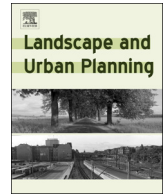




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Research Paper

Quantification of anthropogenic food subsidies to an avian facultative scavenger in urban and rural habitats

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ABSTRACT

The provision of anthropogenic food to wildlife is a global phenomenon, and intentional wild bird feeding has become increasingly popular in the last decades. Though there is anecdotal evidence of feeding of avian facultative scavengers in rural areas, most studies of wild bird feeding in Europe and the United States focused on passerines and urban contexts. We aim at quantifying the extent of feeding by private residents to an avian facultative scavenger, the red kite (*Milvus milvus*), in Swiss urban and rural areas by conducting a face-to-face systematic survey (N = 199 randomly selected houses) in a 275 km² study area. 4.6% of urban and 12.7% of rural households regularly fed red kites. While building density negatively affected the probability of households providing food, daily anthropogenic food mass was larger in urban than in rural areas, mainly due to the higher number of households. Daily availability was also larger in winter than in the rest of the year. In total, 47–86 metric tons of anthropogenic food was provided yearly, which represents a maximum daily average of nearly 0.9 kg of food per km². We conclude that intentional (20%) and unintentional (80%) provision of anthropogenic food to facultative scavengers are widespread and well-established human behaviors in Switzerland. These behaviors provide high food availability over the year in both rural and urban areas. The results represent an important basis for understanding the ecological consequences of anthropogenic food provisioning, human-scavenger interactions, and scavenger population dynamics in anthropogenic landscapes.

1. Introduction

The provision of anthropogenic food to wildlife is a global phenomenon that has considerably intensified following human population growth and development (Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín, 2013). The large quantity of food subsidies provided over extensive areas of various landscapes can have important effects on wildlife, such as altering species distribution (Plummer, Siriwardena, Conway, Risely, & Toms, 2015) and behavior (Fedriani, Fuller, & Sauvajot, 2001), and disrupt predator-prey interactions (Rodewald, Kearns, & Shustack, 2011). These effects are expected to cascade through the trophic levels of ecosystems (Oro et al., 2013), and to restructure entire communities (Galbraith, Beggs, Jones, & Stanley, 2015; Wilson & Wolkovich, 2011).

Many bird species are particularly influenced by the presence of anthropogenic food as intentional wild bird feeding became increasingly popular in the last decades (Jones & Reynolds, 2008). Bird feeding

first appeared in northern Europe and spread to many western countries and to parts of the Southern Hemisphere (Reynolds, Galbraith, Smith, & Jones, 2017), reaching a larger percentage of participants (Jones, 2011). People's intention of bird feeding often is to improve survival of birds during the harsh winter months (Reynolds et al., 2017). However, intentional bird feeding is also driven by a range of other motivations, including the possibility of engaging more personally with the surrounding environment (Cox & Gaston, 2016). This is especially a subject of interest in urban ecology, where garden feeding may balance the increasing lack of contact with nature in a fast urbanizing world (Miller, 2005). Studies that quantify feeding of wild birds often not only estimate the mass of food distributed to birds, but also highlight the number of people involved and the ecological and financial implications of this activity. In the US about 57.2 million people feed birds around their houses (U.S. Department of the Interior U.S. Fish and Wildlife Service and U.S. Department of Commerce. U.S. Census Bureau, 2018), and in mainland Europe about US \$220 million are

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spent every year on supplementary food (Jones & Reynolds, 2008).

Generally, changes in food availability have important consequences for the ecology and dynamics of bird populations (Newton, 1988; Robb, McDonald, Chamberlain, & Bearhop, 2008). The availability of food provided by bird feeding activities varies in space and time and therefore affects the spatiotemporal distribution and accessibility of food resources for birds. Bird feeding is shown to have a wide array of both positive and negative effects on avian communities. For example, breeding performance might increase after food supplementation due to improved parental conditions (Robb, McDonald, Chamberlain, Reynolds et al., 2008). In contrast, supplementation can reduce natural selection or cause ecological traps, decreasing the overall breeding performance of the population (Plummer, Bearhop, Leech, Chamberlain, & Blount, 2013). Moreover, survival is shown to be affected by garden feeding in two ways. Garden feeding might enhance survival, if natural food resources are limited (Lieuury, Gallardo, Ponchon, Besnard, & Millon, 2015), or reduce survival due to higher mortality risks in settlements (Bayne, Scobie, & Rawson-Clark, 2012). Other consequences of bird feeding are decreased winter migration (Plummer et al., 2015), faster spread of diseases (Brittingham & Temple, 1988), and altered composition of avian communities (Galbraith et al., 2015). These effects arise due to both an increased amount of food and its altered distribution in space and time (Cortés-Avizanda, Jovani, Carrete, & Donazar, 2012). Although it is crucial for the understanding of the effect of bird feeding on bird populations and their management, knowledge on the spatiotemporal distribution of anthropogenic food resources remains often anecdotal or fragmentary due to the difficulties of its quantification. In particular, large-scale studies comparing both urban and rural areas are still rare. While wild bird feeding is receiving increasing attention in urban contexts (Reynolds et al., 2017), less is known about bird feeding in rural areas. Most studies considering rural areas apply a comparative approach with urban areas (e.g. Tryjanowski et al., 2015). However, the fact that in rural areas the range of anthropogenic food types might differ from urban areas is often neglected (but see Lepczyk, Mertig, & Liu, 2004). For example, in rural areas people may offer agricultural waste, fully aware that birds are feeding on them.

Avian facultative scavengers such as corvids, gulls and raptors use other sources of anthropogenic food than small passerines, for example all sorts of waste, carcasses from road kills and window collisions, and livestock afterbirths (Davis & Davis, 1981; Dean & Milton, 2003; Inger, Cox, Per, Norton, & Gaston, 2016). Recently, scavengers have been shown to provide important ecosystem services in terms of stabilization of food webs, disease mitigation and waste-disposal services (DeVault et al., 2016; O'Bryan et al., 2018). Though these benefits of scavengers to humans are increasingly recognized, negative impacts of large populations or aggregations of facultative scavengers such as increased predation on other wildlife (Fletcher, Aebischer, Baines, Foster, & Hoodless, 2010; Rees, Webb, Crowther, & Letnic, 2015), disease transmission (Carrasco-García, Barroso, Montoro, Perez-Olivares, & Vicente, 2018; Monaghan, Shedden, Ensor, Fricker, & Girdwood, 1985) and other human-wildlife conflicts (Messmer, 2000; Soulsbury & White, 2015) are also increasingly addressed and result in frequent calls for management, particularly in urban landscapes (Špur, Pokorný, & Šorgo, 2017; Washburn, 2012). However, studies quantifying anthropogenic feeding of avian facultative scavengers in urbanized landscapes are limited.

