



Effects of site fidelity, group size and age on food-caching behaviour of common ravens, *Corvus corax*

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The storage of food is widespread among mammals and birds and can be flexibly adjusted to various contexts such as competition, food availability or energetic demands. In bird species, nonbreeders often move through large areas whereby periods of long-term settlement can alternate with short-term visits. In food-caching species these differences in the degree of local settlement might change the benefits gained from storing food, and caching may only be advantageous during periods of prolonged settlement. We examined whether differences in local settlement influence food-caching behaviour of wild common ravens at a local anthropogenic food source with high interspecific and intraspecific competition. We found that individuals with a higher degree of site fidelity (i.e. prolonged periods of local settlement) engaged in food caching more than individuals with less site fidelity (i.e. short periods of local settlement); this effect was even stronger in the presence of potential predators representing a high-risk foraging situation. Further, juvenile ravens were less likely to cache than subadults and adults, and an increasing number of conspecifics present at the feeding site decreased the likelihood of caching. We found considerable individual variation in respect to the area used for caching. We suggest that individuals with higher site fidelity may gain more benefits from caching food and/or that they are more successful in obtaining food potentially due to more experience with the local foraging situation. Research is needed to examine the exact causes of the observed link between food-caching behaviour and the different degrees of site fidelity. Our findings show that differences in movement and settlement decisions can influence ecological aspects such as food acquisition and thus may have important consequences for individual fitness and population dynamics.

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Food caching is a common and flexible strategy among mammal and bird species to store resources for later consumption (Vander Wall, 1990). Several theoretical models and empirical studies have aimed to examine the economics behind an optimal food-caching strategy (Gerber, Reichman; Roughgarden, 2004; McNamara, Houston, & Krebs, 1990) comprising factors such as food scarcity, energetic expenditures, social competition or brain processing capacity. For instance, many species adjust the intensity of caching to the current availability of food by either increasing or

decreasing the frequency of caching when food is abundant (Clayton, Mellor, & Jackson, 1996; Morrison, Pelchat, Donahue, & Hik, 2009; Pravosudov, 2006; Sklepkovych; Montevecchi, 1996) or individuals adjust to the current social context by decreasing or increasing the frequency of caching when competition is high (Emery & Clayton, 2001; Hopewell, Leaver, & Lea, 2008; Lahti et al., 1998).

The storage of food is an investment in future benefits and animals may differ in their timing of cache recovery (Brodin, 2005). Some species use caches as short-term storage which will only last for a few hours or a day (Cowie, Krebs, & Sherry, 1981; Brodin, 1992) whereas others use caches as long-term storage lasting several days or months (Hitchcock & Sherry, 1990; Balda & Kamil, 1992). In the wild, many birds, in particular during nonbreeding phases, roam through large areas and periods of prolonged settlement can

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alternate with short-term visits (Paradis, Baillie, Sutherland, & Gregory, 1998; Silk, Croft, Tregenza, & Bearhop, 2014; Teitelbaum & Mueller, 2019). If caching primarily serves as long-term food storage, only individuals that remain in an area for an extended period of time or revisit the area frequently (i.e. exhibit a high degree of site fidelity) might benefit from caching food whereas individuals that visit an area rarely may benefit more from consuming food directly. In contrast, if caches serve as short-term storage both settled individuals and infrequent visitors can benefit from food caching. However, it remains unknown whether and how differences in site fidelity (i.e. short versus long periods of temporary settlement) in highly mobile species influence food-caching behaviour.

Common ravens frequently cache food for later consumption and forage in groups at highly clumped and/or local food sources. The resources used range from ephemeral sites such as carcasses and road kills (Heinrich, 1988; Marzluff, Heinrich, & Marzluff, 1996) to frequently available sites such as anthropogenic food sources (e.g. farms, zoos and rubbish dumps; Boarman, Patten, Camp, & Collis, 2006; Webb, Marzluff, & Hepinstall-Cymerman, 2012; Loretto, Reimann, Schuster, Graulich, Bugnyar, 2016). Anthropogenic food sources can attract large numbers of nonbreeding ravens, and thus cannot be monopolized by a single territorial pair. Consequently, breeding pairs and nonbreeders alike cope with fierce competition by repeatedly carrying away pieces of food for scatter hoarding (Heinrich & Pepper, 1998). This in turn allows other individuals to potentially access food by pilfering caches. As in most corvids, efficient pilfering in ravens relies on observing other individuals making caches (Bednekoff & Balda, 1996a,b; Emery & Clayton, 2001). To reduce the risk of being seen and to allow selective cache defence, ravens engage in a variety of cache protection strategies (Heinrich & Pepper, 1998; Bugnyar & Kotrschal, 2002; Bugnyar, Stöwe, & Heinrich, 2007). In the presence of competitors, ravens start caching earlier (after accessing the food), they move faster and try to cache out of the view of conspecifics (Heinrich & Pepper, 1998). Captive ravens even remember the identity of individuals present during caching (Bugnyar & Heinrich, 2005, 2006; Bugnyar, 2011) and selectively alter their cache protection strategy according to the social status (e.g. dominance rank; Bugnyar & Heinrich, 2006) and visual perspective of conspecifics (Bugnyar, Reber, & Buckner, 2016). While breeding pairs are territorial year-round, nonbreeding ravens vary in their space and resource use. Radio and GPS tracking have revealed the same patterns across different study areas in Central Europe and North America: short- to long-distance movements alternate with short to long periods of temporary settlement around food sources (Loretto et al., 2017; Loretto, Schuster et al., 2016; Webb, Marzluff; Hepinstall-Cymerman, 2012). The individual variation in movement results in different degrees of 'site fidelity' at local resources (Braun & Bugnyar, 2012), which renders ravens an ideal study species to examine how and whether these differences in temporary settlement influence food-caching behaviour.

In this study we aimed to examine how differences in site fidelity affect the food-caching behaviour of common ravens at a local, ephemeral food source with high inter- and intraspecific competition. We recorded caching behaviour at two enclosures in a zoo where wild ravens frequently steal food and which differ in predation risk and food quality (i.e. a wild boar, *Sus scrofa*, enclosure as a low-risk and low-quality food source versus a wolf, *Canis lupus*, enclosure as a high-risk and high-quality food source). First, we investigated whether different degrees of site fidelity influence the number and the likelihood of caching trips of ravens at these food sources. We predicted that individuals with a higher degree of site

fidelity (i.e. those frequently present at the local food sources; hereafter 'locals') would cache more than birds that used this food source less often (hereafter 'visitors'), as locals may benefit more from caches in the long term. We expected this effect to be stronger in the high-risk situation, since locals might have more experience in developing strategies to steal food from wolves. Second, we divided caching trips of ravens into caching nearby (i.e. where the exact location of the cache was observed) versus caching at a distance (i.e. where only the flight direction but not the exact cache location was observed) and asked whether the degree of site fidelity affected this ratio. If locals and visitors both stored food but pursued different strategies we expected that locals would cache more in proximity to the enclosure, potentially as an adjustment to the ephemerality of the food source, while visitors would prefer flying away with food out of the view of conspecifics (Bugnyar; Kotrschal, 2002; Heinrich & Pepper, 1998). Alternatively, locals may fly longer distances to preferred locations that have proven to be safe caching spots in the past whereas visitors may cache more nearby as they lack experience with suitable cache locations further away. Last, we examined whether locals preferred specific cache locations compared to visitors. Using techniques from home range analyses, we quantified the area used for caches nearby and compared it between locals and visitors. Further, for caches at a distance we calculated a mean take-off direction and predicted that locals would fly towards a specific direction more often than infrequent visitors. In addition, we examined in all these analyses the effect of group size and age: we expected caching behaviour to increase with decreasing group size and increasing age.

METHODS

Field Site and Animals

Data were collected in the area of the Cumberland Wildpark (47.804783°N, 13.947862°E), located in a narrow valley in the northern Austrian Alps. Ravens (breeding pairs and nonbreeders) frequently use this park to forage, that is, they steal food from several species of zoo animals (Drack & Kotrschal, 1995). Depending on the season, between 30 (summer) and 120 (winter) ravens can be observed in the park area. From 2007 until 2013, more than 200 ravens were caught with drop-in-traps and individually marked with colour rings and a wing tag. Age was estimated based on the beak and plumage coloration (Heinrich, 1994; Heinrich & Marzluff, 1992) and for the analyses ravens were classified as adults (>3 years), subadults (1–3 years) and juveniles (< 1 year). Breeders are defined as birds territorial throughout the year. They can be distinguished from nonbreeders by their high rates of aggressive and self-aggrandizing behaviours (Heinrich, 1988). At our study site, we typically know their territory and/or have observed them feeding their offspring at the park area after fledging.

