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Article

Central place foraging in a human-dominated landscape: how do common cranes select feeding sites?

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Human infrastructure and disturbance play an important role when animals select resources in human-modified landscapes. Theory predicts that animals trade food intake against costs of movement or disturbance to optimize net energy gain and fitness, but other necessary resources may also constrain the decisions, e.g. when animals repeatedly need to return to a central location, such as a nest, waterhole or night roost. Central place foraging theory states that the probability of occurrence of an animal decreases with the distance to the central location while selectivity for food items or foraging sites providing high net energy gain should increase with distance. We studied foraging patterns of common cranes *Grus grus* feeding in an agricultural landscape adjacent to a wetland to which they return for night roost. We used availability of spilled grains on harvested fields and distance to human settlement as proxy for site quality (i.e. increased likelihood of increased net energy gain with increased food availability and less disturbance). As predicted by theory, our results clearly show that cranes were more likely (more than twice as high resource selection function scores) to select foraging sites close to roosts. However, contrary to predictions, the selection of high quality sites in terms of high food availability decreased with distance to roost sites. Nevertheless, our results indicate that cranes were more likely to select sites with low risk of human disturbance far from roost sites, and were more tolerant to disturbance close to roost sites. How different species respond to the local and environmental conditions will increase the understanding of the species' resource requirement, and also where in the landscape to prioritize conservation or management actions (e.g. mitigation of human disturbance and crop damage prevention to sustain agricultural production).

Keywords: agriculture, conservation conflict, crop protection, geese, *Grus grus*, stubble fields

Introduction

Knowledge of how animals select resources in the landscape is central to understanding habitat requirements and population distribution (Boyce and McDonald 1999).

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Optimal foraging theory predicts that animals trade food intake against costs of movement and handling time to optimize net energy gain and consequently fitness (MacArthur and Pianka 1966). The selection of profitable foraging sites may therefore be constrained by movement costs, but also other factors causing increased cost, such as predation risk and human disturbance due to antipredator behaviour such as vigilance (Orians and Pearson 1979, Brown and Kotler 2004, Tablado and Jenni 2017). Moreover, many animals repeatedly return to a central location, such as a nest, water-hole or night roost site (Pinaud and Weimerskirch 2005, Chudzińska et al. 2015, Rozen-Rechels et al. 2015). To account for movement constraints (i.e. repeated movements to a central location), the central place foraging theory was elaborated from the principles of optimal foraging theory (Orians and Pearson 1979, Kacelnik 1984, Olsson et al. 2008). Central place foraging theory was initially developed to explain how birds maximize energy returns when traveling to and from a nest carrying prey of different size and showed that load size tends to increase with foraging distance from the nest (Orians and Pearson 1979). In more previous studies, central place foraging has been used to also explain distribution patterns in habitats differing in quality in relation to the distance to the central place (Rosenberg and McKelvey 1999, Olsson et al. 2008, Chudzińska et al. 2015). Habitat quality has been defined as foraging sites providing high net energy intake e.g. by high food availability (Ford et al. 2015). There are two main predictions derived from central place foraging theory; 1) the probability of occurrence of an animal decreases with the distance to the central location, and 2) selectivity for high-quality foraging sites increases with increasing distance to the central location to compensate for energetic costs of movements (Schoener 1971, Orians and Pearson 1979, Rosenberg and McKelvey 1999).

In addition, to travel distance and food availability, predation risk and human disturbance affect an animal's decisions (Olsson et al. 2008, Chudzińska et al. 2015). For example, disturbance may increase vigilance and thereby decrease time spent foraging and consequently affecting habitat quality (Brown 1999, Olsson et al. 2008, Jensen et al. 2016). Further, the capability to optimize net energy intake may be facilitated by social information, i.e. cues of high-quality foraging sites based on presence of conspecifics (Fernández-Juricic et al. 2004, Boyd et al. 2016). Thus, all these factors need to be considered to thoroughly understand habitat requirements, species distribution and potential negative effects on fitness (Lima and Dill 1990, Bechet et al. 2004, Wang et al. 2011). Such understanding is also important for decisions regarding management and conservation strategies, for example predicting resource requirement of the species, spatial distribution of wildlife damage to human livelihoods and how to optimize the use of damage preventive measures (Sutherland et al. 2004, Nilsson et al. 2016).

