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Predicting anthropogenic food supplementation from individual tracking data

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Many wildlife species consume food or refuse provided by humans. To understand the effect of anthropogenic food subsidies on wildlife populations, we first need to quantify where and when individuals can access such food sources. The Red Kite *Milvus milvus* is an opportunistic raptor species and uses both inadvertent and deliberate food subsidies provided by citizens. Here we present a new approach using global positioning system (GPS)-tracking data to predict where anthropogenic food subsidies probably occur. We tracked 497 individuals with solar-powered GPS transmitters over an average of 3.2 (range 1–9) breeding seasons in Switzerland, and combined these data with locations of 125 known feeding sites obtained through interviews. We used two sequential random forest models, at both individual movement and population levels, to predict where anthropogenic food subsidies were attended by Red Kites. The first model classified locations that were frequently and regularly revisited, and successfully predicted 85% of locations that were within 50 m of an externally validated feeding site. These predicted locations were aggregated in 500-m grid cells to calculate the proportion of individuals and locations associated with predicted food subsidy. A second model related the presence of known food subsidies to the aggregated predictions. In our study area, 80% of known anthropogenic food provision locations could be correctly identified using Red Kite tracking data, but data sparsity beyond the core range of tracked individuals limits predictions of anthropogenic food subsidies at larger geographical scales. Nonetheless, biologging data can identify ephemeral food sources, and facilitate an assessment of the importance of anthropogenic food subsidies for the fitness of individuals in tracked populations.

Keywords: biologging, human food subsidies, raptor, telemetry.

Human activities often produce food waste that can be consumed by wildlife (Parfitt *et al.* 2010). These anthropogenic food subsidies can affect the demography and behaviour of many opportunistic animal species, such as seabirds consuming unwanted catch discarded by fishing vessels (Navarro *et al.* 2009, Bugoni *et al.* 2010, Wagner & Boersma 2011, Bicknell *et al.* 2013), vultures becoming dependent on expired livestock (Donazar *et al.* 2009, Margalida & Colomer 2012, Fluhr *et al.* 2017, Tauler-Ametller *et al.* 2017) and terrestrial scavengers feeding routinely on human refuse (Kolowski & Holekamp 2008, Weiser & Powell 2011b, Plaza & Lambertucci 2017, Katzenberger *et al.* 2019, Langley *et al.* 2021). However, despite much general knowledge about which species use what form of human food subsidies, the extent to which these subsidies affect the demography of populations is still poorly understood (Robb *et al.* 2008, Newsome *et al.* 2015, Shutt & Lees 2021, Bailey & Bonter 2022, Broggi *et al.* 2022, Griffin & Ciuti 2023).

To improve our understanding of how human food subsidies affect the demography of populations, it will be necessary to objectively quantify to

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what extent individuals rely on such subsidies. Dietary contributions of different sources can be quantified using individual dietary assessments (Weiser & Powell 2011a, Swan *et al*. 2020, Cecchetti *et al*. 2021, Ouled-Cheikh *et al*. 2021), but these approaches are generally very labour-intensive and limited to short time periods over which sampling can be maintained. By contrast, long-term telemetry data from an increasing number of animals could be used to quantify certain methods of food acquisition (Caron-Beaudoin *et al*. 2013, Alarcón & Lambertucci 2018, Bennison *et al*. 2018, Jetz *et al*. 2022). The use of long-term telemetry data to quantify an individual's use of human food subsidies would then facilitate analyses that relate an individual's demographic performance to its proportional use of human food subsidies.

The analysis of telemetry data has benefited from multiple analytical advances to identify and classify animal behaviours (Jonsen *et al*. 2003, 2023, Garriga *et al*. 2016, Michelot *et al*. 2016, Browning *et al*. 2017, McClintock & Michelot 2018, Wang 2019, Kays *et al*. 2023). Similarly, telemetry data have been used extensively to identify spatial areas where multiple individuals congregate (Louzao *et al*. 2009, Montevecchi *et al*. 2012, Buechley *et al*. 2018, Hindell *et al*. 2020, Beal *et al*. 2021, Davies *et al*. 2021). The regular and persistent occurrence of human food subsidies would probably be characterized by the combination of predictable foraging behaviour of multiple individuals at the same location (Orros & Fellowes 2015, Arkumarev *et al*. 2020, Peters *et al*. 2022). Combining approaches that identify individual behaviour with approaches that detect the congregation of individuals thus opens the possibility to use telemetry data from multiple individuals to identify where human food subsidies occur (Webb *et al*. 2008, Mateo-Tomás *et al*. 2023).