The red kite (*Milvus milvus*) is a large European avian facultative scavenger listed as near threatened at the IUCN red list. In Great Britain, it became the target of intentional garden bird feeding (for quantification see Orros and Fellowes 2014, 2015) after a successful reintroduction (Carter, 2007). On the European mainland persistent illegal killing (Beryn & Gaillet, 2008; Smart et al., 2010) and declines in its major breeding areas (Germany: (Mammen, 2009), France: (Pinaud, Passerault, Hemery, & Bretagnolle, 2009) and Spain: (Cardiel, 2006)) recently reduced the chances of recovery for the species. The ongoing

range expansion and increasing breeding densities of red kites in Switzerland are of great importance for the preservation of the species (Knaus, Antoniazza, Wechsler, Guélat, Kéry, Strebler, & Sattler, 2018). There is observational evidence that in Switzerland feeding of red kites by private residents occurs regularly, in particular during winter. Little is known about the extent of these feedings and their spatiotemporal occurrence, and thus, it is crucial to investigate their role for Swiss red kite populations.

Here, we aim at quantifying the extent of intentional and unintentional feeding by private residents and the availability of anthropogenic food for red kites across a highly populated landscape in Switzerland. We conducted a systematic survey using a random selection of houses for interviews designed to quantify the proportion of households involved in feeding red kites. As in garden feeding of other bird species (Lepczyk et al., 2004), we expect differences in the probability of feeding and in the amount of food provided between urban and rural sites, in particular due to a higher frequency of unintentionally provided food in rural areas. The attitude towards bird feeding might depend on bird density or the density of human observers. We therefore predict that the feeding probability is positively associated with proxies of high natural food availability (arable fields, forest edges) and negatively with proxies of human presence (density of houses, amount of forest, low elevation). We also expect more frequent feedings and larger amount of food fed in the winter season (December – February) than in the rest of the year (March – November), because people should rather support red kites during the cold season when food resources are thought to be scarce than in the growing season. We suggest that the amount of anthropogenic food available to red kites by feeding carried out by private residents represents an important but previously neglected source of food for multiple scavenging species. The results provide new insights into an understudied type of bird feeding and into the rural-urban gradient of the availability of anthropogenic food for facultative scavengers.

2. Methods

2.1. Public survey

The survey to investigate the occurrence of garden feeding of red kites was conducted between summer and fall 2016 in a 275 km² study area in Switzerland, consisting primarily of the Sense district of the canton of Fribourg and partly of the Bern-Mittelland district of the canton of Bern (Fig. 1). The hilly landscape is situated between 500 and 1130 m.a.s.l., with most of the area located around 600–900 m.a.s.l. The landscape is mostly dominated by agricultural fields but is considerably populated in villages and small cities. Building density was estimated at 59 buildings per km².

We selected households participating in the survey by using the building layer of the Swiss digital topographic model (vector25 © swisstopo; DV002232.1), which provided positional data of all the potential survey buildings within the study area. A random sample of 199 buildings was selected within the study area. Since in urban areas density of buildings was much higher than in rural areas, we opted for a stratified random sample to better cover the whole study area. A sampling ratio of 1:2 buildings between urban and rural areas avoided clustering of the sample locations in urban areas. Urban and rural areas were defined by the borders of the *settlement* land-cover type on the digital map. Whenever no person was found at the selected survey household (N = 14 households; 7%), the closest house was used as replacement household. This random sample allowed for systematic recording of small and less frequent feeding sites. It was used to estimate the total number of feeding households in the whole study area, which in turn was used to estimate the amount of food distributed at these small feeding sites over the study area. Respondents feeding red kites were divided into persons intentionally providing food (intentional feeders) and persons observing red kites feeding from their

