RESEARCH ARTICLE

Caching behaviour by red squirrels may contribute to food conditioning of grizzly bears

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Abstract

We describe an interspecific relationship wherein grizzly bears (*Ursus arctos horribilis*) appear to seek out and consume agricultural seeds concentrated in the middens of red squirrels (*Tamiasciurus hudsonicus*), which had collected and cached spilled grain from a railway. We studied this interaction by estimating squirrel density, midden density and contents, and bear activity along paired transects that were near (within 50 m) or far (200 m) from the railway. Relative to far ones, near transects had 2.4 times more squirrel sightings, but similar numbers of squirrel middens. Among 15 middens in which agricultural products were found, 14 were near the rail and 4 subsequently exhibited evidence of bear digging. Remote cameras confirmed the presence of squirrels on the rail and bears excavating middens. We speculate that obtaining grain from squirrel middens encourages bears to seek grain on the railway, potentially contributing to their rising risk of collisions with trains.

Keywords

Ursus arctos, *Tamiasciurus hudsonicus*, cache pilferage, food conditioning, caching behaviour

Introduction

As an alternative to foraging independently, many animals steal food from other individuals. This behaviour is widespread in birds and mammals, can occur within and among species, and includes the active pursuit of prey-carrying individuals as well as the pilfering of resources from hoards or caches. Such strategies may be occasional and opportunistic, such as for the kleptoparasitism exhibited by several gull species (*Larus* spp.; Brockmann and Barnard 1979, Giraldeau and Beauchamp 1999), and the reciprocal pilfering of caches that occur in several species of small mammals (Vander Wall and Jenkins 2003). These strategies can also occur as a prevalent form of foraging, as in magnificent frigatebirds (*Fregata magnificens*; Gilardi 1994, Vickery and De L Brooke 1994) or via specialization by some individuals, such as that which occurs in house sparrows (*Passer domesticus*; Barnard and Sibly 1981). Pilfering species often have size, mobility, or numerical advantages relative to the individuals that provide the food, including when wolves (*Canis lupus*) steal carcasses from solitary cougars (*Felis concolor*; Kortello et al. 2007). Host species often exhibit counter strategies to deter thieves, which include defence by red squirrels (Gerhardt 2005), scatter hoarding by western scrub-jays (*Aphelocoma californica*; Dally et al. 2006) and use of hiding material by cougars (Beier et al. 1995).

Inter-specific opportunities to steal food create the potential for food conditioning, which is defined simply as the capacity to associate food with another species (Mattson et al. 1992). Food conditioning of wildlife by people contributes to human-wildlife conflict all over the world (reviewed by Donaldson et al. 2012), especially in urban areas (Gehrt 2004). Bears (*Ursus* spp.) are particularly prone to food conditioning (Hopkins et al. 2012), which also makes them more likely to exhibit conflict behaviour (Hopkins et al. 2014a). Experience-based knowledge of this association by wildlife managers is the reason that preventing food conditioning has become a mainstay of wildlife management in protected areas (Herrero 1970, McCullough 1982).

Preventing food conditioning is especially difficult for anthropogenic products that are dispersed in time and space via sources that are ubiquitous and difficult to contain. One such situation is the deposition of agricultural products spilled by trains in the mountain parks of Canada which likely contributes to attraction and associated mortality of grizzly bears on the railway (Bertch and Gibeau 2010, Gangadharan et al. 2017). Wheat (*Triticum* spp.) and other agricultural seeds spill from the bottom-emptying hopper cars, which are prone to slow leaks and occasional larger spills (Dorsey 2011, Shepherd 2014). For this reason, Canadian Pacific, which owns the railway through Banff National Park, avoids siding trains in the park overnight and attempts to remove agricultural seed spills before they can attract bears and other wildlife (K. Roberge, personal communication).
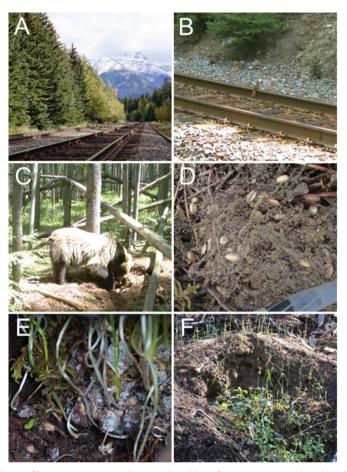
Here we explore the possibility that red squirrels contribute to the targeting of bears to agricultural seeds on the railway, where they are at risk of being hit by passing trains, by conditioning them to agricultural seeds in concentrated caches in their