The common crane *Grus grus* (hereafter crane) is a protected migratory bird that has recovered from being threatened to extinction to a current population in Europe

of ~ 500 000 individuals (Harris and Mirande 2013); it uses wetlands as central night roost locations and commonly gather in large flocks to forage in surrounding agricultural landscapes at staging sites along the flyway (Vegvari and Tar 2002, EC 2009, Nilsson et al. 2019). Agricultural landscapes provide a high abundance of high-energy forage and although cranes may cause damage to growing crops, they prefer to forage on spilled cereal grain on stubble fields when available (Sugden et al. 1988, Guzman et al. 1999, Nilsson et al. 2016). Cranes are known to use foraging sites with high availability of spilled grain to optimize net energy intake (Alonso et al. 1995, Bautista et al. 1995). The availability of spilled grain varies over time and space due to harvest, tilling, sprouting and consumption (Chudzińska et al. 2015, Nilsson et al. 2016). Adult cranes have few natural predators and the predation risk is thus of minor importance (Munoz Pulido and Alonso 1992), but their foraging behaviour may still be limited by fear of human disturbances, such as traffic, human settlements and scaring activities (Franco et al. 2000, Amano et al. 2008, Vegvari et al. 2011).

Our aim was to test whether cranes select foraging sites according to the central place foraging theory, and whether selection of foraging sites is influenced by disturbance. We used data derived from cranes equipped with GPS-transmitters combined with spatial data on human settlements and roads and detailed field surveys of food availability. While most studies use proxies for quality, such as habitat types (Chudzińska et al. 2015, Rozen-Rechels et al. 2015), we measure food availability directly in the field but also added distance to human settlement as a measure of foraging site quality. We investigated the following question: Do food availability, distance to roost sites and human disturbance affect foraging patterns? Considering that cranes repeatedly return to the same roost site, we predicted that they select for fields close to roost sites and exhibit stronger selectivity for high quality sites associated with higher net energy intake i.e. high availability of spilled grain (e.g. less time searching for food within sites) and low risk of human disturbance (e.g. less time spent on vigilance) with increasing distance to roost site.

Material and methods

Study system

We conducted the study in Kvismaren (59°10'N/15°22'E), in the boreonemoral zone of south-central Sweden (Fig. 1). The area is flat and dominated by productive farmland (~ 66%), well suited for cultivating cereals, ley and potatoes. Crops are generally harvested between August and early October, but the timing varies due to crop type and weather. The average precipitation in September is 50–75 mm (SMHI 2017). The core of the area is a nature reserve consisting of two shallow eutrophic lakes, 2.5 km apart, surrounded by narrow strips of grazed wetlands. The area is assigned under the Ramsar convention of wetlands and as an EU Natura

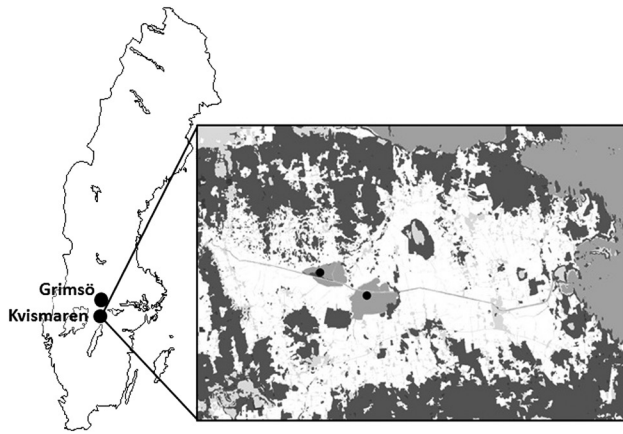


Figure 1. Cranes were captured and equipped with GPS transmitters at Grimsö 2012–2014 ($n=19$). The study was conducted in Kvismaren. The core of the area consists of two protected wetlands/shallow lakes where the cranes roost overnight (black dots). The wetlands are mainly surrounded by arable land (white) and to a lesser extent by forested areas (dark grey).

