Biological Conservation 262 (2021) 109306

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Using movement ecology to evaluate the effectiveness of multiple human-wildlife conflict management practices

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ARTICLE INFO

Keywords:
Common crane
Disturbance
Diversionary feeding
Human-wildlife coexistence
Refuge areas
Scaring

ABSTRACT

Human-wildlife conflicts are universally growing, threatening sustainable coexistence and demanding increasing conservation efforts. While such conflicts are commonly tackled by combining different management practices, how each component contributes to management effectiveness usually remains unclear. This challenge can be addressed by integrating individual-based movement ecology with detailed information on the variety of management practices applied. Using a high-resolution movement dataset of common cranes (*Grus grus*) wintering at the agricultural landscape of the Hula Valley (Israel), we assessed their individual-level responses to three conflict management activities – intensive scaring, allocation of refuge areas and diversionary feeding – quantified in space and time throughout the wintering period. We found that diversionary feeding combined with active scaring reduced the cranes' core activity area and led to a significant shift in habitat preference. Low refuge area availability combined with low intensity diversionary feeding required compensation by higher scaring efforts. However, even intensive feeding was insufficient to prevent cranes from foraging on sensitive crops when refuge fields were highly limited. While most cranes heavily relied on the feeding station, a smaller group consistently avoided it and relied on refuge areas and sensitive crops despite scaring efforts. To achieve a more balanced management plan in our case study, provisioning of diversionary food should be much lower, and refuge areas should be designated based on crane habitat selection rather than solely on residual crops. Generally, we stress that quantitative behavioral analysis of target species that incorporates sub-populations with consistent behavioral variation, is important for effective combination of multiple management practices.

1. Introduction

Human-wildlife conflicts are ubiquitous and often pose a substantial and growing threat to conservation efforts worldwide (Woodroffe et al., 2005; Dickman, 2010). Such conflicts can arise, for example, when species occupy agricultural lands, lured by anthropogenic superabundant food resources often due to destruction and fragmentation of their natural habitats (Fox et al., 2005; Firbank et al., 2008; Fox et al., 2017) or when forced into them as a consequence of factors such as extreme weather events (Goswami et al., 2021). Close contact between humans and wildlife often leads to crop damage, livestock depredation, increased disease transmission and in extreme cases, attacks on humans (Nyhus and Tilson, 2000; Woodroffe et al., 2005; Kilpatrick et al., 2009). The incurred costs, paid by local communities, frequently promote negative public opinion towards certain species, protected areas and nature conservation overall, leading in some cases to culling of animal populations (Treves and Karanth, 2003; Treves et al., 2006). Consequently, various management methods have been implemented worldwide to mitigate such conflicts and promote sustainable human-wildlife coexistence (Treves et al., 2009; König et al., 2020).

During the 20th century, 64% of the world's wetlands disappeared due to human use and land reclamation (Gardner et al., 2015). Laws and acts promoting wetland protection and restoration have been successful in some areas, leading to increased waterbird abundance. Yet these protected areas – frequently embedded in agriculture and aquaculture matrices – often provide insufficient food resources, prompting birds to forage in surrounding agricultural areas (Kleijn et al., 2014; Jankowiak et al., 2015; Runge et al., 2015). The ensuing human-wildlife conflict, in turn, further confounds conservation plans and threatens biodiversity (Reis et al., 2017; Nilsson et al., 2019).

Populations of large grazing birds in Europe and North America have increased rapidly over the last 50 years due to exploitation of resources

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https://doi.org/10.1016/j.biocon.2021.109306
Received 28 October 2020; Received in revised form 9 August 2021; Accepted 16 August 2021

in agricultural landscapes, habitat conservation and hunting bans (Fox et al., 2005). For example, protection from hunting and large-scale habitat restoration enabled the recovery of the Rocky Mountain population of sandhill crane (*Grus canadensis*) rose from 400 individuals in the mid-1940s to ~20,000 recently (Harris and Mirande, 2013), and migratory geese in Poland now tend to select roosting sites within protected areas in regions of intensive agriculture (Jankowiak et al., 2015). The combination of rising bird populations and the inability of protected areas to fulfil resource needs leads to consumption, trampling and contamination of crops and rising conservation-agriculture conflicts at staging sites (Leito et al., 2015; Fox et al., 2017; Montràs-Janer et al., 2019).

To solve such conflicts at the stopover and wintering grounds of large grazing birds, management practices such as active disturbance (scaring) from sensitive crops, establishment of undisturbed refuge fields, creation of diversionary feeding areas, compensation to farmers and even restricted culling have been implemented (for recent reviews, see Fox et al., 2017, Austin et al., 2018). While scaring is effective in increasing the energetic costs of feeding on sensitive crops (Tombre et al., 2005; Parrott and Watola, 2008; Simonsen et al., 2016), it may lead to habituation over time or promote more extensive foraging (Fox and Madsen, 1997; Nolet et al., 2016). For example, white-fronted geese (*Anser albifrons*) exposed to intense scaring, are expected to consume more grass to compensate for the cost of extra flying (Nolet et al., 2016). Refuge fields (non-disturbed fields for birds to feed in) and diversionary feeding are helping to divert birds from sensitive crops by creating superior and safe feeding opportunities (Vickery and Gill, 1999; McKay et al., 2001; Austin and Sundar, 2018), but their establishment and maintenance frequently require large investments. Diversionary feeding provides artificial food in a limited area and may thus also lead to overcrowding and high risk of disease spread (Austin and Sundar, 2018). For example, wintering cranes in Japan became increasingly dependent on supplemental feeding in sites which attract also other waterfowl species susceptible to avian influenza (Amano, 2009; Okuya et al., 2015).

Frequently, due to the complexity of these systems, a single solution is not effective enough for conflict resolution, and a combination of techniques is required (Conover, 2001; Fox et al., 2017; Austin and Sundar, 2018). For example, implementation of a combination of scaring and refuge areas was successful in reducing geese-agriculture conflict in Scotland (Cope et al., 2005). However, even though at many sites, multiple management practices are implemented simultaneously, the direct contribution of the different methods is rarely analyzed (but see Cope et al., 2005 and Tombre et al., 2013). Therefore, to develop a cost-effective, data-driven management program, the integrated contributions of these multiple management practices to the program's success must be simultaneously evaluated (Conover, 2001; White and Ward, 2010). Furthermore, while space-use patterns of birds within agricultural habitats have been extensively studied using tracking devices (Krapu et al., 2014; Nilsson et al., 2016; Dorak et al., 2017; Kleinhenz and Koenig, 2018; Nilsson et al., 2020), the birds' reactions to specific management practices were not analyzed. Some management practices directly constrain animal movement by creating disturbances or barriers (Goswami and Vasudev, 2017), while other practices do not impose such constraints yet can still influence movement and space use of free-ranging animals by manipulating their foraging decisions (Owen et al., 2017). In both scenarios, better understanding of animal response to management requires information about animal movement, motivating the incorporation of movement ecology approaches (Nathan et al., 2008) in conflict-reduction studies, as has been recently highlighted for conservation management actions more generally (Barton et al., 2015; McGowan et al., 2016; Doherty and Driscoll, 2018).