Data Collection

Between April and December 2013 (on 115 days) we observed ravens' caching behaviour in the morning during the feeding of wild boars and wolves. The food for wild boars comprises a mixture of pellets, bread, vegetables, fruits and occasionally kitchen leftovers, meat or entrails. Thus, the quality is usually lower than that of the food for wolves which only consists of meat. Ravens have never been seen to be harmed by a wild boar suggesting that foraging near them is relatively low risk, whereas co-feeding with wolves can be considered 'high risk', since each year around 5–10 ravens get killed (Bugnyar & Kotrschal, 2001, for recent years

Loretto & Bugnyar, n.d.). As soon as the zoo animals are fed, ravens try to steal pieces of food which is frequently followed by caching trips as described by Heinrich and Pepper (1998). From a fixed position around 30 m away from the feeding point the observer (K.B.) recorded which individually marked raven left with food. Ravens were observed during caching in 500 cases (hereafter referred to as nearby caches), from which most were recorded close to the wild boar enclosure, which is surrounded by a more open habitat than the wolf enclosure. In 1185 cases the ravens flew further away with food out of the view of the observer (hereafter referred to as distant caches). Although, in these cases we did not see the cache being made, we still consider it as a caching trip, as the food items are usually too large for direct consumption and ravens usually quickly returned without food. However, we cannot exclude the possibility that they lost the food to another individual. We marked all observations on a detailed map of the study area (Map Data, Google, scale 1:10 000). For the nearby caches we recorded the cache location and for the distant caches we recorded the last location where the individual was seen. These data were then entered into QGIS 2.18.1 (an Open Source Geospatial Foundation Project: <http://qgis.osgeo.org>, QGIS Development Team, 2016) to extract the spatial coordinates. In addition, we collected data on the presence of all marked individuals (on 97 of the 115 days; data collection required at least two people observing simultaneously, one for the food caches and one for the presence of ravens). At each feeding site (wild boars and wolves) we observed for about 20 min (until most of the food was gone) and recorded all marked ravens present. Based on this, we calculated each individual's site fidelity, i.e. the proportion of days it was present throughout the study. For simplification we refer to individuals close to 1 as 'locals' and individuals close to 0 as 'visitors'; however, all analyses are based on the continuous variable.

In addition, we performed daily observations after the feeding of the zoo animals (1100–1200 and 1400–1900 hours; at least 2 h after the feeding) and entered all sightings of marked ravens onto a map of the study area. The observer walked once or twice per day along a standardized route in the zoo. The route encompassed both feeding sites and the area identified as most frequently used by ravens at this study site (Loretto, Reimann et al., 2016). This was done to compare the overlap of space use between individuals during caching with the space use during the rest of the day.

Ethical Note

Our research adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. Ravens were trapped, blood sampled and marked according to the procedure described in Braun and Bugnyar (2012) and with a licence from the commission for animal experimentation of the Austrian government (BMWF-66.006/0010–11/10b/2009 and BMWF-66.006/0009–II/3b/2012). As the study itself was noninvasive and based on behavioural observations only, it was not classified as an animal experiment in accordance with the Austrian law (§ 2. Federal Law Gazette No. 114/ 2012). The monitoring and ringing programme of the Konrad Lorenz Forschungsstelle is authorized by the Central Administration of Upper Austria.

Data Analysis

Effects on the number of caching trips

We analysed effects on the number of caching trips using a generalized linear mixed model (GLMM) with a Poisson error distribution and a log link function. As the response variable we included the number of caching trips per individual (i.e. combining

the number of nearby and distant caches) and per day (i.e. referring only to those days when the individual was present during the feeding). As fixed effects we included degree of site fidelity, age class, foraging site and group size with an interaction between degree of site fidelity and foraging site. Age class was included as a categorical variable (juvenile, subadult, adult), as well as foraging site (low risk = wild boar enclosure, high risk = wolf enclosure). The fixed effect degree of site fidelity was included as a continuous variable ranging from 0 to 1 (Appendix Fig. A1) and group size represented the total number of marked individuals present during the feeding on that day (Appendix Fig. A2). The number of marked ravens correlated strongly with the total number of ravens present and thus could be used as a reliable proxy for group size (Pearson correlation: $r = 0.73$, $P < 0.01$, based on estimations made by the same observer during 2013 and 2014; with an estimated mean for the total number of marked and unmarked ravens of 42 and a maximum of 80 ravens per day). Further, we included day and individual identity as random factors.

Although the data were not zero-inflated, the average number of recorded caching trips per individual and day was rather low (mean = 0.486, maximum = 9). Therefore, we also modelled the probability of an individual making a caching trip as a logistic regression, by transforming the response variable to binary values (GLMM, error distribution = binomial, link = logit).

Our data set also includes observations from six territorial, breeding individuals. Since only adult ravens can be territorial it would be confounding with age class if added as a factor into the model. Thus, we repeated the same models by simply excluding these individuals from the analysis.

Nearby versus distant caching

We examined the influence of the same fixed effects as described above (i.e. degree of site fidelity, age class and group size) on an individual's decision to cache nearby (i.e. where the exact location of the cache was observed) or at a distance (i.e. where only a flight direction but not the exact cache location was observed). We created a GLMM (binomial distribution) with the number of nearby and distant caches for each individual and each day it was present as the response variable. We included day and individual identity as random factors. For the analysis we focused on the data collected at the wild boar enclosure as few nearby caches were observed at the wolf enclosure ($N = 21$). We recalculated the same model excluding the territorial individuals.

Individual preferences for cache locations

First, we quantified the area used for nearby caches using home range estimation methods. We only included individuals for which nearby food caches were directly observed at least 15 times. We followed an approach described in Loretto, Reimann, et al. 2016 which is based on kernel density estimation using the plug-in method to select the smoothing parameter with the 'ks' r package (Duong, 2019). We calculated the 95% utilization distribution of each individual's caching area and used these values as the response variable in a linear model to test whether any of the previously described fixed factors (degree of site fidelity, age class and number of observations per individual) influenced the size of individual caching areas.

To assess the size of the total area used for nearby caching (i.e. the area where we could directly observe caching), we estimated the 100% utilization distribution for all caching observations of nearby caches from all individuals. Next, we calculated the percentage of the total area used for caching by each individual.

To test whether the space use of individuals during caching was more separated from that of other ravens than during the rest of the

day, we also calculated the 95% utilization distribution of each individual's space use during the day outside of feeding events. Then, we calculated the spatial overlap of all dyadic combinations of individuals during caching and compared it with the spatial overlap of dyads outside the feeding events. We used the kernel density-based global two-sample comparison test for all dyadic combinations (Duong, Goud; Schauer, 2012). The test statistic gives the probability that the utilization distributions of two individuals (three-dimensional overlap) are from the same distribution (see also Loretto, Reimann et al., 2016). To test whether ravens have a lower overlap during caching than in other situations, we used for each dyadic combination the calculated P value as the response variable in a GLMM (family = beta, link = logit). We included the identities of the individuals being compared as a random factor and the context (caching versus locations outside feeding events) as a fixed factor.

Second, we quantified the mean direction to distant caches. For this analysis we again used only data collected at the wild boar enclosure, since the topography and the surrounding forest at the wolf enclosure strongly biased ravens' flight directions. For every individual with more than three observations we calculated the mean resultant length (Jammalamadaka & Sengupta, 2001) with the 'circular' r package (Agostinelli & Lund, 2017), which is a value ranging from 0 to 1, with 1 indicating that all flights went in exactly the same direction. The mean resultant length per individual was then used as the response variable in a generalized linear model (GLM, error distribution = beta, link = logit) with the following fixed factors: degree of site fidelity, age class and number of observations per individual. The latter parameter was included to control for the fact that mean direction is not simply influenced by the number of observations. We repeated the same analysis including only ravens that had been observed more than 12 times to avoid any bias from the low number of observed flight directions for some individuals.

