). On the contrary, in grasslands we found prolonged foraging duration during HM only in May and July (2A). Nevertheless, with the exception of April, storks also seemed to revisit grassland fields during HM significantly more often than those during non-HM (2B).

concentration of harvest activities in croplands during these months.

Contrary to our expectation, for grasslands we did not observe significantly longer foraging duration during HM than during non-HM throughout the breeding season. Intensively managed grassland is usually mown twice a year, which lowers its vegetation height over the breeding season (Griffiths et al., 2020; Itzerott & Kaden, 2006; Johst et al., 2001). Moreover, natural grasslands are generally characterized by lower vegetation and are continuously accessible (Olsson & Rogers, 2009). These could explain why, unlike in croplands, we observed storks to spend a considerable amount of their foraging time also during non-HM in grasslands. In contrast to croplands,

prey density is generally higher in grasslands (Böhning-Gaese, 1992; Vickery et al., 2001), and when they are mown, vegetation is left in the fields allowing prey to hide and remain available to storks (Rachel, 2006). Mowing usually occurs in the middle of the breeding season (Sackl, 1989), and storks are known to use grasslands disproportionately during such activities because they represent their most productive habitats (Thomsen & Struwe, 1994). Accordingly, we found significant selection of grasslands during HM from ~May to mid-July, when foraging in grasslands during non-HM was only proportional to its availability or even avoided in croplands.

During the early breeding season (~April), foraging habitat use is mainly determined by vegetation growth
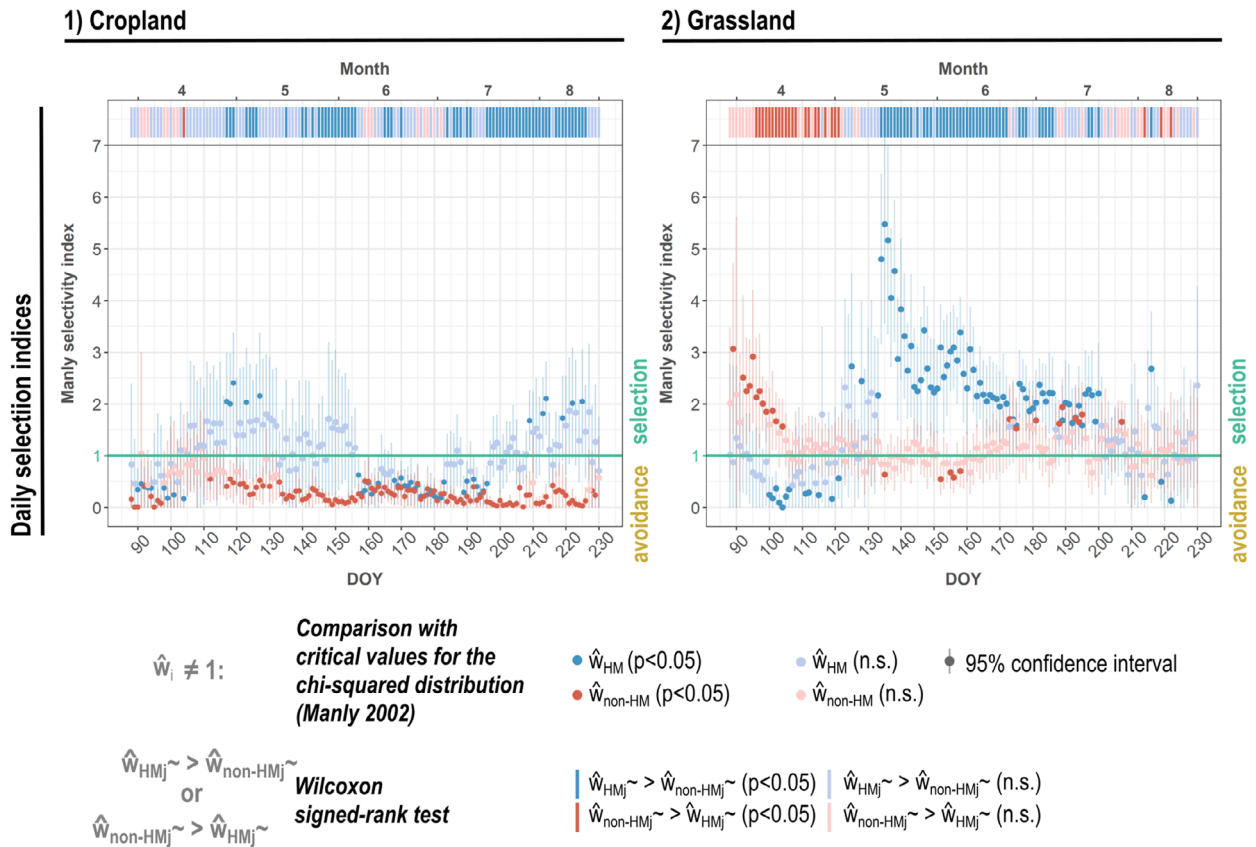
Figure 6. Summary of the daily values of the Manly selectivity index [$\hat{w}_i$] for croplands (1) and grasslands (2) during HM and non-HM throughout the breeding season 2014. The storks used cropland fields during HM most of the breeding season proportional to their availability [$\hat{w}_i \sim 1$] (see 1). The general tendency of $\hat{w}_i$ pointed towards selection (>1), however, selection was only significant on a few days in ~ early May as well as in August. Cropland fields during non-HM were significantly avoided most of the days throughout the breeding season [$\hat{w}_i < 1$]. In grasslands, we found significant selection of HM [$\hat{w}_i > 1$] by storks from May to mid-July (see 2). Storks' usage of grasslands during non-HM was, with the exception of April, mostly proportional to its availability [$\hat{w}_i \sim 1$]. On croplands and grasslands, we found that storks used fields during HM proportionally more than fields during non-HM compared the relative availability of those habitats ($\hat{w}_{HMj}\sim > \hat{w}_{non-HMj}\sim$). However, in grasslands, this difference was significant only from mid-May to mid-July. Additionally, we observed storks using grassland fields during non-HM in significantly higher proportions than grassland fields during HM throughout April ($\hat{w}_{non-HMj}\sim > \hat{w}_{HMj}\sim$).