2000 special protection area. The shallow lakes and the surrounding agricultural landscape provide both suitable roost sites and favorable foraging conditions for cranes and other large grazing birds such as bean geese, *Anser fabilis fabilis*, and greylag geese, *Anser anser*. Kvismaren has been a staging site for large grazing birds for the last 30 years and is the site in Sweden hosting most cranes during autumn, with maximum numbers of 15 500–24 200 cranes in 2009–2019 (Månsson and Nilsson unpubl.). The number of cranes in Kvismaren progressively increases from August to the end of September and all cranes leave at about the same time when the weather conditions become suitable in the beginning of October. The large concentration of foraging cranes and geese causes damage to crops (Frank et al. 2019, Montràs-Janer et al. 2019). Commonly used preventive measures are scaring (e.g. scarecrows, pennants and propane cannons), diversionary fields (i.e. supplying food at undisturbed locations) and occasional local culling (Hake et al. 2010, Cusack et al. 2018). The level of scaring activity was however hard to quantify as it was an uncoordinated activity carried out by farmers and managers.

Capturing and tagging

We captured and tagged 19 juvenile cranes with backpack GPS-transmitters between 2012 and 2014 (for details of the methods, see Månsson et al. 2013). Fourteen juvenile cranes were tagged with Vectronic GPS-plus bird backpacks (Vectronic Aerospace, Berlin, Germany) and five cranes with solar-cell transmitters (Cellular Tracking Technologies, Rio Grande, USA). The captures were conducted within a 30 km radius of Grimsö Wildlife Research Station (59°43'N/15°28'E, 85 km north of Kvismaren; Fig. 1) in July and early August (late part of the breeding period). The juvenile cranes migrated with their parents to Kvismaren in late August or early September before continuing their migration. During the staging period

in Kvismaren, the transmitters were programmed for 8 days of intensive positioning (1 location per 30 min from dawn to dusk) evenly distributed during the period from when the cranes arrived to the study area until they left. Each individual was only monitored during its first autumn staging period in Kvismaren. The family group normally split at the wintering grounds in January, and we thus assume that each juvenile was accompanied by the parental pair and occasionally by one sibling during the study period (Alonso et al. 1984). The effect of the GPS transmitters on foraging and movement of cranes are not known. However, previous studies on birds show that the amount of discomfort and time spent preening may increase (Robert et al. 2006). However, studies have also shown non-significant effect on reproductive success or foraging behavior as long as the transmitter load was low in relation to body weight (Phillips and Croxall 2003, Burnside et al. 2019). To minimize the potential effects of the transmitters, we kept transmitter weights < 3% of crane body weights (Phillips and Croxall 2003). All captures and tagging fulfilled ethical requirements for research on wild animals after approval from the Animal Ethics Committee of central Sweden (C104/10 and C53/13).

Field surveys

To study individual selection of foraging sites and food availability within arable stubble fields, we surveyed locations ($n=124$) used by the cranes for crop type and spilled grain availability, during the days of intensive positioning. To exclude flight locations, only fields with two or more consecutive crane locations were chosen (i.e. fields visited less than 30 min were excluded). At each field, one of the locations was randomly selected for survey. An equal number of random locations representing availability in the landscape (hereafter 'available locations') were surveyed. Available locations were randomly distributed within stubble fields less than 11 km from the two wetland roost sites, corresponding to the maximum daily flight distance from the wetland roosts earlier defined by the studied cranes. Both used and available locations were surveyed after sunset the same day as visited by the targeted individuals i.e. immediately when the cranes had left for night roost to avoid disturbance. At each location we noted crop type and counted number of unsprouted grains (i.e. spilled grain availability) at three plots (0.2×0.2 m), at the focal location, 5 m north and south of the location, respectively. The mean spilled grain availability of the three plots was used in the analysis and was rescaled to kernels dm^{-2} in the modeling procedure.

Data processing

Crop types were pooled into three categories; barley, wheat and other. The category 'other' included oat, rye and cereal mix, because each of these types had too few observations to be included separately. Distance to human disturbance was assessed as the shortest distance to roads (excluding agricultural roads only passable with tractors and 4WD

vehicles), houses or farms derived from the GSD Terrain map (Lantmäteriet 2016) in ArcGIS ver. 10.3.1. Similarly, the distance from locations to the roost site was calculated in ArcGIS.