Model validation and inference

All models were calculated using the statistical software R, version 3.5.3 (R Development Core Team, 2019). For GLMMs we used the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015) and for the GLM with beta distribution the package 'glimm4mb' (Fournier et al., 2012), respectively. For every model, we compared the second-order form of Akaike's information criterion (AICc) to account for small sample sizes, Hurvich & Tsai, 1989) with the AICc of the corresponding null (intercept) model. We thus made sure that the fixed factors better explain the variation of the response variable than the null model (i.e. $\Delta\text{AICc} \leq 2$) and controlled for the Type 1 error rate (Forstmeier & Schielzeth, 2011). We included an interaction term only if the AICc of the model with the interaction performed better than one without it. We examined the model residuals for homogeneity of variance, violation of normality assumptions or other departure from model assumptions and model fit using graphical methods (i.e. qq plot of residuals and random effects, fitted values versus residuals, Korner-Nievergelt et al., 2015).

For the inference of the GLMMs, we obtained Bayesian parameter estimates with their 95% credible intervals (CrI). We used improper prior distributions, namely $p(\beta) \propto 1$ for the coefficients, and $p(\sigma) \propto \frac{1}{\sigma}$ for the variance parameters. To get the posterior distribution we directly simulated 10 000 values from the joint posterior distribution of the model parameters using the function `sim` of the `r` package 'arm' (Gelman and Su, 2018). The 95% CrI represents an estimate for the mean with a probability of 0.95.

If one group's CrI does not overlap the mean of the other group, the groups can be considered different from each other. For regression slopes of continuous variables, we can assume a meaningful relationship if the 95% CrI does not include zero (Korner-Nievergelt et al., 2015). Besides the Bayesian posterior means and their respective 95% CrI, we also provide the posterior probability $P(\beta)$ of our hypotheses, i.e. the likelihood that the groups differ from each other or for regression slopes that the slope is larger than zero.

RESULTS

In the course of this study, we observed 74 marked ravens (33 adults, 18 subadults, 23 juveniles) on average on 23.8 days (range 1–93 days) at the feeding of wild boars and wolves. Of these, 21 were marked during the study and therefore could have been observed on 16–31 days (mean = 29.1), while all other ravens could have been present throughout the study period, i.e. they had been marked before the study started and were also seen in the area after it had finished. In total, we observed 74 individually marked ravens caching 500 times nearby and 1185 times flying away with food. Of these 74 ravens, 36 were never observed to cache nearby, 23 were never seen to cache at a distance and 18 were never seen performing either behaviour.

Effects on the Number of Caching Trips

Ravens with a higher degree of site fidelity (i.e. a longer period of being present at the study site) performed on average more caching trips per day (Table 1, Fig. 1). As predicted this effect was even stronger for foraging in the high-risk situation with a slope increase of 73.9% (95% CrI: 31.4–125.7%) compared to an increase of 38.8% (95% CrI: 9.7–74.9%) in the low-risk situation. Since the data were z -transformed for the analysis these values refer to the mean degree of site fidelity (60.2% of the days present in the study site) and an increase in the degree of site fidelity by one SD (29.4%). However, ravens made 58.8% fewer caching trips in the high-risk than in the low-risk situation (Table 1, Fig. 1). As expected, an increasing number of ravens at the foraging site had a decreasing effect on the number of caching trips; the probability of $P(\beta) = 1$ for the prediction of this effect shows that all 10 000 values simulated from the posterior distribution were lower than zero (Table 1). The data suggest with a likelihood of $P(\beta) = 0.991$ that adults performed more caching trips than juveniles and with a likelihood of $P(\beta) = 0.998$ that juveniles performed fewer caching trips than subadults (Table 1, Fig. 1).

When excluding all observations of the six territorial breeders, the results only slightly differ in the effect sizes (Appendix Table A1, Fig. A3). Further, we found the same effects using a logistic regression model to predict the probability of a caching trip (Appendix Tables A2, A3, Fig. A4, A5).

Nearby versus Distant Caching

We found that ravens with a higher degree of site fidelity were more likely to cache nearby (Table 2, Fig. 2), which was also true when excluding the territorial breeders (Appendix Table A4, Fig. A6). We found no effect of group size (approximated by the number of marked ravens) in both models with and without territorial individuals. Juveniles were more likely to cache food nearby than adults (i.e. the CrI of the log-transformed model

Table 1
Estimated model coefficients explaining the number of caching trips per individual and day

Parameter	Log-transformed model estimates			Back-transformed estimates as % change ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Hypothesis	$P(\beta)$
Intercept ^b	-1.025	-1.381	-0.67	-64.112	-74.865	-48.814	$P(A > J)$	0.991
Juveniles, J	-0.801	-1.467	-0.133	-55.103	-76.929	-12.455	$P(J > S)$	0.998
Subadults, S	0.246	-0.31	0.801	27.867	-26.692	122.884	$P(S > A)$	0.807
Degree of site fidelity, Sf	0.328	0.093	0.559	38.777	9.734	74.929	$P(Sf > 0)$	0.998
High-risk foraging, Hr	-0.731	-0.881	-0.58	-51.875	-58.577	-43.986	$P(Lr > Hr)$	1
No. of marked ravens, N	-0.32	-0.433	-0.202	-27.38	-35.173	-18.262	$P(N < 0)$	1
Sf*Hr ^c	0.216	0.054	0.375	24.132	5.557	45.447	$P(Sf*Hr > 0)$	0.995

The GLMM with Poisson error distribution includes the following explanatory variables: age class, degree of site fidelity, foraging site, number of marked ravens and the interaction between degree of site fidelity and foraging site. The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as log-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability $P(\beta)$ of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.294 and SD(N) = 5.402, referring to the centred parameters mean (Sf) = 0.602 and mean(N) = 20.061.

^b The intercept represents adults A and low-risk foraging Lr.

^c These estimates are relative to the effect of Sf (representing Lr); to calculate the absolute slope we add their posterior distributions on the log-scale leading to back-transformed estimates of 73.912% (credible intervals: 2.5% = 31.409%, 97.5% = 125.681%) for a 29.4% increase in site fidelity.

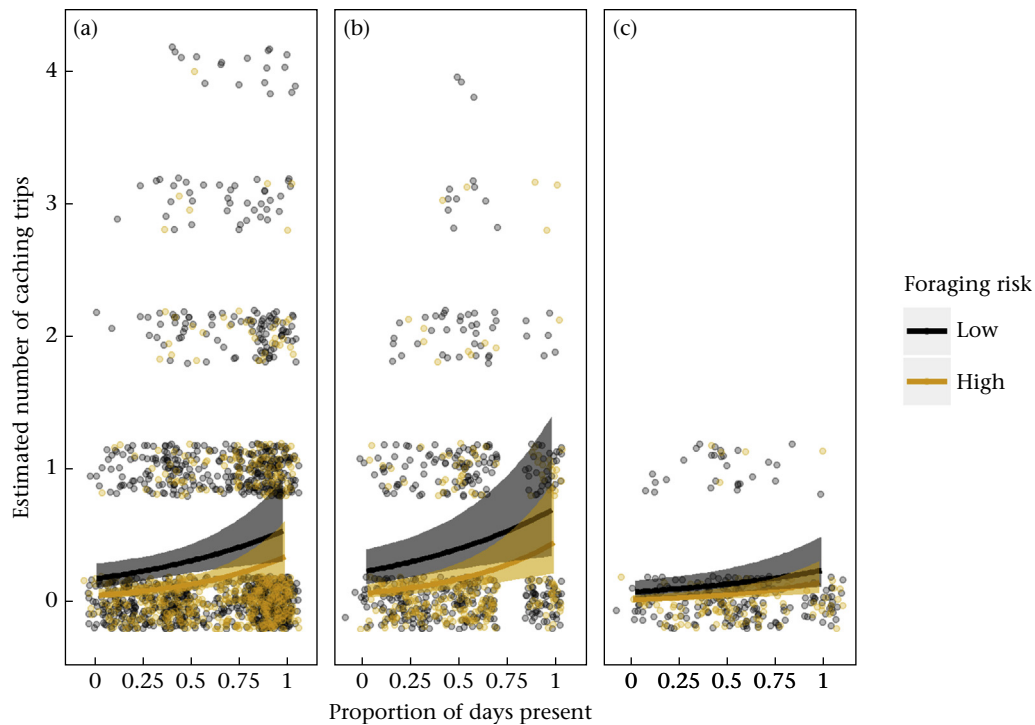


Figure 1. The effect of the proportion of days present at the foraging site (i.e. degree of site fidelity) on the number of caching trips in the low- versus high-risk situation for each age class. (a) Adults, (b) subadults and (c) juveniles. Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.1 in the x and y directions to better illustrate their distribution. We cropped the y axis above four caches, which excludes 11 cases of an adult raven caching more than four times per day.

estimates for juveniles (Table 2) does not include zero in the data set including territorial ravens). When excluding territorial individuals the CrI includes zero, which means that there is no longer a meaningful difference from adults (intercept); still, given the relatively high probability of $P(\beta) = 0.962$, we argue that there is a difference (Appendix Table A4). Similarly, subadults had a higher likelihood of caching nearby than adults ($P(\beta) = 0.96$), but again the CrI from the model estimates for subadults includes zero with and without territorial individuals. There was no difference between juveniles and subadults ($P(\beta) = 0.23$ for all data and $P(\beta) = 0.26$ when excluding territorial individuals; Table 2, A4, Fig. 2, A6).