In this study, we aimed to examine the utility of using detailed data on movements and activities of both humans and animals in assessing the effectiveness of multiple management practices in mitigating an agriculture-wildlife conflict. We focus on the common crane (*Grus grus*) whose growing population sizes and gregariousness in the non-breeding season create conflicts with farmers along their migration flyways (Deinet et al., 2013), leading to the establishment of various management programs (Nilsson et al., 2016; Austin and Sundar, 2018). In the Hula Valley, Israel, wintering crane numbers increased substantially (from 10,000 in the 1990s to 50,000 in 2018) in a relatively small area, giving rise to eco-tourism but also to intensified conflict with local farmers (Shanni et al., 2012). As a consequence, a management project was established that includes refuge areas, motorized vehicles to scare cranes from sensitive crops and a diversionary feeding station that operates during the winter. While initially considered a "huge success" (Nemtzov, 2002), this management plan was later met with growing criticism mainly due its high overall cost caused by a rise in the number of wintering cranes. In addition, although multiple management practices are simultaneously used and are centralized (rather than applied per farmer), the combined effectiveness of the project's different components has not hitherto been evaluated.

We used GPS tracking to quantify the responses of individual wintering cranes to three management practices, each depicted in fine detail (movement of scaring vehicles, allocation of refuge areas, and food provision at a diversionary feeding station) throughout the 120-day wintering period during which cranes inhabit this agricultural landscape. We assessed management success by quantifying the preference of cranes to forage in sensitive crops vs. refuge areas and the amount of time they remained within the diversionary feeding station during its operation. While scaring acts to directly constrain movement, designation of refuge areas and diversionary feeding aims at manipulating cranes' foraging behavior and demonstrate how management can influence movement through its effect on animal decision-making processes. We hypothesize that individual cranes would tend to (a) favor refuge areas, (b) remain within the diversionary feeding station when sufficient food is supplied and (c) avoid sensitive fields after scaring events.

2. Methods

2.1. Study area

Over the last two decades, the Hula Valley in northern Israel (33°06′N, 35°36E) became a globally important common crane wintering and stopover site for migratory populations breeding in eastern Europe and western Russia (Leito et al., 2015; Pekarsky et al., 2015). The valley is an intensive agricultural area that provides superior feeding opportunities for cranes, especially during fall and early winter (Appendix A, Section A1). The landscape also includes two relatively small natural protected wetland areas that provide the cranes with attractive undisturbed roosting sites but lack cultivated land, and several rural settlements scattered throughout the valley. An uncultivated 85-hectare area inside one of the natural protected areas was designated as an undisturbed crane diversionary feeding station (Appendix A, Fig. A1).

2.2. Capturing and tagging

We caught and tagged 35 cranes at the pre-migration staging site in western Russia (Ryazan area; 54°56′N, 41°02E) during the summers of 2016 and 2017 and one in the Hula Valley in early spring, 2016. Of these, 21 wintered in the Hula Valley during 2017–18 and were included in the current study. The cranes were trapped using alpha-chlorolose (see Markin, 2013; Hartup et al., 2014) and processed in accordance with protocols approved by the Department of Environment of the Ryazan district, Russia (permit CK19-7154) and the Israel Nature and Parks Authority (permit 2015/41169).

Captured birds were color-ringed and fitted with leg-mounted, solar-powered, GPS-GSM transmitters (20 OrniTrack-L40: Ornitela, Lithuania;

one e-obs GmbH, Germany). Morphological measurements were taken, and body feathers were collected for molecular sexing. The maximal total mass of a transmitter plus rings used for attachment was (mean ± STD) 0.8 ± 0.09% (range: 0.7–1%; 35 g–42 g) of the cranes' average mass.

Three-dimensional GPS positions were recorded every 3–30 min depending on battery status; more specifically, sampling resolution was set to 3 or 5 min when battery charge was above 50% and to 30 min when charge level was below this threshold. All data were remotely downloaded through GSM. We included in the analysis 21 cranes whose main wintering area (>75% roosting time) was the Hula Valley. Since cranes forage during the day (Nilsson et al., 2018), daytime positions (from the time they leave the roost until they return at night) were used (mean ± STD number of days per crane = 122 ± 22). For analyses requiring a higher sampling resolution, we used crane days with <5 min GPS sampling interval ($n = 18$ cranes, mean ± STD number of days per crane = 96 + 32).

Preliminary analysis of the tracking data revealed that most (~80%) tagged cranes concentrated their activity at the diversionary feeding station upon its operation. The remaining birds, however, exhibited a markedly different space use pattern, consistently avoiding the feeding station (see Results). We thus subdivided tagged cranes to two groups – DF-dependent and DF-independent ones – and examined variation in movement patterns and in response to management activities between the two groups.

2.3. *Landscape classification and crane management quantification*

To classify the landscape to different landcover types, we first excluded areas irrelevant for crane foraging (water bodies, settlements, roads and non-agricultural land). We then used a basic land-use map of the remaining area divided into functional units (fields), which we updated to incorporate crop rotation dynamics for every agricultural unit (cultivated or not) through interviews with local farmers (Appendix A, Section A1). Next, we classified the fields into *sensitive* areas susceptible to crane damage and are the target of scaring efforts (see below), and *refuge* areas where cranes are not intentionally disturbed. Sensitive areas include (1) newly sown *annual* crops (e.g. wheat, potato) that are damaged by cranes as they dig or feed on seeds and (2) *perennial* alfalfa crops that are less sensitive but susceptible to trampling. Refuge areas include (1) post-harvested fields with residual crops attractive to cranes (legumes, grain and watermelon), (2) almond and pecan orchards, (3) all other post-harvested or non-sensitive agricultural units (including non-cultivated), and (4) the designated feeding station (see below). The non-flooded habitat in the protected areas was classified as “other” refuge as it is non-disturbed and non-cultivated. Crop rotation agricultural practices lead to land units switching between refuge and sensitive throughout the season. More specifically, sensitive areas become more abundant once sowing starts in late fall, and thus, as the season progresses, less refuge areas containing residual crop (except for orchards) are available for crane foraging (Appendix A Fig. A2). Consequently, only the feeding station is specifically designated for cranes in the management plan, while all other refuge areas functionally act as designated refuge as long as they are insensitive to crane damage.

In order to prevent agricultural damage, organized disturbance worker vehicles (DWV) are responsible for scaring cranes away from sensitive fields from sunrise to sunset to match crane activity time. We collected DWV movement data using second-hand smartphones running the AndroSensor application (freely available at https://bit.ly/2IwJUdu) sampling at 2 Hz. The data were manually downloaded, sub-sampled to 0.1 Hz and filtered to contain only days where ≥10% of the workday was recorded.