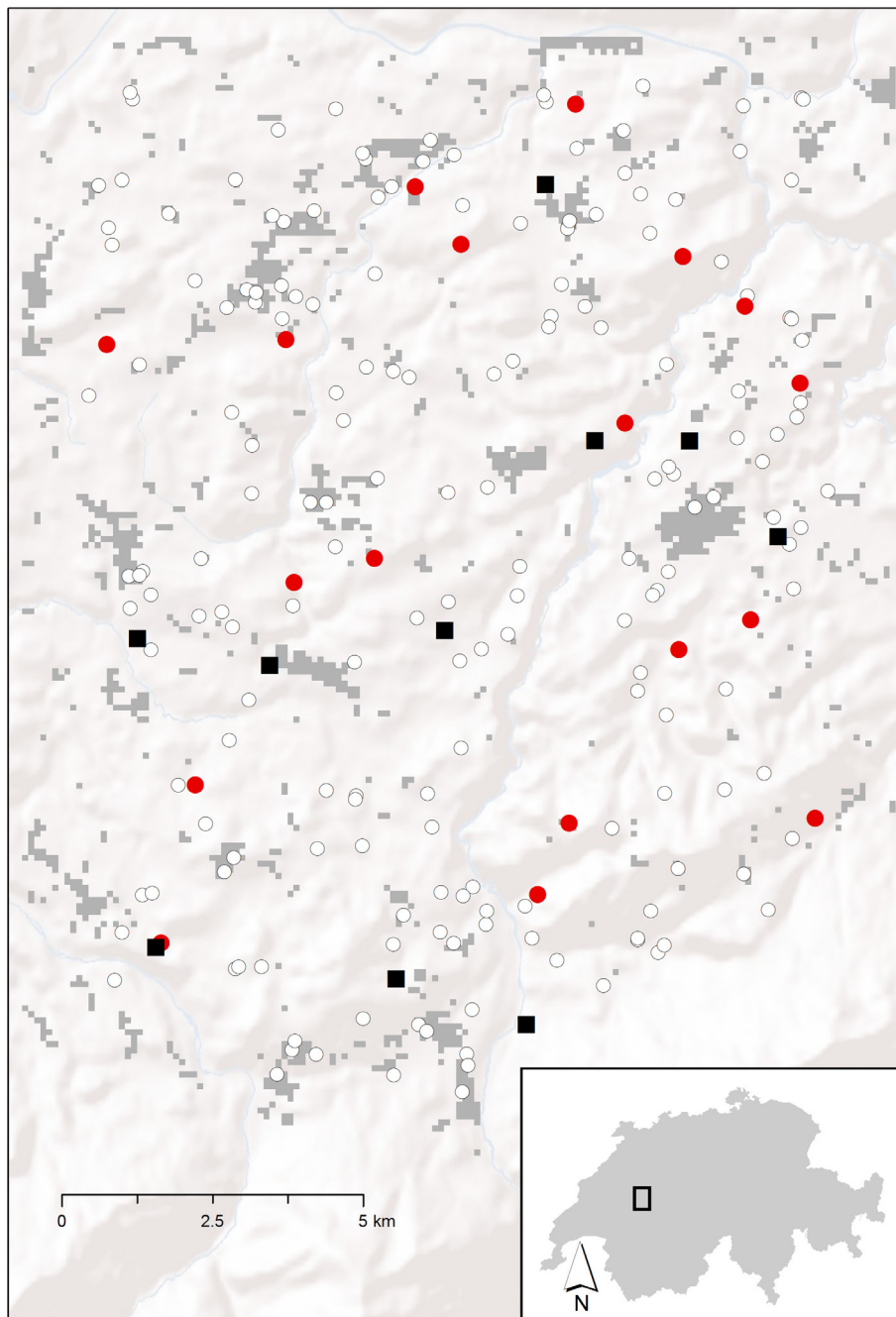


Fig. 1. Distribution of the surveyed houses (non-random sample) and their feeding habits in the study area. White points: non-feeders; red points: year-round feeders; black squares: winter feeders. Background map: Shaded Relief Copyright:© 2014 Esri.

discarded food sources not specifically targeted at them (non-intentional feeders).

Participants and other locals indicated 11 additional households potentially feeding red kites (see questions [Table 1](#)). These participated also in the survey resulting in a non-random sample of 210 surveyed households. Aggregations of soaring red kites conspicuously indicate extensive and predictable feeding sites over large distances. Considering the vast observation effort (1031 work days in 2016) in terms of a red kite monitoring in the study area, we are confident that these additional households cover a high proportion of the few large feeding sites within the study area. The non-random sample (random plus indicated) was used to obtain a minimum estimate of the amount of food distributed using only the known feeding sites of our sample. Moreover, we used the non-random sample for a food distribution modeling

approach in a presence–absence framework extrapolating feeding probabilities over the whole study area using generalized linear modeling of presence of feeding in relation to landscape variables.

We favored a short face-to-face interview to account for the possible reluctance of filling a written questionnaire about an activity of putatively ambiguous legality. The questionnaire for the interviews was based on the one used by [Orros and Fellowes \(2014\)](#) in the UK ([Table 1](#)). People were asked whether they fed red kites, and if they did, they were asked to specify the frequency and seasonality of feeding, type of food used, and number of years they had been feeding. Intention of feeding (intentional vs. unintentional) was assigned based on how people were providing food and on their motivation for feeding kites. After the interview, building type was recorded. No other personal data were collected, and spatial coordinates of the households were used for

Table 1

Questionnaire to investigate red kite feeding. Questions were asked face-to-face and in a conversational way with no fix order. Precise answers were noted down if they did not match any of the offered options.

Questions	Possible answers
Do you feed, or have you ever fed, red kites in your garden?	Yes/Yes, but not anymore/No
At what times of year do (or did) you feed red kites?	All year/Autumn-Winter/Spring-Summer/Winter-Spring/Other
How often do (or did) you usually feed them?	Daily/Several times a week/Once or twice a week/Fortnightly/Monthly/Less often /Other
What types of food do (or did) you put out for red kites? (select all that apply)	a) Meat/Kitchen scraps/Carcasses/Placenta/Other If meat: b) with bones/without bones c) cooked/raw
When you feed (or fed) red kites, approximately how much food do (or did) you usually put out at one time?	< 200 g/200–400 g/400–600 g/600–800 g/800–1000 kg/ > 1 kg/Other
Have you ever observed red kites coming to feed from the given food?	Yes/No
Approximately how long have you been feeding red kites? (Or for how long did you feed in the past).	< 3 months/3–5 months/6–11 months/1–2 years/2–3 years/3–5 years/5–10 years/ > 10 years
Do you know anybody who feeds red kites?	Yes/No

reference only.

2.2. Data analysis

2.2.1. Total number of feeding households in the study area

For an estimation of the number of households feeding red kites in the whole study area, we assumed that our random sample (without the indicated households) included a representative sample of the households in the study area. We estimated the proportion of feeding households from the random sample for both urban and rural areas. Then, we calculated the rate of inhabited households by dividing the total number of buildings present in the Sense district by the number of inhabited households from official statistics ([Office for Statistics Canton of Fribourg STATA, 2015](#)). This proportion was then used to estimate the number of inhabited households in urban and rural areas. The number of households feeding red kites in the study area was finally obtained by multiplying the proportion of feeding households with the respective total number of inhabited households. In the same way, we used the proportion of intentionally feeding households in urban and rural areas to calculate the total number of households that intentionally feed red kites.

2.2.2. Amount of food provided by surveyed households

To calculate the amount of food provided by all the surveyed households, we first transformed the frequency and seasonality categories of the feeding events indicated by people into a continuous number of feeding days in a year. When transforming frequency, “several times a week” counted as 3.5 days/week, and “once or twice a week” counted as 1.5 day/week. When transforming the mass categories placed at each feeding, “less than 200 g” counted as 100 g, “more than 1 kg” counted as 1500 g, and for the rest the mid value was used (e.g. 400–600 g counted as 500 g). We assumed that year-round feeding households provided food over a period of 90 days during the winter season (December – February) and 275 days during the rest of the year (March – November). Winter-feeding households provided only for the former. Consequently, the proportion of households providing food during the winter season was equal to the sum of the proportion of winter-feeding households and year-round feeding households, whereas the proportion of households providing food during the rest of the year was equal to the proportion of year-round households. Using these continuous values, it was possible to estimate the average daily mass provided by a household during winter and the rest of the year in urban and rural areas. To investigate differences between the two times of the year, we tested daily mass provided by Student’s *t*-test, and type of food by χ^2 -test. Similarly, we tested for differences in average number of feeding days, total mass provided per year and type of food used between households in urban and in rural areas. Significance level α was 0.05.