Individual Preferences for Cache Locations

From 13 individuals we observed at least 15 nearby caches, sufficient to calculate the individual's caching area with kernel-based home range estimations (Fig. A7a). Again, the predictor variables (i.e. age class, degree of site fidelity and the number of observations per individual) did not improve the penalized model fit over the null model. This indicates that the variation in the size of each individual's caching area cannot be explained by any of these variables. Each individual used on average 27.51% of the total area for caching food (minimum = 8.97%, maximum = 57.40%).

Table 2
Model coefficients for the estimated probability of caching close to the foraging site per individual and day

Parameter	Log-transformed model estimates			Back-transformed estimates as probability ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Hypothesis	$P(\beta)$
Intercept ^b	-1.118	-1.903	-0.322	0.246	0.13	0.42	$P(A < J)$	0.998
Juveniles, J	1.828	0.241	3.413	0.862	0.56	0.968	$P(J > S)$	0.232
Subadults, S	1.176	-0.15	2.503	0.764	0.463	0.924	$P(S > A)$	0.96
Degree of site fidelity, Sf	1.011	0.421	1.597	0.733	0.604	0.832	$P(Sf > 0)$	1
No. of marked ravens, N	0.041	-0.198	0.277	0.51	0.451	0.569	$P(N < 0)$	0.365

The GLMM with binomial error distribution includes the following explanatory variables: age class, degree of site fidelity and number of marked ravens (data are only available for the low-risk situation). The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as logit-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability $P(\beta)$ of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.296 and SD(N) = 5.448, referring to the centred parameters mean (Sf) = 0.598 and mean(N) = 20.134.

^b The intercept represents adults A.

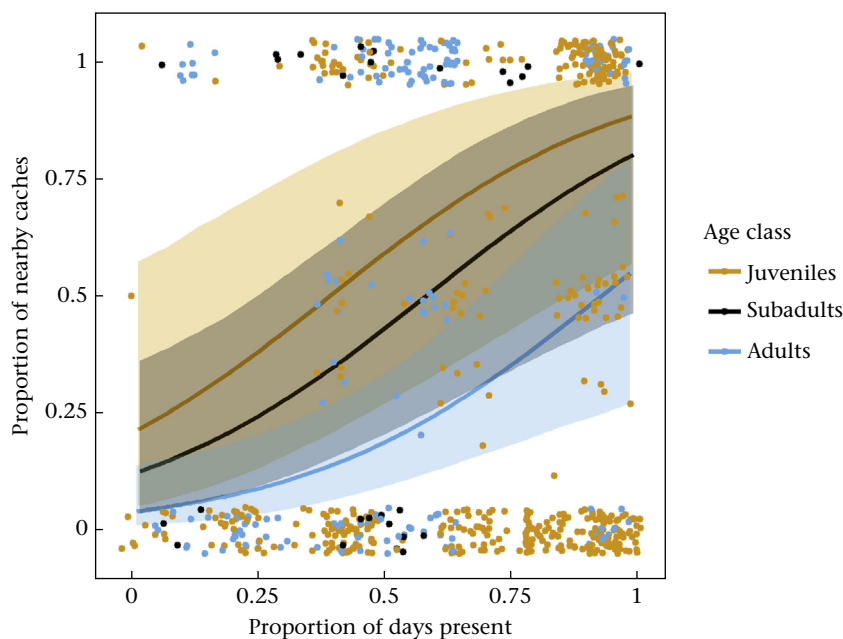


Figure 2. The effect of the proportion of days present at the foraging site (i.e. degree of site fidelity) on the probability of caching near the foraging site for each age class (data are only available for the low-risk situation). Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.05 in the x and y directions to better illustrate their distribution.

The model explaining the spatial overlap between individuals revealed that ravens overlapped more in their general space use during the day ($\beta_1 = 0.69$, $SE = 0.19$, $P < 0.001$) than during caching ($\beta_0 = -3.28$, $SE = 0.30$), although the area used during the day was much larger than that during caching (Fig. A7b). Note that the raw data for this model were P values generated from a test of the three-dimensional overlap of all dyadic combinations. In this case a smaller estimate means that the space use of a dyadic combination differed more from each other compared to dyads with larger estimates. In this context note that unmarked ravens were also present and including these would probably have changed the estimated overlap.

We analysed a data set of 739 observed flight directions (i.e. distant caches) from 35 individuals (number of observations per individual: minimum = 3, mean = 20.74, maximum = 99) leaving the wild boar enclosure. The full model with the predictor variables (i.e. age class, degree of site fidelity and number of observations per individual) did not improve the penalized model fit over the null model. This indicates that the variation in the mean resultant

length (Appendix Fig. A8) per individual cannot be explained by any of these variables. To avoid a potential bias from individuals with very few observations, we repeated this analysis for the 17 individuals with more than 12 observed flight directions (number of observations per individual: minimum = 14, mean = 37.53, maximum = 99) and found similar results.

DISCUSSION

Food-caching species can flexibly adjust the storage of food to various contexts (Emery & Clayton, 2001; Gerber, Reichman; Roughgarden, 2004; McNamara et al., 1990). In this study, we have shown that individual variation in movement patterns (i.e. short versus long periods of local settlement) affects food-caching behaviour in ravens. We found that individuals with a higher degree of site fidelity cached more food than individuals with a lower degree (i.e. short periods of local settlement). However, differences in local settlement were not related to the area used for caching and the direction of caching trips. We speculate that the observed

variation between 'locals' and infrequent 'visitors' may emerge from differences in the benefits gained from caching and/or differences in the success at acquiring food.

Nonbreeding ravens move through large areas where short- to long-distance movements alternate with short to long periods of temporary settlement around food sources (Loretto et al., 2017; Loretto, Schuster, et al., 2016; Webb, Marzluff, Hepinstall-Cymerman, 2012). We found that individuals with a higher degree of site fidelity (i.e. prolonged, local settlement) cached more often than infrequent visitors and they preferentially cached near the enclosure whereas visitors cached further away. These findings might reflect differences between locals and visitors in the benefits gained from food storage. Locals may benefit more from caching as they will remain in the area for a prolonged period and can use food storage as a long-term energy reserve (ravens can remember their cache locations for at least 2 weeks; Heinrich & Pepper, 1998). The relation between food storage and space use may be comparable to that in parids. Food-hoarding species such as marsh tits, *Poecile palustris*, are often highly territorial and live in stable social units whereas nonhoarding species such as great tits, *Parus major*, roam through large areas in loose flocks (Ekman, 1989). Thus, storing food for later consumption will benefit highly resident species but not vagrant ones.

More site-faithful individuals are also likely to be more familiar with the highly competitive foraging situation at this resource, where most food usually depletes within 10 min. In experimental set-ups in captivity it has been shown that ravens complete caching trips much faster in the presence of competitors than when alone (Heinrich & Pepper, 1998) and they reduce the time it takes to cover the caches with substrate (Bugnyar et al., 2016). Thus, ravens are expected to minimize the time spent caching as much as possible if resources deplete fast and competition is high. Individuals with high site fidelity might have more practice in dealing with the trade-off between caching safely and doing so quickly. We found that locals more often cached close to the food source than infrequent visitors and thus they probably saved travelling time and returned faster to the ephemeral food source. Unfortunately, we could not directly measure the duration of each individual's caching trip. Further, locals might be more familiar with the physical environment and thus better at using specific obstacles such as trees, rocks or small hills to prevent others observing them while caching, as indicated by observations in captivity (Bugnyar & Kotrschal, 2002).