Diversionary feeding was confined to a specific, well-defined area (the feeding station) and commenced after fall migration, when the wintering crane population stabilizes, and winter-sowing drastically increase crane pressure on sensitive crops. Corn seeds were spread throughout the day using a tractor-mounted fertilizer spreader operated by a contractor as part of the management project. We recorded the amount of food distributed daily throughout the season. Based on diversionary feeding patterns, we divided the season into three feeding periods: (1) Before, (2) Low, and (3) Intensive (Table 1).

2.4. *Activity area and overlap*

To estimate home ranges, we fitted a continuous-time stochastic movement model (ctmm) followed by AIC best model selection for each individual during. The analysis included only the before and intensive feeding periods (Table 1) to quantify home range change once the feeding station was fully operational and for individuals with data for more than 10 days for each period ($n = 18$; Appendix A Section A2). The selected models were used to construct autocorrelated kernel density estimation (AKDE) home ranges (Fleming et al., 2015), which explicitly incorporates autocorrelation in movement data and has been shown to consistently outperform other home-range estimators (Noonan et al., 2019). We estimated both general (95%) and core home ranges (50%). To quantify the overlap between the core activity area and feeding station, we summed the probability mass function within the feeding station polygon for each individual to estimate the predicted time fraction within it ($n = 21$; Appendix A Section A2). The calculation was done using the ‘ctmm’ package (Calabrese et al., 2016) in R v.3.5.2 (R Core Team, 2020).

2.5. *Movement data segmentation*

Cranes almost always walk within a certain habitat and fly between habitat patches, implying that interpatch, rather than intrapatch, movements represent decisions to shift among foraging units or habitats (Alonso et al., 1995). For quantifying crane habitat selection and the crane-DWV interactions movement data was segmented into “moves” (flights between foraging sites) and “stops” (walking at the foraging site; Appendix A Section A3). The segmentation was performed only on daytime positions taken outside of the roost because this is the time when cranes are foraging (Nilsson et al., 2018). Only days with median GPS sampling interval < 6 min were included in the analysis.

2.6. *Habitat preference*

We evaluated crane habitat selection using a step-selection function (SSF, Fortin et al., 2005). While most SSF applications implicitly assume that movement decisions are made at the spatial and temporal scales of observation (here GPS sampling intervals), these scales are often chosen arbitrarily and might fail to properly represent the scales relevant to the biology of focal species and the properties of the study system (Bastille-Rousseau et al., 2018). We thus adjusted the SSF's implementation to be more suitable for animals flying over rather than moving through (by walking) habitats, using our “moves” and “stops” segmentation (for details, see Appendix A Section A4). This analysis assumes that cranes shift to another spatial unit or another landcover type mostly by flying

Table 1
Division of the season into three periods based on different intensities of diversionary feeding.

Period	Timing	Feed weight	Prop. total refuge area (mean ± STD)[a]	Prop. sensitive crops (mean ± STD)[a]
Before	20 Oct.-04 Dec.	0 kg	0.29 ± 0.04	0.24 ± 0.07
Low	05 Oct.-21 Dec.	<5000 kg	0.22 ± 0.01	0.37 ± 0.02
Intensive	22 Dec.-28 Feb.	>5000 kg	0.16 ± 0.02	0.49 ± 0.04

[a] Proportions are out of the entire study area.

(Section 2.5), while walking occurs mostly within habitats and seldom leads them to shift to another spatial unit or a different landcover type. Exploration of our movement dataset revealed strong support in this assumption. Each "stop" was assigned to one of the classified landcover types, and those occurring in excluded areas (Section 2.3) or assigned to more than one landcover type were discarded (Appendix A Section A3).

Because of the temporal variation of "stop" length, we used "stop" duration, before the "move", as covariates instead of only relying on presence data. No correlation between move length and time spent in the habitat before the flight (rho = 0.03) or after (rho = 0.02) was found. For each observed foraging location, we constructed 20 random "moves" with the same starting point (Forester et al., 2009) using turning angles drawn from a random distribution. Creation of random "moves" continued until 20 random "moves" ending in a classified landcover type were created. "Move" distances and "stop" durations were drawn from an empirical distribution based on the segmented behavior of all individuals throughout the entire season (Appendix A Fig. A4). Modelling was performed using MATLAB R2017a (The Mathworks Inc.).

To compare time spent by an individual crane in different landcover types at used vs. available locations, we applied conditional logistic regression using the 'survival' (Therneau and Grambsch, 2000) R package. The SSF was of the following form:

$$w(x) = exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

where β_1 to β_n are the estimated coefficients describing the strength of selection (time spent) of landcover types x_1 to x_n. We run this analysis separately for each tagged individual to examine variation among individuals.

2.7. Crane-DWV interaction quantification

Thresholds and criteria for crane-DWV interactions were defined based on 130 observations of such interactions obtained over six days, an interview with the scaring team coordinator regarding the effective distance of the various scaring methods, and the distribution of crane-DWV distances from the movement data collected (Appendix A Section A5). To define an interaction, we only used to "stop" (Appendix A Section A3) occurring in sensitive areas as cranes are never intentionally scared away from other types of cultivated land. "Stops" occurring in the same functional unit (field) were grouped and only the final point before leaving the field was considered as crane-DWV interaction, since every time workers spot cranes on a sensitive field, they would scare them away and scaring measures would continue until the birds departed from the field resulting in a 100% success rate. Furthermore, an interaction was only considered when DWV was within a 300 m radius from a crane. Situations in which cranes left a sensitive field without being scared were defined as cases when the DWV in charge of that field was >1000 m away. Since not all scaring techniques are effective for distances >300 m, interactions falling in the range of 300–1000 m were excluded from the analysis because we could not definitively determine if crane desertions were associated with scaring activity. We could track only a portion of the DWV's activity each day, and thus analyzed only the crane-DWV interactions or lack thereof in areas where tagged DWVs were active.

2.8. Statistical analyses

To compare home ranges between periods, we used Wilcoxon signed-rank tests. To test whether the core activity area overlap with the feeding station was associated with age or sex, we used a binomial generalized linear model.

To calculate the proportion of time the cranes spent in the feeding station we divided the number of daytime positions inside the feeding station polygon (Appendix A Fig. A1) by the total number of daytime positions. The optimal amount of corn to maximize the proportion of time cranes spent at the feeding station was found by fitting a three-parameter logistic curve and comparing to other candidate models using the 'drc' (Ritz et al., 2015) R package (Appendix A Section A6).

The effect of season and food amount on time spent at the feeding station was analyzed using a Type II Wald chi-square test on a generalized linear mixed model with beta distribution and crane identity as a random factor, using the 'glmmTMB' (Brooks et al., 2017) R package.

