How common ravens (*Corvus corax*) exploit anthropogenic food sources through time and space in a semi-transformed, alpine environment

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Abstract

From large-scale agriculture and farming to concentrated fishing discards, garbage dumps, game carcasses and bird feeders, human action has been increasingly affecting natural systems and animal species through the deliberate and unintentional provisioning of food resources. Anthropogenic food sources (AFSs) are often more spatially concentrated, easily accessible, abundant and stable than natural food sources. The common raven, *Corvus corax*, is a behaviourally flexible and ecologically adaptable species that has managed to thrive in human transformed landscapes by exploiting these anthropogenic sources of food. The aim of this research was to investigate how raven individuals vary in their use of different AFSs through space and time. I used data from a long-term GPS tracking initiative in the Upper Austrian Alps to investigate (1) the space-use of non-breeding raven individuals across this landscape to answer the questions: (2) what types of AFSs are most extensively used by ravens in this landscape, and what factors predict individual variation in AFS use (i.e., apparent reliance on and access to resources), specifically (3a) the number of AFSs visited and (3b) the probability of being at AFSs at any given point in time. Movement patterns can reveal information on the foraging decisions made by individuals, including how they use different AFSs. Non-breeding raven individuals exhibited great variation in how they moved around and used the landscape. The number of AFSs visited, but not the probability of being at an AFS (at any given point in time), varied among individuals with different ranging behaviour and of different age class (i.e., juvenile and adults) and origin (i.e., captive-bred-released and wild-caught), suggesting that experience affects AFS-use. Non-breeders differed in their use of AFSs by season, visiting the highest number of AFSs but having the lowest probability being present at an AFS in winter, potentially indicative of high foraging competition under stressful environmental conditions. They were also found to extensively exploit resources in spring, both visiting high numbers of AFSs and having a high probability of being present at an AFS, perhaps due to decreased competition (e.g., from breeders) and increases in food availability. The category (i.e., wildpark, refuse site, hut) of AFSs also influenced the probability of an individual being present at the site, likely because of differences in resource quality, quantity and replenishing rate. A very few foraging sites were highly popular, while over half attracted less than 5 individuals throughout the study. By exploiting AFSs, raven population numbers have increased across their range, raising conservation concerns (i.e., predation on threatened species and human-wildlife conflict). With a better understanding of the patterns of AFS-use and the factors influencing these patterns, I suggest that strategies to manage ravens in this semi-transformed, alpine environment should focus on controlling the supply of food at AFSs at a regional scale.

Key words Non-breeder, food subsidy, space-use, resource-use, hyperpredation

Introduction

Human activity is rapidly transforming natural landscapes across the world, altering the quantity and quality of resources in the environment (Ditchkoff et al. 2006; Soulsbury & White 2015) and driving ecological change (Lowry et al. 2013; Song et al. 2018). From large-scale agriculture and farming to concentrated fishing discards, garbage dumps, game carcasses and bird feeders, human action has increasingly affected natural systems through the provisioning of food resources (Johnston 2001; Oro et al. 2013). Although humans have both deliberately and unintentionally supplied food to wild animals since hunter-gatherer times, the modern widespread occurrence of novel anthropogenic food sources in the environment creates distinct foraging conditions to which species must adapt to persist (Shochat et al. 2010; Lowry et al. 2013; Cereghetti et al. 2019).

Anthropogenic food sources (AFSs) are spatially concentrated, easily accessible, abundant and stable (in both space and time) compared to natural food resources, which are often sparsely distributed and ephemerally present (Oro et al. 2013). According to optimal foraging theory, an individual should forage at AFSs if it is energetically advantageous to do so, to maximise their net energy gains and ultimately their fitness (Pyke et al. 1977). In maximising benefits relative to costs, each individual is faced with various trade-offs. For instance, individuals experience costs associated with food-searching efforts, such as time and energy spent, opportunity costs (i.e., lost reproductive opportunities) and increased predation risk (Loretto et al. 2016b). At AFSs, individuals can also experience costs from high levels of competition if heavily exploited by conspecifics and heterospecifics (van Overveld et al. 2018), and increased predation (Chamberlain et al. 2009). In foraging at an AFS, one of the trade-offs incurred is between the costs associated with searching versus those associated with foraging. In socially and or cognitively complex species, foraging trade-offs can differ among individuals based on social interactions. These include competition (Newsome et al. 2015) and cooperation (Focardi et al. 2015), dominance status (Goldberg et al. 2001; van Overveld et al. 2018), and the ability to gain knowledge of and access to a food site (Deygout et al. 2010; Boucherie et al. 2019; Riotte-Lambert & Matthiopoulos 2020).

In the foraging context created by the presence of AFSs, individual trade-offs can be influenced by the availability of natural resources in the environment and the availability of anthropogenic resources themselves, which is often determined by human activity (Contesse et al. 2004; Monsarrat et al. 2013; Stofberg et al. 2019). This can generate scheduled patterns in anthropogenic food availability across temporal scales (e.g., diurnal human activity cycles, crop harvesting, hunting or recreation seasons) or locations (e.g., roads, recreational trails), that species learn and benefit from tracking (Oro et al. 2013; Riotte-Lambert & Matthiopoulos 2020; Spelt et al. 2021). For instance, in response to both seasonal decreases in natural food abundance and increases in anthropogenic food availability, populations of various taxa globally have been observed to forage more at AFSs than natural food sources, including Griffon vultures *Gyps fulvus* (Monsarrat et al. 2013), black bears *Ursus americanus* (Lewis et al. 2015), grey wolves *Canis lupus* (Petroelje et al. 2019), chacma baboons *Papio ursinus* (Walton et al. 2021), corvid species *Corvidae* (Preininger et al. 2019) and black-capped chickadees *Poecile atricapilla* (Wilson 2001).

In addition to facing different trade-offs, resource-use among individuals within a population can vary according to dietary preferences (Newsome et al. 2015), ranging patterns (Hidalgo-Mihart et al. 2004; Petroelje et al. 2019), and the foraging techniques and social interactions needed to acquire food (Bugnyar & Kotrschal 2001; Deygout et al. 2010; Boucherie et al. 2019). These differences in foraging behaviour generate individual, population and ecosystem-level impacts (Wilson et al. 2020). In some cases, high-quality and highly abundant AFSs can improve reproduction and survival and might lead to increases in population densities (Contesse et al. 2004; Marzluff & Neatherlin 2006; Newsome et al. 2015; Kumar et al. 2019). Conversely, poor-quality AFSs, exploited under conditions of scarce natural resources, can also have negative health impacts (Wilcoxen et al. 2015) and decrease fitness (Mennechez & Clergeau 2006; Sauter et al. 2006). The growth or decline of populations associated with the exploitation of AFSs affects ecosystem functioning, for example, through trophic-cascades or community structure changes (Oro et al. 2013; Soulsbury & White 2015).

The fitness of individuals in human-modified landscapes is not only affected by the presence of AFSs, but also by disturbances, including noise and light pollution and direct human interference, and opportunities, such as artificial structures and shelters (Shochat et al. 2010; Lowry et al. 2013). Species in such landscapes therefore need to be behaviourally and physiologically flexible to cope with and tolerate these different opportunities and disturbances. Some species, for example, may exhibit temporal avoidance behaviour (Lowry et al. 2013; Wilson et al. 2020) and only forage at AFSs during periods of low human activity to avoid disturbance and conflict (Buehler et al. 1991; Contesse et al. 2004; Spelt et al. 2021; Walton et al. 2021). The challenging and dynamic conditions created by anthropogenic areas tend to favour ecological generalists, species that thrive in heterogenous environments, and synanthropic species - wild species cohabiting with humans and depending on anthropized areas to varying degrees (Johnston 2001; Devictor et al. 2008; Shochat et al. 2010).

The common raven, *Corvus corax*, is a generalist (scavenger and omnivore) and synanthrope that thrives in human-dominated landscapes. The social and cognitive complexity, behavioural adaptability, and ecological flexibility of ravens have allowed them to extensively capitalize on AFSs despite anthropogenic disturbances including direct persecution (Marzluff & Neatherlin 2006; Zawadzka & Zawadzki 2014).

Across the common raven's range in the northern hemisphere, individuals congregate at food sites to feed, socialise and roost in large numbers, sometimes exceeding hundreds of individuals (Webb et al. 2009; Baltensperger et al. 2013; Mateo-Tomás et al. 2015; Loretto et al. 2016b). The extensive use of an increasing number of AFSs has supported the growth and spread of raven populations across their range (Webb et al. 2004; Oro et al. 2013; Loretto et al. 2016a; Boarman & Heinrich 2020). Their adaptation to stable, abundant AFSs has benefitted them through increases in reproduction (Marzluff & Neatherlin 2006), both adult (Marzluff & Neatherlin 2006) and offspring survival (Webb et al. 2004; Webb et al. 2011), and decreases in winter mortality (Engel & Young 1992; Preston 2005; Baltensperger et al. 2013). However, this growth in raven abundance has raised ecological and conservation concerns (McMahon et al. 2020).

In addition to their seed dispersal and carrion eating roles at the ecosystem level, ravens are also predators (Boarman & Heinrich 2020). As they increase in number, their predatory nature has the potential to impact biodiversity via trophic cascades (Merta et al. 2009; Baltensperger et al. 2013; Mateo-Tomás et al. 2015; McMahon et al. 2020) but also see (Madden et al. 2015). In North America, for example, raven populations subsidized by AFSs have been found to negatively affect threatened species (Webb et al. 2004; Marzluff & Neatherlin 2006) including the greater sage-grouse *Controcercus urophasianus* (Bui et al. 2010; Coates et al. 2016), desert tortoises *Gopherus agassizii* (Kristan III & Boarman 2003), and western snowy plovers *Charadrius nivosus nivosus* (Demers & Robinson-Nilsen 2012) through hyperpredation (i.e., an increase in generalist predator to natural prey ratio, and thus predation rates, following the introduction of an alternative resource or prey) (Smith & Quin 1996; Courchamp et al. 2000). In Europe, common ravens predate on black grouse *Tetrao tetrix* (Merta et al. 2009; Policht et al. 2019; Cukor et al. 2021), and are suspected to affect mountain hare *Lepus montanus* (Storch & Leidenberger 2003). Even as prey populations decline, raven numbers and predation rates can still remain high (Kristan III & Boarman 2003). Spill-over predation can also occur where ravens, subsidized by AFSs, begin to invade adjacent areas, inflating predation and affecting the trophic networks there (Oro et al. 2013; Coates et al. 2016).

Increasing raven population numbers also worsen the existing conflict between ravens and humans. Ravens have been reported to predate upon newborn pigs and sick or injured lambs and calves, feed on newly planted seeds and break open silage bales (Marchand et al. 2018; Preininger et al. 2019). Economic costs incurred and conflict result in both legal and illegal raven persecution by shooting and poisoning at AFSs (Restani et al. 2001; Marzluff & Neatherlin 2006; Mateo-Tomás et al. 2015). Given the conservation concerns and potential for ecosystem-level impacts arising from raven populations subsidized by AFSs, understanding raven ecology, behaviour and demography in the context of anthropized landscapes is critical to managing this species and the potential conservation risks it poses (Webb et al. 2011; Marchand et al. 2018; Ferguson et al. 2021).

Ravens vary dramatically in how they exploit AFSs (Preston 2005; Loretto et al. 2016a; Loretto et al. 2016b). The extent to which attributes of individuals themselves (i.e., preferences, socio-cognitive factors), their traits (i.e., age, origin and sex) and external factors (i.e., type of AFS, climate) shape variation in AFS exploitation is not completely understood (Braun & Bugnyar 2012; Webb et al. 2012; Loretto et al. 2016b; Boucherie et al. 2019). Movement patterns can reveal information on the foraging decisions made by raven individuals, including how they use different AFSs. In understanding the patterns of AFS-use and the factors influencing these patterns, ravens can be better managed to address their conservation impacts. In this study, I used data from a long-term GPS tracking initiative in the Upper Austrian Alps to investigate (1) the space-use of raven individuals across the landscape to answer the questions: (2) what categories of AFSs are most extensively used by ravens in this landscape, and what factors predict individual variation in AFS use (i.e., apparent access to and reliance on food sources), specifically (3a) the number of AFSs visited and (3b) the probability of being at an AFS at any given point in time.

In line with initial findings published on this population and other raven study systems, I predict that space and resource use will vary widely among individuals, within cohorts (i.e., age class, origin, but not sex [see (Webb et al. 2009; Webb et al. 2012; Loretto et al. 2016b)]) and across seasons (Loretto et al. 2016b). I expect that with increasing space use, more AFSs will be explored and exploited. As foraging trade-offs can vary based on experience and social ranking, individuals of different origin and age class may use AFSs differently. Seasonal differences are expected to arise as during winter months, natural resources in the environment are depleted and thermoregulatory expenses increase, and as seasonal food sources like ski and alpine huts become available (Restani et al. 2001; Loretto et al. 2016b). Lastly, I expect that the different types of AFSs, varying in quality, quantity and rate of resources supplied, influence the probability of an individual being at an AFS (i.e., individuals are more likely to visit rich year-long than seasonal food sites).

Human activity is increasingly altering pristine ecosystems, making it important to understand how anthropogenic changes affect species and how species cope in response. This study fills an important knowledge gap for the common raven in understanding its adaptability and flexibility within human transformed landscapes at the individual and cohort level. The use of and dependency on AFSs ultimately has consequences for individual fitness (i.e., survival and reproduction), population dynamics, and ecosystem functioning (Oro et al. 2013). Understanding how common ravens use AFSs, whether there are individual differences in this, and what predicts these, will aid the management of these food sites and raven populations. Furthermore, patterns from this population of ravens will better inform predictions on how other intelligent, behaviourally flexible populations and species exploit rich and reliable AFSs.

Methods

Study site and species

Common ravens were trapped in the inner Alm valley in the Northern Austrian Alps for GPS tracking (Figure 1). The valley has an elevation profile ranging from approximately 500 to 2,515 metres above sea level. Below the timberline, the forest landscape is semi-transformed by residential, recreational and other anthropogenic activity. The weather in this region is highly seasonal, dropping below 0˚C across winter months and averaging up to 25˚C in the summer. Snowfall and reduced daylight hours are experienced from November to March.

Rich anthropogenic food sources are distributed across the mountainous landscape. Ravens congregate at these AFSs in large numbers to forage, socialize and roost. Wildlife parks, compost sites and garbage dumps provide food throughout the year while farms, ski huts, restaurants and hotels operate more seasonally, with the latter three peaking in food supply across winter months. Natural food resources in this environment include carcasses, live meat, grains, insects and fruits, but these are highly ephemeral and limited, particularly in winter (Boarman & Heinrich 2020).