Here we use long-term telemetry data of an opportunistic bird of prey, the Red Kite *Milvus milvus*, to predict the occurrence of human food subsidies. The Red Kite is a widespread raptor in central Europe, and benefits from anthropogenic food supplementation (Orros & Fellowes 2014, 2015, Cereghetti *et al*. 2019, Aebischer & Scherler 2021, Sanz-Zuasti *et al*. 2022). The degree to which individuals rely on human food subsidies may affect their survival and reproductive output (Catitti *et al*. 2022, Nägeli *et al*. 2022, Scherler *et al*. 2023b), but so far it has not been possible to quantify the relative use of human food subsidies at an individual level. To better understand the spatial extent of anthropogenic food provisioning and to support future analyses relating the survival and productivity of individuals to their use of human food subsidies, we therefore developed an approach that uses the tracking data of Red Kites in two sequential machine-learning models to identify places where the tracked behaviour of kites is consistent with the recorded behaviour of tracked kites at known anthropogenic feeding sites. We present the approach and demonstrate how the output could be used in future analyses relating a quantitative metric of human food subsidy to individual fitness parameters.

METHODS

Study area and tracking data collection

Our study area was located in western Switzerland in the cantons of Fribourg and Bern, and ranged over approximately 1377 km^2 from the lowlands of the Swiss plateau to the foothills of the Swiss Alps (482–1763 m above sea level). The area is characterized by agriculture (56.25%), managed forests (26.95%), settlements (8.4%) and unproductive land (8.4%), with a very dispersed structure of farms that facilitates a high breeding density of Red Kites (Scherler *et al*. 2023a). The Red Kite is a facultative scavenger with an opportunistic diet spectrum, and regularly visits anthropogenic feeding sites, which are provided in the form of compost heaps, manure heaps containing small carcasses or animal parts, and individual food provisioning sites of private residents (Cereghetti *et al*. 2019, Welti *et al*. 2020, Nägeli *et al*. 2022). Their typical foraging behaviour includes low searching flights over fields, with frequent turns and circling to detect prey from the air, but also includes walking on the ground to obtain small prey items (e.g. injured animals after a field was mown). Prey and other food items can be obtained either in low swooping flights, or by sitting on the ground and extracting small prey from the ground or manipulating carcasses (Aebischer & Scherler 2021, Sanz-Zuasti *et al*. 2022).

As part of a long-term research project, we tracked 497 individual Red Kites from 2015 to 2024 using harness-attached solar-powered global positioning system (GPS) tags of different manufacturers with similar locational precision to within

10 m (Aebischer & Scherler 2021, Orgeret *et al.* 2023, Scherler *et al.* 2023b). These logger attachments have been shown to cause no adverse effects on survival and breeding performance of birds (Peniche *et al.* 2011, Sergio *et al.* 2015, Longarini *et al.* 2023). Birds were tracked with varying temporal resolutions ranging from one location every 2 min to a location every 60 min, with occasional gaps of several hours (see Fig. S1 for data distribution). Data points that suggested unrealistic movements (due to a speed >35 m s^{-1}) were eliminated. We used all data from all birds at the temporal resolution at which they were recorded, but also repeated the analysis with all tracking data resampled to one location per hour, matching the temporal data resolution that is generally available from most Red Kite datasets in Europe (Maciorowski *et al.* 2019, García-Macía *et al.* 2022, Literák *et al.* 2022). We present the results from the analysis with all data in the main text, and show the qualitatively similar results from data at 1-h resolution in the electronic Supplementary material.

We first extracted movement metrics from the tracking locations to inform behaviours (Kays *et al.* 2023). Specifically, step length, speed and turning angle for each step between two subsequent GPS locations were calculated using the R package 'amt' (Signer *et al.* 2019). We hypothesized that presence at a feeding site would typically involve slow speeds, short step lengths and high turning angles (Spiegel *et al.* 2013, Arkumarev *et al.* 2020, Mateo-Tomás *et al.* 2023). The number of revisits to the same location and the amount of time spent within a 50-m radius around each location were calculated using the R package 'recurse' (Bracis *et al.* 2018).

After having calculated movement metrics for all tracks, we filtered the tracking data to within the borders of Switzerland to remove locations during migration and at distant wintering sites, resulting in 8 788 005 GPS locations. These locations were then further filtered to remove locations at night, because Red Kites are diurnal foragers. Red kites nest in forest, but both natural and anthropogenic feeding is unlikely to occur in forest, and we therefore removed all locations within 2810 forest fragments (obtained from https://www.swisstopo.admin.ch/en/landscape-model-swisstlm3d) where Red Kites are unlikely to forage. Because anthropogenic feeding generally occurs near permanent human habitation (Orros & Fellowes 2014), all locations more than 50 m away from buildings larger than 65 m^2 were also removed unless they were within 50 m of an experimental feeding site (see below). Although many smaller barns and shelters exist, these buildings generally serve as storage for machinery or hay and are unlikely to support permanent human habitation. Our building size cut-off therefore ensured that only locations near permanently inhabited buildings where people could in theory provide food for Red Kites were retained. All the above filtering steps reduced our data to 856 630 GPS locations of 497 individuals.