To analyze the influence of DWV on crane movement, we calculated the time a crane spent at a field before being scared and the time passed until returning to the same field. To assess the effect of scaring and crop type on foraging cranes, we applied an aligned rank transform ANOVA (ART-ANOVA) for non-parametric factorial analyses with crane ID as a random factor, using the 'ARTool' (Wobbrock et al., 2011) R package. We carried out within-group comparisons using the 'ARTool' pair-wise contrast function and between-group comparisons using a Mann-Whitney *U* test with Bonferroni-Holm's p adjustment. To evaluate the DWV return rate, we calculated the mean return time per field per day and compared it between crop types and periods (Table 1) using ART-ANOVA, with DWV identity as a random factor.

Prior to statistical analysis, Levene's test was performed to ensure homogeneity of variance, and data was pooled when needed. Shapiro-Wilk tests were performed to ensure normal distribution when parametric tests were used.

3. Results

3.1. Activity area

Before the feeding station operation (Table 1), the median daily and core activity areas were 29.16 km^2 (range: 5.89–73.45) and 5.66 km^2 (range: 1.1–18.87), respectively. During the intensive feeding period (Table 1), the predicted time fraction (based on AKDE home range calculation) within the feeding station for 17 individuals (DF-dependent, see Methods) was on average 44% (range: 12–71%, Fig. 1) while for 4 individuals the predicted time fraction was <1% (DF-independent). Age or sex had no significant effects on the tendency of the core activity area to overlap with the feeding station (quasibinomial GLM; age: $p = -1.15$, $p = 0.26$, sex: $p = -1.66$, $p = 0.11$). For both DF-dependent and -independent groups, core and daily activity areas were reduced in the intensive feeding period, but this trend was statistically significant only for DF-dependent cranes (Wilcoxon signed-rank test, $p < 0.001$ DF-dependent; $p = 0.13$ DF-independent; Fig. 1).

3.2. Habitat preference

Before the start of the operation of the feeding station, habitat preference was generally similar among DF-dependent and DF-independent cranes (Fig. 2.a, Appendix B Table B3). During this period, the cranes spent around 70% of their daily time in refuge areas, selecting for fields containing post harvested residual legumes, grain and watermelon (LGW) and almond and pecan orchards (AP), but avoiding other refuge sites where anthropogenic food is not expected (OTH; Fig. 2.a, Appendix B Table B1 and Fig. B1). The cranes also avoided sown annual (AN), but not perennial (PRN), fields (Fig. 2.a, Appendix B Table B1).

During the low feeding period, the DF-dependent cranes shifted to prefer the feeding station. They spent 35% of their daily time in other refuge areas, but these were no longer preferred compared to their availability (Fig. 2b, Appendix B Table B1 and Fig. B1). Additionally, once the low feeding period began, these cranes strongly avoided sensitive annual and perennial fields (Fig. 2.b, Appendix B Table B2). During the intensive feeding period, avoidance of sensitive annual fields was even more pronounced and the DF-dependent cranes' presence there dropped to 1% of daily time, but they no longer avoided perennial fields (Fig. 2.c, Appendix B Table B2 and Fig. B1).

The DF-independent cranes had a higher preference for refuge areas

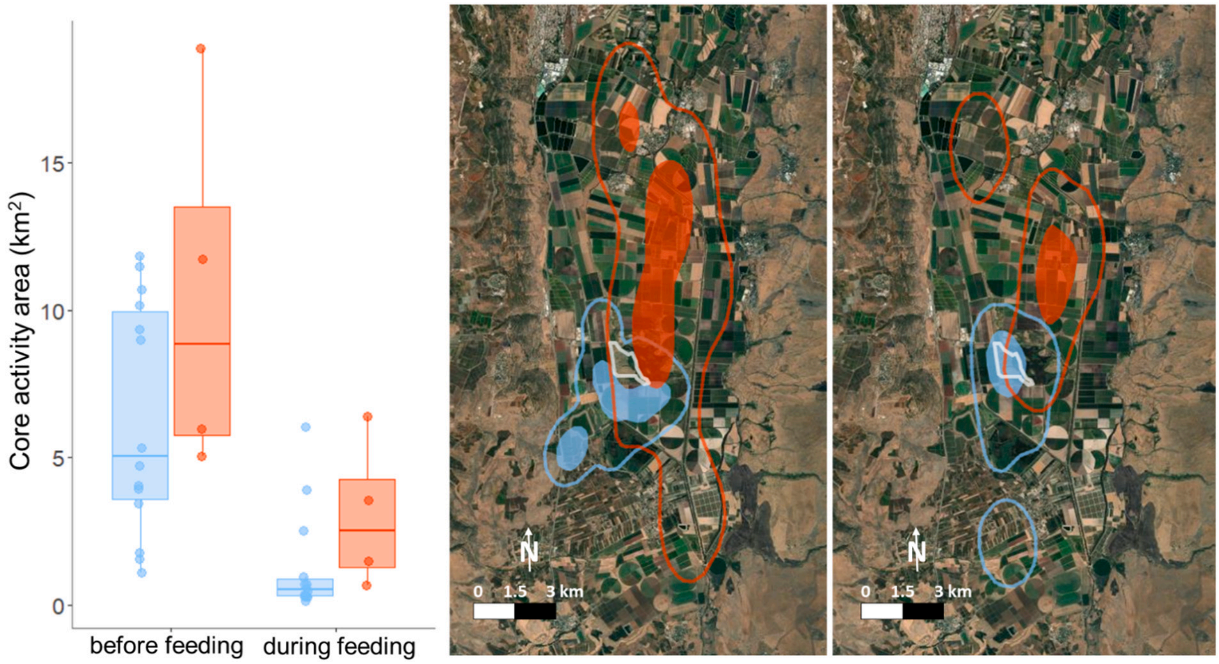

Fig. 1. (a) Change in crane core activity area (50% Auto-correlated Kernel Density Estimate for each individual) before and during the diversionary feeding periods. The asterisk indicates a significant difference ($p < 0.05$). Individuals whose core activity overlaps with the feeding station (DF-dependent, $N = 14$) are shown in blue and those avoiding it (DF-independent, $N = 4$) are shown in red. Sample daily activity area (outlined, 95%) and core activity area (shaded, 50%) of one DF-dependent (#170591) and one DF-independent (#170831) individual (b) during the period before the feeding station was operational and (c) during the period of intensive feeding (Table 1) are depicted. Not all areas of the same individual are connected. Night roost sites are indicated by blue stars and the diversionary feeding station is outlined in white. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