2.2.3. Total amount of food distributed and spatial modeling of anthropogenic food availability

We applied two approaches for the extrapolation of red kite feeding over the entire study area. First, we used only the random sample to extrapolate the food distributed over the whole study area at the building level. We multiplied the average daily mass provided by each household during the winter season and the rest of the year by the estimated number of households feeding red kites in the whole study area during the two time periods. Second, the probability of feeding could not only vary between urban and rural areas and between seasons, but also in relation to landscape variables surrounding the buildings. Thus, we investigated the effect of landscape variables on the probability of a household feeding by using generalized linear models with a binomial error distribution (logistic regression). With the aim of projections into landscape, a random sample of the absence points considering the full range of potential landscapes is important, but a random sample of occurrence points is not necessarily needed. Therefore, we used feeding occurrence of the non-random sample including the randomly selected and the indicated households as response variable. This resulted in a probability that a selected household in a given 1 ha cell was feeding depending on the surrounding landscape variables. The probability of feeding was then used to calculate the total amount of food provided in the whole study area by including the information on building density in the cell and the amount of food provided by a feeding household in the extrapolation over all cells in the study area.

Feeding or non-feeding were entered as response variable in a joint and in separated models for the winter season and the rest of the year, while landscape variables in the surrounding of each household were entered as explanatory variables. The separated seasonal models were used for projections and estimation of the total food distributed. We extracted land cover type by rasterizing the Swiss vector-based map (vector25 © swisstopo; DV002232.1) at a very fine resolution (5 m × 5 m), and then calculated the proportion of each land cover variable at a 100 m resolution (1 ha). We extracted elevation from the Copernicus EU-DEM ([European Environmental Agency, 2013](#)) and re-sampled the original 25 m × 25 m resolution data to the same 100 m × 100 m resolution. Using buildings data from the Swiss vector-based map, we also calculated the number of buildings within each 1 ha cell.

Organisms can respond to different variables at different scales. In a first step, we therefore explicitly optimized the size of the ecological neighborhood at which feeding probability responded to each environmental variable (the characteristic scale), following [Fattebert et al. \(2018\)](#) and [Zeller, Vickers, Ernest, and Boyce \(2017\)](#). We first computed a disk kernel smoothing on each landscape variable at four ecological neighborhoods (300 m, 500 m, 700 m and 900 m) using the package ‘smoothie’ ([Gilleland, 2013](#)) in R (v. 3.4.3, [R Core and Team, 2017](#)). For each variable, we then fitted univariate logistic regressions at each neighborhood, including the original 100 m scale. We selected the

univariate model with the lowest value of the Akaike's Information Criterion corrected for small sample size (AICc) to identify the characteristic scale of each variable.

In a second step, we fitted a multivariable logistic regression using the optimized scale for each environmental variable. We first screened for collinearity among all environmental variables at their selected characteristic scales using a threshold Spearman's rho ($|r| > 0.6$), and retained 'number of buildings', 'elevation', 'proportion of forest', and 'proportion of agricultural fields' (including meadows and arable fields) as predictors. We also included distance to the nearest forest and distance to the nearest field as explanatory variables in a full model. We then reduced the model by conducting a manual backward-stepwise model selection procedure, removing all non-significant variables from the multivariate model until the effects of all remaining variables were significant $P < 0.05$ (Fattebert et al., 2018; Hosmer, Lemeshow, & Sturdivant, 2013) to receive model estimates for predictions into space.

The resulting separate models, one for feeding in the winter season and one for feeding during the rest of the year, were used to spatially project the probability of a household feeding in a cell to all 1 ha cells of the landscape with at least one building (urban cells with at least one building: 14.3 km²; rural cells with at least one building: 43.7 km²). Then the amount of food provided in each 1 ha cell was calculated by multiplying the probability of a household feeding in a cell by the number of buildings present in the cell, resulting in the number of households feeding in that cell, and by the average mass fed per feeding household in the given area and season.

2.2.4. Red kites supported

The minimum and maximum number of red kites that could be supported by garden feeding was calculated by dividing the total mass of food daily provided by the minimum and maximum daily food requirements of red kites. Thus, we assumed full consumption of the provided food by red kites, neglecting that parts of the provided food could be consumed by other species. Published minimum and maximum daily food requirements of red kites of 80 g and 180 g were used (see Carter, 2007).

3. Results

3.1. Feeding households in the survey

A total of 210 households were surveyed: 199 randomly sampled and 11 selected because indicated to be feeding red kites (Table 2). In

Table 2

Summary of the survey results obtained with the random and the non-random samples, split by urban and rural areas. Number of feeders and their intentionality are given for both samples, while number of feeding years and type of food distributed are only given for the random and non-random sample respectively. In parentheses proportion (%) is given.

Random sample (N = 199)		Urban (N = 65)	Rural (N = 134)
Feeders:	all	3 (4.6%)	17 (12.7%)
	intentional	1 (1.5%)	3 (2.2%)
Feeding years:	< 2 years	1	–
	2–3 years	–	5
	3–5 years	–	5
	5–10 years	1	5
	> 10 years	1	2
Non-random sample (N = 210)		Urban (N = 66)	Rural (N = 144)
Feeders:	all	4 (6.1%)	24 (16.7%)
	intentional	2 (3.0%)	9 (6.3%)
Food type:	meat	1	6
	afterbirth	1	9
	kitchen scraps	1	7
	carrion	1	2

the random sample, 20 feeding households (10.1%) were found, while thanks to the additional 11 indicated households, 8 feeding households were added to the non-random sample (13.3% feeding households in the non-random sample). The feeding households were distributed over the whole study area (Fig. 1). The proportion of feeding households was greater within rural areas than within urban areas (12.7% vs. 4.6% in the random sample; 16.7% vs. 6.1% in the non-random sample), and in both areas, unintentional provision of food tolerated to be consumed by red kites was the most common form of garden feeding (Table 2). All the feeding households were either farmhouses or houses with gardens, with a proportion in the random sample of 85% ($n = 17$) and 15% ($n = 3$) respectively. Of the 20 feeding households in the random sample, only one (5%) was a very recent feeder (less than 2 feeding years), while the other were either feeding for 2–5 years (50%, $n = 10$) or for more than 5 years (45%, $n = 9$) (Table 2).