Finally, local ravens might have an advantage over visitors directly in the acquisition of food, which subsequently allows them to engage more in caching activities. Locals cached more than visitors, and this effect was even stronger in the high-risk foraging situation with higher food quality (Fig. 1, Table 1). This indicates that locals may be better at judging the behaviour of the zoo animals which is particularly advantageous when stealing meat from the wolf enclosure where predation risk is high. Besides interspecific competition and predation risk, intraspecific competition can also play an important role. Ravens frequently socialize and regularly form social bonds as nonbreeders. Having bonding partner(s) is key for obtaining a high dominance rank (Braun & Bugnyar, 2012) and particularly advantageous during and after conflicts (Fraser & Bugnyar, 2010; Loretto, Fraser, & Bugnyar, 2012; Szpl; Ringler; Bugnyar, 2018). Being better embedded in the social environment, that is, having more and stronger social bonds, may give local birds another advantage over visitors in the competition for food. Highly site-faithful individuals might have a better knowledge of the rank relations with others which can help them avoid conflicts and they

may be better at judging when they can risk caching food without the cache being pilfered.

The propensity to cache food has a strong genetic component ('innate' behaviour) whereas other food storage behaviours are probably learned and can improve over time (Clayton, 1992, 1994; Heinrich & Pepper, 1998; Bugnyar et al., 2007). For instance, the risk of cache pilferage is a common reason for cache loss and can be prevented by learning to hoard further away or behind obstacles out of view of conspecifics. In our study, we found that juveniles cached less food than older individuals (Fig. 1, Table 1) which might be caused by the lack of experience and an increased risk of cache loss. In ravens, age can roughly predict dominance rank (Braun & Bugnyar, 2012), whereby older ravens will displace juveniles. This can hinder juveniles in accessing food in the first place (compare Pravosudov, Mendoza, & Clayton, 2003). Further, juveniles that manage to get and cache a food item face a high risk of pilfering as they cannot protect their caches against dominant birds and they may still have to learn about others' pilfering skills and, notably, how to avoid being seen by others when caching (Bugnyar et al., 2007).

Several bird species have developed strategies to prevent cache loss from conspecifics such as scatter hoarding, ceasing, reducing or delaying the onset of caching in the presence of potential thieves (Vander Wall & Smith, 1987), relocating caches in response to being observed (Emery & Clayton, 2001; Dally, Emery, & Clayton, 2006), hiding from view (Bugnyar & Kotrschal, 2002; Dally et al., 2006; Pravosudov, Roth II & LaDage, 2010) and making false caches (Heinrich & Pepper, 1998). For instance, black-capped chickadees, *Parus atricapillus* (Stone & Baker, 1989) and nuthatches, *Sitta europaea* (Carrascal & Moreno, 1993) cache less in the presence of others to minimize the risk of pilferage. We found similar results in ravens: caching activity decreased with an increasing number of conspecifics present (Table 1). The decrease could be a by-product of having limited access to food, that is, if individuals have to share the available food with many conspecifics, they get a smaller proportion for themselves and consequently have less to cache. Alternatively, it could be the result of an active decision where birds prefer immediate food consumption over caching since the risk of pilfering is higher. This active decision-making process has recently been linked to foraging success at the same study site (Gallego-Abenza, Loretto, & Bugnyar, 2019). In captivity, ravens have even demonstrated that they can adjust food-caching behaviour to the social context in various experimental settings (Bugnyar & Heinrich, 2006; Bugnyar; Reber & Buckner, 2016). Future studies will need to measure food intake under different social conditions and test whether ravens can flexibly switch between immediate food consumption and caching according to audience composition.

We hypothesized that ravens do not scatter their caches randomly in the valley but prefer some areas, for example where they have successfully cached in the past. We thus expected experienced ravens, that is, older and/or local birds, to show site preferences compared to inexperienced ravens. However, we found no indication that the caching area or the mean direction of caching trips differed between age classes or was affected by the degree of site fidelity. We found large individual differences in the direction of caching trips: some individuals were very consistent in their flight direction, while others varied extensively, which may reflect different caching strategies. In addition to the area used for caching, we calculated for each individual the area used throughout the day outside the main feeding events. The caching areas of ravens in the morning were less spatially overlapping than during the rest of the day, which indicates that the birds avoided each other more during

caching than during other daytime activities. Other studies have also revealed that nonbreeding ravens overlap considerably in space, especially at food sources or night roosts (Heinrich, 1988; Wright, Stone, & Brown, 2003; Loretto, Reimann et al., 2016). However, a recent radiotracking study on the same population found that particularly subadult and adult local nonbreeders show a high preference for individually distinct sites on a small scale (e.g. a group of trees), where they spend most of the day (Loretto, Reimann et al., 2016). We speculate that these areas could also represent their preferred cache locations, but the current data do not support this interpretation.

Conclusion

In this study, we have shown that differences in the degree of site fidelity can influence the food-caching behaviour of common ravens. We speculate that these differences may emerge from differences in the benefits gained from caching or in the access to food and/or may be influenced by locals being more experienced with the physical and social environment. However, the exact causes of the observed link between food-caching behaviour and different degrees of site fidelity remain to be tested. Many animals live in so-called fission–fusion societies, where group cohesion and individual membership change-over time (Aureli et al., 2008). Individuals differ in their tendency to remain in or leave a certain location or group (i.e. site fidelity) and the causes and consequences of these differences in movement patterns are not well understood (Nandintsetseg et al., 2019; Spiegel, Leu, Bull, & Sih, 2017; Teitelbaum & Mueller, 2019). What are the benefits of remaining in an area versus frequently visiting different sites and do these differences lie in the degree of mobility of individuals or in individual-specific traits or are they caused by environmental conditions? The variation in movement patterns probably causes individual differences in various behaviours such as the acquisition of resources (e.g. degree of food caching). Research is needed to better understand the causes of these differences and their consequences for individual fitness and population dynamics.

Author Contributions

M.L. conceived the study; K.B. collected the data; M.L. and K.B. analysed the data; K.B. and M.L. drafted the manuscript with comments from T.B.; T.B. acquired funding. All authors read and approved the final manuscript.

Data Availability

Data and R scripts used for the analysis are available at <https://osf.io/vmdja/>.

Declaration of Interest

None.

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Appendix

Table A1

Estimated model coefficients explaining the number of caching trips per individual and day as in Table 1 when excluding territorial breeders

Parameter	Log-transformed model estimates			Back-transformed estimates as % change ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Hypothesis	P(β)
Intercept ^b	-1.04	-1.408	-0.67	-64.647	-75.544	-48.816	P(A > J)	0.993
Juveniles, J	-0.842	-1.491	-0.176	-56.898	-77.479	-16.16	P(J > S)	0.999
Subadults, S	0.237	-0.292	0.765	26.721	-25.313	114.907	P(S > A)	0.81
Degree of site fidelity, Sf	0.248	0.024	0.478	28.116	2.431	61.356	P(Sf > 0)	0.984
High-risk foraging, Hr	-0.833	-1.007	-0.666	-56.524	-63.475	-48.604	P(Lr > Hr)	1
No. of marked ravens, N	-0.309	-0.424	-0.195	-26.613	-34.568	-17.737	P(N < 0)	1
Sf*Hr ^c	0.247	0.059	0.439	28.006	6.056	55.182	P(Sf*Hr > 0)	0.994

The GLMM with Poisson error distribution includes the following explanatory variables: age class, degree of site fidelity, foraging site, number of marked ravens and the interaction between degree of site fidelity and foraging site. The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as log-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability P(β) of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.289 and SD(N) = 5.408, referring to the centred parameters mean (Sf) = 0.602 and mean(N) = 20.313.

^b The intercept represents adults A and low-risk foraging Lr.

^c These estimate are relative to the effect of Sf (representing Lr); to calculate the absolute slope we add their posterior distributions on the log-scale leading to back-transformed estimates of 65.677% (credible interval: 2.5% = 24.414%, 97.5% = 118.314%) for an 28.9% increase in the degree of site fidelity.