Table 2. Comparison of storks' daily proportional habitat use during HM and non-HM relative to the availability of those habitats in croplands and grasslands.

	Wilcoxon signed-rank test	Total (% of days in breeding season)	Significant ($P < 0.05$) (% of days in breeding season)
Cropland	a) $\hat{w}_{HMj\sim} > \hat{w}_{non-HMj\sim}$	87.4%	41.7%
	b) $\hat{w}_{non-HMj\sim} > \hat{w}_{HMj\sim}$	12.6%	0.7%
Grassland	c) $\hat{w}_{HMj\sim} > \hat{w}_{non-HMj\sim}$	62.9%	31.8%
	d) $\hat{w}_{non-HMj\sim} > \hat{w}_{HMj\sim}$	37.1%	15.9%

(Böhning-Gaese, 1992; Rachel, 2006). According to our hypothesis, non-HM should identify times when vegetation is already too high and should therefore be avoided.

In April, however, we found storks avoiding croplands during non-HM/HM and even selecting grasslands during non-HM. We therefore suggest that periods in which only

Table 3. Summary of the effects of various predictors (fixed effects) on storks' foraging habitat selection (modeled with GLMMs for the combined LC [considering cropland and grassland fields together]).

		Model	Predictors	Estimate (SE)	Marginal R^2
Landcover: combined LC	Response: presence/pseudo-absence (visit)	M1	Landcover (Grassland)	0.40 (0.02)***	0.234
			Distance	−5.65 (0.78)***	
		M2	Landcover (Grassland)	0.65 (0.02)***	0.257
			Distance	−5.72 (1.15)***	
			NDVI	−1.53 (0.29)***	
		M3	Landcover (Grassland)	0.55 (0.02)***	0.270
			Distance	−5.84 (1.12)***	
			HM_Amp	4.42 (0.54)***	
		M4	Landcover (Grassland)	0.58 (0.02)***	0.262
			Distance	−5.74 (1.08)***	
			NDVI	−1.35 (0.29)***	
			HM_Dist	−1.59 (0.28)***	
		M5	Landcover (Grassland)	0.5 (0.02)***	0.273
			Distance	−5.86 (1.06)***	
			HM_Amp	4.23 (0.58)***	
			HM_Dist	−1.08 (0.29)***	
		M6	Landcover (Grassland)	0.90 (0.03)***	0.163
			Distance	−5.92 (1.17)***	
			NDVI	−1.24 (0.36)***	
			HM_Dist	−1.64 (0.30)***	
			NDVI_Range	1.83 (0.84)*	
		M7	Landcover (Grassland)	0.83 (0.03)***	0.247
			Distance	−6.02 (1.08)***	
			HM_Amp	4.46 (0.75)***	
			HM_Dist	−0.97 (0.33)**	
			NDVI_Range	1.53 (0.85)[†]	

The marginal R^2 indicate how much of the variance was explained by the different (fixed) predictor combinations. SE, standard error.
P-values: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, [†]$P < 0.1$.

variations in vegetation height distinguish prey availability may not be captured appropriately with the half-maximum. The latter was derived using intra-annual NDVI profiles and may therefore have been influenced by the increased sensitivity of this index to growing vegetation (Payero et al., 2004).