Inventory of anthropogenic feeding sites

Between 2017 and 2020 we surveyed 567 households in our study area and mapped the location of 125 known anthropogenic feeding sites (Cereghetti *et al.* 2019, Heiniger 2020), none of which were more than 50 m from a building larger than 65 m^2. These included private households providing occasional pieces of meat, and farms, butchers, shops and restaurants routinely providing waste materials several times a week. Also included were feeding platforms that were operated by the Swiss Ornithological Institute as part of other ecological studies, which were more than 50 m from inhabited buildings and provided small pieces of meat that Red Kites could pick up while swooping low over the platform (Baucks 2018, Catitti *et al.* 2022, Nägeli *et al.* 2022, Witczak 2023). In addition, similar interviews were used in 2018 to obtain a second, independent, dataset of 71 feeding sites that were withheld and only used for model validation (Cereghetti *et al.* 2019). We collectively refer to all these known places of human food subsidy as 'feeding sites'.

All our Red Kite tracking data were then annotated to label all GPS locations within 50 m of a known feeding site as 'anthropogenic feeding locations', and this label was limited to locations that coincided in time with experimental intermittent food provisioning. A total of 18 608 GPS locations (2.2% of the retained GPS locations) were thus labelled to be near a known anthropogenic feeding site and were available for training predictive models. We collectively refer to GPS positions of individual birds where foraging was inferred or predicted as 'feeding locations'.

Predicting the probability of anthropogenic food supplementation

Anthropogenic feeding sites attract Red Kites regularly, and we therefore expected data patterns at two distinct hierarchical levels that could indicate the presence of an anthropogenic feeding site. At the individual level, locations with low speed, high turning angles, and high and consistent revisitation rates over a specified time window (year) would indicate the presence of a persistent or recurring foraging place (Webb *et al.* 2008, Arkumarev *et al.* 2020, Kays *et al.* 2023). However, such locations may be indicative of both natural and artificial foraging areas. For this reason, we considered that at a second level, several individuals would exhibit similar behaviour in the same place and congregate in areas with regular anthropogenic food supplementation near human settlements. Our analytical approach therefore proceeded in two steps, namely (1) to predict the occurrence of feeding behaviour at the level of individual GPS locations, and (2) to aggregate these individual feeding locations in spatial units to identify those units where several individuals repeatedly exhibit behaviour consistent with anthropogenic feeding.

Prediction of feeding behaviour at the individual level

In the first step we used a random forest model to predict whether locations occurred within 50 m of anthropogenic feeding sites or not. A random forest is a powerful machine-learning algorithm that can extract useful information from many predictor variables (Breiman 2001, Cutler *et al.* 2007, Pichler & Hartig 2023), and has been used to distinguish other movement behaviours (Nathan *et al.* 2012, Thiebault *et al.* 2018, Dickinson *et al.* 2021, Yu *et al.* 2021, Carneiro *et al.* 2022). We used 19 predictor variables (Table S1) that were calculated and assigned to each GPS location of our tracking data, and the GPS locations were split into training and test data in a grouped random fashion to maintain an equal proportion of feeder to non-feeder locations in both the training (n = 12 467) and test (n = 6809) data subsets. We fit the models in the R package ‘ranger’ (Wright & Ziegler 2017) using 2500 classification trees, two variables evaluated at each split, and evaluated variable importance through an internal permutation algorithm (Boulesteix *et al.* 2012, Janitza *et al.* 2013). For the purpose of fitting the model, all locations that were not within 50 m of a known anthropogenic feeding site were classified as ‘absences’. However, our knowledge of anthropogenic feeding sites was not exhaustive, and the validation data can only indicate the presence (but not the absence) of a feeding location. We therefore calculated the proportion of GPS locations that were within a 50-m radius of a known anthropogenic feeding site and were correctly predicted as ‘anthropogenic feeding’ in our withheld testing data, and calculated the continuous Boyce index in the R package ‘modEvA’ (Boyce *et al.* 2002, Hirzel *et al.* 2006, Márcia Barbosa *et al.* 2013). This index is the correlation between model predictions and predicted frequencies along different prediction classes, and ranges between −1 and 1, with values close to 0 indicating that the model has no discriminative ability.

Aggregating feeding individuals at the population level

Because predicted ‘anthropogenic feeding’ locations may occur in many places with similar behaviours, including ephemeral natural foraging areas, and do not by themselves indicate the presence of an anthropogenic feeding site, we aggregated the predicted probabilities of all GPS locations to identify locations where several individuals would exhibit similar behaviour in the same place. All GPS locations were therefore first classified as either ‘predicted to exhibit behaviour consistent with anthropogenic feeding’ or not by the above model using a probability threshold that was equal to the prevalence of ‘presence’ cases (0.04) in the training data (Liu *et al.* 2005). These predicted ‘feeding’ locations were then aggregated in 500-m hexagonal grid cells to summarize visitation patterns at the population level. We calculated the number and proportion of predicted ‘feeding’ locations over the total number of GPS locations in a grid cell, and also calculated the number and proportion of predicted ‘feeding’ individuals over the total number of individuals occurring in each grid cell. This summary information was then used in a second random forest model, which used six variables representing the number and proportion of locations and individuals per grid cell (Table S1) to predict whether an anthropogenic feeding site was present in that grid cell. This model was based on 3732 grid cells with sufficient data (at least 10 Red Kite GPS locations), of which 193 (5.2%) contained known anthropogenic feeding sites.