To understand the way in which ravens use AFSs, I focus on the non-breeding members (i.e., non-breeders) of the population. Non-breeders make up majority of the individuals congregating at AFSs (Restani et al. 2001; Webb et al. 2011; Loretto et al. 2016b). The non-breeder demographic comprises sexually immature juveniles (within their first year) and sub-adults (2nd and 3rd year), and sexually mature adults (3rd year onwards) that lack either a partner or defendable breeding territory (Braun & Bugnyar 2012). Within this population, some adults can take 10 years or more to attain breeding status as breeding territories (10km^2 or more in size) are limited and likely fully occupied across the landscape (Braun & Bugnyar 2012). With a life expectancy of 10 to 15 years in the wild, ravens therefore spend a considerable amount of time as non-breeders, as opposed to territorial breeders (Webb et al. 2012; Teitelbaum & Mueller 2019).

I sourced movement data from a total of 76 non-breeding common ravens from the inner Alm valley region, tracked between the 1st of July 2017 and 30th of April 2020 (note that part of the study period was affected by the first lockdown in response to the coronavirus pandemic from 16th March to the 20th of April 2020). Of the individuals tracked within this time period, 11 were tracked since 2017, 40 since 2018 and 25 since 2019. At the time of trapping, 52 individuals were tagged as juveniles, 16 as sub-adults, and 8 as adults. There were 56 wild-caught and 20 captive-bred-released-released individuals (see below), and 46 females and 30 males. Sex was determined from blood samples collected when individuals were trapped. Age class was assigned based on the colouration of the mouth lining (pink for juveniles, black for sub/adults) and plumage (slightly brown for juveniles, black for sub/adults) (Loretto et al. 2016b) (Appendix 1).

Wild-caught individuals (n=56) were caught using drop-in traps (Stiehl 1978) baited with meat and bread, placed in Cumberland Wildpark (47˚48’19.08” N, 13˚56’55.32” E) and captive-bred individuals (n=20) were released into the wild from a spacious outdoor aviary (80m^2) at the Konrad Lorenz Research Station (47°48’ 56.16” N, 13°57’1.4” E) (Figure 1). At the research station, raven-raised offspring from a colony of ravens held in captivity are released into the wild, typically at the beginning of September in their first year. The captive-bred-release research line focuses on controlled early life experiences (i.e., if a raven grows up with one or several siblings), including some cross-fostering to disentangle genetic and environmental effects. Captive-bred-release individuals are GPS tagged to understand vagrancy patterns (i.e., if they remain near the release site or explore other areas) in relation to brood sizes. The mortality rates within the first few months post-release are comparable with those of wild ravens (approximately 50%) (pers. comms. Thomas Bugnyar). Once released, individuals generally successfully integrate into the non-breeding local population within a month or two (Braun & Bugnyar 2012). Individuals released from captivity may differ in how habituated they are to humans and how experienced they are with the surrounding landscape, consequently using anthropogenic landscapes and food resources differently. All individuals were fitted with backpack-style, solar-powered GPS loggers (OrniTrack-25 with elevated solar panels, Ornitela, Lituania; https://www.ornitela.com/25g-transmitter). Similar to GPS loggers described and used in Loretto et al. (2016b), these weighed 27g and never exceeded 3% of the bird’s bodyweight. Data from the loggers were automatically uploaded onto the Movebank database (www.movebank.org).

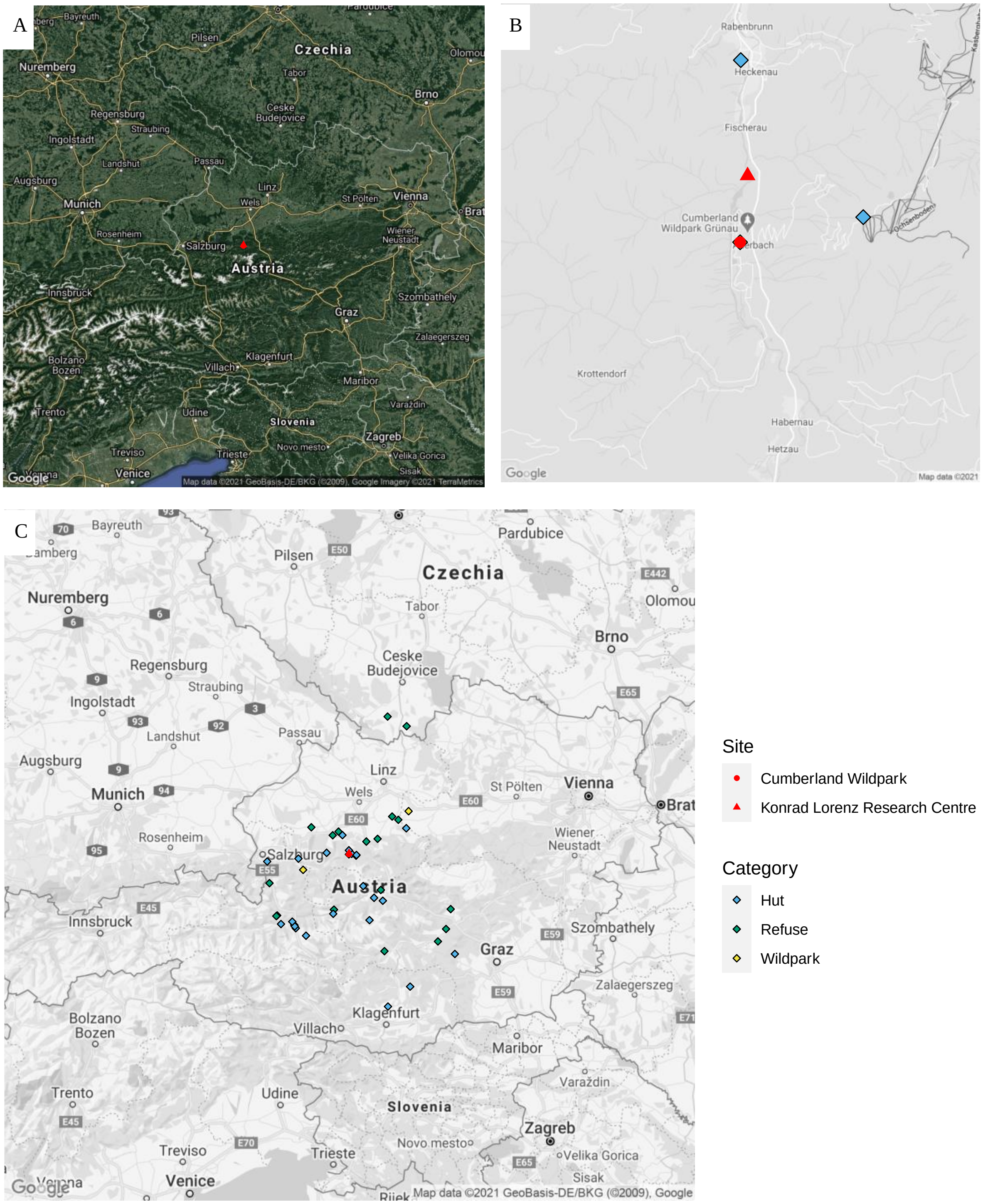

Figure 1 Map of the (A) the study region, highlighting (B) Cumberland Wildpark, where wild non-breeders were caught and trapped, and the Konrad Lorenz Research Centre, from where captive-bred non-breeders were released. Although individuals were GPS-tagged in the narrow Alm valley, they were found to use (C) anthropogenic food sources, identified according to category (i.e., hut, refuse, wildpark), across central Austria. Two refuse sites (F10 and F11 in Appendix 2) were in the Czech Republic, just beyond the Northern Austrian border.

Data analysis

In this study, I first (1) quantified the use of space by each raven individual. To understand individual variation in how anthropogenic food sources were exploited, I (2) used movement tracks to identify extensively used AFSs, then looked at how (3) individual identity, selected traits (i.e., sex, origin, age class, ranging behaviour) and external conditions (i.e., season, category of AFS) affected (a) the number of AFSs visited by individuals and (b) the probability of an individual being at an AFS at any given point in time.

Following Loretto et al. (2016b), I divided the data according to astronomical seasons using the equinox dates of March 21, June 21, September 23 and December 21 as they reflect changes in food resource distribution and availability (Table 1). These dates also roughly correspond to seasonal changes in raven behaviour (Braun & Bugnyar 2012). Nest building and breeding occurs between February and March (i.e., winter); chicks hatch in spring; towards the end of May, fledglings leave the nest with their parents, and by July, move around independently (i.e., summer). Individuals were tracked for different lengths of time, and so the number of common ravens for which GPS tracking data was available in each season varied across the study duration (Table 1; Appendix 1 contains more information on tracking duration for each bird). Tracking ended for various reasons including bird death, battery failure and GPS backpack loss.

Table 1 The number of different individuals (n = 76) for which GPS tracking data was available, by each season and year (total n = 406, with some individuals tracked in more than one season), from the 1st of July 2017 and 30th of April 2020.

Season	Date	2017	2018	2019	2020
Winter	21st December – 20st March		11	43	49
Spring	21st March – 20th June		18	47	45
Summer	21st June – 22nd September	1	35	46	
Autumn	23rd September - 20th December	11	47	53	

As some individuals were tagged for over a year, I calculated age classes by subtracting the year of hatching from the year in which they were tracked. As individuals hatch in spring, the end of spring across all years marked when an individual transitioned between age classes. Individuals tagged within their first year were categorised as juveniles, and by the following summer, were categorised as adults (> 1 year old). Although sexually maturity occurs at around three years of age (Webb et al. 2009), I grouped sub-adult and adult individuals in the same category (i.e., the ‘adult’ category) as only data from non-breeding individuals were included in this study. Additionally, in terms of age estimates, the merged adult category is more robust because age estimations for adults alone are difficult to infer relative to individuals in their first three years.

(1) Estimation of space use

To understand the movement activity of individuals across the landscape, I quantified the use of space by each raven individual. For every individual, in each season and year in which it was tracked (Table 1), I estimated the area within the 95% contour of the utilization distribution (UD) (Appendix 1).The utilization distribution describes the probability of where an animal occurs in an area at any randomly chosen moment (Powell & Mitchell 2012). By using available location information, it provides an indication of how intensively certain areas are used relative to others. The area within the 95% contour (95% UD) is frequently used as a measure of home range, capturing the space-use of individuals throughout their life activities (e.g., including breeding). As the UD measured in this context only represents individuals in their non-breeding stage, where they move around nomadically, the 95% contour more accurately refers to their activity range rather than home range (Loretto et al. 2016a; Teitelbaum & Mueller 2019). I reported the 95% UD estimates for individuals of different sex, age-class and origin, and across the four seasons. The 95% UD estimates were also produced for use as a predictor variable in downstream analyses.

I estimated the 95% UD using the dynamic Brownian Bridge Movement Modelling (dBBMM) approach in the “move” package in R (Kranstauber et al. 2020). The dBBMM approach builds on previous UD estimations by considering both the sequence of fixes along a trajectory and the time between fixes. It is particularly useful in estimating the UD for data with non-regularly sampled tracks, accounting for temporal autocorrelation and high data volumes (Kranstauber et al. 2012). Data were collected from sunrise to sunset and with varying sampling frequency depending on the available energy of the solar powered batteries in the tracking units. Consequently, the sampling frequency was sometimes as fast as every second to 5 minutes over summer months, and every 1-2 hours in winter. To estimate the dBBMMs I used the following parameters: margin of 13, window size of 31, an estimated location error of 20 m, raster cell size of 100m, “timestep” as 1 minute, and in calculating the variance, I excluded time lags that exceed 5 hours.

(2) Identifying extensively used anthropogenic food sources

To estimate individual differences in the use of AFSs by the ravens, I used movement tracks to first identify which AFSs were being used by tagged individuals. I mapped out the GPS fixes for all individuals tracked between December 2018 and December 2019 on Google Earth (Gorelick et al. 2017). As individuals spend extended periods of time at long-term and stable AFSs (Loretto et al. 2016b; Boarman & Heinrich 2020), I selected fixes that were a minimum of 15 minutes apart. The high-resolution satellite imagery allowed me to locate clusters (i.e., 10 or more GPS fixes within a non-overlapping radius of 200 metres) of fixes across the landscape. Focussing on these clusters, I was able to identify which ones were at or near obvious anthropogenic features, including farmhouses, compost sites, ski huts and wildlife parks. From this analysis, I extracted the GPS coordinates (taken as the centre point of a single or group of clusters) for a total of 47 sites.

Field surveys for these identified sites were conducted in Austria with the assistance of a field technician from the Konrad Lorenz Research Centre, where possible given lockdown restrictions in response to the coronavirus pandemic. The purpose of the field surveys was to verify if the sites were indeed AFSs, and to obtain a description of the sites. Out of 47 sites that were identified, 28 sites were visited. Among these 28 sites, only 26 could be verified and described. The other two sites that were visited but could not be surveyed were a ski-field, which was closed and inaccessible, and a farmhouse, where the car got stuck in snow en route (F21 and F31, Appendix 2). Among the 26 verified sites, 3 were excluded as they were found to be roosting and /or socialising areas near buildings (e.g., trees near farmhouses) that were not provisioning food. Two of these sites were situated in close proximity (<0.8 km) to composting stations (F06 and F33 in Appendix 2), and the third was ~1.15km away from a wildlife park (F01 in Appendix 2). Of all the sites that were identified remotely and subsequently verified on the ground, 88.5% (i.e., 23 out of 26) were indeed AFSs.

The remaining 21 remotely identified sites that were not visited due to pandemic-related travel constraints were still included in the analysis, based on the above ground-truthing which suggests the vast majority were likely to be AFSs. The final sample of 44 food sources included 11 compost sites; 7 waste management centres; 5 farms; 18 ski huts, hotels and restaurants; and 3 wildlife parks (hereafter referred to as wildparks). For sites that were not visited on the field, the identity and type of site were inferred from landmark names and satellite imagery on Google Earth. The different types of AFSs were grouped into broader categories based on similarities in site descriptions obtained from the field surveys (Table 2 reports the general description by type of AFS; Appendix 2 contains descriptions of each site surveyed).

Table 2 General description of the types of AFSs (i.e., wildparks, compost sites, waste management centres / dumps, ski huts, hotels and restaurants, private farms) and the broader categories (i.e., wildparks, refuse sites, huts) into which they were grouped.

Category	Type of AFS	Description
Wildparks (n = 3)	Wildparks	Wildparks have animal enclosures (e.g., bears, boars, wolves) within which food is supplied to animals daily.
Refuse sites (n = 18)	Compost sites	Contain long, tall (~1.5m) rows of household and organic waste matter, mixed with woodchips and sawdust.
	Waste management centres / dumps	Combine both organic and non-organic material. Non-organic waste included bales and large piles of plastics.
Huts (n = 23)	Ski huts, hotels, restaurants	Particularly active in winter, when numerous tourists and alpine visitors visit. Some sites dispose garbage in the forest next to the main building.
	Private farms	Some farms were found to have small composting area close to buildings where barnyard animal waste is processed. At the end of winter, when animals are moved out to the fields, the barn compost is often raked out to compost in warming weather. Other farms had offal piles and other waste available for ravens to scavenge, increasing in abundance over the hunting season.