Table A2
Model coefficients for the estimated probability of caching trips per individual and day

Parameter	Logit-transformed model estimates			Back-transformed estimates as probability ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	Hypothesis	Hypothesis	2.5%	97.5%	Prediction	$P(\beta)$
Intercept ^b	-0.669	-1.133	-0.207	0.339	0.244	0.448	$P(A > J)$	0.991
Juveniles, J	-0.815	-1.639	-0.009	0.307	0.163	0.498	$P(J > S)$	0.998
Subadults, S	0.321	-0.393	1.058	0.579	0.403	0.742	$P(S > A)$	0.807
Degree of site fidelity, Sf	0.386	0.075	0.689	0.595	0.519	0.666	$P(Sf > 0)$	0.998
High-risk foraging, Hr	-1.178	-1.408	-0.955	0.235	0.197	0.278	$P(Lr > Hr)$	1
No. of marked ravens, N	-0.445	-0.61	-0.275	0.391	0.352	0.432	$P(N < 0)$	1
Sf*Hr ^c	0.361	0.126	0.595	0.589	0.531	0.645	$P(Sf*Hr > 0)$	0.995

The GLMM has the same structure as the model for Table 1 but a binomial instead of a Poisson error distribution and includes the following explanatory variables: age class, degree of site fidelity, foraging site, number of marked ravens and the interaction between degree of site fidelity and foraging site. The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as log-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability $P(\beta)$ of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.294 and SD(N) = 5.402, referring to the centred parameters mean (Sf) = 0.602 and mean(N) = 20.061.

^b The intercept represents adults A and low-risk foraging Lr.

^c These estimates are relative to the effect of Sf (representing Lr); to calculate the absolute slope we add their posterior distributions on the logit-scale leading to back-transformed estimates of 0.677 (credible interval: 2.5% = 0.594, 97.5% = 0.751) for an 29.4% increase in the presence pattern.

Table A3
Model coefficients for the estimated probability of caching trips per individual and day as in Table A2 when excluding territorial breeders.

Parameter	Logit-transformed model estimates			Back-transformed estimates as probability ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	Hypothesis	Hypothesis	2.5%	97.5%	Prediction	$P(\beta)$
Intercept ^b	-0.709	-1.197	-0.218	0.33	0.232	0.446	$P(A > J)$	0.981
Juveniles, J	-0.871	-1.677	-0.039	0.295	0.158	0.49	$P(J > S)$	0.994
Subadults, S	0.299	-0.408	0.996	0.574	0.399	0.73	$P(S > A)$	0.791
Degree of site fidelity, Sf	0.305	0.009	0.606	0.576	0.502	0.647	$P(Sf > 0)$	0.978
High-risk foraging, Hr	-1.193	-1.441	-0.945	0.233	0.191	0.28	$P(Lr > Hr)$	1
No. of marked ravens, N	-0.428	-0.593	-0.259	0.395	0.356	0.436	$P(N < 0)$	1
Sf*Hr ^c	0.33	0.076	0.588	0.582	0.519	0.643	$P(Sf*Hr > 0)$	0.994

The GLMM has the same structure as the model for Table 1 but a binomial instead of a Poisson error distribution and includes the following explanatory variables: age class, degree of site fidelity, foraging site, number of marked ravens and the interaction between degree of site fidelity and foraging site. The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as log-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability $P(\beta)$ of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.289 and SD(N) = 5.408, referring to the centred parameters mean (Sf) = 0.602 and mean(N) = 20.313.

^b The intercept represents adults A and low-risk foraging Lr.

^c These estimates are relative to the effect of Sf (representing Lr); to calculate the absolute slope we add their posterior distributions on the logit-scale leading to back-transformed estimates of 0.652 (credible interval: 2.5% = 0.567, 97.5% = 0.731) for an 28.9% increase in the presence pattern.

Table A4
Model coefficients for the estimated probability of caching close to the foraging site per individual and day when excluding territorial breeders

Parameter	Log-transformed model estimates			Back-transformed estimates as probability ^a			Posterior probability of the hypothesis being true	
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Hypothesis	$P(\beta)$
Intercept ^b	-0.678	-1.415	0.057	0.337	0.195	0.514	$P(A < J)$	0.962
Juveniles, J	1.325	-0.148	2.787	0.79	0.463	0.942	$P(J > S)$	0.255
Subadults, S	0.817	-0.335	2.007	0.694	0.417	0.882	$P(S > A)$	0.912
Degree of site fidelity, Sf	0.959	0.43	1.497	0.723	0.606	0.817	$P(Sf > 0)$	1
No. of marked ravens, N	0.096	-0.132	0.329	0.524	0.467	0.581	$P(N < 0)$	0.204

The GLMM with binomial error distribution includes the following explanatory variables: age class, degree of site fidelity and number of marked ravens (data are only available for the low-risk situation). The table gives the mean, the 2.5% and the 97.5% quantiles of the posterior distribution as Logit-transformed model estimates and for an easier interpretation as back-transformed estimates. Further, we present the posterior probability $P(\beta)$ of the hypothesis being true, i.e. either one categorical variable is different from another one or the effect of a continuous variable is larger/smaller than zero.

^a Since the continuous variables were z-transformed for the analysis, the unit of the slope represents one SD of the parameter SD (Sf) = 0.292 and SD(N) = 5.461, referring to the centred parameters mean (Sf) = 0.598 and mean(N) = 20.393.

^b The intercept represents adults A.

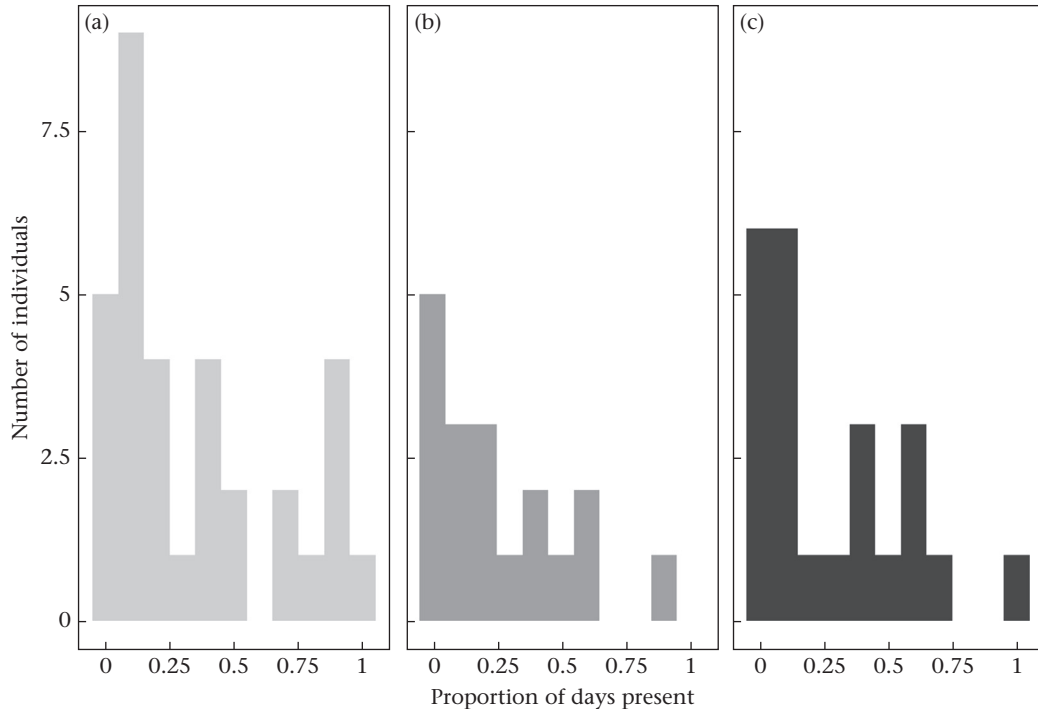


Figure A1. Histograms showing the distribution of the proportion of days present (i.e. the degree of site fidelity) for each age class. (a) Adults, (b) subadults and (c) juveniles.