With the exception of April, our results indicate that storks tended to favor HM over non-HM throughout large and critical parts of the breeding season. Compared to their relative availability, they used croplands and grasslands proportionally more during HM than during non-HM. Furthermore, our models including temporal predictors were able to improve predictions of their foraging habitat selection. We found that storks were more likely to select fields closer to their nests – typical for central place foragers – and during HM (supported by the positive effect of higher (positive) HM_Amp values). Although, in grasslands, storks did not favor fields during HM throughout the breeding season (as seen in croplands) but only from May to mid-July, this period is critical for the breeding success. While one adult must remain in the nest throughout incubation/early nestling-rearing

phase (Böhning-Gaese, 1992; Johst et al., 2001), parents can later forage simultaneously and more frequently (Moritzi et al., 2001). This period overlaps largely with the grassland mowing in Europe (Pfeifer & Brandl, 1991; Sackl, 1989). Accordingly, we registered the highest proportion of foraging visits in grasslands from May to mid-July (DOY 121–196: 71.9%) and found, supported by habitat selection models, that storks tended to select grassland habitats during HM. The influence of both, distance and HM_Amp, corresponds with previous studies postulating that storks' foraging habitat selection is affected by nest distance and quality (Alonso et al., 1991; Gadenne et al., 2014; Johst et al., 2001), where quality in agricultural landscapes is determined by vegetation height and agricultural activities (Moritzi et al., 2001). Given the agreement of our findings with previous research, we propose that the half-maximum proxy allows to coarsely discriminate temporal changes of habitat conditions which influence storks foraging behavior during breeding season. However, these may not necessarily relate only to variations in vegetation height, as we had expected, but also to the prey availability in their foraging habitats.
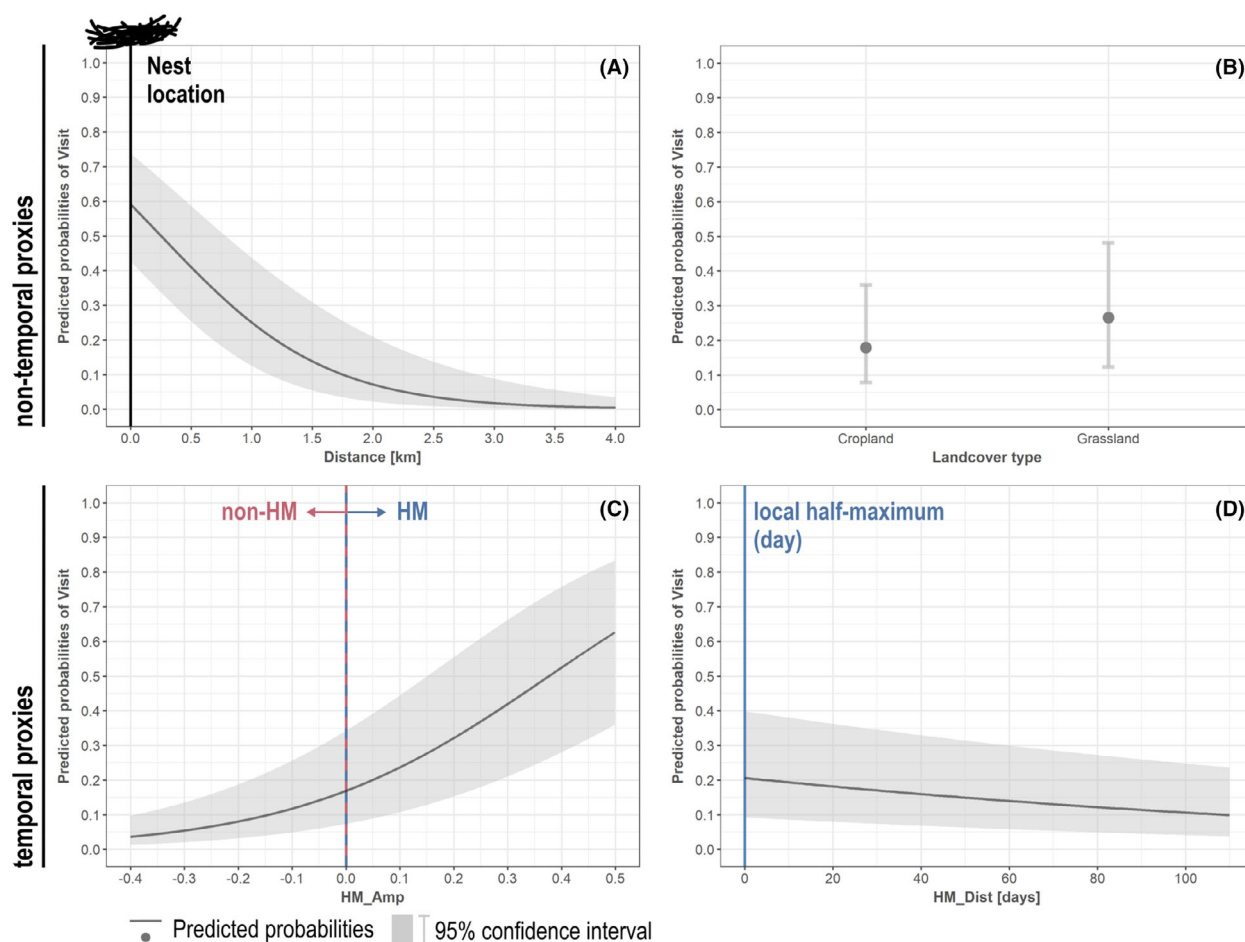
Figure 7. Predicted values (marginal effects) for the fixed model terms of the best-performing (in terms of marginal R^2) model (GLMM; Table 3: M5) for storks' foraging habitat selection based on all presence/pseudo-absence samples (cropland and grassland fields = combined LC). The model indicates that storks are more likely to select grasslands over croplands (B) as well as fields in close proximity to their nests (A) with higher (positive) HM_Amp values (C). The temporal proximity to the closest local half-maximum day (HM_Dist) (D) appears to have only little influence on the birds' decision to forage in a certain field.