(3) Estimating the use of specific anthropogenic food sources by raven individuals

To measure the number of AFSs visited by individuals and their probability of being at an AFS, I set a buffer around each AFS, and considered individuals inside the buffers to be actively using the site. As non-breeding ravens congregate at AFSs in large numbers to forage, socialize and roost, buffers were set to encompass buildings and surrounding trees. I examined how the number of revisitations at each site changed with buffers ranging between 0 to 150m in radius using the 'recurse' package in R (Bracis et al. 2018). Because each site had its own optimal radius, site-specific buffers were selected based on the best estimate of the distance above which revisitations no longer increased with increasing radius size, or at the maximum of 150m, beyond which individuals were not considered to be actively using the site. For wildparks and huts, optimal buffer radii had a median of 80m (range: 40 – 150m). Refuse sites had larger radii of median 100m (range: 50 – 150m) (Appendix 2).

Statistical analysis

All analyses were conducted in R (version 1.4.1103) (Team 2021). I used generalized linear mixed models (GLMMs) and multi model inference with the 'glmmadmb' (Skaug et al. 2010; Fournier et al. 2012) and 'MuMIn' (Barton 2020) packages to test which factors influenced the number of AFSs visited and the probability of being at an AFS. Collinearity among predictors was checked for using the variance inflation factor in the "car" package (Fox et al. 2019), all of which were less than 2, indicating that none of the predictors were collinear (O'Brien 2007).

To estimate the number of AFSs visited by individuals, each was scored based on whether a GPS fix was within a buffer or not, for each bird in each season in which it was tracked (n = 406). The proportion of GPS fixes within and outside a buffer was used to determine their probability of being at an AFS. This was estimated for each category of AFS (i.e., wildpark, refuse site, hut) visited by different birds across the seasons in which they were tracked (n = 762 as some individuals visited more than one category of AFS; Appendix 1). Individuals were tracked for different lengths of time, and so the number of common ravens for which GPS tracking data was available in each season varied across the study duration (Table 1; Appendix 1).

The number of different AFSs visited by each bird per season was modelled using a Poisson error distribution with a log-link function. The global model included sex, origin (i.e., wild-caught or captive-bred-released), age class (i.e., juvenile, adult), season (i.e., autumn, winter, spring, summer), local activity range (95% UD), and the total number of fixes as fixed factors. Individual identity was included as the random factor to account for non-independence in the data (Burnham & Anderson 2002). Although the number of AFSs visited by individuals was scored based on whether a GPS fix was within a buffer or not, I included the total number of fixes in the model to control for variation due to irregular sampling intervals.

For each individual per season, the probability of being inside an AFS was modelled using the cbind syntax (i.e., proportion of all GPS fixes within AFS buffers versus those outside) with a binomial distribution and logit-link function. The global model included sex, origin, age class, season, local activity range, and the category of AFS (i.e., wildpark, refuse site, hut) as fixed factors, and individual identity as the random factor. The total number of fixes was not included as a fixed factor as it was already accounted for while calculating the proportion of GPS fixes within AFS buffers versus outside.

I used a multi-model inference approach to compare all possible nested models within each global model. In this approach several competing hypotheses are examined by calculating all potential fixed effect combinations. The resulting ranked and weighted models are indicative of the relative support for each hypothesis (Burnham & Anderson 2002; Grueber et al. 2011). Models were ranked according to Akaike's Information Criterion corrected for small sample sizes (AICc). Candidate sets of top-ranking models were retained for model averaging at four different cut-offs (ΔAICc less than and equal to 2, 4, and 6, and models less than or equal to the 95% confidence summed weights). I compared the candidate sets of models from each cut-off and reported the model average for the set resulting from a cut-off at ΔAICc <= 2 as the relative importance and effect sizes of the parameter estimates were similar across all cut-offs. I also wanted to avoid overly complex models, as the inclusion of parameter estimates from models with poor weights are likely to be spurious and result in model overfitting (Grueber et al. 2011) (Appendix 3 contains details on the candidate sets of top-ranking models at all four ΔAICc cut-offs).

For all model averaged outputs, I report the direction and magnitude of the parameter estimates, unconditional standard errors (Unc. SE), 95% confidence intervals (95% CI), z-values, and the relative variable importance (RVI) of the model parameters. Unconditional SEs incorporate model selection uncertainty compared to standard SEs which only consider variance (Grueber et al. 2011). Estimates were considered to be significant if 95% confidence intervals excluded zero.

All summary metrics are reported as the mean ± 1 standard error (range, n).

Ethics statement

The ethics permit for the GPS tagging of raven individuals was obtained by the Corvid Lab, Department of Behavioural and Cognitive Biology, University of Vienna, under the approval number 'BMBWF-66.006/0015-V/3b/2018' and is valid until 30/06/2022.

Results

My analysis included a total of 3,697,079 fixes from 76 individuals from the 1st of July 2017 to the 30th of April 2020. The average number of GPS fixes and tracking days per individual (n = 76) were 48646 ± 8307 (33 – 254964) fixes and approximately 322 ± 20 (3 – 662) days.

(1) Estimation of space use

The average 95% UD estimation from each individual and season in which it was tracked was 133.04 ± 0.17 km^2 (0.06 – 3281.66 km^2, n = 406). Average 95% UD areas were smaller for juveniles 72.20 ± 0.15 km^2 (0.06 – 3281.66 km^2, n=151) and captive-bred-released individuals 49.40 ± 0.29 km^2 (0.21 – 3281.66 km^2, n = 118) than adults 169.06 ± 0.26 km^2 (0.11 – 1561.11 km^2, n = 255) and wild-caught individuals 167.00 ± 0.21 km^2 (0.06 – 2677.85 km^2, n = 288), but not between males 142.86 ± 0.22 km^2 (0.06 – 3281.66 km^2, n = 173) and females 125.75 ± 0.28 km^2 (0.08 – 2677.85 km^2, n = 233) (Figure 2). Average 95% UD areas across all individuals were largest in winter at 307.27 ± 0.57 km^2 (0.11 – 3281.66 km^2, n = 103), followed by autumn (mean = 118.36 ± 0.20 km^2; 0.08 – 1182.98 km^2, n = 111), spring (mean = 67.62 ± 0.22 km^2; 0.06 – 2150.85 km^2, n = 110) and summer (mean = 21.81 ± 0.04 km^2; 0.11 – 204.18 km^2, n = 82) (Figure 2, Figure 3).

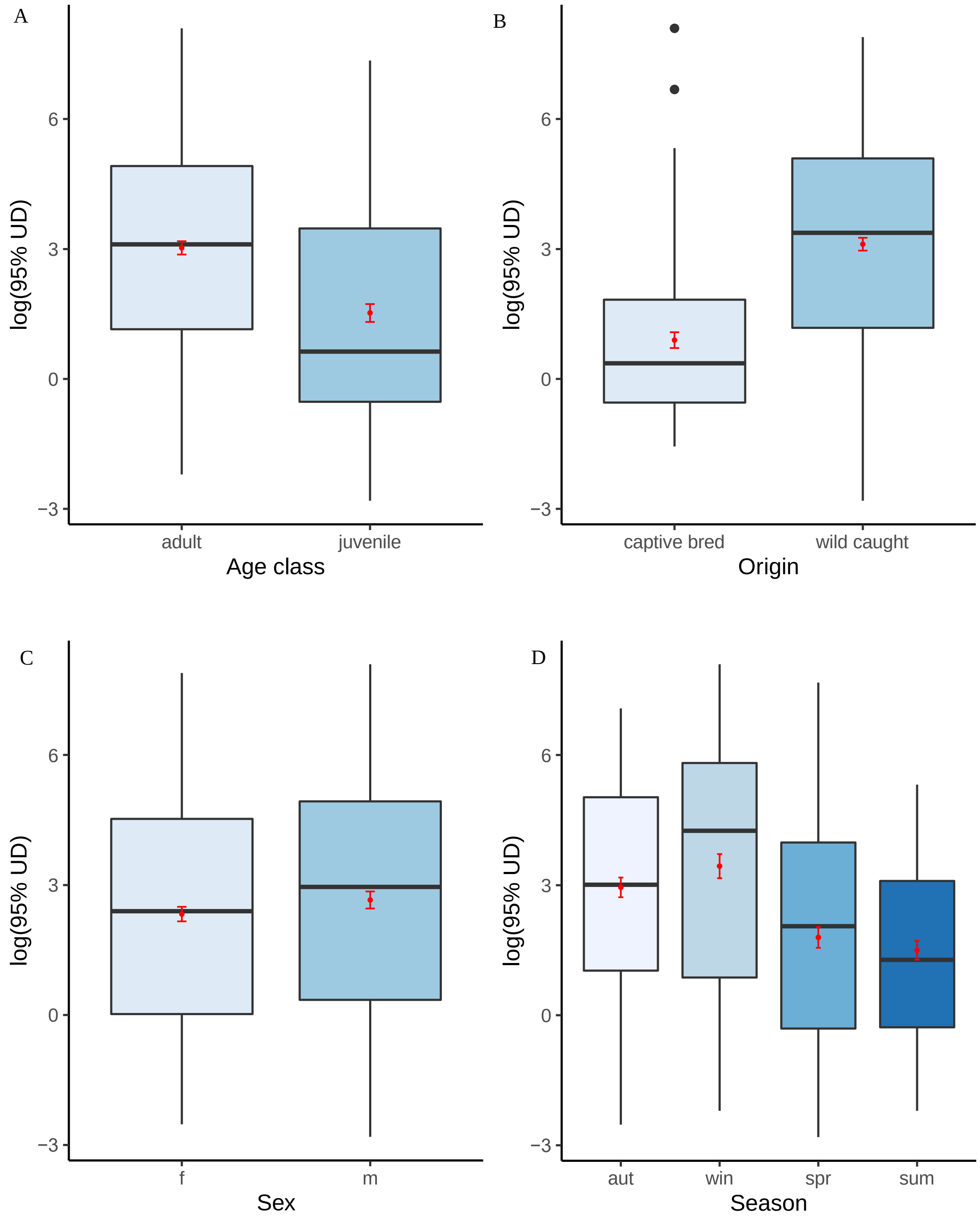

Figure 2 The 95% UD estimations, presented here on a logarithmic scale, were smaller for (A) juveniles (n = 151) and (B) captive-bred-released individuals (n = 118) than adults (n = 255) and wild-caught individuals (n = 167), but not between (C) males (n = 173) and females (n = 233). The 95% UD sizes were largest in (D) winter followed by autumn, spring and summer. The average 95% UD sizes ± 1 standard error are presented in red.

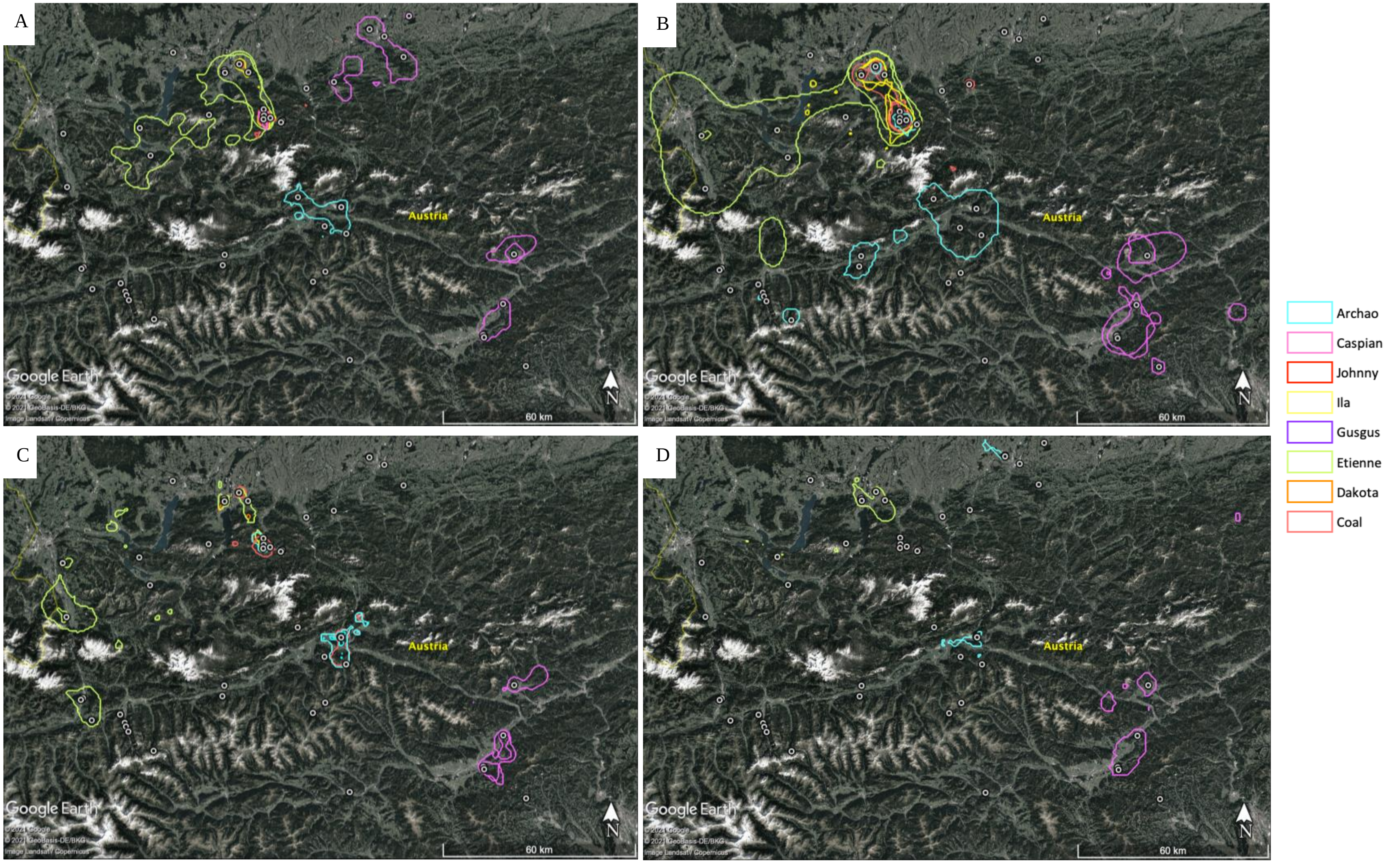

Figure 3 Spatial distribution of 8 GPS tagged ravens in central Austria. The coloured polygons represent the different individuals' 95% UDs, showing how these vary between the seasons (A) autumn, (B) winter, (C) spring and (D) summer). White circles represent anthropogenic foraging sites (note that not all foraging sites are depicted).