To assess the quality of the predictions, we used an independently collected dataset of feeding sites obtained through interviews conducted in 2018 (Cereghetti *et al.* 2019) to assess what proportion of those grid cells with known feeding sites was correctly predicted by the model, and also provide the same continuous Boyce index as for the first model above.

Projection across Switzerland and quantification of attendance

We used the two models above to project the distribution of predicted anthropogenic feeding sites across Switzerland during the entire year, and extracted the proportion of time that individuals spent at those sites to demonstrate the utility of these projections. The probability of the presence of an anthropogenic feeding site was then predicted across all 500-m grid cells within Switzerland (n = 359 869) from which a minimum of 20 GPS locations from at least two individually tracked Red Kites (n = 17 948) existed. To estimate the amount of time individual Red Kites spent at predicted feeding sites, we first interpolated the raw tracking data to 15-min intervals using the R package adehabitatLT (Calenge 2006), and intersected those data with the 17 948 grid cells for which predicted probabilities of feeding sites were available. To demonstrate how our predictions could be used, we then quantified the time spent by individuals at anthropogenic feeding sites by multiplying the predicted probabilities with the number of interpolated GPS locations (each representing 15 min) of each individual in that grid cell. The amount of time spent at anthropogenic feeding sites per day for each individual was then summarized, and we present the mean and 95% quantiles of daily attendance metrics across age classes, sexes and seasons (breeding season from 10 March to 20 June and non-breeding season from 21 June to 9 March).

RESULTS

The tracking data were randomly split into 573 941 locations for training the first random forest model, and 282 689 locations for validation, and we report the performance of the model on external validation data that were not used to train the model. The first random forest model classified 5783 of 6809 known presences at anthropogenic feeding sites correctly (85%), and also predicted that 31 552 of 276 995 (11%) other GPS locations (that were not within 50 m of a known feeding site) were consistent with behaviour at anthropogenic feeding sites (Boyce index = 0.999). The variables that contributed the most to classifying GPS locations as near an anthropogenic feeding site were the number of revisits to that location, the number of days on which it was visited, the frequency of visits and the number of days between the first and the last visit to a location, whereas speed had only moderate explanatory power and turning angle had very low explanatory power (Table S1). The best predictor not associated with revisitation or duration of attendance was ‘distance to nest’, and indicated that anthropogenic feeding behaviour was more likely at distances greater than 500 m from nests. Known feeding sites at which GPS locations were erroneously not predicted to exhibit feeding behaviour were characterized by greater step lengths, lower revisitation rates and less time spent compared with correctly predicted locations, whereas locations that were erroneously predicted to be within 50 m of a feeding site had the highest time span between the first and last visits to that location (Fig. S2).

Combining the training and test data, there were 88 650 locations of 1377 bird-seasons predicted by the first random forest model that were consistent with foraging at anthropogenic feeding sites. We summarized these locations in 500-m grid cells, which resulted in 2979 out of the 4337 grid cells with sufficient data in the study area containing predicted ‘anthropogenic feeding sites’, compared with 193 grid cells where the existence of an anthropogenic feeding site was known from ground validation. The proportions of feeding locations across all 3732 grid cells ranged from 0% to 41% of GPS locations in each grid cell, and the proportion of feeding individuals ranged from 0% to 51% of individuals that occurred in a grid cell.

The second random forest model, predicting the occurrence of anthropogenic feeding sites per grid cell based on six predictor variables (Table S1), correctly predicted 57 of the 71 feeding sites (80%) in our external validation data identified by independent interviews (Fig. 1; Boyce index = 0.847). The most important variables for this model were the proportion of feeding individuals and locations, and the total number of GPS locations that were present and classified as ‘feeding’. Predicted probabilities of the study area grid cells containing a known anthropogenic feeding