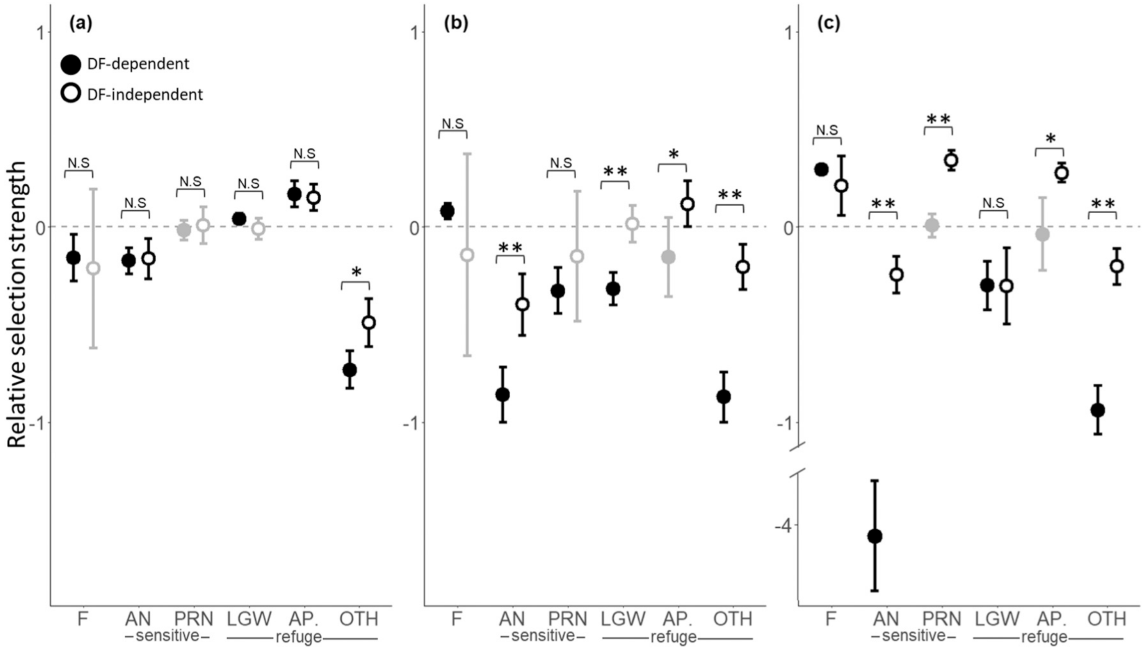

Fig. 2. Step-selection parameter estimates (based on time spent at the habitat), with error bars indicating 95% confidence intervals, of individuals feeding at the feeding station (DF-dependent cranes, solid circles) and individuals avoiding it (DF-independent cranes, open circles) (a) before the feeding station is operational, (b) during low intensity feeding and (c) during intensive feeding (Table 1). Please note the broken Y-axis in panel c. Confidence intervals >0 indicate preference and < 0 indicate avoidance. Black and grey indicate significant ($p < 0.05$) and insignificant effects respectively (Appendix B table B1). Habitat covariates include the feeding station (F), post harvested fields containing legumes, grain, watermelon (LGW) and almond or pecan orchards (AP), newly sown annual crops (AN) and perennial crops (PRN; see Appendix A Table A1 for more details). $^*p < 0.05$, $^{**}p < 0.001$ (Appendix B Table B3).

(spending 74% of their time there) during the low feeding period compared to the DF-dependent cranes, a lower avoidance of sensitive annual fields and no avoidance of sensitive perennial fields (Fig. 2.b, Appendix B Table B2 and Fig. B1). During the intensive feeding period, DF-independent cranes had a significantly greater preference for almond and pecan orchards, and lesser avoidance of other refuges compared to

DF-dependent cranes, but like them they no longer preferred post-harvested residual legume, grain and watermelon fields (Fig. 2.c, Appendix B Table B2). They strongly preferred perennial fields (spending 30% of their time there) and had a significantly weaker avoidance of sensitive annual fields than DF-dependent cranes (Fig. 2. c, Appendix B Table B2 and Fig. B1). During the intensive period, the DF-independent birds showed a significant increase in their preference for the feeding station, and spent on average only 3% of their daily time there (Fig. 2. c, Appendix B Table B1 and Fig. B1).

3.3. Feeding station influence

Before the feeding station was operational, DF-dependent cranes spent 3 ± 2% (average + STD) of their daily activity time at the station area (Fig. 3). During the low feeding period, a mean of 3398 kg of corn (range: 2100-5600) was provided daily, and DF-dependent cranes spent 44% (±8%) of their daily activity time at the station. During the intensive feeding period, a mean of 8769 kg of corn (range: 4300-12,140) was provided, and DF-dependent cranes spent 84% (±8%) of their daily activity time at the station (Fig. 3). The upper asymptote of the logistic regression, representing the optimal amount of corn to maximize the proportion of time cranes spent at the feeding station, was 0.85 and the 95% estimated effective dose was 6456 kg (Fig. 3). Not only the amount of food ($\chi^2 = 67.6$, $p < 0.001$) but also the intensity of feeding ($\chi^2 = 53.3$, $p < 0.001$) significantly affected the time the cranes spent at the feeding station. As indicated by post-hoc comparison, all months had significantly different crane presence at the station, with February having the highest even though the amount of food provided was not increased during this time (rho = −0.18, $p < 0.001$).

3.4. Active disturbance impact

We collected 7119 h of movement data from an average of 6.5 DWV per day (range: 1–13). The median of the mean daily DWV revisit time to the same field was 47 min (range: 5–152). This time was shortest during the low feeding period (ART-ANOVA: $F_{5,4188} = 13.40$, $p < 0.001$, Appendix B Fig. B2.a.).

We identified 627 interactions (see 2.7) between GPS-tagged cranes and DWVs on sensitive fields, and 119 instances in which a crane left a sensitive field without interacting with a DWV. Cranes that left without being scared stayed at the fields longer than cranes which were scared, with no difference between field types (median of 30 min. vs. 18 min, respectively; ART-ANOVA: scared: $F_{3,61} = 5.\ 47$, $p < 0.05$, field type: $F_{1,61} = 2.39$, $p = 0.13$, Fig. 4.a). The tendency to return to the same field was slightly lower for actively scared cranes compared to those that left the field without scaring, but this difference was not statistically significant (ART-ANOVA: $F_{3,65} = 3.24$, $p = 0.08$, Fig. 4.b).

The highest number of crane returns within the same day occurred around 40 min (Appendix B Fig. B3) after the scaring event, independent of period or field type (ART-ANOVA: period: $F_{5,\ 241} = 0.87$, $p = 0.42$, field type: $F_{5,241} = 0.02$, $p = 0.88$). For same day returns, the probability of a crane returning to the perennial field from which it was scared was twice higher compared to an annual field (ART-ANOVA: $F_{1,32} = 9.81$, $p < 0.01$, Fig. 4.c.); however, the DWV revisit time was not different between these two types of fields (ART ANOVA: $F_{5,4188} = 1.13$, $p = 0.29$, Appendix B Fig. B2.b.).