(2) Identifying extensively used anthropogenic food sources

To determine potential AFSs, I analysed clusters from 15-minute GPS fix intervals for all individuals tracked between December 2018 and December 2019 on Google Earth (Gorelick et al. 2017). I identified and used a total of 44 year-long and seasonally available AFSs across the central Austria in the analysis, with two refuse sites (F10 and F11 in Appendix 2) situated in the Czech Republic (just beyond the Northern Austrian border) (Figure 1). More than half the sites (n = 26) were visited by 5 or fewer individuals, while a few sites (n = 6) were visited by more than 20 individuals. The most popular site attracting a total of 74 different individuals across the study period was Cumberland Wildpark (F01, wildpark) followed by 46 at Kompostierung Gattinger (F02, compost site) and 45 at Kasbergalmhütte (F36, restaurant) (Appendix 2).

(3a) Number of anthropogenic food sources visited by individuals

The number of AFSs visited by individuals for each bird per season in which it was tracked was 2.7 ± 0.1 AFSs (1 – 12, n = 406) on average. The model set resulting from a cut-off of ΔAICc <= 2, produced a total of three top models (Table 3, see Appendix 3 for the other model sets). Origin, age class, season and 95% UD were most important predictors and featured in all the top models. Relative to these predictors, the total number of fixes and sex had an importance of 27% and 25% respectively. Both predictors featured once across the three top models.

There was strong evidence that juveniles visited fewer AFSs than older individuals (> 1 calendar year) (95% CI: -0.380, -0.077), while wild-caught individuals visited more AFSs than captive-bred-released individuals (95% CI: 0.233, 0.704). On average the number of AFSs visited were 2.3 ± 0.2 (1 – 12, n = 151) for juveniles and 3.0 ± 0.2 (1 – 9, n = 255) for adults, and 1.8 ± 0.1 (1 – 6, n = 118) for captive-bred-released and 3.1 ± 0.1 (1 – 12, n = 288) for wild-caught individuals. Individuals with a large 95% UD size also visited more AFSs than individuals with smaller ones (95% CI: 0.029, 0.139).

Individuals visited significantly fewer AFSs in autumn (95% CI: -0.475, -0.142) and summer (95% CI: -0.583, -0.187) compared to winter, and significantly more in spring compared to summer (CI: 0.034, 0.415) (Appendix 4). The average number of AFSs visited was highest in winter at 3.5 ± 0.2 (1 – 9, n = 103) food sites per individual, followed by spring (mean = 2.8 ± 0.2; 1 – 12, n = 110), autumn (mean = 2.4 ± 0.2; 1 – 7, n = 111) and summer (mean = 2.2 ± 0.1; 1 – 6, n = 82) (Figure 4).

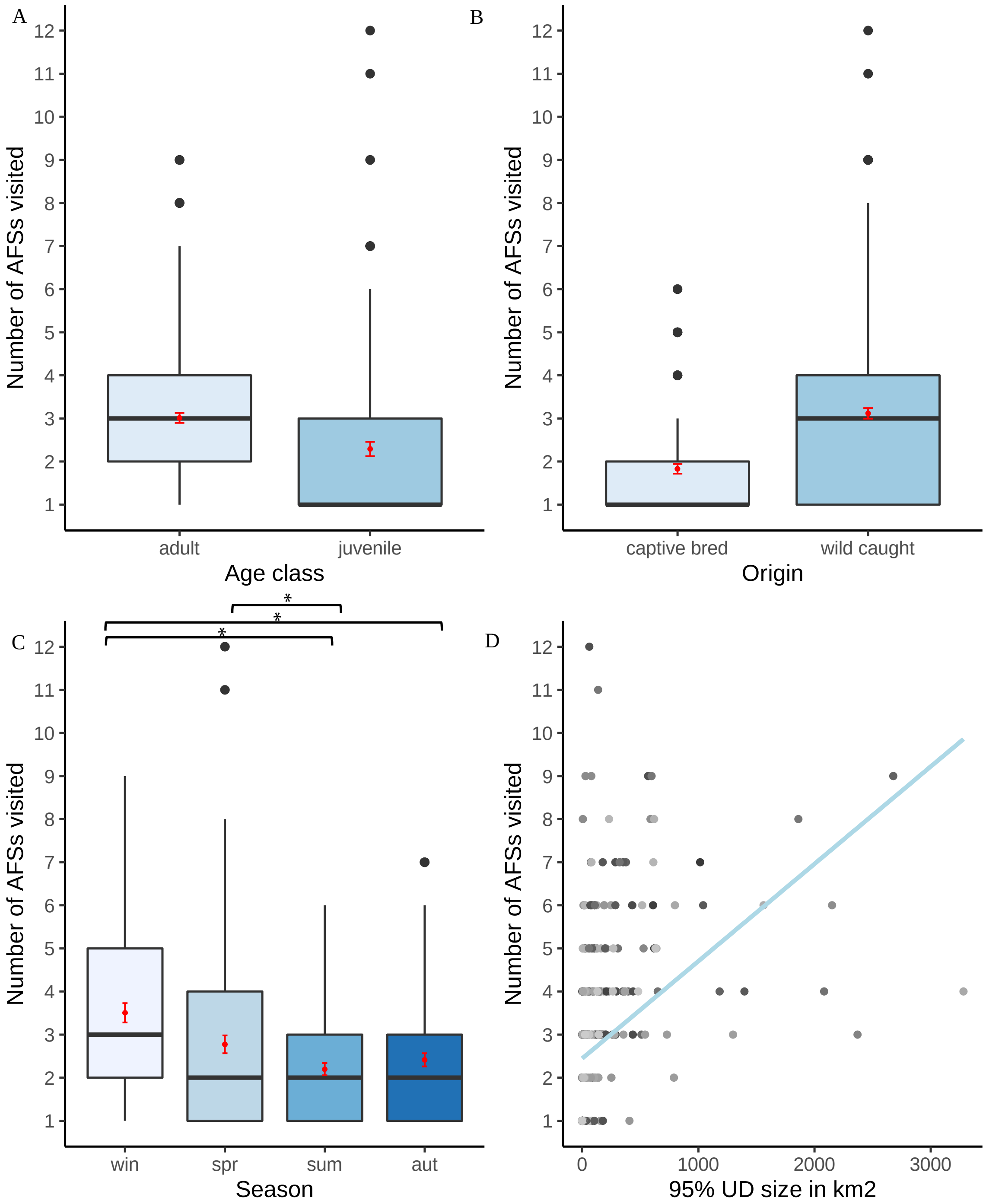

Figure 4 The number of anthropogenic food sources (AFSs) visited was lower for (A) juveniles (n = 151) and (B) captive-bred-released individuals (n = 118) than adults (n = 255) and wild-caught individuals (n = 167). The number of AFS visited was significantly more in winter (n = 103) compared to autumn (n = 111) and summer (n = 82), and in spring (n = 110) compared to summer (significant differences between seasons are indicated with an asterisk *). For (A – C), the average number of AFS visited ± 1 standard error are presented in red. Plot (D) shows that as 95% utilization distribution sizes (95% UD) increased, so did the number of AFSs visited (linear regression line fit; $R^2 = 0.16$, p-value = < 2.2e-16).

(3b) The probability of an individual being present at an AFS

For each category (i.e., wildpark, refuse site, hut) of AFS visited by different birds across the seasons in which they were tracked, the average number of GPS fixes recorded inside a buffer was 1767.9 ± 325.2 (1 – 12117, n = 762), corresponding to an average proportion of 9.59 ± 0.49% (0.00 – 87.40%, n = 762) of the total fixes. The model set resulting from a cut-off of ΔAICc <= 2, produced a total of six top models (Table 3, see Appendix 3 for the other model sets). Relative to the category of AFS (the most important predictor, featuring in all top models); season had an importance of 89% and featured in 5 out of 6 of the top models; UD had 30% (2 out of 6 models); age class had 18%, sex had 12% and origin had 11% (1 out of 6 models).

Individuals had a significantly higher probability of being at wildparks compared to refuse sites (95% CI: -1.277, -0.031) and huts (95% CI: -3.968, -0.998). Individuals also had a significantly higher probability of being at refuse sites than at huts (95% CI: 0.278, 3.380) (Appendix 4). The average proportion of points inside AFS buffers was 16.10 ± 0.90% (0.41 – 16.20%, n = 347) for wildparks, 6.50 ± 0.40% (0.39 – 4.78%, n = 234) for refuse sites and 1.03 ± 0.10% (0.02 – 3.49%, n = 181) for huts (Appendix 4). Individuals had a significantly higher probability of being at AFSs in spring than autumn (95% CI: 0.212, 1.654) or winter (95% CI: 0.034, 1.444). The average proportion of points inside AFS buffers was highest in spring (mean = 14.00 ± 1.30%; 0.003 – 87.39, n = 199), then summer (mean = 12.70 ± 1.45%; 0.002 – 78.20%, n = 135), autumn (mean = 6.63 ± 0.52%; 0.01 – 34.54%, n = 198), and winter (mean = 6.50 ± 0.54%; 0.01 – 37.46%, n = 230) (Figure 5).

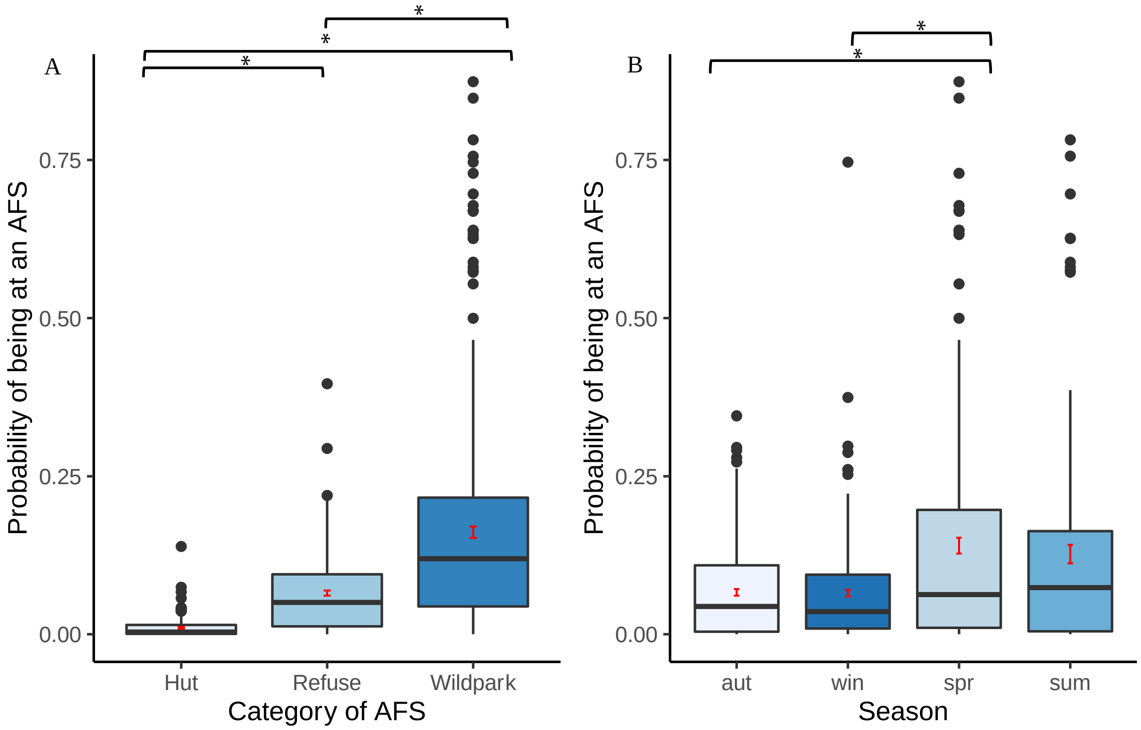

Figure 5 The probability of being at an AFS was higher at (A) wildparks (n = 347) than refuse sites (n = 234) and huts (n = 181), and (B) in spring (n = 199), than summer (n = 135), autumn (n = 198) and winter (n = 230) (significant differences between category of AFS and seasons are indicated with an asterisk *).

Table 3 Model averaging outputs for the top model set at ΔAICc <= 2 cut-off for **(a)** the number of anthropogenic food sources (AFSs) visited in relation to sex, origin (i.e., wild-caught or captive-bred-released), age class (i.e., juvenile, subadult/adult), season (i.e., autumn, winter, spring, summer), local activity range (95% UD), and the total number of fixes as fixed factors, and **(b)** the probability of visiting an anthropogenic food source in relation to sex, origin, age class, season, local activity range, and the category of AFS (i.e., wildpark, refuse site, hut). The number of model parameters (Df), log-likelihood (logLik), Akaike information criterion corrected for small sample size (AICc), ΔAICc, and model weights (ώᵢ) are presented for all models less than or equal to the ΔAICc of 2. Estimates, unconditional standard errors (Unc. SE), 95% confidence intervals (95% CI), z-values, and the relative variable importance (RVI) are presented for the top models. Fixed factors highlighted in bold have 95% CIs that do not contain zero.

a) Response: number of AFS visited
(n = 406 UD estimates from 76 birds)

Top model set	Df	logLik	AICc	ΔAICc	ώᵢ
Age class + Origin + Season + 95%UD	8	-711.52	1439.4	0.00	0.384
Age class + Origin + Season + 95%UD + Total no. fixes	9	-711.03	1440.5	1.11	0.220
Age class + Origin + Season + 95%UD + Sex	9	-711.12	1440.7	1.28	0.202
Effect size of explanatory terms	Estimate	Unc. SE	95% CI	z-value	RVI
Intercept	0.463	0.132	(0.203, 0.722)	3.496	-
Juvenile †	**-0.228**	**0.077**	**(-0.380, -0.077)**	**2.954**	**1.00**
Wild-caught†	**0.469**	**0.120**	**(0.233, 0.704)**	**3.903**	**1.00**
Winter ‡	**0.385**	**0.101**	**(0.187, 0.583)**	**3.805**	**1.00**
Autumn ‡	0.076	0.100	(-0.120, 0.272)	0.762	“
Spring ‡	**0.224**	**0.097**	**(0.034, 0.415)**	**2.305**	**“**
95% UD	**0.084**	**0.028**	**(0.029, 0.139)**	**2.980**	**1.00**
Total fixes	0.036	0.025	(-0.034, 0.107)	1.007	0.27
Maleŧ	0.090	0.063	(-0.106, 0.285)	0.899	0.25

†Age class: ‘adult’, †origin: ‘captive-bred-released’, ‡season: ‘summer’, and ŧsex: ‘female’ were used as reference categories

b) Response: probability of being at an AFS
(n = 762 proportions from 76 birds)