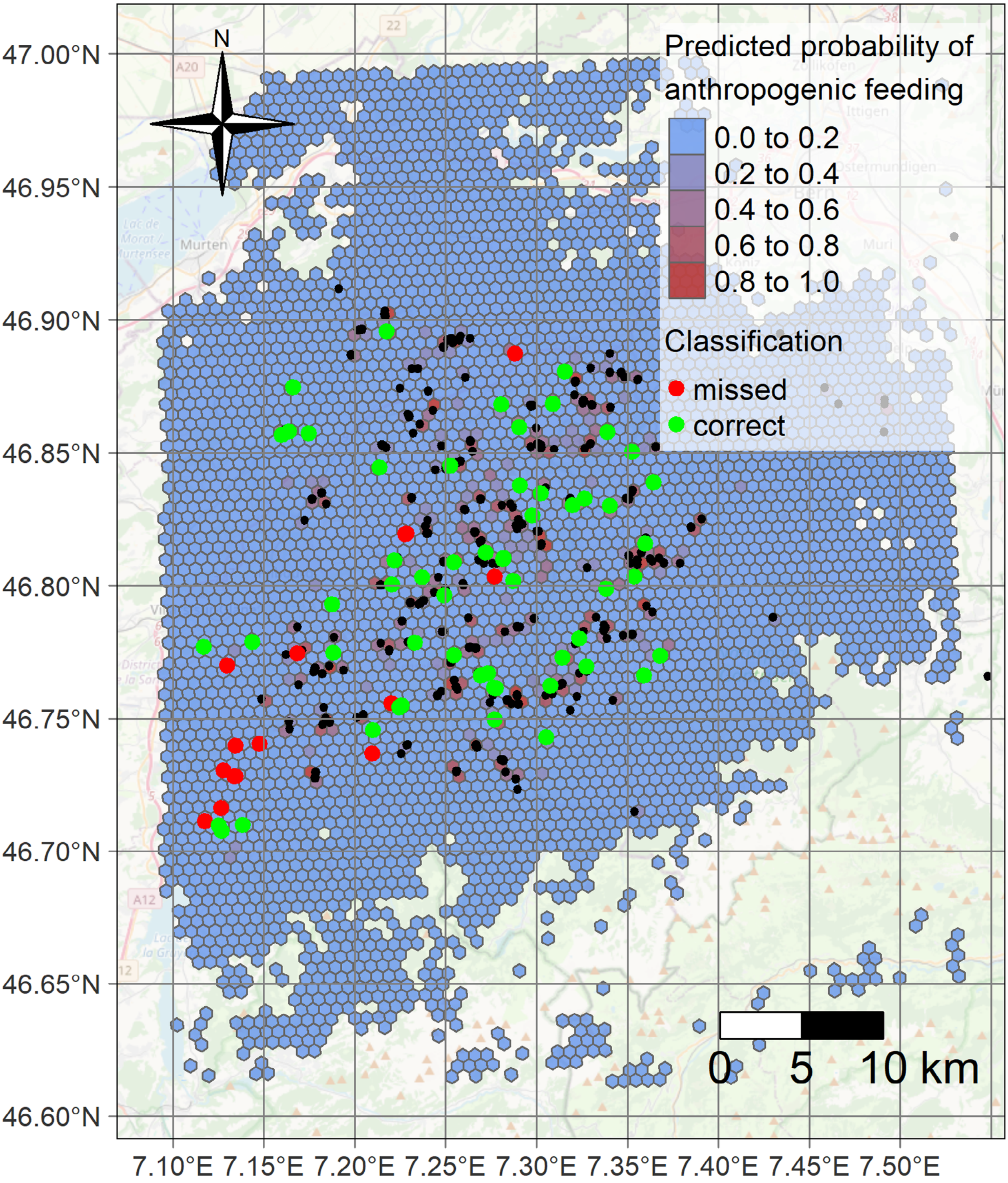

Figure 1. Predicted probabilities of the presence of anthropogenic feeding sites in the main Red Kite study area in Western Switzerland. Black points indicate known feeding sites that were used to train models, grid cells are coloured according to the predicted probability of anthropogenic feeding occurring in that grid cell from blue (low) to red (high), and points show feeding sites from independent validation data that were correctly predicted (green, n = 57) or missed by predictions (red, n = 14).

site ranged from 0.002 to 0.947 (Fig. 1). Grid cells with a 'missed' prediction had fewer GPS locations overall, with fewer locations and individuals classified as feeding, compared with correctly predicted grid cells (Fig. S3). Correct predictions of known anthropogenic feeding sites had a minimum of 294 GPS locations from a minimum of 29 individuals within a given 500-m grid cell.

Example application of predicted anthropogenic feeding sites

Due to the concentrated occurrence of our tracked Red Kites within our study area, we eliminated 95% of grid cells across Switzerland because they did not meet data requirements for prediction (e.g. <20 GPS locations in these grid cells). Of the remaining 17 948 grid cells with sufficient data, 3.7% were predicted to contain anthropogenic feeding sites with a probability exceeding the threshold for anthropogenic feeding sites (Fig. 2).

Using the predicted probabilities for the presence of anthropogenic feeding sites in grid cells across Switzerland, we found that most individual Red Kites spent on average 1–3 h per day within 500 m of such feeding sites (Fig. 3). There was no obvious pattern of usage among ages and sexes, nor between breeding and non-breeding seasons, and there was large variability among individuals in feeding site attendance. This individual variability could now be used as an explanatory variable to investigate the reproductive performance or survival of individuals.