3.2. Food provided by surveyed households

Among the 28 feeding households of the non-random sample, 100% ($n = 28$) provided food during the winter, and 64.3% ($n = 18$) provided food during the rest of the year. In winter, provision of anthropogenic food was also more intense: average daily mass of food provided by a household was moderately higher than during the rest of the year (Table 3). But given the high variance, no statistical difference was found ($t = -0.583$, $df = 37.82$, $p = 0.563$). When summed, the daily food mass provided in winter was almost twice the mass provided during the rest of the year (Table 3). The proportion of food provided only by intentional feeders made up 28% of the total daily sum of food provided in the winter season and 46% during the rest of the year. Average daily mass of intentional feedings alone was higher during winter than during the rest of the year ($179 \text{ g} \pm 222 \text{ SD}$ vs. $142 \text{ g} \pm 222 \text{ g SD}$), and the same was found for the sum of daily food mass intentionally provided (1.97 kg in the winter season vs. 1.57 kg

Table 3

Summary of the anthropogenic food provided by the surveyed households in the random and the non-random samples. Average daily mass of food distributed per household, average number of feeding days, sum of the daily mass of food distributed across the study area and number of potentially supported red kites are given separately per season (winter and rest of the year) and per area (urban and rural). In parentheses (\pm SD) standard deviation is given. Study area: Sense and Bern-Mittelland districts, Switzerland.

Random Sample (N = 199)			
Feeders: winter season	Urban (N = 3)	Rural (N = 17)	Total (N = 20)
Average mass fed [g/day]	258 (± 137)	235 (± 275)	239 (± 257)
Feeding days	51 (± 36)	26 (± 16)	30 (± 21)
Total mass fed [g/day]	774	4002	4776
Red kites daily supported	4–10	22–50	27–60
Feeders: rest of the year			
Urban (N = 3)	Rural (N = 10)	Total (N = 13)	
Average mass fed [g/day]	257 (± 137)	141 (± 235)	168 (± 217)
Feeding days	157 (± 109)	86 (± 46)	103 (± 67)
Total mass fed [g/day]	772	1415	2187
Red kites daily supported	4–10	8–18	12–27
Non-Random Sample (N = 210)			
Feeders: winter season	Urban (N = 4)	Rural (N = 24)	Total (N = 28)
Average mass fed [g/day]	274 (± 117)	227 (± 267)	234 (± 250)
Feeding days	44 (± 34)	29 (± 21)	31 (± 23)
Total mass fed [g/day]	1097	5435	6531
Red kites daily supported	6–14	30–68	36–82
Feeders: rest of the year			
Urban (N = 4)	Rural (N = 14)	Total (N = 18)	
Average mass fed [g/day]	273 (± 116)	167 (± 260)	190 (± 237)
Feeding days	133 (± 102)	105 (± 65)	111 (± 72)
Total mass fed [g/day]	1093	2337	3430
Red kites daily supported	6–14	13–29	19–43

during the rest of the year). Consequently, the number of red kites that could be supported daily, considering the minimum and maximum food mass needed by a red kite per day, was nearly doubled in winter compared to the rest of the year (Table 3). This difference, although not as strong, was also observed when considering intentional feeders of the survey only, which could daily support 11–25 individuals in the winter season and 9–20 individuals in the rest of the year.

Among all 28 feeding households of the non-random sample, the most common food made available to kites was livestock afterbirth (10), followed by kitchen scraps (8), meat (7, both raw and cooked from different animals), and carrion (3). Intentional feeders favored provision of meat (7, often slaughter waste), followed by kitchen scraps (3) and then carrion (1). Considering the full sample, no significant difference between seasons was found regarding the type of food provided ($\chi^2 = 2.330$, $df = 4$, $p = 0.675$). We also found no differences between urban and rural provision of food regarding number of feeding days in a year ($t = -1.223$, $df = 3.45$, $p = 0.298$) or type of food provided ($\chi^2 = 1.4$, $df = 4$, $p = 0.844$). Total mass provided in a year by urban households doubled the mass provided by rural households, but statistically only tended to be higher in urban households due to high within-group variation (urban: $99.8 \text{ kg} \pm 42.5 \text{ kg SD}$, rural: $47.2 \text{ kg} \pm 74.9 \text{ kg SD}$; $t = -2.012$, $df = 6.68$, $p = 0.086$).

3.3. Estimated number of feeding households in the study area

Inhabited houses represented 83.6% of all buildings in the study area. Thus, the total number of inhabited houses in the study area was estimated at 9897, with 6374 located in urban areas and 3523 in rural areas. Considering the proportions of feeding households in urban and rural areas estimated from the random sample ($N = 20$ feeding households; Table 2), we estimated a total of 293 feeding households in urban areas and 447 feeding households in rural areas over the entire study area. When considering differences in feeding participation between winter and rest of the year (Table 3), we estimated all 293 urban households and 447 rural households to be feeding in winter, and 293 urban households and 263 rural households to be feeding the rest of the year (Table 4). In total, we therefore estimated 740 households (7.5% of all households) feeding red kites in the study area. The proportion of intentionally feeding households was 1.5% and 2.2% in urban and rural areas, respectively, resulting in an estimated number of 96 intentional feeders in urban areas and 76 in rural areas, totaling 172 intentionally feeding households in the entire study area (1.7% of all households).

3.4. Anthropogenic food availability

Using the random sample, we estimated the total daily mass distributed in rural areas of the study area to 105.05 kg in winter and 37.08 kg in the rest of the year. In urban areas, it amounted to 75.59 kg in winter and to 75.30 kg in the rest of the year. This summed up to a total of 47.2 metric tons of food provided by humans over the study area in a year. This amount of food would support 1004–2258 red kite individuals daily in winter and 624–1404 individuals during the rest of the year. Using the non-random sample for the same extrapolations, we end up with 51.0 metric tons of anthropogenic food per year in the study area

Using the non-random sample, we investigated the probability that a selected household in a 1 ha cell was feeding in relation to environmental variables. Scale optimization resulted in the best scale for building density at the 500 m diameter, for proportion of forest at the 700 m diameter, for proportion of open fields at the 100 m diameter, and for the elevation at the 300 m diameter (Table S1). The average probability was 1.66 (CI = 0.89–3.19) times higher in winter than in the rest of the year (Fig. 2a). However, although we found a higher number of households feeding in winter, the effect of season was not significant ($p = 0.11$; see Table S2), most probably due to low sample size. After model reduction, only the number of buildings showed an

Table 4

Estimates of the available anthropogenic food in the study area according to the extrapolation of the random sample and the spatial model, subdivided by urban and rural areas and by winter season and rest of the year. Total annual food mass, total daily food mass and range of red kites potentially supported according to minimum and maximum food mass requirement estimates are given for both extrapolation methods. Extrapolation of the random sample also presents the estimated number of feeding households, while average daily food mass available per ha with at least one building (\pm SD) is given for the spatial model extrapolation. Study area: Sense and Bern-Mittelland districts, Switzerland.