Statistical analysis

Selection of foraging sites was analyzed with a resource selection function, where used locations were compared to available locations (Lele and Keim 2006). As we could not exclude the possibility that available locations were actually used by cranes (Lele and Keim 2006, Lele et al. 2013), we assessed relative resource selection estimates (i.e. RSF scores) and fitted a generalized linear mixed model with a binomial error structure and a logit link function (R package lme4; Bates et al. 2015). Spilled grain availability and distance to human disturbance were log-transformed to reduce skewness of distribution, $\log_e(x+1)$ (Zuur et al. 2010). For the model selection, we included used and available locations (binomial) as response variable and crop type (categorical), distance to roost site, $\log_e(1 + \text{spilled grain availability})$, $\log_e(1 + \text{distance to human disturbance})$, the interaction effects of spilled grain availability \times distance to roost site, as well as of distance to human disturbance \times distance to roost site as explanatory variables. Crane identity was added as random intercept to account for unbalanced number of locations per individual. The results from a first model setup showed that the estimates for barley and wheat were comparable (i.e. overlapping 0) (Supplementary material Appendix 1 Table A1, A2) and were therefore combined into one category in the final model setup (i.e. in total two categories: wheat/barley and other). Model estimates from the categorical variables represent absolute numbers rather than the difference to the estimated intercept, i.e. RSF-scores. Positive RSF scores demonstrate use of the resource in larger proportion than what is available, i.e. selection, a negative score demonstrates underuse in relation to availability, i.e. avoidance, and a score of zero indicates that animals do not select or avoid the resource. Model selection was carried out according to Burnham and Anderson (2002) using the function 'dredge' (R package MuMIn; Barton 2013). The top-ranked model was selected based on AIC and was used to model the associated fitted

values and their 95% confidence intervals after repeated simulations ($n = 1000$) (R package arm: Gelman et al. 2014). All analyses were done in R ver. 3.2.3 (<www.r-project.org>).

Results

Our results showed that spilled grain availability was more than two times higher on stubble fields used by cranes (range: 0–64.1, median 2.4 kernels dm^{-2}) than average availability (range: 0–26.8, median 1.0 kernels dm^{-2}) suggesting that cranes select sites with high food availability. However, according to model estimates foraging decisions by cranes were also influenced by distance to roost site, distance to human disturbance and crop type at the stubble fields (Table 1, 2). Our findings revealed that distance to roost affects selection of foraging sites as cranes selected for higher availability of spilled grain at shorter distances to roost sites and the selection of high food availability gradually decreased with increasing distance to roost sites (Table 2, Fig. 2). Our results demonstrate, although with only $\Delta\text{AIC} = 0.67$ to the third best model without any of the interaction terms (Table 1) that crane selectivity for food availability in relation to distance to roost sites also differed between crop types on stubble fields. On barley and wheat stubble fields, cranes selected for high food availability at short and mean distances to roost sites but the use was in proportion to availability at far distance to roost sites (Fig. 2). Our results further indicated, that selection of foraging sites in relation to features like roads and houses (i.e. human disturbance) was related to distance to roost site (Table 1, Fig. 3). Human disturbance seemed to play a minor role close to roost sites, whereas cranes increasingly selected foraging sites at further distance from human disturbances as the distance to roost site increased (Table 1, Fig. 3).

Discussion

As predicted by central place foraging theory, we found that cranes are more likely to select foraging sites close to the roost sites (more than twice as high RSF scores). However, contradictory to predictions, cranes showed selectivity for foraging

Table 1. Multi-model inference from the RSF (the binomial generalized mixed models) with the binomial response variable set as 1 for used locations and 0 for available locations and cereal stubble type (e.g. barley/wheat and other), spilled grain availability ($\log_e((\text{kernels} + 1)/\text{dm}^2)$), distance to roost site (km), distance to human disturbance ($\log_e(\text{km} + 1)$) and the interaction between spilled grain availability and distance to roost and between distance to roost and distance to human disturbance as explanatory variables. Crane identity was fitted as a random factor. Only the models within $\text{AIC} > 10$ were included in the table.