While our results emphasize the potential of time series for characterizing small-scale vegetation dynamics in ecological-meaningful ways, some analytical challenges remain: First, storks respond quickly to harvest/mowing events, not only because these activities make prey items re-accessible but because they increase prey availability in the short-term (Johst et al., 2001; Moritzi et al., 2001; Olsson & Rogers, 2009). While the half-maximum allows to roughly identify periods with favorable foraging conditions (HM) mainly in terms of accessibility, prey availability is likely to vary considerably throughout these times and is highest close to mowing/harvest dates. Remote sensing sensors like Sentinel-1/-2 are promising to further investigate these temporal variations. Linking Landsat with Sentinel-2 (S2) imagery can increase the temporal resolution of optical data up to 2 days (Roy &

Yan, 2018), while Sentinel-1 data (S1; synthetic radar aperture) are available at regular temporal intervals due to their independence from sunlight and cloud cover (Vroey et al., 2021). Both data sources have recently been applied successfully to detect harvest/mowing events by identifying residuals from an idealized NDVI growing trajectory (S2/Landsat) (Griffiths et al., 2020) or through methods based on interferometric coherence (S1) (Vroey et al., 2021). These data and methods have not been an option for the current study as these satellites were not/ only recently launched at the time the telemetry data was acquired. Nevertheless, future studies should examine whether they are sufficiently accurate to narrow down the periods with increased prey availability for storks following agricultural practices and focus on differences between croplands/grasslands.

Second, while NDVI is correlated with vegetation greenness and allows assessing vegetation development (Pettorelli et al., 2005; Pettorelli et al., 2011), it can also be influenced by topography, soil background or standing water (Griffiths et al., 2020; Kerr & Ostrovsky, 2003; Payero et al., 2004). Furthermore, vegetation senescence before mowing/harvest leads to a steady decrease in NDVI (Veloso et al., 2017), which can cause commission errors of HM in the absence of management activities, for example in natural grasslands. To rule out such biases, validation data with explicit information on mowing/harvest dates are needed, but seldomly available (Estel et al., 2016; Griffiths et al., 2020). Nevertheless, the half-maximum is an established proxy that has already been validated (Estel et al., 2016). Additionally, our findings are consistent with previous research and the breeding areas of the studied storks are located in an agricultural landscape where natural vegetation is rare. This makes us confident that HM captured favorable foraging conditions for storks; the post-harvest/mowing periods.