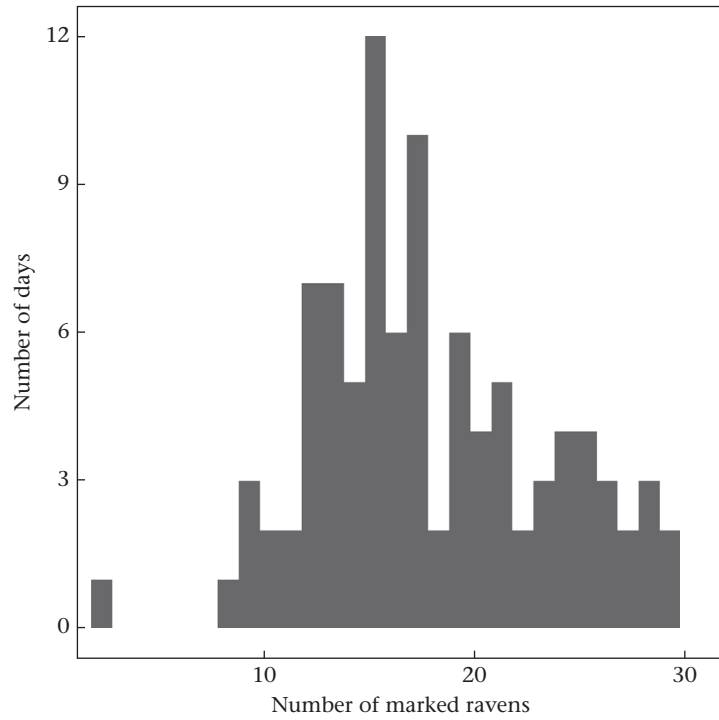


Figure A2. Histogram showing the number of marked ravens during observations at the daily feedings.

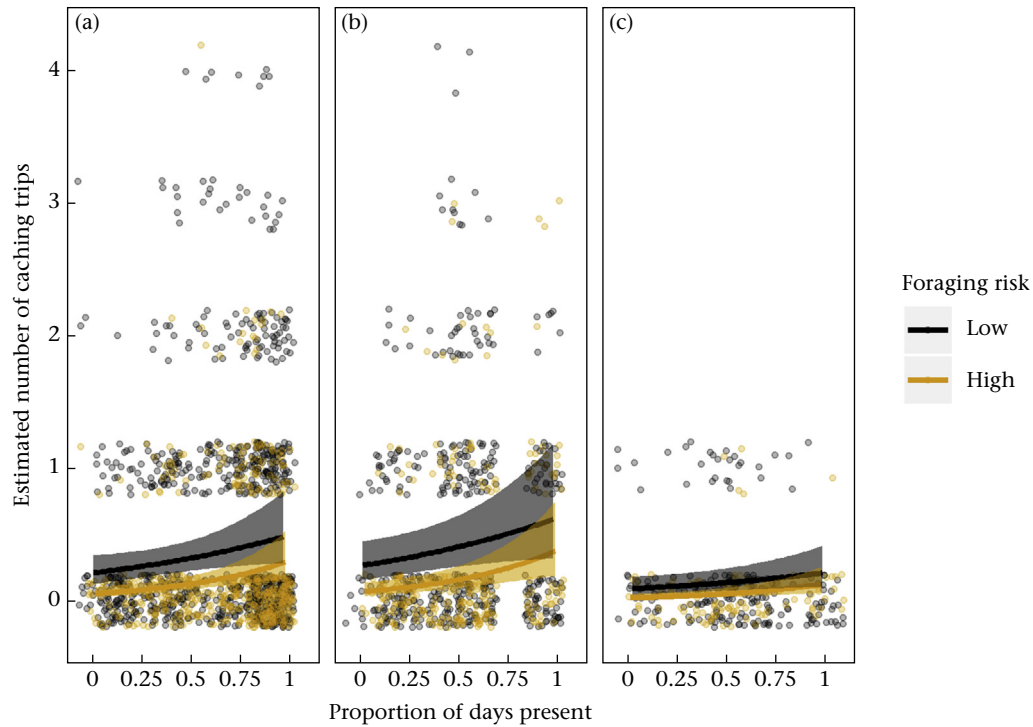


Figure A3. The effect of the proportion of days present at the foraging site (i.e. degree of site fidelity) on the number of caching trips in the low- versus high-risk situation separated for each age class as in Fig. 1 but excluding territorial breeders. (a) Adults, (b) subadults and (c) juveniles. Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.1 in the x and 0.2 in the y direction to better illustrate their distribution. We cropped the y axis above four caches, which excludes three cases where an adult raven cached more than four times per day.

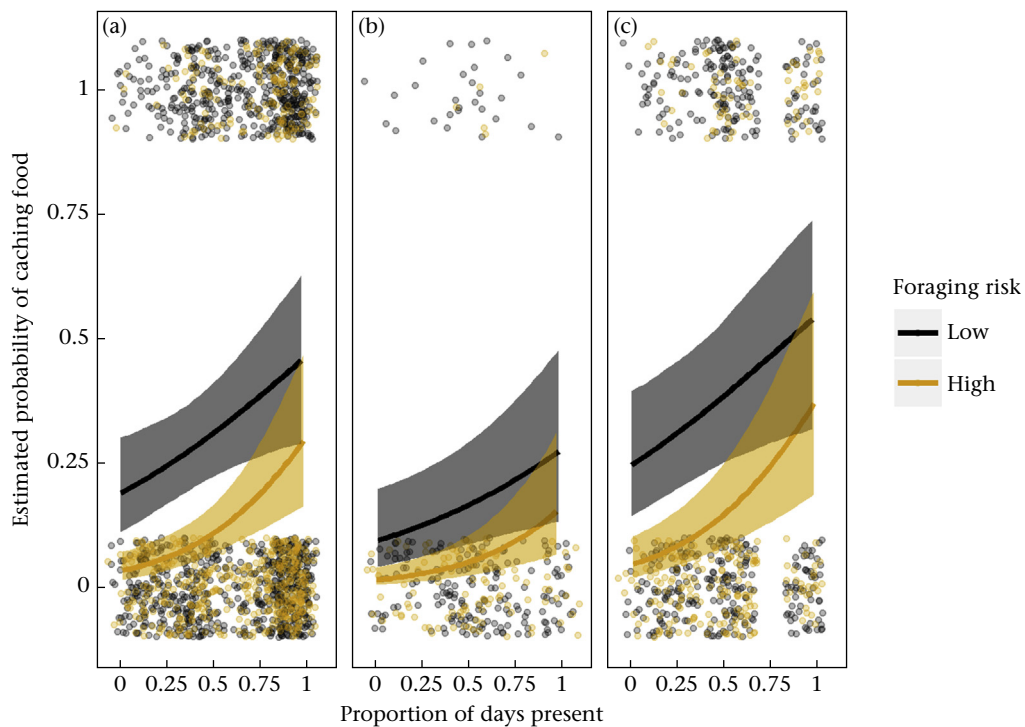


Figure A4. The effect of the proportion of days present (i.e. degree of site fidelity) at the foraging site on the probability of a caching trip in the low- versus high-risk situation separated for each age class. (a) Adults, (b) subadults and (c) juveniles. Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.1 in the x and y directions to better illustrate their distribution.