Model	AIC	ΔAIC	Weight
stubble + human + roost + grain + grain \times roost + human \times roost	291.7		0.29
stubble + human + roost + grain + human \times roost	292.1	0.36	0.24
stubble + human + roost + grain + grain \times roost	292.1	0.39	0.24
stubble + human + roost + grain	292.4	0.67	0.20
stubble + human + roost + human \times roost	298.1	6.43	0.01
stubble + grain + grain \times roost	298.6	6.94	0.01
stubble + human + roost	298.8	7.10	0.01
stubble + roost + grain	299.0	7.25	0.01

Table 2. Parameter estimates (RSF scores) from the top-ranked model (Table 2) and standard errors of the binomial generalized mixed model. In the model the binomial response variable was set as 1 for used locations and 0 for available locations and categorical stubble type (barley/wheat, other) and continuous variables distance to roost site (km), spilled grain availability ($\log_e((\text{kernel} + 1)/\text{dm}^2)$), distance to human disturbance ($\log_e(\text{km} + 1)$), the interaction between spilled grain availability and distance to roost site was set as explanatory variables and crane identity fitted as a random factor. All estimates are absolute values (i.e. not in comparison with the intercept). The estimates for the categorical explanatory variables (barley/wheat stubble and other stubble) represent intercept (RSF scores) and the estimates for continuous variables represent slopes. SE=standard error.

Model variables	Estimate	SE	p-value
dist roost	-0.18	0.11	0.11
dist human	0.22	0.09	0.93
grain availability	1.11	0.37	< 0.01
barley/wheat stubble	0.02	0.70	0.97
other stubble	-2.06	0.93	0.03
dist human \times dist roost	0.56	0.37	0.13
grain availability \times dist roost	-0.11	0.06	0.05

sites with high food availability (i.e. high net energy intake in the vicinity of the roost sites while the selectivity decreased with distance. Yet, in line with predictions, our findings indicated that cranes were gradually becoming more risk averse, selecting for high quality foraging sites located further away from human disturbance with increasing distance to roost.

Our findings correspond with previous studies showing a decreasing probability of crane presence with distance to roost site (Bautista et al. 1995, Nilsson et al. 2016, 2019), presumably because cranes strive to reduce energetic costs of movement (Gils and Tijssen 2007, Elliott et al. 2009, Rozen-Rechels et al. 2015). The decreasing strength of selection for food availability with distance to the central place is more intricate to explain. For instance, it contradicts foraging patterns of cranes at a wintering site in Spain, where cranes used higher-quality sites and foraged more intensively at far distances to roost sites (Alonso et al. 1987). However, optimal and central place foraging theories rely on the assumption that individuals must have full information of the surrounding landscape to be capable to optimize net energy intake (MacArthur and Pianka 1966, Charnov 1976). This assumption may be violated in agricultural landscapes especially during the autumn harvesting period because of high unpredictability in food availability due to crop characteristics and farming practices (e.g. harvesting and tilling) causing food availability to vary from day to day within and between fields and in the landscape (Chudzińska et al. 2015, Nilsson et al. 2016). Moreover, since cranes repeatedly depart and arrive to roost sites, we suggest that they get a better overview of the surrounding landscape especially close to roosts that also facilitate more informed decisions about foraging sites. It is also important to consider that our study, similar to most GPS-studies, rely on a sample of the total daily foraging bouts of the individual. Olsson et al. (2008) suggests that selection of within-site patches may be independent of distance

to roost sites as the total energy gain along a daily foraging bout of multiple foraging sites may explain foraging behavior better than selection of unique sites. In our study we were restricted by capacity of batteries in GPS-devices (i.e. limited fix rate) and the time-consuming surveys of spilled grain. However, with solar panel charged transmitters and improved land cover data it may in future studies be possible with more intensive sampling for more comprehensive understanding of selection in relation to net energy gain.

Cranes, similarly to geese and many other gregarious animals, identify good foraging sites by using foraging conspecifics as informative cues and the higher occurrence of cranes close to the roost sites may provide better information about where the profitable foraging sites occur and thus enhance the selection for those (Amano et al. 2006, Boyd et al. 2016). The higher densities of conspecifics close to the roost sites may also be important in forming selection patterns due to competition, which can be expected to gradually decrease with increasing distance to roost sites. Lowered competition may compensate for the energetic cost of moving further away, resulting in a decreased need for selection of sites with high food availability. The potential tradeoff between high competition close to roost sites and energetic costs of moving far from roost sites may affect the relative energetic value of identical levels of spilled grain availability at different distances to roost sites (Bautista et al. 1998, Stillman et al. 2002). Therefore, to improve our understanding of the selection of foraging sites of these birds, we suggest that the interaction between food availability and competition as well as the significance of social information from conspecifics would need further investigation.