Random Sample			
Feeders: winter season	Urban	Rural	Total
No feeders	293	447	740
Total annual mass [kg]	6803.46	9454.05	16257.51
Total daily mass [kg]	75.59	105.05	180.68
Red kites daily supported	420–945	584–1313	1004–2258
Feeders: rest of the year			
No feeders	293	263	556
Total annual mass [kg]	20707.78	10197.83	30905.61
Total daily mass [kg]	75.30	37.08	112.38
Red kites daily supported	418–941	206–464	624–1405
Spatial Modeling			
Feeders: winter season	Urban	Rural	Total
Total annual mass [kg]	11715.93	21505.14	33221.07
Total daily mass [kg]	130.2	238.9	369.1
Average daily mass [g/ha]	91 (\pm 77)	55 (\pm 36)	64 (\pm 52)
Red kites daily supported	723–1627	1327–2987	2050–4614
Feeders: rest of the year			
Total annual mass [kg]	21696.95	31146.78	52843.73
Total daily mass [kg]	78.9	113.3	192.2
Average daily mass [g/ha]	55 (\pm 50)	26 (\pm 17)	33 (\pm 32)
Red kites daily supported	438–986	629–1416	1067–2402

important effect for both feeding in winter and during the rest of the year (estimate = -1.14 ± 0.39 SE; $Z = -2.93$; $p = 0.004$). High number of buildings within 500 m resulted in reduced probability of a household feeding. The probability was also higher in rural than in urban areas (Fig. 2a).

While the probability that a selected household in a 1 ha cell was feeding declined with the building density, the average amount of food provided per ha (calculated by using the feeding probability) was higher in urban than in rural areas (Fig. 2b) because urban areas showed larger number of buildings per ha. The estimated daily mass of food provided per ha in urban areas was two times the mass provided in rural areas, although it must be noted that the variance was high (Table 4, Fig. 3). Nevertheless, more food was provided in the entire rural area than in the entire urban area, because the urban area was considerably smaller than the rural area (Table 4). Daily food mass per ha was also higher in winter than during the rest of the year (Fig. 3). This arises from both the higher probability of a household feeding and the higher average amount of food provided in winter. The number of red kites that could be supported was consequently higher in rural than in urban areas, and higher in the winter than in the remaining time of the year. When combining the results of both seasons and areas using the spatial modeling approach to estimate food provided over the entire study area, we found that on average, 0.86 kg of anthropogenic food was available per day per km^2 , which could support about 5–11 red kites per km^2 (based on minimum and maximum of food mass daily needed by a red kite). Annually, the provision of anthropogenic food summed up to 86.1 metric tons for the entire study area. Of this amount, 20% came from intentional feeders, leaving 80% for unintentionally placed waste known to be targeted by red kites.

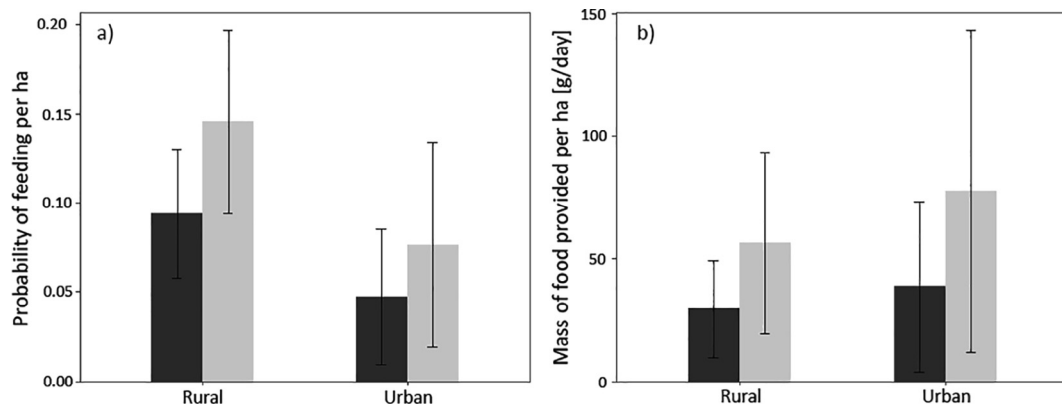


Fig. 2. (a) Probability of feeding occurrence per hectare, and (b) amount of food provided daily per hectare in relation to area type. Light grey bars: winter season feeding; dark grey bars: rest of the year feeding. Error bars represent standard deviation.

4. Discussion

Our results show (1) that the proportion of households providing food to red kites in our study area is around 7.5%, (2) that this proportion, and thus the probability of a household feeding was considerably higher in rural than in urban areas, and (3) that winter feeding rate was 1.7 times higher than in the rest of the year. Due to the larger amount of buildings, the mass provided per area was higher in urban than in rural areas, suggesting an increased food availability in urban areas. Thus, the provision of anthropogenic food to red kites is a widespread and well-established human behavior in western Switzerland. This provision includes both intentional feeding and unintentional feeding of waste known to be targeted by red kites. To our knowledge, this is the first report of the amount of food regularly distributed by private households to a scavenger bird species in mainland Europe. Although the percentage of people involved in red kites feeding

was low compared to feeding of passerine birds, the mass of food distributed would be enough to support a considerable number of red kites individuals.