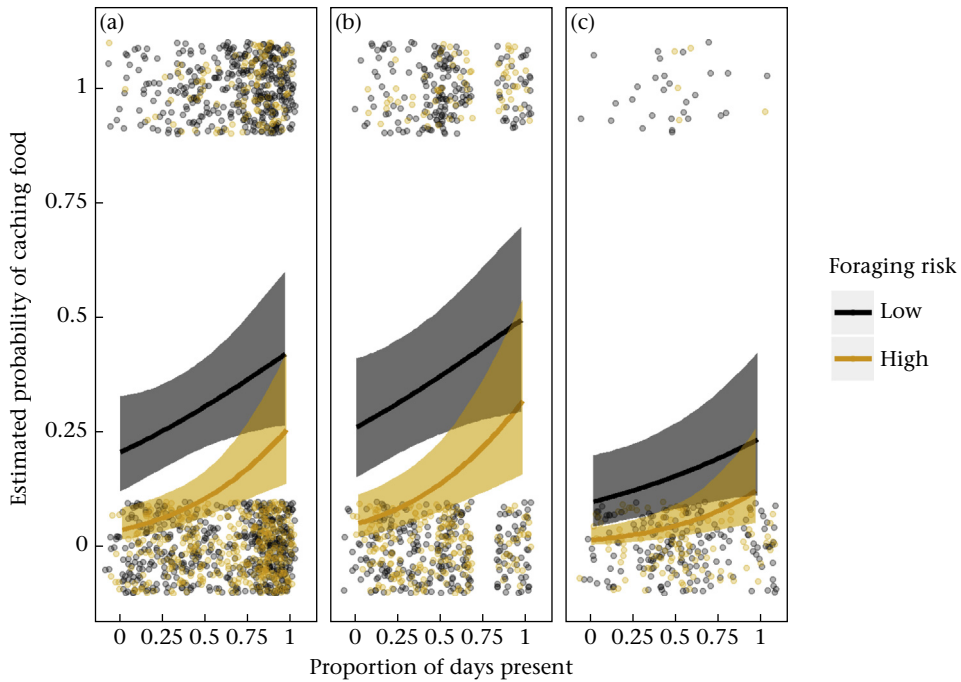


Figure A5. The effect of the proportion of days present (i.e. degree of site fidelity) at the foraging site on the probability of a caching trip in the low- versus high-risk situation for each age class as in Fig. A4 but excluding territorial breeders. (a) Adults, (b) subadults and (c) juveniles. Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.1 in the x and y directions to better illustrate their distribution.

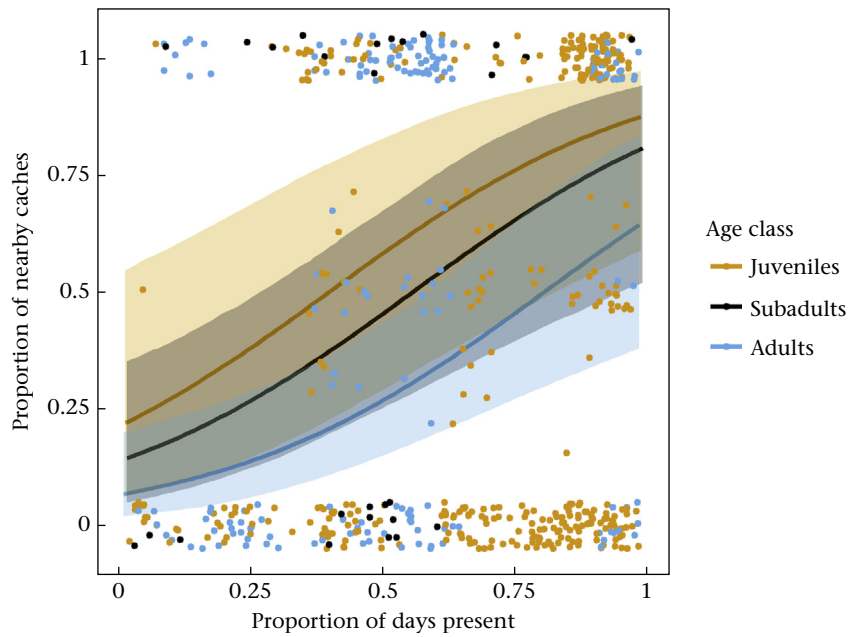


Figure A6. The effect of the proportion of days present at the foraging site (i.e. degree of site fidelity) on the probability of caching nearby for each age class (data are only available for the low-risk situation), as in Fig. 2 but excluding territorial breeders. Raw data and regression lines with 95% credible intervals are shown. Since many data points have the same value, we added a random noise of up to 0.05 in the x and y directions to better illustrate their distribution.

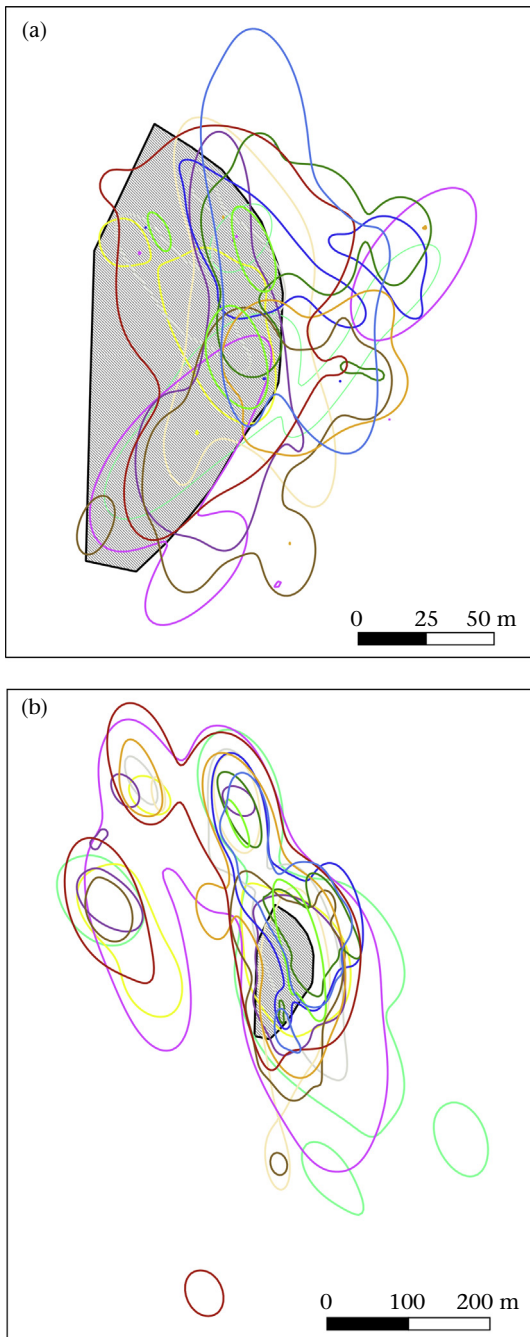


Figure A7. Map of the study site showing different coloured polygons which represent (a) the caching area of different individuals and (b) the area where the same individuals were observed during the day outside feeding events. For every raven with at least 15 observed caches we calculated the 95% utilization distribution of the caching area and the area used during the rest of the day using kernel density estimation. The grey area represents the wild boar enclosure as one of the main food sources for ravens at this study site.

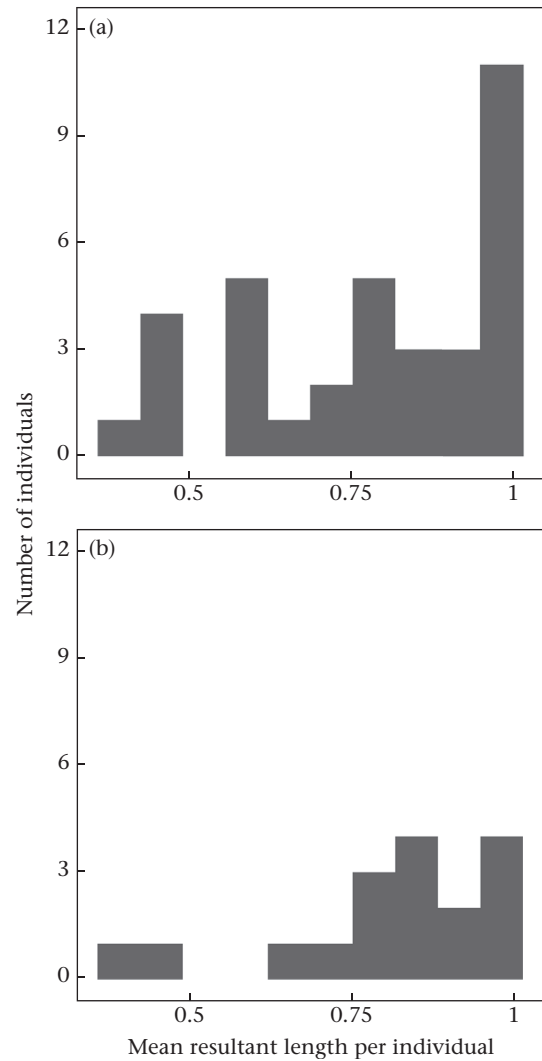


Figure A8. Histogram showing the mean resultant length for each individual with at least (a) three and (b) 12 observations of flying away with food from the wild boar enclosure. The mean resultant length ranges from 0 to 1, with 1 indicating that all flights went in the same direction. None of our predictor variables could explain the variance of the mean resultant length. See text for details of the models.