Top model set	Df	logLik	AICc	ΔAICc	ώᵢ
Season + Category of AFS	7	-151.34	316.8	0.00	0.140
Season + Category of AFS + 95%UD	8	-150.74	317.7	0.83	0.092
Season + Category of AFS + Age class	8	-150.80	317.8	0.97	0.086
Season + Category of AFS + Sex	8	-151.74	318.5	1.71	0.060
Season + Category of AFS + Origin	8	-151.29	318.8	1.93	0.053
Category of AFS + 95% UD	5	-154.35	318.8	1.94	0.053
Effect size of explanatory terms	Estimate	Unc. SE	95% CI	z-value	RVI
Intercept	-1.871	0.338	(-2.535, -1.208)	5.526	-
Hut+	**-2.483**	**0.757**	**(-3.968, -0.998)**	**3.277**	**1.00**
Refuse+	**-0.654**	**0.317**	**(-1.277, -0.031)**	**2.058**	**“**
Summer‡	0.605	0.424	(-0.185, 1.395)	1.502	0.89
Winter‡	0.194	0.389	(-0.607, 0.994)	0.474	“
Spring‡	**0.933**	**0.453**	**(0.212, 1.654)**	**2.536**	**“**
95% UD	-0.265	0.181	(-0.745, 0.216)	1.080	0.30
Juvenile †	0.284	0.158	(-0.251, 0.818)	1.040	0.18
Maleŧ	0.153	0.105	(-0.365, 0.672)	0.580	0.12
Wild-caught†	-0.094	0.099	(-0.655, 0.467)	0.329	0.11

+Category of AFS: ‘wildpark’, ‡season: ‘autumn’, †Age class: ‘adult’, ŧsex: ‘female’, and †origin: ‘captive-bred-released’ were used as reference categories

Discussion

Using broad-scale movement patterns inferred from high resolution spatial and temporal data, I was able to investigate how 76 individual non-breeding ravens used anthropogenic food sources across a semi-transformed alpine landscape within a period of 2 years and 9 months. Variation among individuals and cohorts (i.e., age-class and origin), and in response to external conditions (i.e., season and category of AFS) resulted in differences in how AFSs were exploited. Knowing which individuals exploit AFSs, when they exploit them, and the differences in the resources being exploited might improve our understanding of how this socially and cognitively complex species thrives in alpine environments, and could ultimately inform effective management strategies.

Individuals exhibited great variation in how extensively they moved around the landscape, with juveniles and captive-bred-released individuals exhibiting smaller range sizes compared to adults and wild-caught individuals; and across seasons with birds ranging furthest in winter, followed by autumn, spring and summer. Differences in ranging behaviour and between individuals of different cohorts (i.e., age class and origin) were reflected in the number of AFSs visited, but not the probability of an individual being at an AFS. Although individuals of different cohorts were equally likely to visit AFSs, adults and wild-caught individuals used notably more different AFSs than juveniles and captive-bred-released individuals, suggesting that experience affects AFS use. In winter, the number of different AFSs visited by ravens was the highest, but contrary to my expectation, their probability of being at an AFS was lowest. This could indicate a high level of foraging competition under stressful environmental conditions, with non-breeding birds attempting to visit a large number of AFSs, but moving on quickly from each one. Interestingly, the highest probability of individuals being at an AFS occurred during spring, and individuals still visited a large number of sites, perhaps due to changes in competition and seasonal anthropogenic food availability. The category of AFS influenced the probability of an individual being at an AFS, with individuals visiting wildparks and refuse sites (where anthropogenic food is provided year-round) more than huts (where anthropogenic food provision is seasonal). Few sites were found to attract over 40 individuals while more than half of the sites attracted less than 5. The quality, quantity and rate at which resources replenish at sites may influence patterns in how individuals exploit these resources. These patterns are discussed further below.

Many wild animal species have been observed to alter their ranging behaviour in response to the presence of AFSs (Hidalgo-Mihart et al. 2004; Lowry et al. 2013; López-López et al. 2014; Newsome et al. 2015; Petroelje et al. 2019) but also see (Margalida et al. 2017). In ravens and other corvids, individuals have been found to exhibit more specific use of landscape by opportunistically adapting to AFSs (i.e., exploit areas with AFSs more than those without in the environment) (Storch & Leidenberger 2003; Walker & Marzluff 2015; Loretto et al. 2016b). In the foraging context created by the presence of AFSs, studies on non-breeding ravens have previously reported 95% UD estimates ranging from 1.4 km^2 up to 6,675km^2, with averages from across diverse habitats including 791km^2 in Central France (from control ravens in the study) (Marchand et al. 2018), 1,746km^2 in Central Washington (Rossi 2019), 19.5km^2 in the Olympic Peninsula (Webb et al. 2012); and at least 1800km^2 in western Maine (Heinrich 1988b). For the population I studied, Loretto et al. (2016b) estimated a local activity range of 337.53 km^2 for 10 individuals, which was higher than my findings (133.04 km^2, n=76), ranging between 0.86 – 1,732.57 km^2, compared to my estimates of 0.06 – 3281.66 km^2.

As noted by Loretto et al. (2016b), 95% UD estimates across studies can vary depending on regional differences, sample sizes, sampling frequency and analytical method (Walter et al. 2015). I employed a Dynamic Brownian Bridge Movement Modelling approach to estimate the ranges of 76 non-breeders, while for instance Rossi (2019) used Brownian bridge models on 7 non-breeders and Loretto et al. (2016b) employed Kernel Density Estimations for 10 non-breeders (mostly sub-adult and juvenile individuals in all three studies). Despite these differences, it is evident that non-breeding common ravens, who move around nomadically in this life-stage (Teitelbaum & Mueller 2019), exhibit dramatic variation in their local activity ranges, with some individuals retaining their vagrant way of life and others localising their movement behaviour.

The differences in local activity ranges among individuals were reflected in differences in resource use. I found that wide-ranging (i.e., vagrant) individuals visited more AFSs than individuals with smaller local activity ranges (i.e., local). However, ranging behaviour did not affect ravens' probability of being at an AFS. In this system, observations at a single communal food source have highlighted differences in the frequency at which individuals visit the food source (Braun & Bugnyar 2012; Loretto et al. 2017). Taken together with my findings, the lack of difference in the probability of being at an AFS can be explained by individuals with smaller ranges frequently exploiting one or two AFSs, while vagrant individuals infrequently exploit many AFS. Rossi (2019) also report such a pattern among the non-breeding ravens in Central Washington.

Individuals may exhibit more vagrant or local ranging behaviours-based trade-offs they face. In being vagrant, individuals reap the benefits of exploiting new resources, and suffer reduced intraspecific competition for food, particularly at popular AFSs (Loretto et al. 2016a). In contrast, individuals moving within a small area may benefit from familiarity with their social and spatial environment (Wright et al. 2003; Loretto et al. 2017). Under competitive foraging scenarios at AFSs, locals may benefit from knowing better places to cache food (i.e., hide food), how to avoid risky conflicts and with whom to form allies (Loretto et al. 2017; Boucherie et al. 2019; Beck et al. 2020).

Among non-breeding ravens, trade-offs in space and resource use also depend on an individual's experience and knowledge of the foraging context (Boucherie et al. 2019). I found that juveniles and captive-bred-released individuals exhibited a smaller average local activity range and visited fewer AFSs than adults and wild-caught individuals, but did not have a higher probability of being at AFSs. Juveniles and captive-bred-released individuals' (who are always released as juveniles) lack familiarity with the landscape and knowledge about alternative AFSs, and fear novel or unknown things, explaining why they only visit few food sources (Heinrich 1988a; Kijne & Kotrschal 2002; Lowry et al. 2013; Loretto et al. 2017). The range of 95% UD sizes exhibited by individuals in both the age class and origin cohorts, however, suggests that individuals may be in the process of learning the landscape and differ in exploratory behaviour.

Webb et al. (2009), found that once juveniles leave their natal territory, they are more likely to go to the nearest communally-used AFS rather than a closer, non-communal foraging site. Although competition at communal AFSs can be high, the inability and inexperience of juveniles and captive-released individuals can prevent them from exploiting other resources. For instance, juveniles rank low in dominance hierarchies and require larger groups to form alliances and reduce conflict, competition and defences at food sources (Heinrich 1988b; Webb et al. 2009). With age, individuals can lower risks and costs associated with travelling across unknown areas by relying on learning and memory (Preston 2005; van Overveld et al. 2018; Riotte-Lambert & Matthiopoulos 2020). In developing a spatial knowledge of AFSs in the landscape, individuals also have the potential to exhibit spatial preferences (Loretto et al. 2016a). Therefore, although individuals of different origin and age class are equally likely to visit AFSs, experience gives adults and wild-caught individuals a competitive edge. In knowing and using more AFSs, they can avoid high levels of competition, particularly when subsequent generations of fledged juveniles flock at popular sites (Restani et al. 2001).

Seasonal changes in environmental conditions can bring about a shift in foraging and socialising tactics (Engel & Young 1992). Winter in temperate climates creates environmentally stressful conditions. Avian scavengers, like ravens, can experience higher food-searching costs in low temperatures, high snow cover (which hides natural food sources), short day lengths and limited opportunities for good flight conditions (e.g., fewer thermals in winter reduces flight distance and duration) (Restani et al. 2001; Preston 2005; Monsarrat et al. 2013; Loretto et al. 2016b; Marchand et al. 2018).When coping with such environmental changes, AFSs can represent comparatively high-energy resources and attract individuals. Studies on populations of ravens in Greenland (Restani et al. 2001), the Austrian Alps (Loretto et al. 2016b), Alaska

(Baltensperger et al. 2013), and North Wales (Wright et al. 2003), have all noted increases in the number of individuals present at AFSs over winter. However, crowds also increase the competition for food. High levels of competition, yet the increased need for food sources, may explain why individuals were found to have the lowest probability of being at an AFS in winter. Consequently, individuals may need to visit a greater number of sites to mitigate these high levels of competition (Loretto et al. 2016b). The large range sizes in winter may reflect both the increased number of food sources visited and the seasonally wide-spread availability of resources in the landscape (e.g., huts).

In spring, individuals had the highest probability of being at a food source and, second only to winter, visited the most AFSs. Although contrary to what was expected, this suggests that individuals still rely highly on AFSs after harsh winters (perhaps to recoup condition) (Norberg 1996). Individuals may be more able to access sites due to reduced levels of competition or seasonal increases in AFS availability. Breeders, who rank highest in social dominance and guard food sources, remain within their territories during the breeding season (Marzluff & Neatherlin 2006; Webb et al. 2012). In the presence of breeders, non-breeders need to group in large numbers to overcome defences, particularly where territories overlap with AFSs (Marzluff et al. 1996). For food sources not encompassed by breeder territories, during the springtime breeding season, non-breeder individuals, particularly younger ones, may therefore be more present at more AFSs because of reduced competition. Observations based at a landfill in Greenland noted a seasonal use of the resource by ravens, with sub-adults and non-territorial adults, but not breeding adults, likely to forage there in spring (Restani et al. 2001). Additionally, in spring, more food becomes available as large amounts of garbage melt out of the snow (Baltensperger et al. 2013), and as organic waste is raked out of barns to compost in the warming weather (Table 2). Increases in offal piles at farms across hunting seasons (1st August to 31st December for stag, and 1st May to 31st October for roe deer) may also explain the higher probabilities of being at AFSs in summer and autumn than winter.

The seasonal patterns in resource use I found for the non-breeding ravens of Austria are similar to patterns observed in France, where individuals were concentrated at landfills from June – September (summer), whereas their presence decreased and movements increased from September to March (autumn and winter) (Marchand et al. 2018). In southwestern Idaho, Engel and Young (1992) found that ravens (14 adults, 5 sub-adults and 7 juveniles) fed at AFSs 3 times more in spring relative to other seasons. Although they did not distinguish between sexually mature breeding and non-breeding adults, they proposed that dramatic increases in feeding in spring could reflect increases in energy demand for gonad development for the breeding season (Engel & Young 1992). However, how and to which extent this is applicable for non-breeders is unclear.

When AFSs are stable in space and time, environmental predictability increases, which in turn can influence the costs and benefits of foraging, making some sites more popular than others (van Overveld et al. 2018; Riotte-Lambert & Matthiopoulos 2020). The availability of resources themselves, and the quality and quantity by which they replenish can result in individuals differentially exploiting resources. For instance, the quality of refuse sites is likely to be lower than wildparks and huts, as individuals forage through piles of waste and potentially risk ingesting and encountering harmful foods.

In this system, individuals were most likely visit wildparks, followed by refuse sites and huts. However, the reliance on wildparks was probably heavily influenced by the inclusion of Cumberland Wildpark, where wild-caught individuals were trapped, and less than 2km away from where captive-bred individuals were released. Most, if not all, tracked individuals in this study therefore had knowledge of this site. This is further supported by the fact that 74 of the 76 individuals visited the site over the tracking duration, making it the most popular one. In comparison, the other two wildparks – Wildtierpark Kleefeld and Tierpark Stadt Haag – were visited by only 4 and 3 individuals respectively (F39 and F35 in Appendix 2). To address this issue, future studies could include the distance from each AFS to the site of capture and release in the model.

It is also possible that in addition to individuals knowing the site, Cumberland Wildpark attracted large numbers of individuals based on the quality and reliability of food supplied. Cumberland Wildpark has animal enclosures (grey wolf/ brown bear *Canis lupus/Ursus arctos*, wild boar *Sus scrofa*, and red/fallow deer *Cervus elaphus*/*Dama dama*) where food is supplied between 8 to 10am daily, lasting between 10 – 40 minutes per enclosure (Braun & Bugnyar 2012; Loretto et al. 2017), and evening feeding of carnivores on a less predictable schedule (pers. comm. Cumberland Wildpark). The morning food provided at this site is frequently replenished, with both high spatial constancy and temporal consistency (Riotte-Lambert & Matthiopoulos 2020).

The reduced probability of being at huts reflects the seasonal availability of this resource, although this may also be an artefact of huts appearing intermittently in the dataset. In the Bavarian Alps, Storch and Leidenberger (2003) found that ravens were not more present or numerous at popular tourist alpine and skiing huts than the control sites they identified. However, they did observe that ravens were abundant at these sites in autumn, when most tourists visit the area. Together with my findings, this could suggest that ravens visit sites when more activity and food is available. Furthermore, they reported that ravens were found to visit huts independently of visitor presence, suggesting that individuals may be strongly attracted to the food source despite potential human disturbances.

Limitations

Part of the study period was affected by the first lockdown in response to the coronavirus pandemic from 16th March to the 20th of April 2020. During this time, restrictions included the closure and limited operation of wildparks, hotels, restaurants and ski huts, although informal food kiosks appeared (Sozialministerium 2021). While waste disposal and compost sites remained open, residents were urged to reduce waste (Sozialministerium 2021). Less predictable AFSs from road-kills are also suspected to be lower under lockdown measures with the limited movement of people and associated vehicle traffic (Manenti et al. 2020). The impact of these lockdowns on non-breeders, and their response to the abrupt change in food sources are unknown. Given the long-term duration of the data used in the study, I do not expect the 1-month lockdown to impact the overall results presented here.