DISCUSSION

We predict the probability of anthropogenic food subsidies used by Red Kites across Switzerland based on tracking data, and provide another example of how biologging of wild animals can be used as a remote sensing tool to detect or quantify human activities or natural hazards (Navarro

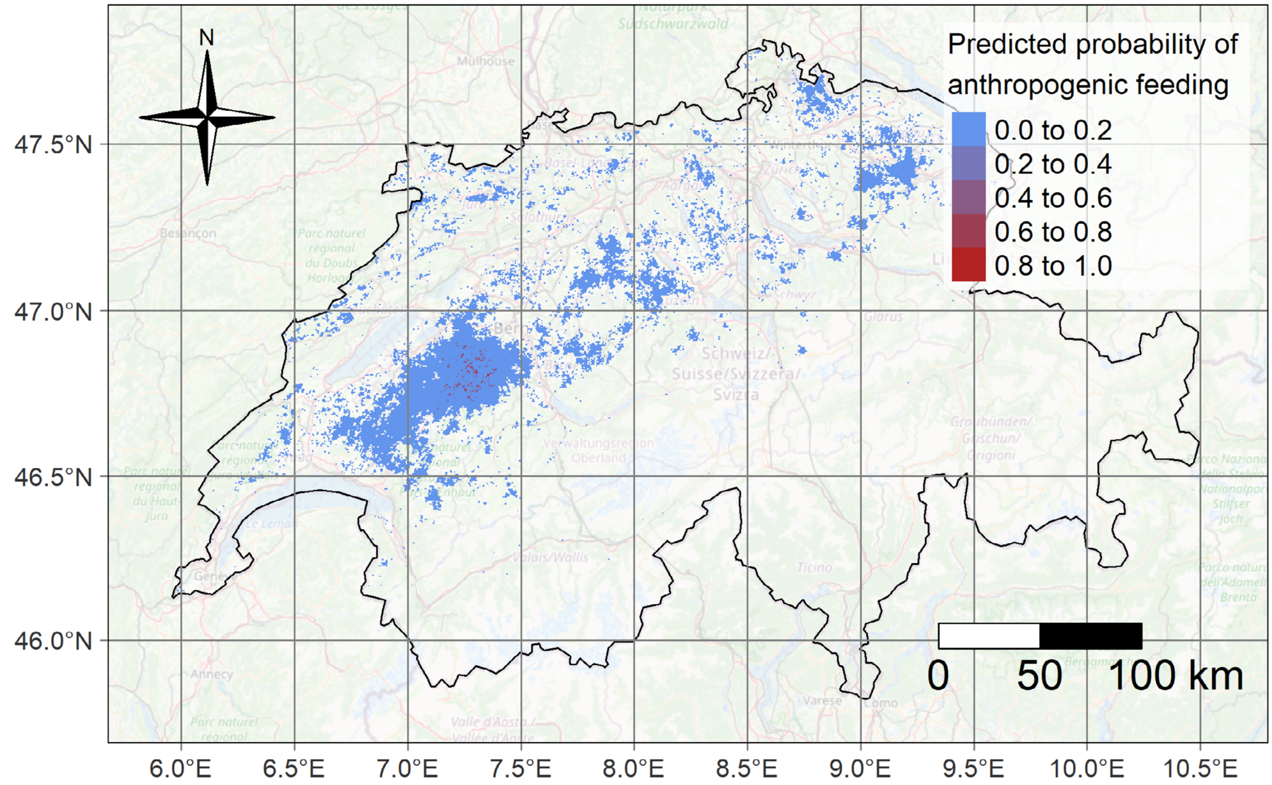

Figure 2. Predicted probability of the presence of anthropogenic feeding sites in Switzerland based on Red Kite GPS-tracking data. All coloured grid cells contain a minimum of 20 GPS locations and are coloured according to the predicted probability of anthropogenic feeding occurring in that grid cell from blue (low) to red (high). Note that predictions are not possible outside of coloured grid cells because of insufficient GPS-tracking data.

Figure 3. Predicted mean (and 95% quantiles) daily time (in hours) that individual Red Kites in different age classes and sexes spent in 500-m grid cells with predicted anthropogenic feeding sites during the breeding (upper panel, 10 March to 20 June) and non-breeding season (lower panel, 21 June to 9 March). Time spent was calculated as the number of 15-min interpolated GPS locations multiplied by the predicted probability of anthropogenic feeding sites in each grid cell.

et al. 2016, Weimerskirch *et al.* 2020, Wikelski *et al.* 2020). The results provide a useful input layer for the study of fitness consequences of food subsidies for Red Kite individuals by estimating a relative index for the use of human food subsidies. The models performed well in our study area in Switzerland, but broader applicability and transferability are limited by the density of tracking locations that are required to reliably infer the presence of human food subsidies.