In addition to food availability, the crane selection of foraging sites was influenced by crop type and disturbance. Risk of human disturbance possibly increases the foraging costs due to increased vigilance and thus limits the cranes' selection of foraging sites with high availability of spilled grain, especially at far distances to roosts (i.e. trade-offs in energy budgets). Similarly, previous studies have found that cranes avoid areas close to roads or villages (Franco et al. 2000, Vegvari et al. 2011, Wang et al. 2011), and that geese and swans abandon fields when approached by humans or at high traffic intensities (Madsen 1985, Rees et al. 2005). The more pronounced effect of disturbance at far distances to roost sites is likely the result of cranes having more knowledge of the landscape and disturbance close to roost sites, but also due to higher densities of conspecifics and closeness to roost sites that may contribute to a perception of safety (Caraco et al. 1980, Brown 1988, Beauchamp 2002, Wang et al. 2011). Scaring activities such as propane cannons, human silhouettes and flags are common in the study area, and lethal scaring occurs occasionally and likely more frequent in relation to roads or houses where fields are easily accessible. The frequency and response to direct scaring is however hard to quantify as it is done by farmers and managers on an ad hoc basis. Nevertheless, the unknown frequency and spatial distribution of scaring in the study area likely adds uncertainty

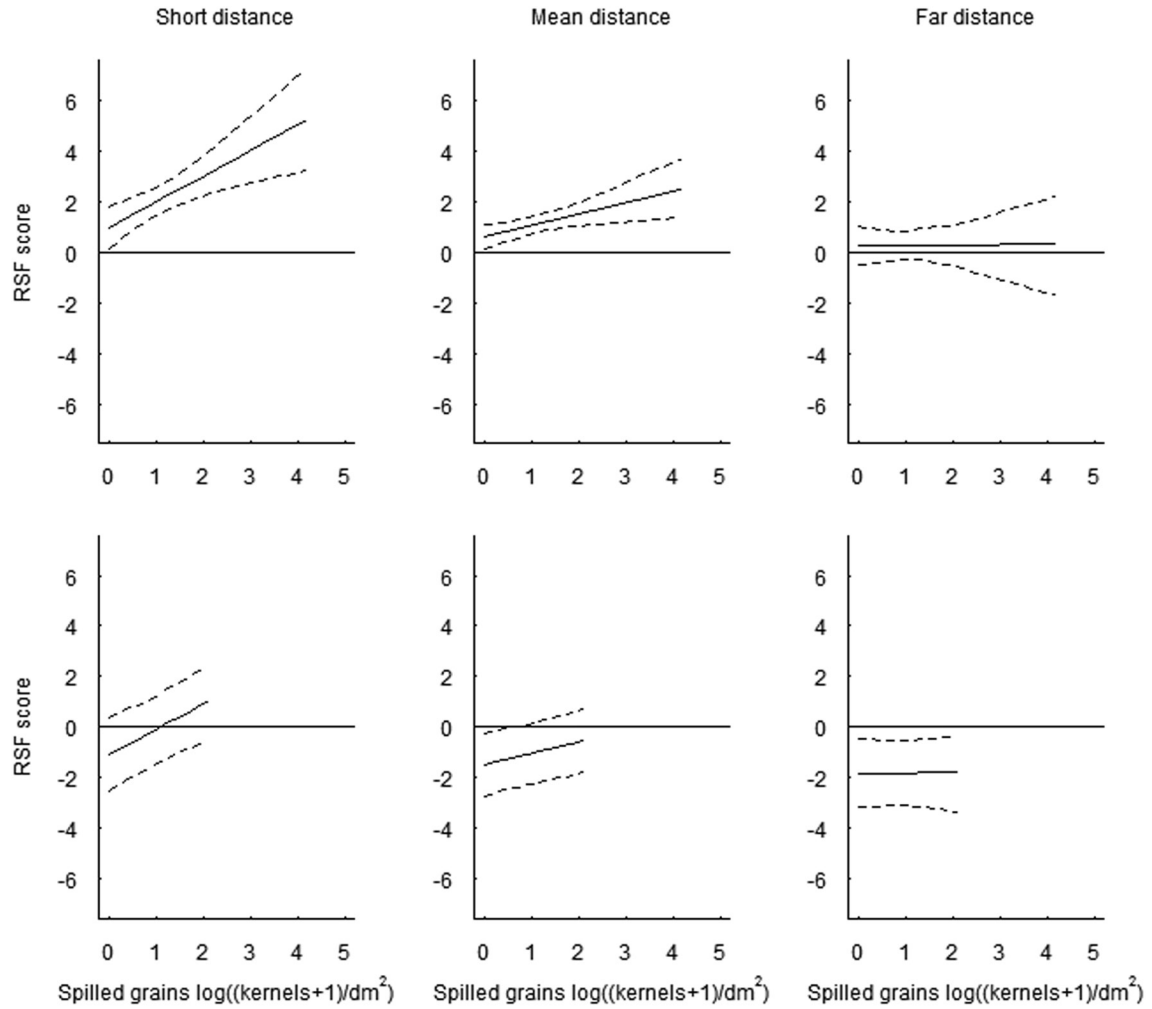


Figure 2. RSF scores (positive predicted values \pm C.I. indicate selection and negative values avoidance, whereas values overlapping 0 indicate use in proportion to availability) in relation to spilled grain availability at short (1.00 km), mean (5.91 km) and far (10.00 km) distances to roost sites, respectively, at wheat/barley stubble fields (upper row) and other stubbles (lower row). For the predictions, distance to human disturbance is kept constant to its median 0.18 ($\log_e(\text{km} + 1)$). Predictions (solid lines) and confidence intervals (95%; dashed lines) are derived from 1000 model simulations using the top-model estimates (Table 2). Predictions are only plotted for the range of available data on the x-axis.