Given the restrictions posed by the coronavirus pandemic, not all sites could be visited on the field. The ground-truthing of 26 sites identified using the ravens' movement patterns revealed that 3 were not in fact AFSs. If this misidentification rate also applies to the remaining 21 sites that were unable to be visited, then approx. 5 sites may not have been AFSs. This uncertainty might create some noise in the data, but given the large sample size of sites that were verified, it seems unlikely this will affect the interpretation of the results.

Implications, management recommendations and conclusion

Increases in raven populations have been linked with human activity (Restani et al. 2001; Marzluff & Neatherlin 2006). When raven abundances increase, new members are added to the non-breeder demographic (Marzluff & Neatherlin 2006). These population increases, particularly concerning the non-breeders, can lead to ecosystem level impacts including the predation of species of concern and human-wildlife conflict (Marzluff & Neatherlin 2006; Marchand et al. 2018; McMahon et al. 2020). Regarding the predation of species however, Madden et al. (2015) found that from 42 studies there was no overall negative impact of corvids on prey species (i.e., declines in prey bird populations are not exclusively due to corvid predation). Other limiting factors, such as the presence of other predators can still result in prey bird population declines (Bodey et al. 2011; Cukor et al. 2021).

In the Austrian Alps study system, raven-related concerns are mostly linked to human-wildlife conflict, namely crop damage and potential depredation of livestock. Focussing on the use of specific AFSs by non-breeders in this study revealed exploitation of anthropogenic resources but with variation at the individual (i.e., variation in space-use) and cohort levels (i.e., age-class and origin), and in response to external conditions (i.e., season and food availability) (Riotte-Lambert & Matthiopoulos 2020). Given these findings, should population management of ravens become desirable, the most effective and easiest to implement strategy would be to manage the resources themselves that are exploited by individuals (Webb et al. 2004; Baltensperger et al. 2013).

As individuals can range far and wide, and use alternative AFSs, management strategies, if implemented, would need to be done on a regional scale. Considering the category of resources in the Austrian landscape and the bias introduced by Cumberland Wildpark, management strategies may be most effective for refuse sites. Strategies can include measures such as dump closures, burning or covering garbage, and restrictions on agricultural activities to reduce agricultural waste (Engel & Young 1992; Marzluff & Neatherlin 2006). Targeting refuse sites may prove to be difficult given the sizes of their operation, which tend to be larger than huts and wildparks. However, emerging laser technologies may make such large-scale management achievable and effective (Blackwell et al. 2002; van Dooren 2019). Improved waste management at huts and restrictions to prevent illegal dumping at these sites may be the easier to implement, however would make the least difference. In theory, managing resources should reduce population growth by reducing fitness (i.e., survivorship) (Marzluff & Neatherlin 2006).

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Appendix 1 *General information on the 76 individuals (ID, Name) that were tracked within the period from 1st of July 2017 to 30th of April 2020, including sex (m = male, f = female), origin (w = wild-caught, c = captive-bred-released) and death status (N = no, Y = yes). Age class calculated by subtracting the year of hatching from the tracking year in summer. Juveniles, sub-adults and adults are presented as three separate categories in this table, but sub-adults and adults were merged into a single 'adult' category for data analysis. The number of tracked days, fixes and anthropogenic food sources visited are presented for each season and year. The 95% contour area of the utilization distribution (95% UD) is also presented (n = 406).*

ID	Name	Sex	Origin	Dead	Date of tagging	Last GPS fix	Hatched in	Age class	Tracking year	Season	No. days	No. fixes	95% UD (km^2)	No. AFS visited
1	AJ	m	w	N	19 December 2019	19 March 2020	2019	juvenile	2019	aut	2	35	1.98	1
									2020	win	90	689	287.77	3
2	Alfon	m	w	Y (predation by eagle owl)	12 May 2019	08 March 2020	2018	juvenile	2019	spr	40	4128	0.24	1
								sub-adult	2019	sum	94	12355	16.36	3
									2019	aut	90	3585	620.97	5
									2020	win	72	851	1015.27	7
3	Archao	f	w	N	22 March 2019	30 April 2020	2017	sub-adult	2019	spr	91	13923	16.4	2
								sub-adult	2019	sum	94	16793	56.93	3
									2019	aut	87	2118	126.47	2
									2020	win	91	789	610.19	6
									2020	spr	41	1834	114.87	3
4	Arthemis	m	c	Y (suspected dead)	04 September 2018	12 February 2020	2018	juvenile	2018	sum	19	1291	0.78	1
									2018	aut	89	5662	1.71	1
									2019	win	90	5097	206.7	4
									2019	spr	93	15945	0.7	2
								sub-adult	2019	sum	94	16304	1.69	4
									2019	aut	90	4196	19.17	5
									2020	win	45	509	4.08	1
5	Bababa	m	w	N	19 September 2018	08 November 2018	2018	juvenile	2018	sum	4	106	5.3	2
									2018	aut	47	2765	116.17	3
6	Caspian	m	w	N	21 September 2018	30 April 2020	2018	juvenile	2018	sum	2	148	0.48	1
									2018	aut	80	1177	430.9	6
									2019	win	90	645	294.66	4
									2019	spr	93	3064	61.54	4
								sub-adult	2019	sum	94	3207	204.18	3
									2019	aut	32	44	82.64	1
									2020	win	71	363	436.06	3

									2020	spr	41	1492	150.48	3
7	Cava	m	w	N	04 November 2018	30 April 2020	2018	juvenile	2018	aut	47	1382	285.96	7
									2019	win	90	5140	568.26	9
									2019	spr	93	16776	61.59	12
								sub-adult	2019	sum	94	12297	103.35	5
									2019	aut	90	1076	262.11	3
									2020	win	78	440	438.16	4
									2020	spr	41	1918	53.04	3
8	Cebu	f	w	N	13 September 2018	30 April 2020	2017	sub-adult	2018	sum	10	1512	10.64	2
									2018	aut	89	5372	93.07	2
									2019	win	90	7284	70.55	6
									2019	spr	93	17394	6.37	1
								sub-adult	2019	sum	94	14606	83.77	6
									2019	aut	90	1883	178.3	1
									2020	win	91	1116	281.53	3
									2020	spr	41	2011	26.49	2
9	Christiane	f	w	N	18 December 2017	26 October 2018	2017	juvenile	2017	aut	3	279	0.2	1
									2018	win	90	2410	33.61	1
									2018	spr	93	59110	18.41	3
								sub-adult	2018	sum	94	25854	22.22	4
									2018	aut	34	4893	176.91	7
10	Clara	f	w	N	27 October 2018	30 April 2020	2018	juvenile	2018	aut	55	826	1041.59	6
									2019	win	90	3435	352.74	7
									2019	spr	93	14104	28.57	5
								sub-adult	2019	sum	94	10105	127.04	5
									2019	aut	90	1734	170.27	3
									2020	win	91	984	1396.59	4
									2020	spr	41	1991	286.36	6
11	Clove	m	c	N	10 October 2017	30 April 2020	2017	juvenile	2017	aut	72	847	1.5	1
									2018	win	90	7041	0.4	1
									2018	spr	92	89402	0.27	1
								sub-adult	2018	sum	94	51089	0.77	1
									2018	aut	89	4273	10.52	2
									2019	win	90	3032	1.44	2
									2019	spr	93	14569	0.73	1

								sub-adult	2019	sum	94	9530	2.05	3
									2019	aut	90	2651	16.87	2
									2020	win	91	1231	197.43	5
									2020	spr	41	2018	104.45	1
12	Coal	f	c	N		04 September 2018	30 April 2020	2018	juvenile	2018	sum	19	1225	0.58	1
									2018	aut	89	2032	6.58	2
									2019	win	90	1596	133.52	3
									2019	spr	93	13652	1.56	3
								sub-adult	2019	sum	94	11328	3.07	3
									2019	aut	90	3373	31.31	5
									2020	win	91	1555	84.22	5
									2020	spr	41	2000	105.19	6
13	Coqui	f	w	N	29 November 2019	30 April 2020	2014	adult	2019	aut	22	213	1182.98	4
									2020	win	91	1034	2677.85	9
									2020	spr	41	1987	376.7	7
14	Dakota	f	w	N	29 November 2019	30 April 2020	2019	juvenile	2019	aut	22	155	0.92	1
									2020	win	74	362	1.87	2
									2020	spr	41	1634	31.03	3
15	Dandelion	f	c	N	10 October 2017	30 April 2020	2017	juvenile	2017	aut	72	661	1.74	1
									2018	win	90	8406	0.64	1
									2018	spr	92	146821	0.4	1
								sub-adult	2018	sum	94	55272	1.02	1
									2018	aut	89	5568	15.89	2
									2019	win	90	2976	3.27	2
									2019	spr	93	15052	0.55	2
								sub-adult	2019	sum	94	13548	1.06	2
									2019	aut	90	3328	14.09	2
									2020	win	91	1327	2.67	2
									2020	spr	41	2005	1.09	1
16	Default	f	w	N	19 September 2018	03 April 2019	2018	juvenile	2018	sum	4	283	57.52	3
									2018	aut	77	2179	510.76	3
									2019	win	77	881	350.61	4
									2019	spr	15	1630	158.33	4
17	Dessert	f	w	N	14 April 2019	30 April 2020	2018	juvenile	2019	spr	68	12210	7.31	5
								sub-adult	2019	sum	94	8496	20.29	3

									2019	aut	90	3129	129.98	4
									2020	win	91	1487	109.57	6
									2020	spr	41	2001	10.23	3
18	Escher	f	w	Y (found in weak condition)	13 December 2018	17 May 2019	2018	juvenile	2018	aut	8	102	8.57	1
									2019	win	90	2378	1.41	2
									2019	spr	59	6771	0.54	1
19	Etienne	m	w	N	05 December 2018	30 April 2020	2018	juvenile	2018	aut	16	154	201.65	3
									2019	win	90	2292	322.36	7
									2019	spr	93	10245	74.5	7
								sub-adult	2019	sum	94	7944	91.93	4
									2019	aut	68	707	651.28	4
									2020	win	50	236	2082.25	4
									2020	spr	41	1766	307.29	5
20	Fabio	f	w	N	13 September 2018	30 April 2020	2018	juvenile	2018	sum	10	1289	0.47	1
									2018	aut	89	1649	2.92	1
									2019	win	90	2110	1.28	2
									2019	spr	93	11361	0.96	1
								sub-adult	2019	sum	94	8949	1.74	2
									2019	aut	90	1678	11.06	2
									2020	win	91	945	58.88	5
									2020	spr	41	2002	59.96	4
21	Farewell	m	w	N	06 December 2018	05 March 2020	2018	juvenile	2018	aut	15	188	184.92	3
									2019	win	90	2785	597.43	9
									2019	spr	93	15424	137.44	11
								sub-adult	2019	sum	94	14800	53.88	4
									2019	aut	90	2439	396.43	4
									2020	win	76	744	1860.71	8
22	Gema	f	w	N	04 November 2018	20 November 2018	2018	juvenile	2018	aut	17	253	0.81	1
23	Gisla	f	c	N	19 July 2017	30 April 2020	2016	sub-adult	2017	sum	66	14740	0.4	1
									2017	aut	89	12476	2.01	1
									2018	win	90	9401	0.64	2
									2018	spr	91	143561	0.3	1
								sub-adult	2018	sum	94	38006	0.53	1
									2018	aut	89	2535	18.11	2
									2019	win	91	1001	2.52	3

									2019	spr	92	6140	0.55	3
								adult	2019	sum	94	3448	18.99	2
									2019	aut	89	1309	17.23	3
									2020	win	91	572	3.23	2
									2020	spr	41	1169	0.91	1
24	Gloria	m	w	Y	16 August 2018	14 December 2018	2017	sub-adult	2018	sum	38	5034	0.28	1
									2018	aut	83	2802	1.39	1
25	Gluco	f	w	N	19 October 2019	30 April 2020	2019	juvenile	2019	aut	54	296	0.62	1
									2020	win	65	348	4.72	2
									2020	spr	40	1062	1.01	1
26	Gusgus	m	c	N	04 September 2018	11 January 2019	2018	juvenile	2018	sum	19	246	0.46	1
									2018	aut	74	505	0.5	1
									2019	win	22	242	0.71	1
27	Gwen	f	w	N	05 December 2018	30 April 2020	2018	juvenile	2018	aut	16	177	4.32	1
									2019	win	90	724	23.05	3
									2019	spr	93	1575	1.6	1
								sub-adult	2019	sum	94	2824	1.83	2
									2019	aut	72	470	20.28	1
									2020	win	44	214	2370.07	3
									2020	spr	41	473	12.42	1
28	Hedda	f	w	N	18 May 2018	02 April 2020	2008	adult	2018	spr	34	32885	0.11	1
								adult	2018	sum	94	15727	0.13	1
									2018	aut	89	1074	0.14	1
									2019	win	90	1510	0.11	1
									2019	spr	93	6848	0.13	1
								adult	2019	sum	94	7456	0.11	1
									2019	aut	88	669	0.13	1
									2020	win	73	347	0.14	1
									2020	spr	14	123	0.15	1
29	Hektor	f	w	N	21 September 2019	30 April 2020	2010	adult	2019	aut	68	696	111.4	2
									2019	win	37	145	528.47	5
									2020	spr	41	224	153.85	3
30	Hickory	f	c	N	30 August 2019	30 April 2020	2019	juvenile	2020	sum	24	483	1.34	1
									2019	aut	90	1230	105.64	3
									2019	win	91	810	6.32	2