Human food subsidies are known to attract scavengers and can lead to the aggregation of many animals (Orros & Fellowes 2015, Newsome & Van Eeden 2017, Plaza & Lambertucci 2017, Khawar Sultan 2021). We show that tracked Red Kites exhibit recognizable behaviour around human food subsidies, which can be used to predict where such subsidies occur, as has been shown for other scavenger species (Arkumarev *et al.* 2020, Peters *et al.* 2022, Mateo-Tomás *et al.* 2023). Compared with many natural foraging areas, which can be ephemeral in nature and provide food for only a brief temporal window, anthropogenic feeding sites were frequently revisited over the entire season, leading to a high number of revisitations and high total amount of time spent in those locations. Similar revisitation patterns also occur at nest-sites of birds (Picardi *et al.* 2020, Ozsanlav-Harris *et al.* 2022, Eisaguirre *et al.* 2023), but unlike nests of solitary nesting species like the Red Kite, anthropogenic feeding areas are generally visited by multiple individuals. As a consequence, identifying anthropogenic feeding sites was more likely in areas where multiple tracked individuals exhibited revisitation behaviour, indicating feeding.

We provide an example of how the predicted distribution of anthropogenic feeding sites could be used to quantify an individual's use of human food subsidies, and we found very large individual variation in the use of such feeding sites. Supplementary feeding has been shown to increase breeding success and survival of some raptors (González *et al.* 2006, Sweikert & Phillips 2015, Pearson & Husby 2021). Individual variation in the use of feeding sites could indicate individual specialization in foraging strategies (Johnson *et al.* 2022), which may lead to differences in either survival (Nebel *et al.* 2023) or productivity (Zabala & Zuberogoitia 2014, Otterbeck *et al.* 2015, Cecere *et al.* 2020). The causes of individual differences could be a result of the distance to the nearest feeding site (Hilgartner *et al.* 2014), or social dominance and competitive ability, because attending communal feeding sites where multiple individuals may compete for resources may not be equally beneficial for individuals of different inherent quality (Francis *et al.* 2018, Shutt & Lees 2021, Catitti *et al.* 2022, 2024). For some age and sex classes, the amount of time individuals spent at anthropogenic feeding sites may need to be interpreted with caution: for example, some adult females spent on average up to 18 h per day in grid cells with predicted feeding sites during the breeding season, which may be a consequence of a nest being located within 500 m of a feeding site and very high nest attendance therefore resulting in the apparent high attendance at a predicted 'feeding site' (Aebischer & Scherler 2021, Sanz-Zuasti *et al.* 2022, Scherler *et al.* 2023a).

Measures such as the mean daily attendance at anthropogenic feeding sites will nonetheless be invaluable to assess whether survival, reproductive output or age at first breeding in Red Kites varies depending on an individual's relative use of human food subsidies (Cereghetti *et al.* 2019, Catitti *et al.* 2022, Nägeli *et al.* 2022). Although our results are encouraging and show that tracking data can be used to identify feeding sites (Arkumarev *et al.* 2020, Heiniger 2020, Mateo-Tomás *et al.* 2023), we caution that the approach is fundamentally limited by the amount of tracking data available. For example, our predictions across Switzerland were unable to identify anthropogenic feeding sites across broad regions where none, or only a few, of our tracked Red Kites had ventured. Nonetheless, for our tracked population of individuals the potential fitness consequences of individual variability in using human food subsidies can now be investigated using the model predictions that we provide.

Another potentially useful application of our approach could be in translocation or reintroduction projects where all released animals are tracked with GPS tags. For these re-established and potentially vulnerable populations, the tracking data could be used to identify potential feeding sites to assess their quality and safety for the translocated population (Ferrer *et al.* 2018, Arkumarev *et al.* 2020, 2022, Dixon *et al.* 2020, Badia-Boher *et al.* 2022).

Our prediction of anthropogenic feeding sites proceeded in two steps, with the first step emulating a behavioural classification based on individual GPS locations. Unlike in many other classifications of animal behaviour from GPS-tracking data (Jonsen *et al.* 2003, 2023, Garriga *et al.* 2016, Michelot *et al.* 2016, Browning *et al.* 2017, McClintock & Michelot 2018, Wang 2019, Kays *et al.* 2023), we found that speed and turning angle had only a very small influence on distinguishing locations near anthropogenic feeding sites, but that parameters related to frequent revisitation and the amount of time spent were far more important. We speculate that slow speed and acute turning angles may also occur at natural foraging areas, which may differ from anthropogenic feeding sites by their temporal persistence and revisitation rate. Because our models relied principally on the same key variables regardless of the data resolution (see supplementary results in Data S1 for analysis with 1-h resolution data), we consider it unlikely that the temporal resolution of our data affected the importance of predictor variables. However, very high-resolution tracking and accelerometer data (in seconds) that may distinguish precise body motions and behaviours could potentially improve model performance if such data can reliably distinguish between feeding and non-feeding behaviours.

Erroneous predictions in this step of the analysis occurred primarily due to individuals spending less time near actual feeding sites, or flying over them at higher-than-expected speeds (Fig. S2). Such behaviours occur naturally when birds fail in their breeding attempt and no longer return to an anthropogenic feeding site, or if they pass a feeding site after the provided food has already been consumed. Predictions of 'feeding' locations where no anthropogenic feeding site was known within 50 m were associated with much higher average time intervals between subsequent visits, which could indicate occasional feeding sites that were not revealed by our interviews, with a less regular food provision and hence less regular visitation by kites.