Third, storks' favor of certain foraging habitats is also dependent on their anthropogenic management (Radovic & Tepic, 2009). Hayfields, for example provide high energy yields primarily around mowing while extensively managed and natural grasslands produce lower yields yet are continuously available (Johst et al., 2001; Olsson & Rogers, 2009; Struwe & Thomsen, 1991). Here, we made a distinction solely between croplands and grasslands because no finer thematic landcover classification was available. This coarse separation has proven to be sufficient in other studies (Moritzi et al., 2001; Radovic & Tepic, 2009; Zurell et al., 2018). Our attempt to characterize agricultural management variations of the fields using the NDVI_range predictor was further not successful as it worsened the performance of some habitat selection models. A finer habitat separation should therefore be pursued in future studies to better describe and account for temporal variations in habitat conditions resulting from differently managed fields.

Finally, storks' habitat use/selection is in parts opportunistic (Latus & Kujawa, 2005; Sackl, 1989) and also known to be affected by individual experience, the presence of conspecifics or regional differences in habitat composition (Alonso et al., 1991; Böhning-Gaese, 1992; Pfeifer, 1989; Zurell et al., 2018). Hence, although the inclusion of temporal predictors improved habitat selection modeling, the explained variance (marginal R^2) of the models remained relatively low (Table 3). In addition, we considered longer foraging duration – in line with foraging theory – as an indicator of habitat type preference in our analysis of habitat use. Foraging time can however, also be prolonged when storks are unable to locate enough prey in low quality landscapes (Johst et al., 2001)

or shortened when prey is so ample that the carrying/digestive capacity of the bird is quickly reached. These aspects were beyond the scope of our study, which more generally aimed to characterize and assess the influence of environmental dynamics on storks' habitat use/selection with time series. Nevertheless, we suggest that future research could refine our findings and investigate the phenomenon more holistically, and also use species-rather than landscape-centered methods (e.g. conditional logistic instead of logistic regression).

Animals' habitat selection, use and ultimately biodiversity at local/regional scales, are affected by agricultural practices and vegetation phenology which continuously alter habitat suitability (Dunning et al., 1995; Johst et al., 2001; Pressey et al., 2007). The need to monitor, understand and predict the impact of such environmental dynamics is urgent and necessary to develop appropriate management and conservation strategies (Durant et al., 2005; Kerr & Ostrovsky, 2003; Pettorelli et al., 2011). Hence, it is important to identify meaningful ecological proxies that allow capturing habitat dynamics at the thematic/spatial/temporal scales and resolutions that are relevant for the species of interest and its targeted behavior (Cord et al., 2013; He et al., 2015; Roever et al., 2013). Albeit its widespread use, NDVI may not always be the best choice for this objective, as seen in our habitat selection models in grasslands, where it had no significant effect. Here, we utilized time series to derive the half-maximum, an established proxy for leaf-unfolding/loss of canopy structure (Bradley et al., 2007; Fisher et al., 2006), and highlighted its capabilities to coarsely distinguish temporal variations of prey accessibility in storks' foraging habitats. Despite the challenges, such meaningful temporal proxies can aid to create more realistic species-centered landscape scenarios in habitat models (Dunning et al., 1995). Linked to data on individual fitness or population demographics they may eventually allow unravelling the consequences that arise from environmental change for animals (Pettorelli et al., 2005; Pettorelli et al., 2011). Storks' breeding success for instance, has been suggested to be influenced by agricultural management (Johst et al., 2001; Pfeifer & Brandl, 1991) but this linkage is not yet conclusively clarified. Nevertheless, it could possibly be explored further with proxies that enable to characterize temporal variations in prey availability/accessibility in ecological meaningful ways.

Overall, using the white stork as an example, our study demonstrates that time series are suitable means to effectively characterize small-scale vegetation dynamics affecting fine-scale animal behaviors in agricultural landscapes. We hope that our findings provide an incentive to use them more frequently in ecological research and to

develop proxies that are ecologically meaningful. We also suggest that future studies should test the applicability and effectiveness of already established remote sensing proxies. This task requires knowledge from both, animal ecology and remote sensing, making interdisciplinary collaborations desirable and recommended (Pettorelli et al., 2014).

Acknowledgments

Funding Information

References

Alonso, J.C., Alonso, J.A. & Carrascal, L.M. (1991) Habitat selection by foraging White Storks, *Ciconia ciconia*, during the breeding season. *Canadian Journal of Zoology*, **69**(7), 1957–1962.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**(1), 1–48.

Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B. & Mysterud, A. (2012) A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist*, **180**(4), 407–424.

BKG. (Ed.) (2016) Digitales Landbedeckungsmodell für Deutschland - LBM-DE2012. pp. 1–18.

Böhning-Gaese, K. (1992) Zur Nahrungsökologie des Weißstorchs (Ciconia ciconia) in Oberschwaben: Beobachtungen an zwei Paaren. *Journal für Ornithologie*, **133**(1), 61–71.