									2020	spr	41	1981	1.86	2
31	Hillary	f	w	N	08 December 2017	22 May 2019	2013	adult	2017	aut	13	1308	1.81	1
									2018	win	90	12577	29.39	9
									2018	spr	92	119198	6.24	8
								adult	2018	sum	94	46366	0	2
									2018	aut	89	7798	46.52	3
									2019	win	90	5053	78.53	9
									2019	spr	64	11263	16.53	6
32	Hofer	f	w	N	13 May 2019	30 April 2020	2018	juvenile	2019	spr	39	3291	15.28	3
								sub-adult	2019	sum	94	3992	12.38	2
									2019	aut	89	1429	148.26	3
									2020	win	91	1486	588.77	8
									2020	spr	40	1940	2150.85	6
33	Ila	m	c	N	04 September 2018	30 April 2020	2018	juvenile	2018	sum	19	1285	0.57	1
									2018	aut	89	3801	5.84	3
									2019	win	90	2895	145.38	4
									2019	spr	93	15534	0.67	2
								sub-adult	2019	sum	94	13167	3.69	3
									2019	aut	90	2391	36.81	5
									2020	win	86	629	146.14	4
									2020	spr	41	986	6.64	2
34	Ivy	f	c	Y (predation)	10 October 2017	19 January 2019	2017	juvenile	2017	aut	72	1429	0.69	1
									2018	win	90	9058	0.54	1
									2018	spr	92	153566	0.25	1
								sub-adult	2018	sum	94	65850	0.45	1
									2018	aut	89	5085	10.96	2
									2019	win	30	227	0.88	1
35	Jacky	f	c	Y (predation)	10 October 2017	17 December 2017	2017	juvenile	2017	aut	69	620	4.58	1
36	Jehova	f	w	N	03 November 2019	22 February 2020	2019	juvenile	2019	aut	26	127	0.08	1
									2020	win	5	14	0	1
37	Johnny	f	c	N	10 October 2017	25 May 2018	2017	juvenile	2017	aut	72	896	0.27	1
									2018	win	90	3666	0.29	1
									2018	spr	66	96599	0.21	1
38	Jojoba	f	w	N	20 September 2018	18 October 2019	2018	juvenile	2018	sum	3	239	25.43	1
									2018	aut	89	3877	251.33	2

									2019	win	90	5100	187.91	6
									2019	spr	93	15158	0	3
								sub-adult	2019	sum	94	10230	53.3	3
									2019	aut	27	625	407.13	1
39	Junior	f	w	N	26 September 2018	02 November 2018	2018	juvenile	2018	aut	38	2138	182.23	3
40	Lana	f	w	N	15 June 2018	02 October 2019	2017	juvenile	2018	spr	6	6820	0.15	1
								sub-adult	2018	sum	94	53937	6.77	4
									2018	aut	89	2005	20.04	3
									2019	win	90	1674	9.73	1
									2019	spr	93	15895	0.86	1
								sub-adult	2019	sum	94	7410	36.47	2
41	Lava	f	w	N	13 September 2018	30 April 2020	2017	sub-adult	2018	sum	10	907	0.43	1
									2018	aut	89	687	10.6	1
									2019	win	90	1791	0.63	2
									2019	spr	93	16501	14.42	4
								sub-adult	2019	sum	94	10952	75.44	2
									2019	aut	90	2451	729.42	3
									2020	win	91	1333	789.56	2
									2020	spr	41	1969	230.67	4
42	Lewis	m	w	N	21 September 2019	30 April 2020	2014	adult	2019	aut	69	930	205.86	5
									2020	win	56	283	1298.05	3
									2020	spr	41	1925	134.51	2
43	Lisa	m	w	N	01 May 2018	30 April 2020	2016	sub-adult	2018	spr	51	25497	11.12	6
								sub-adult	2018	sum	94	37508	7.5	2
									2018	aut	89	4282	157.27	1
									2019	win	90	6334	542.28	3
									2019	spr	93	8386	31.09	3
								adult	2019	sum	94	8217	22.34	2
									2019	aut	90	3057	124.7	2
									2020	win	91	1587	355.73	3
									2020	spr	41	2017	139.92	2
44	Ljubica	m	w	N	13 May 2019	30 April 2020	2018	juvenile	2019	spr	39	2577	0.17	1
								sub-adult	2019	sum	94	9844	45.68	3
									2019	aut	88	1259	247.32	6
									2020	win	38	168	366.86	4

									2020	spr	40	301	166.31	3
45	Loco	f	w	N	14 September 2018	30 April 2020	2018	juvenile	2018	sum	9	243	3.09	1
									2018	aut	89	941	5.3	1
									2019	win	90	1656	0.49	1
									2019	spr	93	9681	0.35	1
								sub-adult	2019	sum	94	6585	1.04	1
									2019	aut	90	988	5.72	2
									2020	win	79	420	268.74	3
									2020	spr	41	2003	4.47	1
46	Lydia	m	w	N	05 June 2018	30 April 2020	2017	juvenile	2018	spr	7	6895	0.21	1
								sub-adult	2018	sum	94	58420	3.3	4
									2018	aut	89	4537	138.34	2
									2019	win	90	3270	101.54	4
									2019	spr	93	11130	1.16	2
								sub-adult	2019	sum	94	8624	7.36	3
									2019	aut	90	3015	20.5	1
									2020	win	91	1107	24.56	3
									2020	spr	41	2007	23.82	2
47	Mario	m	w	Y (predation by lynx)	10 October 2017	10 April 2019	2017	juvenile	2017	aut	72	878	0.33	1
									2018	win	90	8585	0.28	1
									2018	spr	92	142847	0.06	1
								sub-adult	2018	sum	94	66553	0.55	1
									2018	aut	89	4480	11.21	2
									2019	win	90	5094	6.54	4
									2019	spr	22	3448	1.95	1
48	Mayer	f	w	N	03 March 2018	30 April 2020	2017	juvenile	2018	win	18	5919	6.91	3
									2018	spr	92	141530	2.22	4
								sub-adult	2018	sum	94	48572	20.1	4
									2018	aut	89	4464	215.09	4
									2019	win	90	1864	195.09	5
									2019	spr	93	16584	10.96	5
								sub-adult	2019	sum	94	16293	41.82	4
									2019	aut	90	2322	125.5	6
									2020	win	68	515	77.07	3
									2020	spr	41	2001	103.86	2

49	Minerva	m	c	N	04 September 2018	30 April 2020	2018	juvenile	2018	sum	19	387	1.04	1
									2018	aut	89	654	5.02	1
									2019	win	77	306	23.31	2
									2019	spr	93	2279	87.07	3
								sub-adult	2019	sum	13	1116	4.05	1
									2019	aut	43	783	27.11	1
									2020	win	91	734	3281.66	4
									2020	spr	41	1969	798.5	6
50	Mombu	m	w	N	14 December 2018	30 April 2020	2018	juvenile	2018	aut	7	86	3.5	1
									2019	win	90	1903	2.81	3
									2019	spr	93	8816	0.9	2
								sub-adult	2019	sum	94	3347	3.48	2
									2018	aut	89	1040	63.94	5
									2019	win	74	337	277.62	3
									2019	spr	41	1551	108.37	3
51	Nacht	m	w	N	13 November 2018	16 February 2020	2017	sub-adult	2019	aut	38	537	56.35	2
									2018	win	90	3039	126.24	5
									2019	spr	93	8330	20.19	6
								sub-adult	2019	sum	53	807	15.82	2
									2020	win	5	15	0	1
52	Nane	f	w	Y (predation)	25 October 2017	27 October 2017	2017	juvenile	2017	aut	3	33	2.71	1
53	Napoleon	f	w	N	06 December 2019	30 April 2020	2019	juvenile	2019	aut	15	165	123.38	2
									2020	win	91	860	1561.11	6
									2020	spr	41	2015	370.57	4
54	Neptune	f	c	N	2018-09-04	23 February 2019	2018	juvenile	2018	sum	19	289	0.4	1
									2018	aut	89	847	2.02	1
									2019	win	64	371	2.08	1
55	Pickerl	f	w	N	19 September 2018	30 April 2020	2018	juvenile	2018	sum	4	294	26.6	2
									2018	aut	89	6294	92.18	4
									2019	win	90	4243	161.8	5
									2019	spr	93	17423	12.28	4
								sub-adult	2019	sum	94	17870	17.19	2
									2019	aut	90	2639	189.89	3
									2020	win	91	816	619.05	8
									2020	spr	41	2013	53.82	4

56	Pulipp	m	w	N	2018-05-18	21 November 2019	2017	juvenile	2018	spr	34	36013	1.61	2
								sub-adult	2018	sum	94	50773	9.69	3
									2018	aut	89	4251	189.55	3
									2019	win	90	3162	5	5
									2019	spr	93	14863	0.75	2
								sub-adult	2019	sum	94	11406	22.55	4
									2019	aut	61	3164	59.5	3
57	Pumuckl	f	w	N	13 September 2018	13 January 2019	2006	adult	2018	sum	10	1296	0.51	1
									2018	aut	89	2306	54.01	4
									2019	win	24	176	2.52	1
58	Reese	f	w	N	19 September 2018	16 December 2019	2015	adult	2018	sum	4	337	21.81	1
									2018	aut	89	3675	516.58	6
									2019	win	91	4537	613.01	7
									2019	spr	93	11619	80.9	7
								adult	2019	sum	94	9328	186.63	4
									2019	aut	86	1963	639.11	5
59	Richy	m	w	N	01 May 2018	19 June 2019	2017	juvenile	2018	spr	51	26139	0.27	1
								sub-adult	2018	sum	94	45929	11.16	4
									2018	aut	89	1804	191.44	6
									2019	win	90	2498	231.84	8
									2019	spr	92	6210	27.42	6
60	Rollo	m	c	N	07 October 2017	30 April 2020	2016	sub-adult	2017	aut	75	3696	2.06	2
									2018	win	90	8431	2.25	1
									2018	spr	92	147605	0.26	1
								sub-adult	2018	sum	94	50397	0.47	1
									2018	aut	89	2874	5.92	2
									2019	win	90	1425	0.59	2
									2019	spr	93	13251	0.29	2
								adult	2019	sum	94	9251	0.75	2
									2019	aut	90	1401	1.89	2
									2020	win	67	385	3.71	2
									2020	spr	41	2003	0.31	1
61	Sansa	f	c	N	30 August 2019	30 April 2020	2019	juvenile	2019	sum	24	492	0.58	1
									2019	aut	90	1151	1.43	1
									2020	win	91	840	0.6	1

									2020	spr	41	1968	0.78	1
62	Summer	f	c	Y (predation by eagle owl)	30 August 2019	19 November 2019	2019	juvenile	2019	sum	24	407	0.75	1
									2019	aut	59	594	0.45	1
63	Susa	f	w	N	18 May 2018	26 March 2019	2017	juvenile	2018	spr	34	42924	0.17	1
								sub-adult	2018	sum	94	43929	6.19	4
									2018	aut	89	6628	166.31	3
									2019	win	90	6291	267.9	5
									2019	spr	7	934	66.2	1
64	T-Rex	m	w	N	20 March 2019	30 April 2020	2014	adult	2019	spr	93	1309	1.05	1
								adult	2019	sum	94	1395	1.38	1
									2019	aut	22	57	0.51	1
									2020	win	35	106	1.42	1
									2020	spr	41	277	1.07	1
65	Taco	m	w	N	30 March 2019	30 April 2020	2017	sub-adult	2019	spr	83	5903	8.32	3
								sub-adult	2019	sum	94	3342	8.64	2
									2019	aut	86	473	29.05	1
									2020	win	67	197	263.78	4
									2020	spr	41	374	41.29	3
66	Toma	m	c	N	02 September 2019	30 April 2020	2019	juvenile	2019	aut	62	185	0.22	1
									2020	win	35	166	0.57	1
									2020	spr	41	931	0.52	1
67	Tweety	f	w	N	26 September 2018	30 April 2020	2018	juvenile	2018	aut	86	1722	10.06	2
									2019	win	90	1223	1.73	1
									2019	spr	93	8209	1.16	1
								sub-adult	2019	sum	94	10304	1.9	2
									2019	aut	90	1915	19.82	2
									2020	win	91	800	15.05	2
									2020	spr	41	1989	41.08	5
68	Twinkle	f	c	Y (predation by wolves)	04 September 2018	17 September 2019	2018	juvenile	2018	sum	19	1270	0.6	1
									2018	aut	89	4878	2.87	1
									2019	win	90	1794	1.88	1
									2019	spr	93	11740	0.82	1
								sub-adult	2019	sum	89	7865	0.95	1
69	Uber	f	w	N	29 March 2019	30 April 2020	2017	sub-adult	2019	spr	84	708	89.72	3
								sub-adult	2019	sum	93	584	131.41	4

									2020	win	32	123	629.91	5
									2020	spr	40	319	19.4	3
70	Unesco	f	w	N	15 November 2019	30 April 2020	2019	juvenile	2019	aut	36	619	28.29	2
									2020	win	91	1285	131.65	4
									2020	spr	40	2010	49.46	5
71	Verena	f	w	N	21 December 2018	30 April 2020	2018	juvenile	2019	win	90	831	2.63	1
									2019	spr	93	1658	0.85	1
								sub-adult	2019	sum	94	1762	2.55	2
									2019	aut	85	641	24.5	2
									2020	win	74	660	61.33	3
									2020	spr	41	1838	2.87	1
72	Victor-Peter	m	w	N	19 October 2019	30 April 2020	2019	juvenile	2019	aut	63	527	7.69	2
									2020	win	89	576	482.23	4
									2020	spr	40	1920	53.61	4
73	Viper	m	w	N	15 January 2018	30 April 2020	2017	juvenile	2018	win	43	934	1.58	1
									2018	spr	93	142883	0.54	2
								sub-adult	2018	sum	95	63084	20.54	4
									2018	aut	90	4744	104.66	4
									2019	win	91	6263	57.77	3
									2019	spr	93	16328	8.88	2
								sub-adult	2019	sum	95	8213	30.78	1
									2019	aut	90	2170	130.43	2
									2020	win	91	1824	143.07	3
									2020	spr	41	3115	19.38	1
74	Winter	f	c	N	30 August 2019	30 April 2020	2019	juvenile	2019	sum	24	396	0.25	1
									2019	aut	90	743	0.52	1
									2020	win	82	458	0.51	1
									2020	spr	41	1067	0.78	1
75	Xaba	m	w	N	10 May 2019	11 June 2019	2013	adult	2019	spr	32	872	0.13	1
76	Xerxes	m	c	N	30 August 2019	30 April 2020	2019	juvenile	2019	sum	24	132	0.88	1
									2019	aut	55	203	0.66	1
									2020	win	52	424	24.48	3
									2020	spr	41	1987	15.24	2

Appendix 2 *Information on 23 verified and 21 unverified anthropogenic food sources (AFSs) (including 3 wildparks, 11 compost sites, 7 waste management centres / dumps, 18 ski huts, hotels and restaurants, and 5 private farms). Information on the 3 sites that were verified, but not found to be AFS were excluded from the analysis and are not presented in this table. AFS were grouped into broader categories (3 wildparks, 18 refuse sites and 23 huts) based on similarities in sites that were verified (Y = yes, N = no) and described from the field surveys (see Methods). Buffers were estimated based on revisitation analysis, at the distance where revisitations no longer increased with increasing radius size or at a maximum of 150 metres. Sites are ordered according to the number of different individuals (No. Ind) that were recorded there across the tracking period.*