and variability in the selection of feedings sites by cranes in relation to human disturbance that we were not able to quantify due to the ad-hoc scaring by farmers within the study area.

Foraging site selection by cranes was also influenced by crop type, as wheat and barley was selected over other types of spilled grain (e.g. oat and rye). Similar selection for barley and wheat has been shown in other areas, although selection patterns differ due to local differences in quality and availability of crops (Sugden et al. 1988, Nilsson et al. 2016). Corn and sunflower stubble fields are often selected over barley and wheat in areas where such crops are cultivated (Lovvorn and Kirkpatrick 1982, Alonso et al. 1983), which may restrict generalization between staging sites. Moreover, variation may also depend on season and the internal stage of the birds. Birds preparing for migration are known to maximize fat storage,

favoring energy over protein rich forage, such as cereal grains (Fox et al. 2016), as also supported by our findings. However, the selection of barley and wheat over for example oat and rye is harder to explain as the knowledge about metabolic requirements for cranes are restricted. Nevertheless, differences in for example grain hardness and fatty acid content have been shown to cause variation in nutritional value for livestock (Black 2001).

By detailed measures of food availability and tracking data we were able to test central place foraging theory for cranes in a human-dominated agricultural landscape. Our findings highlight that arable lands should not be viewed as homogeneous feeding areas for cranes but rather as heterogeneous mosaics of fields where the foraging pattern is influenced by distance to roost site, crop stage (Nilsson et al. 2016), food availability and human disturbance. How different species