Bradley, B.A., Jacob, R.W., Hermance, J.F. & Mustard, J.F. (2007) A curve fitting procedure to derive inter-annual phenologies from time series of noisy satellite NDVI data. *Remote Sensing of Environment*, **106**(2), 137–145.

Calenge, C. (2006) The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 1035.

Carrascal, L.M., Alonso, J.C. & Alonso, J.A. (1990) Aggregation size and foraging behaviour of white. *Ardea*, **78**,

399–404. Available from: https://lmcarrascal.eu/pdf/ardea90. pdf. [Accessed 11 September 2020].

Catry, I., Franco, A.M.A. & Moreira, F. (2014) Easy but ephemeral food: exploring the trade-offs of agricultural practices in the foraging decisions of Lesser Kestrels on farmland. *Bird Study*, **61**(4), 447–456.

Chastain, R., Housman, I., Goldstein, J. & Finco, M. (2019) Empirical cross sensor comparison of Sentinel-2A and 2B MSI, Landsat-8 OLI, and Landsat-7 ETM+ top of atmosphere spectral characteristics over the conterminous United States. *Remote Sensing of Environment*, **221** (November 2018), 274–285.

Cord, A.F., Meentemeyer, R.K., Leitão, P.J. & Václav?k, T. (2013) Modelling species distributions with remote sensing data: bridging disciplinary perspectives. *Journal of Biogeography*, **40**(12), 2226–2227.

Duchon, J. (1977) Splines minimizing rotation-invariant semi-norms in sobolev spaces. In: Schempp, W. & Zeller, K. (Eds.) *Constructive theory of functions of several variables*. Berlin Heidelberg: Springer, pp. 85–100.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H. et al. (1995) Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5**(1), 3–11.

Durant, J.M., Hjermann, D.O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. et al. (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters*, **8**(9), 952–958.

Esch, T., Heldens, W., Hirner, A., Keil, M., Marconcini, M., Roth, A. et al. (2017) Breaking new ground in mapping human settlements from space–the Global Urban Footprint. *ISPRS Journal of Photogrammetry and Remote Sensing*, **134**, 30–42.

Esch, T., Metz, A., Marconcini, M. & Keil, M. (2014) Combined use of multi-seasonal high and medium resolution satellite imagery for parcel-related mapping of cropland and grassland. *International Journal of Applied Earth Observation and Geoinformation*, **28**, 230–237.

Estel, S., Kuemmerle, T., Alcántara, C., Levers, C., Prishchepov, A. & Hostert, P. (2015) Mapping farmland abandonment and recultivation across Europe using MODIS NDVI time series. *Remote Sensing of Environment*, **163**, 312–325.

Estel, S., Kuemmerle, T., Levers, C., Baumann, M. & Hostert, P. (2016) Mapping cropland-use intensity across Europe using MODIS NDVI time series. *Environmental Research Letters*, **11**(2), 024015.

Estel, S., Mader, S., Levers, C., Verburg, P.H., Baumann, M. & Kuemmerle, T. (2018) Combining satellite data and agricultural statistics to map grassland management intensity in Europe. *Environmental Research Letters*, **13**(7), 074020.

Fisher, J., Mustard, J. & Vadeboncour, M. (2006) Green leaf phenology at Landsat resolution: scaling from the field to

the satellite. *Remote Sensing of Environment*, **100**(2), 265–279.

Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M. et al. (2016) Costs of migratory decisions: a comparison across eight white stork populations. *Science Advances*, **2**(1), e1500931.

Fleming, C.H. & Calabrese, J.M. (2020) ctmm: continuous-time movement modeling [Internet]. Available from: https://CRAN.R-project.org/package=ctmm. [Accessed 12 March 2020].

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P. & Calabrese, J.M. (2016) Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data. *Ecology*, **97**(3), 576–582.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. et al. (2005) Global consequences of land use. *Science*, **309**(5734), 570–574.

Franke, J., Keuck, V. & Siegert, F. (2012) Assessment of grassland use intensity by remote sensing to support conservation schemes. *Journal for Nature Conservation*, **20** (3), 125–134.

Gadenne, H., Cornulier, T., Eraud, C., Barbraud, J.-C. & Barbraud, C. (2014) Evidence for density-dependent habitat occupancy at varying scales in an expanding bird population. *Population Ecology*, **56**(3), 493–506.