4. Discussion

Like in many other global environmental concerns, human-wildlife conflict management and conservation planning can strongly benefit from the growth in quantity and quality of animal movement data. Although this notion has been emphasized recently (Barton et al., 2015; Doherty and Driscoll, 2018), and a growing number of studies have utilized animal movement data to evaluate and inform human-wildlife conflict management plans (e.g. Nolet et al., 2016; Nilsson et al., 2018), such applications also require detailed information on the management actions in situ to effectively link human activities to animals' response. This integrative approach is exemplified in our study system and summarized in Fig. 5, illustrating the typical behavioral response of most (DF-dependent) cranes to management actions and providing important guidelines to the Hula Valley crane management program. In the following, we first discuss the specific findings of this study and suggest how management practices could be improved, and then highlight some emerging general insights of broader appeal to encourage the use of such an integrative approach in planning sustainable management approaches in other sites.

4.1. Crane management at the Hula Valley

The simultaneous quantification of the spatiotemporal variation in crane movement patterns and management practices revealed some general patterns in our study system (Fig. 5), allowing us to draw informed management recommendations. Before the onset of feeding,

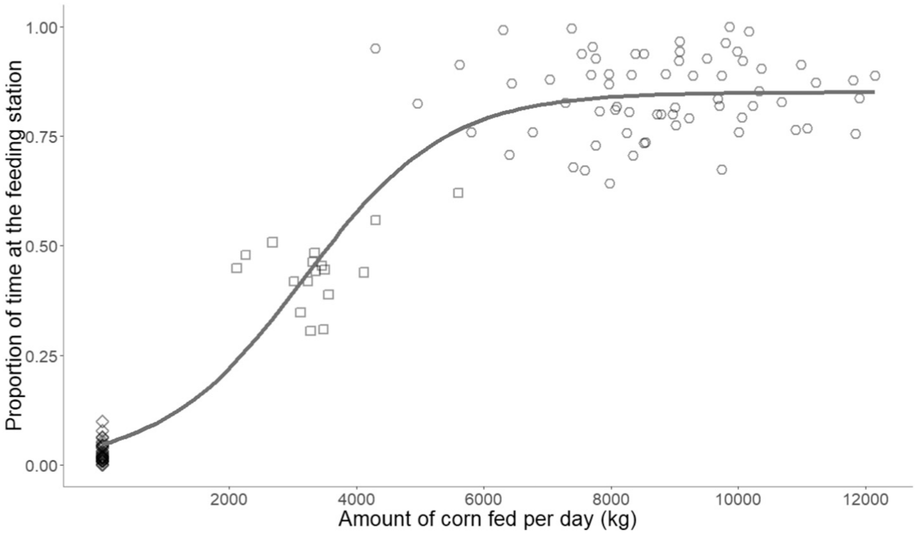

Fig. 3. Proportion of time DF-dependent cranes spent at the feeding station as a function of amount of corn provided. Each point represents the mean daily proportion of time cranes spent at the feeding station before it was operational (diamonds), and during low (squares) and intensive (circles) feeding stages. The line represents a three-parameter logistic curve fitted using daily proportion per individual.

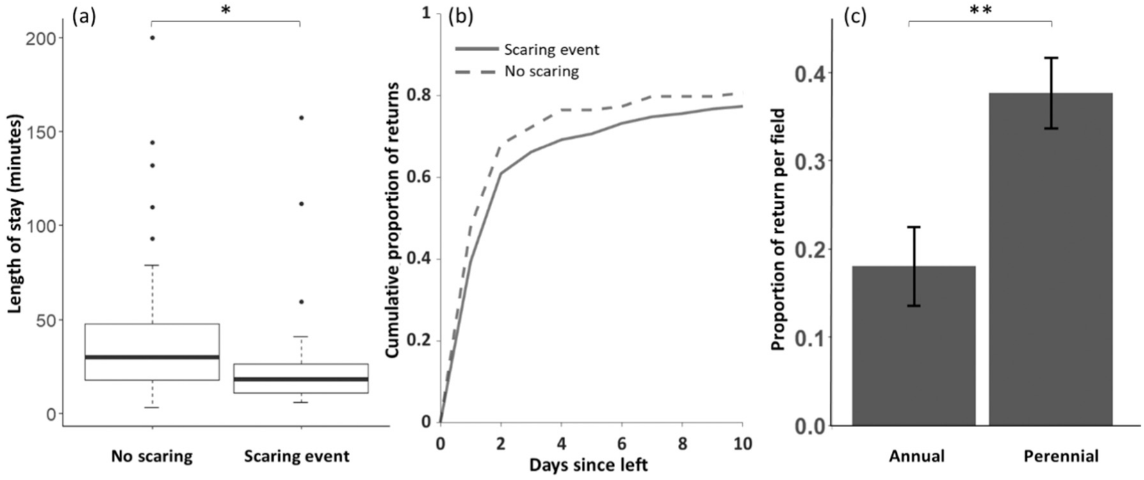

Fig. 4. (a) Time of stay in the field per individual without being scared and after a scaring event. (b) Cumulative proportion of returns during the first 10 days since a crane left a sensitive field without being scared (dashed line) and field after being scared (solid line) (c) The probability of return per individual, for different types of crop (mean ± SE). Asterix indicates significant difference (* $p < 0.05$, ** $p < 0.001$).

there were fewer sensitive crops and higher availability of residual resources in the harvested fields (Fig. 5.a.), allowing for larger core activity areas, stronger preferences for refuge areas and avoidance of sensitive annual crops (Fig. 5.c.). This suggests that the minimal scaring efforts by the disturbance worker vehicles (DWV) in this period were sufficient but also that the presence of multiple refuge areas is essential as cranes spent most of their daily time in these landcover types. As the season progressed, the wintering crane population stabilized (Fig. 5.b.), refuge availability decreased due to winter sowing and due to residual food depletion in the remaining refuge areas; concurrently, the feeding station began operation and the DWV increased their scaring efforts (Fig. 5.a.). The cranes responded by a drop in core activity area and a significant shift in habitat preference from refuge areas across the landscape to the feeding station, and this shift became more pronounced during the intensive feeding period (Fig. 5.c.). Throughout this period, cranes strongly avoided sensitive annual crops while sensitive perennial crops – namely alfalfa – remained more attractive despite scaring efforts (Fig. 5.c, d.).