ID	Latitude	Longitude	Name	Type	Category	Verified	Buffer (in metres)	Description (field surveys)	No. Ind
F01	47.81	13.95	Cumberland Wildpark	Wildpark	Wildpark	Y	80	Wildpark with boar, wolf and bear enclosures, food supplied daily between 8-10am	74
F02	47.96	13.84	Kompostierung Gattinger	Compost	Refuse	Y	60	Outdoor composting with 18 long rows with piles of raw processing material	46
F36	47.81	13.98	Kasbergalmhütte	Restaurant	Hut	N	150		45
F06	47.94	13.78	Unknown	Compost	Refuse	Y	100	Moderate size outdoor private composting facility with 8 long rows of compost	36
F05	47.56	14.27	Abfallwirtschaftsverband Liezen	Compost	Refuse	Y	120	Large composting area within a waste management centre. Large piles of plastic waste under roofed area	26
F03	47.91	14.24	Unknown	Compost	Refuse	Y	80	Outdoor composting in a multi-use area with lots of other construction storage	21
F34	47.49	14.29	Unknown	Hut	Hut	N	90		16
F04	48.06	14.39	Kompostplatz Wolfern	Compost	Refuse	Y	80	Small outdoor composting area	15
F45	47.83	13.95	JUFA Hotel Almtal	Hotel	Hut	N	150		14
F17	47.43	13.80	AWV Schladming	Dump	Refuse	Y	150	Compost site with large unsorted outdoor organic piles (two short and tall maturing rows visible) and some smaller composting piles under the roofed area.	12
F21	47.82	13.72	Feuerkogel	Ski hut	Hut	N	50	Ski field closed and inaccessible	11
F13	47.39	13.22	Unknown	Dump	Refuse	Y	150	Large waste management centre with some outdoor inorganic waste piles and a smaller indoor waste and compost processing area	10
F47	47.80	14.03	Ahornalmhütte	Hut	Hut	N	100		10
F15	47.38	13.21	H&H Recycling	Compost	Refuse	Y	150	Composting area for agricultural waste with long maturing piles (~4m tall) under roofed structures and early-stage outdoor processing, not much plastic	9
F29	47.30	13.41	Burgstallhütte	Ski hut	Hut	Y	60	Ski area	8
F27	47.40	13.79	Natur- und Wellness hotel Höflehner	Ski hut	Hut	Y	120	Ski lodge and wellness centre with large hotel accommodation and restaurant	7
F31	47.33	13.26	Unknown	Farm	Hut	N	40	Car got stuck en route so survey was not conducted.	6
F28	47.25	13.51	Jugendhotel Felseralm	Ski hut	Hut	N	60		6
F08	47.21	14.86	Gobernitz Kompostieranlage	Compost	Refuse	Y	130	Large composting processing site with many stages of compost, including lots of plastic. Roofed area for mature compost and outdoor area for early maturing rows with lots of plastic	5
F18	48.04	14.45	Wachtberg Kompost, company 'Argyl'	Compost	Refuse	Y	50	Small outdoor composting area on a section of the property	5
F46	47.80	14.02	Steyrerhütte	Hut	Hut	N	100		5

F25	47.89	14.13	Altstoffsammelzentrum Micheldorf	Dump	Refuse	N	150		4
F37	47.98	14.53	Unknown	Hotel	Hut	N	80		4
F40	47.78	13.43	Hotel Schafbergspitze	Hotel	Hut	N	50		4
F39	48.10	14.56	Tierpark Stadt Haag	Wildpark	Wildpark	N	90		4
F43	47.59	14.09	Johnsleitner Hütte	Hut	Hut	N	150		4
F16	47.43	14.99	Pichler-reifen	Compost	Refuse	Y	80	Compost site operating at half capacity with lots of plastic and affiliated with lots of nearby buildings (multi-disciplinary companies)	3
F35	47.70	13.48	Wildtierpark Kleefeld	Wildpark	Wildpark	N	65		3
F30	47.31	13.40	Ketzerlehen Bauernhof	Farm	Hut	Y	110	Game farm with a storage shed for possibly processing game carcasses	3
F48	47.94	13.88	Sägewerk Forstinger	Hut	Hut	N	70		3
F42	47.51	14.21	Untergrabner Hütte	Hotel	Hut	N	120		3
F24	47.61	13.14	Struber Entsorgung GmbH	Dump	Refuse	Y	120	Waste management centre with a small section for organic material, but no obvious maturing composting rows. Lots of plastic sorting and compressing. Undercover processing includes a furnace.	2
F38	47.76	13.12	Alpengasthof Fageralm	Hotel	Hut	Y	50	Alpine Guesthouse, where the owner leaves grilled leftovers out for the ravens	2
F10*	48.67	14.54	Unknown	Dump	Refuse	N	100		2
F22	47.14	14.31	AWV Murau	Dump	Refuse	N	90		2
F32	47.34	13.37	Bergrestaurant und Hotel Waldgasthof	Ski hut	Hut	Y	70	Ski area	2
F14	47.29	14.94	Poschacher Kompost	Compost	Refuse	Y	140	Large indoor and outdoor composting area with tall (~4m) and wide rows without much plastic, perhaps agricultural composting	2
F11*	48.74	14.34	Unknown	Dump	Refuse	N	90		1
F12	46.76	14.35	Kompostieranlage St Veit	Farm	Hut	Y	120	Composting area on a section of the property	1
F23	47.12	15.03	Unknown	Farm	Hut	Y	50	Small outdoor composting area on a section of a private farm with a large livestock barn. Plastic in piles.	1
F19	47.32	13.39	Hinterrohrgut, Almhütte	Farm	Hut	Y	50	Small barnyard composting area behind the farmhouse	1
F26	46.89	14.57	Forellenwirt Bacher	Hotel	Hut	N	70		1
F20	47.99	13.57	Arge Kompost	Compost	Refuse	Y	90	Large indoor and outdoor composting area. Over 12 long rows outdoors and 5 long rows under a dome roof	1
F41	47.35	14.16	Feriendorf Hinterwald	Hotel	Hut	N	150		1

Appendix 3 *The candidate sets of top-ranking models for* ***(a)*** *the number of anthropogenic food sources (AFSs) visited and* ***(b)*** *the probability of being at an anthropogenic food source at four different ΔAICc (Akaike's Information Criterion corrected for small sample sizes) cut-offs (less than and equal to 2, 4, and 6, and less than or equal to the 95% confidence summed weights). The global model for (a) included sex, origin (i.e., wild-caught or captive-bred-released), age class (i.e., juvenile, adult), season (i.e., autumn, winter, spring, summer), local activity range (95% UD), and the total number of fixes as fixed factors. The global model for (b) included sex, origin, age class, season, local activity range, and the category of AFS (i.e., wildpark, refuse site, hut) as fixed factors. Individual identity was the random factor in both (a) and (b). The number of model parameters (Df), log-likelihood (logLik), AICc, ΔAICc, and model weights (ώ$_i$) are presented.*

a) Response: number of AFS visited
(n = 406 UD estimates from 76 birds)

Models included under ΔAICc <= 2 threshold	Df	logLik	AICc	ΔAICc	ώ$_i$
Age class + Origin + Season + 95%UD	8	-711.52	1439.4	0.00	0.384
Age class + Origin + Season + 95%UD + Total no. fixes	9	-711.03	1440.5	1.11	0.220
Age class + Origin + Season + 95%UD + Sex	9	-711.12	1440.7	1.28	0.202
Models also included under ΔAICc <= 4 & 6 thresholds					
Age class + Origin + Season + 95%UD + Sex + Total no. fixes	10	-710.63	1441.8	2.41	0.115
Models also included under ΔAICc <= 95% confidence summed weights					
Age class + Origin + Season	7	-715.62	1445.5	6.12	0.018

b) Response: probability of being at an AFS
(n = 762 proportions from 76 birds)

Models included under ΔAICc <= 2 threshold	Df	logLik	AICc	ΔAICc	ώ$_i$
Season + Category of AFS	7	-151.34	316.8	0.00	0.140
Season + Category of AFS + 95%UD	8	-150.74	317.7	0.83	0.092
Season + Category of AFS + Age class	8	-150.80	317.8	0.97	0.086
Season + Category of AFS + Sex	8	-151.74	318.5	1.71	0.060
Season + Category of AFS + Origin	8	-151.29	318.8	1.93	0.053
Category of AFS + 95% UD	5	-154.35	318.8	1.94	0.053
Models also included under ΔAICc <= 4 threshold					
Season + Category of AFS + 95%UD + Age class	9	-150.34	318.9	2.08	0.049
Category of AFS	4	-155.59	319.2	2.40	0.042
Season + Category of AFS + 95%UD + Sex	9	-150.55	319.3	2.51	0.040
Season + Category of AFS + Age class + Sex	9	-150.61	319.5	2.64	0.037
Season + Category of AFS + 95%UD + Origin	9	-150.73	319.7	2.86	0.033
Season + Category of AFS + Age class + Origin	9	-150.78	319.8	2.97	0.032
Category of AFS + 95%UD + Age class	6	-154.01	320.1	3.29	0.027
Category of AFS + Age class	5	-155.14	320.4	3.53	0.024
Season + Category of AFS + Sex + Origin	9	-151.13	320.5	3.67	0.022
Season + Category of AFS + 95%UD + Age class + Sex	10	-150.13	320.6	3.73	0.022
Category of AFS + 95%UD + Sex	6	-154.23	320.6	3.64	0.022
Category of AFS + 95%UD + Origin	6	-154.35	320.8	3.97	0.019
Models also included under ΔAICc <= 95% confidence summed weights					
Season + Category of AFS + 95%UD + Age class + Origin	10	-150.33	321.0	4.13	0.018
Category of AFS + Sex	5	-155.50	321.1	4.25	0.017
Category of AFS + Origin	5	-155.55	321.2	4.35	0.016
Season + Category of AFS + 95%UD + Sex + Origin	10	-150.54	321.4	4.55	0.014
Season + Category of AFS + Age class + Sex + Origin	10	-150.60	321.5	4.66	0.014
Category of AFS + 95%UD + Age class + Sex	7	-153.88	321.9	5.07	0.011
Models also included under ΔAICc <= 6 threshold					
Category of AFS + 95%UD + Age class + Origin	7	-154.01	322.2	5.33	0.010
Category of AFS + Age class + Sex	6	-155.04	322.2	5.35	0.010
Category of AFS + Age class + Origin	6	-155.12	322.4	5.52	0.009
Category of AFS + 95%UD + Sex + Origin	7	-154.23	322.6	5.78	0.008
Season + Category of AFS + 95%UD + Age class + Sex + Origin	11	-150.13	322.6	5.79	0.008

Appendix 4 *Model averaging outputs for the top model set at ΔAICc <= 2 cut-off for* ***(a)*** *the number of anthropogenic food sources (AFSs) visited in relation to sex, origin (i.e., wild-caught or captive-bred-released), age class (i.e., juvenile, subadult/adult), season (i.e., autumn, winter, spring, summer), local activity range (95% UD), and the total number of fixes as fixed factors, and* ***(b)*** *the probability of being at an anthropogenic food source in relation to sex, origin, age class, season, local activity range, and the category of AFS (i.e., wildpark, refuse site, hut). The different reference categories for 'season' and 'category of AFS' are highlighted in bold. The number of model parameters (Df), log-likelihood (logLik), Akaike information criterion corrected for small sample size (AICc), ΔAICc, and model weights ($\acute{\omega}_i$) are presented for all models less than or equal to the ΔAICc of 2. Estimates, unconditional standard errors (Unc. SE), 95% confidence intervals (95% CI), z-values, and the relative variable importance (RVI) are presented for the top models. Fixed factors highlighted in bold have confidence intervals which do not contain zero.*

a) Response: number of AFS visited
(n = 406 95% UD estimates from 76 birds)

Top model set	Df	logLik	AICc	ΔAICc	$\acute{\omega}_i$
Age class + Origin + Season + 95%UD	8	-711.52	1439.4	0.00	0.384
Age class + Origin + Season + 95%UD + Total no. fixes	9	-711.03	1440.5	1.11	0.220
Age class + Origin + Season + 95%UD + Sex	9	-711.12	1440.7	1.28	0.202
Effect size of explanatory terms	Estimate	Unc. SE	95% CI	z-value	RVI
Intercept	0.847	0.127	(0.597, 1.098)	6.637	-
Juvenile ϯ	**-0.228**	**0.077**	**(-0.380, -0.077)**	**2.954**	**1.00**
Wild-caught†	**0.469**	**0.120**	**(0.233, 0.704)**	**3.903**	**1.00**
Autumn ‡	**-0.309**	**0.084**	**(-0.475, -0.142)**	**3.635**	**1.00**
Spring ‡	-0.161	0.085	(-0.328, 0.007)	1.881	"
Summer ‡	**-0.385**	**0.101**	**(-0.583, -0.187)**	**3.805**	**"**
95% UD	**0.084**	**0.028**	**(0.029, 0.139)**	**2.980**	**1.00**
Total fixes	0.036	0.025	(-0.035, 0.107)	1.007	0.27
Maleǂ	0.090	0.063	(-0.106, 0.285)	0.899	0.25

ϯAge class: 'adult', †origin: 'captive-bred-released, **‡season: 'winter'**, and ǂsex: 'female' were used as reference categories

b) Response: probability of being at an AFS
(n = 762 proportions from 76 birds)

Top model set	Df	logLik	AICc	ΔAICc	$\acute{\omega}_i$
Season + Category of AFS	7	-151.34	316.8	0.00	0.140
Season + Category of AFS + 95%UD	8	-150.74	317.7	0.83	0.092
Season + Category of AFS + Age class	8	-150.80	317.8	0.97	0.086
Season + Category of AFS + Sex	8	-151.74	318.5	1.71	0.060
Season + Category of AFS + Origin	8	-151.29	318.8	1.93	0.053
Category of AFS + 95% UD	5	-154.35	318.8	1.94	0.053
Effect size of explanatory terms	Estimate	Unc. SE	95% CI	z-value	RVI
Intercept	-4.182	0.776	(-5.705, -2.659)	5.383	-
Refuse +	**1.829**	**0.790**	**(0.278, 3.380)**	**2.311**	**1.00**
Wildpark+	**2.483**	**0.757**	**(0.998, 3.968)**	**3.277**	**"**
Autumn‡	-0.194	0.390	(-0.994, 0.607)	0.474	0.89
Spring‡	**0.739**	**0.410**	**(0.034, 1.444)**	**2.054**	**"**
Summer‡	0.412	0.397	(-3.70, 1.194)	1.032	"
95% UD	-0.265	0.181	(-0.745, 0.216)	1.080	0.30
Juvenile ϯ	0.284	0.158	(-0.251, 0.818)	1.040	0.18
Maleǂ	0.153	0.105	(-0.365, 0.672)	0.580	0.12
Wild-caught†	-0.094	0.099	(-0.655, 0.467)	0.329	0.11

+ Category of AFS: 'hut', **‡season: 'winter'**, ϯAge class: 'adult', ǂsex: 'female', and †origin: 'captive-bred-released were used as reference categories