Gao, F., Anderson, M.C., Zhang, X., Yang, Z., Alfieri, J.G., Kustas, W.P. et al. (2017) Toward mapping crop progress at field scales through fusion of Landsat and MODIS imagery. *Remote Sensing of Environment*, **188**, 9–25.

Green, R.E., Tyler, G.A., Stowe, T.J. & Newton, A.V. (1997) A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). *Journal of Zoology*, **243**(1), 81–115.

Griffiths, P., Nendel, C., Pickert, J. & Hostert, P. (2020) Towards national-scale characterization of grassland use intensity from integrated Sentinel-2 and Landsat time series. *Remote Sensing of Environment*, **238**, 111124.

Grübler, M.U., Schuler, H., Müller, M., Spaar, R., Horch, P. & Naef-Daenzer, B. (2008) Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biological Conservation*, **141**(12), 3040–3049.

He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S. et al. (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, **1**(1), 4–18.

Itzerott, S. & Kaden, K. (2006) Neuer Algorithmus zur Klassifizierung landwirtschaftlicher Fruchtarten auf Basis spektraler Normkurven. *Photogrammetrie Fernerkundung Geoinformation*, **6**, 509–518.

Johst, K., Brandl, R. & Pfeifer, R. (2001) Foraging in a patchy and dynamic landscape: human land use and the white stork. *Ecological Applications*, **11**(1), 60–69.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science*, **348**(6240), aaa2478–aaa2478.

Kerr, J.T. & Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends in Ecology & Evolution*, **18**(6), 299–305.

Latus, C. & Kujawa, K. (2005) The effect of land cover and fragmentation of agricultural landscape on the density of white stork (*Ciconia ciconia* L.) in Brandenburg, Germany. *Polish Journal of Ecology*, **53**(4), 535–543.

Mack, B., Leinenkugel, P., Kuenzer, C. & Dech, S. (2016) A semi-automated approach for the generation of a new land use and land cover product for Germany based on Landsat time-series and Lucas in-situ data. *Remote Sensing Letters*, **8** (3), 244–253.

Manly, B. (2002) *Resource selection by animals: statistical design and analysis for field studies*. Dordrecht, Boston: Kluwer Academic Publishers.

Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D. et al. (2016) Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, **283**(1833), 20160456.

Moritzi, M., Maumary, L., Schmid, D., Steiner, I., Vallotton, L., Spaar, R. et al. (2001) Time budget, habitat use and breeding success of White Storks Ciconia ciconia under variable foraging conditions during the breeding season in Switzerland. *Ardea*, **89**(3), 457–470.

Muff, S., Signer, J. & Fieberg, J. (2019) Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, **89** (1), 80–92.

Nagendra, H., Lucas, R., Honrado, J.P., Jongman, R.H.G., Tarantino, C., Adamo, M. et al. (2013) Remote sensing for conservation monitoring: assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecological Indicators*, **33**, 45–59.

Nakagawa, S. & Schielzeth, H. (2012) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**(2), 133–142.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**(49), 19052–19059.

Neumann, W., Martinuzzi, S., Estes, A.B., Pidgeon, A.M., Dettki, H., Ericsson, G. et al. (2015) Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Movement Ecology*, **3** (1), 1–13.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, **520**(7545), 45–50.

Nychka, D., Furrer, R., Paige, J. & Sain, S. (2017) *Fields: tools for spatial data [Internet]*. Boulder, CO: University Corporation for Atmospheric Research. Available from: https://github.com/NCAR/Fields. [Accessed 23 November 2019].

Olsson, O. & Bolin, A. (2014) A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia*, **175**(2), 537–548.

Olsson, O. & Rogers, D.J. (2009) Predicting the distribution of a suitable habitat for the white stork in Southern Sweden: identifying priority areas for reintroduction and habitat restoration. *Animal Conservation*, **12**(1), 62–70.

Payero, J.O., Neale, C.M.U. & Wright, J.L. (2004) Comparison of eleven vegetation indices for estimating plant height of alfalfa and grass. *Applied Engineering in Agriculture*, **20**(3), 385–393.

Peggie, C.T., Garratt, C.M. & Whittingham, M.J. (2011) Creating ephemeral resources: how long do the beneficial effects of grass cutting last for birds? *Bird Study*, **58**(4), 390–398.

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H. & Turner, W. (2014) Satellite remote sensing for applied ecologists: opportunities and challenges. *Journal of Applied Ecology*, **51**(4), 839–848.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. et al. (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research*, **46**(1), 15–27.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**(9), 503–510.

Pfeifer, R. (1989) Zur Nahrungssituation und Bruterfolg des Weißstorches *Ciconia ciconia* an zwei Brutplätzen im Rotmaingebiet. *Anzeiger der Ornithologischen Gesellschaft Bayern*, **28**, 117–130.