The activity areas of cranes in the Hula Valley before the onset of diversionary feeding were larger than reported for staging cranes in Sweden estimated using KDE (Nilsson et al., 2018). The KDE method ignores autocorrelation in the data and tends to underestimate home range area size (Fleming et al., 2014; Fleming et al., 2015) and thus the larger home range sizes in our study may be due to incorporation of autocorrelation structure in the data. Later in the season the activity areas shrank, probably due to the attractiveness of the feeding station, DWV scaring efforts in sensitive fields and decreased availability of refuge areas. Interestingly, the activity area decreased both for DF-dependent and DF-independent cranes, further suggesting that the change in activity area size was driven not only by the use of the feeding station but also by the decrease in refuge availability. Refuge area availability in the Hula Valley is being dictated solely by seasonal agricultural practices and thus, unlike specifically designated refuge areas with attractive crops, they are depleted throughout the season due to consumption, degradation, and seasonal crop rotation (Nilsson et al., 2018). Evidently, before the onset of the diversionary feeding, both DF-dependent and DF-independent cranes strongly preferred refuge areas containing residual crops (e.g., peanuts and almonds) and spent most of their time there. However, as the season progressed cranes increasingly avoided the post-harvested fields, probably due to lack of available food remaining in these fields (Fig. 5.c). The almond orchards remained attractive, especially to the DF-independent cranes. Moreover, during the low and intensive feeding periods the avoidance of uncultivated refuges by the DF-independent cranes became weaker, suggesting that after depletion of anthropogenic superabundant food resources they might have to start foraging for more natural food. Similarly, in Spain, cranes switched to feed on acorns and bulbs once the residual grain germinated (Avilés et al., 2002). We suggest, therefore, that as resources remaining in post-harvested fields are depleted, specific fields outside the feeding station should be designated to serve as refuge in the management plan for the duration of the crane wintering period. This practice is also common for managing geese (Jensen et al., 2008) and is expected to make scaring efforts more effective.

Furthermore, as our coupled DWV-crane tracking results showed that cranes had a significantly higher probability of returning to the perennial alfalfa fields they were scared from, this crop can thus be chosen for allocation of designated refuge areas based on their preference. Our coupled DWV-crane tracking further suggested that the scaring efforts were appropriate, as evident in the matching of the frequency of DWV field revisits and the main influx of cranes returning to the field they were chased from. Yet, the fact that there was no influence of scaring on the tendency of cranes to return to fields they departed from, highlights the need for repeated scaring to make it effective.

While diversionary feeding was very effective in the winter months, we found that despite ample food provisioning (above the effective dose) cranes continued to forage on sensitive crops outside the diversionary feeding site. Moreover, during late winter, the cranes spent more time at the feeding station regardless of supplied food amounts, indicating an effect of the diminishing availability of refuge areas rather than a response to the diversionary feeding, as has been shown for other food-limited populations (Calenge et al., 2004; Kubasiewicz et al., 2016). We suggest that the provided corn is insufficient for the cranes' energetic demands, forcing them to seek supplemental nutrients such as protein and calcium elsewhere (Krapu et al., 1985). Although during the non-breeding season cranes' diet is mostly herbivorous, it consistently contains up to 10% food items from animal origin (Reinecke and Krapu, 1986; Bart and Jonathan, 2000; Avilés et al., 2002). Alfalfa fields were used by sandhill cranes to add invertebrates to their diet (Reinecke and Krapu, 1986), potentially explaining why the Hula Valley cranes insistently return to alfalfa fields even when scared from them (Fig. 5.d.) and why they avoided them significantly less than annual sensitive fields (Fig. 5.c.). Further evidence comes from our analysis of cranes' fecal microbiota (Pekarsky et al., 2021), suggesting that DF-dependent cranes likely forage also outside the feeding station to diversify their food, chiefly by feeding on invertebrates in alfalfa fields.

Interestingly, one fifth of the tagged cranes (DF-independent) exhibited a strikingly different behavior, consistently avoiding the feeding station. Individual differences in traits, such as boldness or

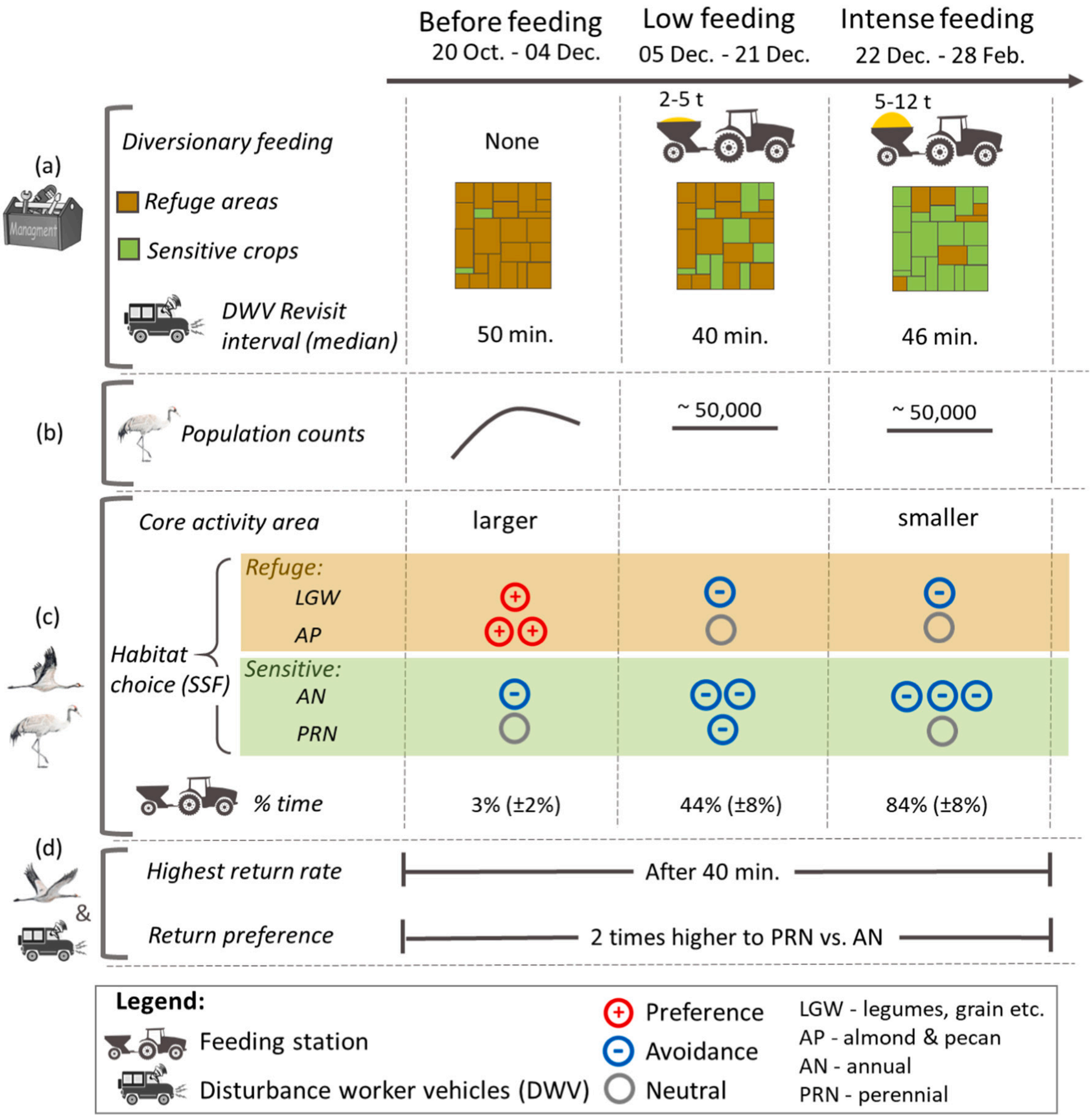

Fig. 5. Summary of the integrative approach for quantification of a multiple human-wildlife conflict management practices, separated into (a) the Hula Valley crane management program, (b) crane population assessment, (c) individual-based effects on movement and habitat selection of the majority of individuals (DF-dependent cranes, see text) and (d) tagged individuals' behaviors after an interaction with a disturbance worker vehicle. For panels a-c, results are represented per period (Table 1) while for panel d, they are pooled for the entire season. For more information regarding habitat types see Appendix A.