The 28 feeding households found in our survey distribute alone more than 1.5 metric tons of food per year, while the maximum estimated annual distribution of food for the entire study area sums up to 47–86 metric tons, 20% of which is intentionally targeted at red kites. According to the maximum estimate, on average, close to 1 kg of anthropogenic food per km² was available daily to facultative scavengers and could support about 5–11 red kites per km², which is far in excess of the density of red kites in the study area: a total of 250–300 red kites were present in the study area during the 2016 breeding season (Cereghetti, 2017). Even according to our minimum estimate of anthropogenic food availability, about 0.5 kg of food per km² was available daily to scavengers, and it could support 3–7 red kites per km². This amount of food is likely to affect the ecology, population dynamics

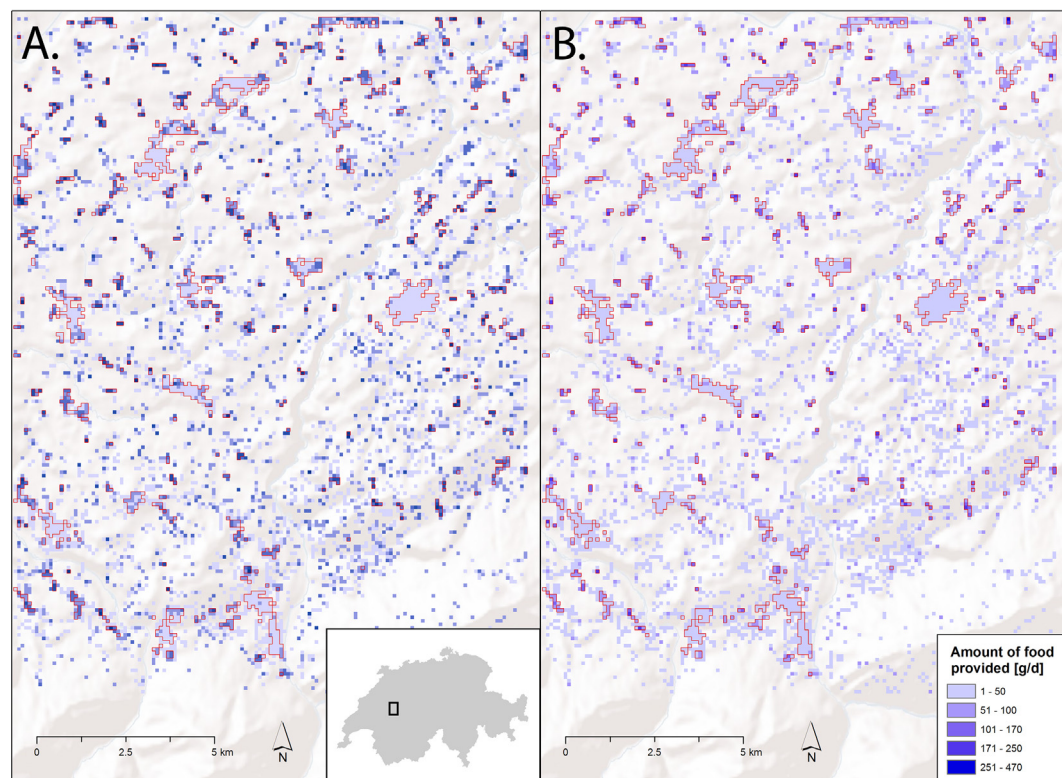


Fig. 3. Spatial prediction of the total amount of food distributed daily per hectare in the study area during the winter season (left, A) and during the growing seasons (right, B). Urban areas are outlined. Background maps: Shaded Relief Copyright:© 2014 Esri.

and behavior not only of red kites, but also of other facultative (or even obligate) scavenger species, mammals included (Reed & Bonter, 2018). The fact that most feeding households have been feeding for several years suggests that this is not a completely new phenomenon and that the amount of anthropogenic food in this area was similar already 10 years ago.

Households in rural areas were more likely to partake in feeding red kites than households in urban areas. Based on our random sample, the proportion of feeding households within rural areas was three times higher than in urban areas (12.7% vs. 4.6%), a result that is similar to the one found by Orros and Fellowes (2015) in the UK. These results highlight the importance of gardens and open spaces, which are more abundant in rural areas due to the lower building density. Also, the uncertainty about the legal situation of feeding red kites might constrain feeders more in highly populated areas. In addition, local farming practices provided a considerable part of rural anthropogenic food by making livestock afterbirth available. Although feeding probability of households was higher in rural than in urban households, the actual availability of anthropogenic food per ha was higher in urban areas. This was due to two factors. First, urban households provided a higher daily amount of food, if they were feeding, and second, the lower probability of a household feeding in urban areas was compensated by the higher number of households. Similarly, Tryjanowski et al. (2015) found that the availability of bird feeders and waste food was higher within the urbanized area. Thus, it is likely that in the last decades urban areas became high quality foraging habitats not only for mammalian, but also for avian facultative scavengers (Contesse, Heggin, Gloor, Bontadina, & Deplazes, 2004; Huijbers, Schlacher, Schoeman, Weston, & Connolly, 2013; Inger et al., 2016; Orros & Fellowes, 2015), potentially resulting in fundamental changes in urban trophic processes and in the selection of individuals with high levels of neophilia (Tryjanowski et al., 2016).

For both urban and rural areas, the availability of anthropogenic food was higher in winter than during the rest of the year, but in rural areas, this increase was more pronounced. We have two not mutually exclusive explanations for this pattern. First, the seasonal accumulation of unintentional food might differ between urban and rural areas. In the traditional Swiss dairy farming systems, calving of cattle resulting in livestock afterbirth occurs more often in winter than during the rest of the year. Second, the opinion of people about the seasonal timing of feeding may differ between urban and rural areas. Rural persons may be aware of the effects of seasonal changes on animal species, and they may see the need of supporting raptors during harsh winter conditions whereas urban persons are less in touch with nature and may base their actions on the fascination of observing raptors regardless of the season. Feeding practices are known to differ depending on the local fauna and culture. For example, feeding of wild birds in Europe is mostly associated with small passerine birds, while in Australia providing meat-derived food is a popular activity (Rollinson, O'Leary, & Jones, 2003). In our study, people were aware that red kites took advantage of anthropogenic food they made available, but they did not prevent red kites from feeding from these resources. This unintentional food was also available for other facultative scavenger species such as carrion crows (*Corvus corone*), common buzzards (*Buteo buteo*) or red foxes (*Vulpes vulpes*). We therefore expect feeding by private residents to have multiple effects on facultative scavengers in general and on red kites as diurnal scavengers in particular because food is provided mostly during daytime and red kites are most competitive at spatially predictable feeding sites (Welti, 2017). The passive positive human-wildlife interactions if people accept red kites to target on waste might be important in the agricultural routine and could be one of the key differences of wildlife feeding between urban and rural areas. However, also in urban ecosystems anthropogenic food for facultative scavengers such as food waste, road kills or bird deaths due to window collisions accumulates. The use of such unintentionally provided food (with or without the awareness of the public) represents an important ecosystem service of

cleaning wastes and carrion (Inger et al., 2016; Sekercioglu, 2006), which is shown also for red kites in the past (Harrison & Reid-Henry, 1988).