The second step of our analysis aggregated individual GPS locations and led to erroneous predictions primarily in areas where insufficient tracking data existed, and where insufficient amounts of tracked individuals exhibited behaviour consistent with attending anthropogenic feeding sites (Fig. S3). Despite some erroneous predictions, we emphasize that the objective evaluation of the predictive accuracy of our analysis is difficult, because we do not have comprehensive knowledge of all anthropogenic feeding sites that occur in our study area. In addition, for many of the known feeding sites we have no reliable information on how often and what size and amount of food they provide. The amount and frequency of food provision can vary enormously (Baucks 2018, Cereghetti *et al.* 2019), and may affect the visitation frequency by Red Kites (Orros & Fellowes 2015). In a different study area, Sahli (2019) reported that individual households can provide 3 kg of meat per day, which would be sufficient to meet the daily energetic requirements of 15 individual Red Kites during the winter (Orros & Fellowes 2014), and may lead to very frequent visitation with highly diagnostic data patterns. However, the deliberate feeding of Red Kites has recently been outlawed in some regions of Switzerland, because of concerns that it would alter the species' behaviour and increase the risk of disease transmission (Blanco *et al.* 2017, Plaza & Lambertucci 2017). Because of the spatially and temporally dynamic occurrence of food provisioning, validating model predictions is exceptionally challenging. Some of our 'erroneous' predictions may in fact be accurate if anthropogenic feeding sites exist that we were not aware of (Mateo-Tomás *et al.* 2023), or if supplementary feeding did not coincide with the presence of our GPS-tracked Red Kites. Given the complicated and possibly error-prone evaluation, our models predicted the known anthropogenic feeding sites surprisingly well, and we are therefore confident that this approach is useful to approximate the relative reliance of individual Red Kites on human food subsidies.

In summary, we show that we can use tracking data to predict the probability of anthropogenic feeding sites, and derive a quantitative index of the proportion of the daytime that Red Kites from our tracked study population spend in grid cells with a high predicted probability of containing an anthropogenic feeding site. These projections make it possible to relate demographic performance to the relative use of predicted human food subsidies, and will increase our understanding of the key demographic drivers underlying the population dynamics of Red Kites (Katzenberger *et al.* 2021, Pfeiffer & Schaub 2023). Ultimately, further studies based on our predictions presented here may allow us to test energy-efficiency relationships (Somveille *et al.* 2018) and examine whether the large extent of anthropogenic feeding in Switzerland has contributed to the species' population increase (Aebischer & Scherler 2021).

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AUTHOR CONTRIBUTIONS

Steffen Oppel: Software; methodology; formal analysis; validation; writing – original draft; writing – review and editing; visualization. **Nathalie Heiniger:** Conceptualization; methodology; writing – review and editing; investigation. **Patrick Scherler:** Conceptualization; methodology; project administration; writing – review and editing; resources; supervision; data curation; investigation. **Valentijn S. van Bergen:** Investigation; data curation; writing – review and editing. **Jérôme Guélat:** Software; data curation. **Robert Weibel:** Conceptualization; methodology; investigation; writing – review and editing. **Martin U. Grüebler:** Conceptualization; funding acquisition; resources; supervision; project administration; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICAL NOTE

Ringing and tagging were permitted by the Amt für Lebensmittelsicherheit und Veterinärwesen (LSVW) of the Canton of Fribourg (Permit No. 2017_29_FR), and the Swiss Federal Office for the Environment (FOEN).

Data Availability Statement

The code and example data to reproduce the models are available at https://doi.org/10.5281/zenodo.13805176. The raw tracking data from Switzerland are available on www.movebank.org with MovebankID of 230 545 451 (Milvusmilvus_GSM_SOI) and 1 356 790 386 (Milvusmilvus_Milsar_SOI_final).

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SUPPORTING INFORMATION

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

Figure 1. Dynamic html version of Figure 1 that allows zooming.

Figure 2. Dynamic html version of Figure 2 that allows zooming.

Data S1. Supplementary results.

Table S1. List of predictor variables and their relative importance in the random forest analysis used to predict anthropogenic food subsidies from Red Kite GPS-tracking data at the level of individual GPS locations and at the level of 500-m grid cells aggregating locations in space and time.

Figure S1. Histogram of the frequency distribution of time intervals between subsequent GPS locations of Red Kites tracked with GPS transmitters between 2015 and 2024 in Switzerland.

Figure S2. Boxplots of the values of predictor variables (see Table S1) at 281610 GPS locations not used for model training that were either correctly predicted to be near an anthropogenic feeding site (correct), or where predictions were incorrect, either because a feeding site was predicted but not known (false pred) or because that location was not predicted to exhibit behaviour consistent with a known existing feeding site (missed pred), assuming a binary classification threshold equal to data prevalence.

Figure S3. Boxplots of the values of predictor variables (see Table S1) in 71 grid cells with known anthropogenic feeding sites that were either correctly predicted (57) or missed (14, assuming a binary classification threshold equal to training data prevalence).