exploratory behavior, have been shown to influence the response of individual animals to novel human-created conditions or disturbances (Martin and Réale, 2008; Tuomainen and Candolin, 2010) and could have led to the different behavioral response shown here. Conversely, behavioral differences may be related to poor physiological condition, as nutritionally-stressed individuals tend to forage in riskier habitats (Beale and Monaghan, 2004) and avoid foraging sites with greater intraspecific competition (Tregenza, 1995). This DF-independent fraction is equivalent to ~10,000 cranes during an average winter in the Hula Valley. While not responding to diversionary feeding, DF-independent cranes selected mostly almond and pecan orchard refuges, probably fulfilling their nutritional demands by foraging on fat rich nuts; yet, they also foraged on sensitive alfalfa crops, further highlighting the importance of applying multiple management practices. Thus, to make the management program more effective, it should be adjusted to accommodate variation among individuals in their response to different management practices. For example, management and damage costs could be reduced by maintaining almond orchards – in which the DF-independent cranes mainly forage without causing any damage – as refuge areas.

In summary, while generally in accordance with our hypotheses, the cranes' response was more complex than hypothesized due to consistent individual behavioral variations, the nontrivial synergistic effects of the different management practices, and the seasonal dynamics of the entire system. Thus, integrating individual-based movement ecology with a spatiotemporal evaluation of the utilized management practices was essential to better understand the response of wild animals to seasonal changes and multiple management practices.

4.2. *Broader implications for wildlife management*

The Hula Valley crane management program applies three types of management practices that are used in many other such programs – diversionary feeding, intensive scaring and allocation of refuge areas. Whereas scaring directly constrain crane habitat use, diversionary feeding and refuge areas indirectly influence their foraging decisions. Such complementary practices should be balanced and can be improved by providing, for instance, multiple food types rather than one (here, corn) to accommodate the target species' nutritional requirements. Furthermore, artificial feeding of wild animals, not only can lead to population growth and diseases transmission but can also create dependency and change behavioral patterns of the target animals, especially mammals (Milner et al., 2014; Murray et al., 2016). Artificial feeding of cervids, for example, led to changes in foraging patterns and home range sizes (Van Beest FM et al., 2010; Ossi et al., 2017). Scaring efforts should be timed to the behavioral response of the animal and should not be intensified before attempting other solutions to avoid excess human effort and elevated food consumption due to energy loss compensation. Additionally, intensive scaring, may not only lead to habituation or higher energetic demands to compensate for energy loss (Nolet et al., 2016; Stone et al., 2017) but could also elevate stress levels and may lead to injury or even death of target animals (Ahlering et al., 2011; Hill, 2018). Thus, while intensive management interventions are frequently essential and unavoidable when other methods are ineffective to mitigate human-wildlife conflicts, supplementary feeding and intensive scaring need to be applied with caution and in the minimal effective dosage. Furthermore, accurate long-term monitoring of the effects on the target populations and efficiency in conflict mediation is needed to ensure responsible management practices.

Refuge fields may be considered as a more moderate intervention and are best designated based on the foraging preference of targeted species, but often (as happens at the Hula Valley), they are allocated according to independent agricultural considerations, irrespective of the behavioral and physiological preferences of the target animals. Animal-designated refuges might help to further decrease food amounts provided by the diversionary feeding and to avoid the risks associated with the consequent overcrowding at the feeding station. In order to encourage farmers to provide refuge areas on their land, subsidies are frequently offered (Eythórsson et al., 2017), which can be further financially supported by increasing efficiency of diversionary feeding, thus reducing overall costs. Moreover, our results also stress the importance of considering that a particular subset of individuals (the DF-independent cranes in our system) may have a consistently different foraging behavior and avoid artificial feeding stations. This understanding should facilitate development of management practices specifically to address their needs while reducing costs of practices that do not target them.

By assessing the efficiency of the different components of the studied conflict, multiple management practices can be better integrated to achieve a more balanced and effective management that promotes coexistence in the long term. To further investigate the contribution of each management practice separately in any system, an experimental framework in collaboration with the stakeholders is needed. For example, food amounts provided at the feeding station could be manipulated to determine the most effective amount for each season, and additional refuge areas could be designated. Moreover, future studies should incorporate financial benefit-cost assessment of management activities (Kubasiewicz et al., 2016). Finally, as we have shown here, all these recommended directions for future research can benefit from integration of movement ecology with human-wildlife conflict management, linking detailed information on movement and activities of both humans and animals to better understand the mechanisms underlying the conflict, and to offer practical solutions.

Data accessibility statement

The code to run the models and conduct the statistics is available on https://github.com/pekarskysasha/conflict_management_practices. All data used in this study will be stored online upon acceptance of the manuscript.

CRediT authorship contribution statement

Sasha Pekarsky: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization, Project administration. **Ingo Schiffner**: Methodology, Writing – Review & Editing, Validation. **Yuri Markin**: Investigation, Writing – Review & Editing. **Ran Nathan**: Conceptualization, Validation, Writing – Review & Editing, Supervision, Funding acquisition.

Declaration of competing interest

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

Acknowledgements

The authors wish to thank to K. Postelnykh, K. Kondrakova, N. Yesraeli, S. Agmon, Y. Charka, G. Shani, N. Valtzer and F. Argyle for help in fieldwork and trapping. We are also grateful to I. Rubin, Y. Davidson E. Naim and O. Bone for coordination with local stakeholders. We thank C. Seif, U. Sadeh, I. Barnea, local farmers and scaring project workers for collaborating on data collection. We also thank the members of Nathan's Movement Ecology lab and especially Y. Bartan, S. Turjeman and D. Shohami for their help at various stages of the research. We thank U. Schlägel for help with SSF analysis. We thank A. Ben-Nun, D. Harel, V. Orlov and M. Meron for help with Hula Valley mapping.

Funding information

This research was supported by a JNF grant 2015-904-01 and BSF grant 60-01-221 to RN. RN also acknowledges support from the Adelina and Massimo Della Pergola Chair of Life Sciences, and the Minerva Center for Movement Ecology.

Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109306.

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