The intentional feeding of red kites in Switzerland and in the UK is uncommon compared to a more traditional winter-feeding of garden birds, and therefore might represent a developing phenomenon in European countries that should be addressed by future research. In our survey, we found evidence for a recent increase in anthropogenic feeding of red kites: no household stopped feeding in the past, but several started recently. Despite our regular presence due to field work we knew only of a handful of intentional feeders in the study area. Thus, intentional feeding was more common than perceived. If these results hold true for other countries, intentional feeding could spread to wider areas in the future. Thus, it can be expected that human-wildlife conflicts will increase and that calls for the management of avian scavengers or their food resources will arise, in particular in urban areas.

The high availability of anthropogenic food is expected to increase reproductive output and survival of red kites and other facultative scavengers (Bino et al., 2010; Contesse et al., 2004), to reduce the stochastic fluctuations inherent in natural systems (Oro et al., 2013), to alter range use behavior (Bino et al., 2010; Monsarrat et al., 2013), and to affect migration behavior (Plummer et al., 2015). This in turn may cascade down through trophic levels by altering predator-prey interactions (Martinson & Flaspohler, 2003; Rodewald et al., 2011) as well as scavenger communities (Newsome et al., 2015; Wilson & Wolkovich, 2011). In particular, bird feeding might be an important factor underlying the range expansion into Alpine valleys and urban settlements, and the increase in breeding and wintering populations of red kites in Switzerland (Aebischer, 2009; Knaus et al., 2018).

Although negative effects of public and private feeding on birds are regularly reported (Blanco, Lemus, & García-Montijano, 2011; Plummer et al., 2013), this is not expected to be the case in our study area: at the moment anthropogenic feeding in Switzerland perfectly follows the recommendations for supplementary feeding of obligate scavengers as a conservation measure (Cortés-Avizanda et al., 2016). First, the food comes from various sources and is not exclusively meat based. Given the diversity of food sources, the risk of imposing an unhealthy diet should be limited (see Blanco et al., 2011). Second, the amount of food made available by red kite feeding is in many cases negligible and the feeding activity is widely distributed over the study area. Consequently, we rarely observed big aggregations of scavengers at feeding sites during the breeding season, minimizing the chances of agonistic encounters that might be detrimental to pairs nesting in the proximity of feeding sites (Carrete, Donázar, & Margalida, 2006), as well as reducing the risks of disease transmission favored by bird aggregations (Brittingham & Temple, 1988; Lawson et al., 2018). In winter, however, aggregations might occur more often at intentional feeding sites that provide large food quantities, potentially provoking considerable human-wildlife conflicts. Third, most feeding events are not scheduled, but depend on factors such as availability of leftovers or timings of livestock births. While the locations of the private feeding sites often are predictable, exact timing remains normally unpredictable. This kind of temporal unpredictability of feeding has been found to favor inter- and intraspecific coexistence in scavengers (Cortés-Avizanda et al., 2012; Duriez, Herman, & Sarrazin, 2012).

Although we are confident that our study presents reliable results, we are aware of its limitations. First, by searching a new household in situations where nobody was at home, we might have biased our random sample versus overestimating feeding households if presence at home is associated with higher feeding probability. However, with only 7% of households affected, this should not be a major problem. Second, though we have a good sample of households in the survey, the low sample size of feeding households limits the complexity of the binomial statistical analysis. We suggest that with a higher sample size, statistical identification of landscape and seasonal effects on feeding probability would have been more reliable. Third, extrapolation of point data into

space is always tricky, in particular with a limited sample of presence points. We faced this issue by using two separate, completely different approaches. While the building-centered extrapolation based on the random sample tends to underestimate the feedings in space because the sampling scheme fails to detect the few large feeding sites found by indication of respondents, the landscape-centered extrapolation based on the non-random sample tends to overestimate the feedings due to extrapolation of the real number of large feeding sites into space. Nevertheless, we believe that the true value is closer to the maximum than the minimum estimation out of two reasons. On the one hand, in the stratified random sample, single remote households tend to be underrepresented although they show the highest feeding probability. On the other hand, the identification of feeders ignores unintentional feeders that were not aware of red kite targeting at the food. The awareness of the feeders about the red kites is not considered in the landscape-centered extrapolation while in the building-centered extrapolation we estimate the number of households that were aware of their feeding. Fourth, we lack information on the socioeconomic status of the surveyed households, which has been found to influence engagement in bird feeding activities (Davies, Fuller, Dallimer, Loram, & Gaston, 2012). Annual income, age, social context, education and interest in wildlife can all be factors affecting participation in red kite feeding (see Davies et al., 2012; Lepczyk et al., 2004). For instance, frequent provision of food to red kites can be an important financial commitment, especially if we consider provision of meat, thus household income could affect the likelihood and frequency of feeding events (Martin & Greig, 2019). People with a greater interest in wildlife might associate the presence of red kites with ecological services such as pest control (Whelan, Wenny, Marquis, & Louis, 2008), which would be considered highly favorable in agricultural landscapes. A more in-depth analysis of the surveyed households and their members is required to shed light on the link between socioeconomic status and the participation in feeding of this scavenger species.

In conclusion, we showed that intentional feeding by private residents and accepted use of unintentional anthropogenic food over large areas provided a vast amount of food to a facultative avian scavenger living in Swiss anthropogenic landscapes. Thus, not only wintering passerines benefit from garden feeding and from positive attitudes toward birds. This phenomenon is likely to be more widespread than previously known and might also strongly affect other less popular facultative scavenger species. However, though we expect effects on red kite population size and distribution as well as on food webs, the ecological consequences of red kite feeding and the resulting human-wildlife interactions remain still to be investigated.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2019.103606>.

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