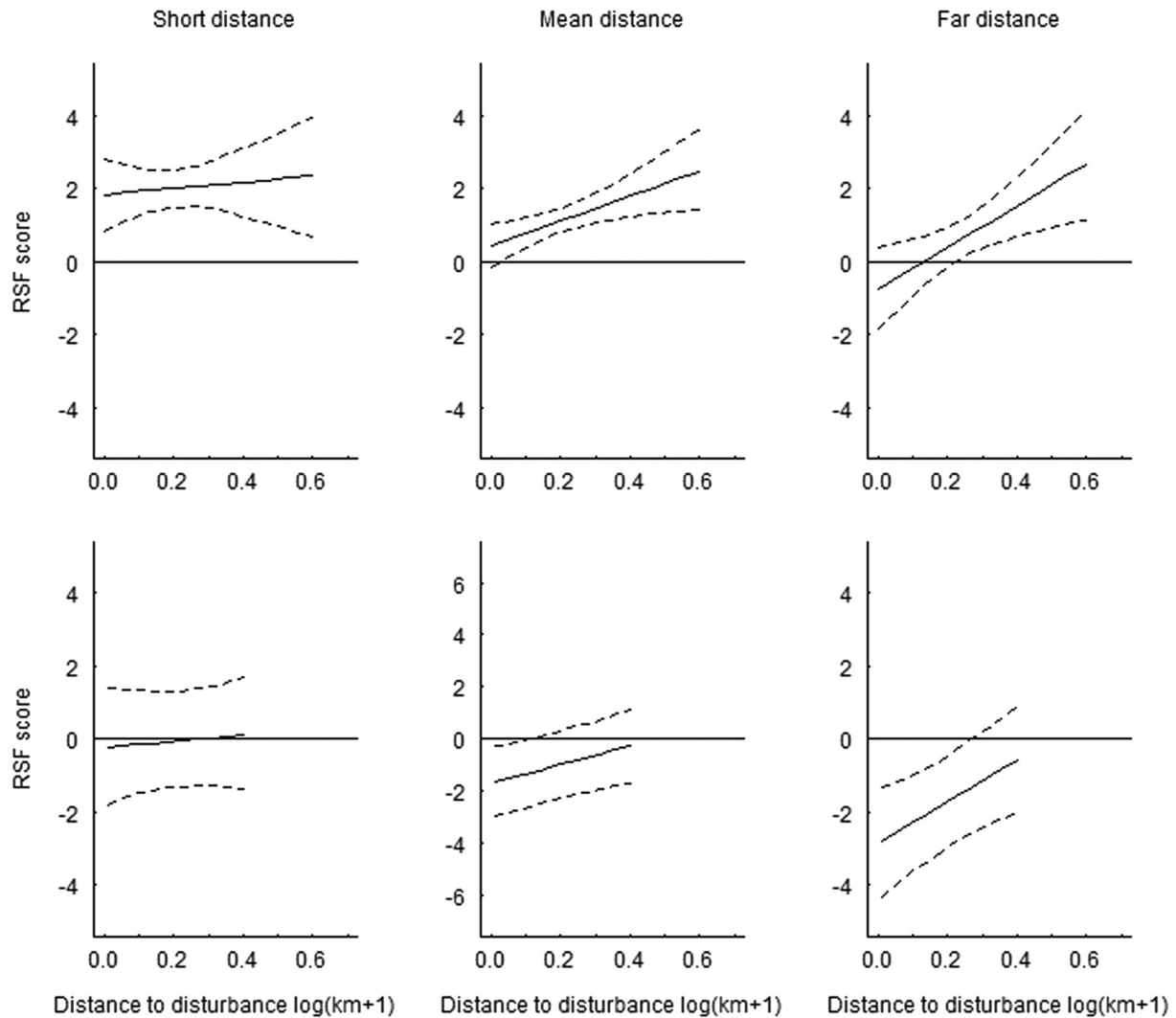


Figure 3. RSF scores (positive predicted values \pm C.I. indicate selection, negative values indicate avoidance and values overlapping 0 indicate use in proportion to availability) in relation to distance to human disturbance at short (1.00 km), mean (5.91 km) and far (10.00 km) distances to roost sites, respectively at wheat/barley stubble fields (upper row) and other stubbles (lower row). Predictions (solid lines) and confidence intervals (95%; dashed lines) are derived from 1000 model simulations using the estimates from the top-ranked model (Table 1, 2). For the predictions, spilled grain availability is kept to its median 1.01 ($\log_e((\text{kernel} + 1)/\text{dm}^2)$). Predictions are only plotted for the range of available data on the x-axis.

respond to local and environmental conditions forms the basis for assessment of the species resource requirement, but can also inform where in the landscape potential conservation conflicts are most likely to occur. Our results can for example be used to facilitate informed implementation of both conservation actions measures (e.g. mitigation of human disturbance) and conflict-mitigating measures (e.g. crop damage prevention). Crop damage caused by cranes and geese is increasing in agriculture landscapes (Montràs-Janer et al. 2019). Our results reveal that crop damage can be mitigated by the use of diversionary fields, preferably stubble fields with high availability of spilled grains, in the vicinity of roost sites as and that distance to human disturbance (e.g. farms and roads) should be considered as it may influence the attractiveness of fields.

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.02487>> (Nilsson et al. 2020).

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Supplementary material (available online as Appendix jav-02487 at <www.avianbiology.org/appendix/jav-02487>). Appendix 1.