Pfeifer, R. & Brandl, R. (1991) Der Einfluß des Wiesenmahdtermins auf die Vogelwelt. *Ornithologischer Anzeiger*, **30**, 159–171.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in Ecology & Evolution*, **22**(11), 583–592.

Rachel, M. (2006) Foraging sites of breeding White Storks *Ciconia ciconia* in the South Wielkopolska region. In: Tryjanowski, P., Sparks, T.H. & Jerzak, L. (Eds.) *The White Stork in Poland: studies in biology, ecology and conservation*. Poznán: Bogucki Wydawnictwo Naukowe, pp. 161–167.

Radovic, A. & Tepic, N. (2009) Using Corine Land Cover Habitat Database for the analysis of breeding bird habitat: case study of white storks (*Ciconia ciconia*) from northern Croatia. *Biologia*, **64**(6), 1212–1218.

Rodríguez, C., Tapia, L., Ribeiro, E. & Bustamante, J. (2013) Crop vegetation structure is more important than crop type

in determining where Lesser Kestrels forage. *Bird Conservation International*, **24**(4), 438–452.

Roever, C.L., Beyer, H.L., Chase, M.J. & van Aarde, R.J. (2013) The pitfalls of ignoring behaviour when quantifying habitat selection. *Diversity and Distributions*, **20**(3), 322–333.

Rotics, S., Kaatz, M., Resheff, Y.S., Turjeman, S.F., Zurell, D., Sapir, N. et al. (2016) The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. *Journal of Animal Ecology*, **85**(4), 938–947.

Roy, D.P. & Yan, L. (2018) Robust Landsat-based crop time series modelling. *Remote Sensing of Environment*, **238**, 110810.

Sackl, P. (1989) Zur Ernährungsbiologie und Habitatnutzung des Weißstorchs. *Vogelschutz in Österreich*, **4**, 6–10.

Struwe, B. & Thomsen, K.-M. (1991) Untersuchungen zur Nahrungsökologie des Weißstorches (*Ciconia ciconia*, L. 1758) in Bergenhusen 1989. *Corax*, **14**, 210–238.

Thomas, D.L. & Taylor, E.J. (1990) Study designs and tests for comparing resource use and availability. *The Journal of Wildlife Management*, **54**(2), 322.

Thomsen, K.M. & Struwe, B. (1994) Vergleichende nahrungsökologische Untersuchungen an Weißstorch-Brutpaaren (*Ciconia ciconia*) in Stapelholm und im Kreis Herzogtum Lauenburg. *Corax*, **15**, 293–308.

Tryjanowski, P., Sparks, T.H., Jakubiec, Z., Jerzak, L., Kosicki, J.Z., Kuzniak, S. et al. (2005) The relationship between population means and variances of reproductive success differs between local populations of white stork (*Ciconia ciconia*). *Population Ecology*, **47**(2), 119–125.

Veloso, A., Mermoz, S., Bouvet, A., Toan, T.L., Planells, M., Dejoux, J.-F. et al. (2017) Understanding the temporal behavior of crops using Sentinel-1 and Sentinel-2-like data for agricultural applications. *Remote Sensing of Environment*, **199**, 415–426.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. et al. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**(3), 647–664.

Vitousek, P.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**(5325), 494–499.

Vroey, M.D., Radoux, J. & Defourny, P. (2021) Grassland mowing detection using sentinel-1 time series: potential and limitations. *Remote Sensing*, **13**(3), 348.

Wang, X., Cao, L., Fox, A.D., Fuller, R., Griffin, L., Mitchell, C. et al. (2019) Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl. *Nature Communications*, **10**(1), 2187.

Zurell, D., von Wehrden, H., Rotics, S., Kaatz, M., Groß, H., Schlag, L. et al. (2018) Home range size and resource use of breeding and non-breeding white storks along a land use gradient. *Frontiers in Ecology and Evolution*, **6**, 79.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Text S1. Simulation of continuous-time movement paths.
Text S2. Pre-processing of Landsat time series and update of field boundaries.
Text S3. Derivation of Manly selectivity index and determination of its statistical significance.

Equation S1. Equations used to calculate HM_Amp, HM_Dist and NDVI_Range.
Table S1. Correlation matrices of the predictors included in the GLMMs.
Table S2. GLMMs – Fixed effects (single LC models).
Table S3. GLMMs - Random effects (combined and single LC models).
Figure S2. Information on visits in croplands and grasslands during the breeding season 2014.