middens. Our work was prompted by the discovery in fall 2013 of a squirrel midden containing agricultural seeds that was visited by a GPS-collared bear (S. Fassina and S. Pollock, personal communication). Although grizzly bears were already known to excavate red squirrel middens to consume the seeds of whitebark pine (*Pinus albicaulis*; Mattson and Reinhart 1997, Hamer and Pengelley 2015), we could find no reference in the literature to bears targeting any other food source in squirrel middens. Red squirrels are active year-round (Gurnell 1984), whereas grizzly bears in this area typically enter partial hibernation between November and March (Graham and Stenhouse 2014). The objectives of this study were to determine if (a) red squirrels occur at higher densities within 50 m of the railway than far from it (~200 m), (b) near middens contain agricultural seeds more often than far ones, and (c) bears visit and excavate middens to consume agricultural seeds. We based our transect positions on expectations that squirrels would collect food items mainly within a close vicinity (<50 m) of their middens (Hurly and Robertson 1987), and would be unlikely to occupy territories with radii of more than 100 m (Rusch and Reeder 1978).

Methods

The study was conducted in Banff (6,836 km²) and Yoho (1,313 km²) National Parks in Canada, along the 134 km section of the Canadian Pacific Railway that runs through the valley bottom (Figure 1A). The railway track within the parks runs from the western border of Yoho National Park (51°14'N, 116°39'W) to the eastern border of Banff National Park (51°8'N, 115°25'W). Common tree species in the study area were lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*). Whitebark pine occurs in our study area, but it is rare and typically is found only at high altitudes (Hamer and Pengelley 2015, Hamer 2017).

We selected 14 sites (11 in Banff and 3 in Yoho National Parks) at which we positioned paired transects of 500 m that were near the railway (15 m from the forest edge within forest cover, and a maximum of 50 m from the railway) and far from it (200 m from the railway within forest cover). Additionally, these 14 sites were chosen to exhibit continuous forest cover and to differ by less than 100 m in altitude between the pairs of transects. When necessitated by breaks in forest cover, the transect was broken into segments of forest-covered areas that summed to 500 m. For each transect, a predetermined route was followed using a hand-held global positioning system (GPS) unit.

On sunny days between August 12th to 28th 2014, we searched for and recorded squirrel activity within 10 m of the transect line, and recorded individuals and signs of both squirrels and bears. This created an area of 1 ha (20 × 500 m) that we searched for a 1 to 2 hour period. For squirrels, within 10 m of the transect line, we recorded visual sightings, acoustic detections, active primary middens, secondary middens and inactive (old) primary middens. We distinguished active from inactive middens by

Figure 1. Evidence of bears interacting with squirrel middens for access to agricultural seeds. **A** Railway in Banff National Park, where agricultural seeds are found on the tracks. **B** American red squirrel on the railway, taken with a remote camera on time-lapse settings **C** Grizzly bear excavating a squirrel midden where bear signs were previously recorded during a survey of an area with high bear use. The photo was taken with a remote camera on hyperfire settings **D** Unsprouted agricultural seeds, visibly wheat and lentil, found at an active midden near the railway that had been recently excavated **E** Moldy sprouted and unsprouted agricultural seeds, visibly chickpeas, wheat, flax, lentils and canola, at an excavated inactive primary midden near the railway **F** Sprouted agricultural plants at an inactive primary midden near the railway.

squirrel occupation (i.e. observed squirrel at midden, freshly clipped pine cones and/or fresh squirrel digging), and primary from secondary middens by size (>4m² vs <1m², respectively). For bears, we recorded evidence of bedding, digging, rubbed trees, claw scratching on trees, digging for ants (in the ground or logs), berry feeding, herbaceous feeding and presence of scat if they occurred within 5 m of a primary midden. If scat was found, we visually inspected it for cone bracts and needles (of pine or spruce) and agricultural seeds. At the start, middle, and end points of each transect, we recorded forest type and canopy cover. The forest type was quantified by the dominant species in

a count of trunks with a diameter at breast height (dbh) greater than 10 cm that were within 25 m of the plot centroid. We used a concave densiometer to quantify canopy cover. Both canopy cover and tree species are known to be predictors of squirrel density (Gurnell 1984). During data collection, the first author was responsible for searching for squirrel and bear signs, and measuring forest type and canopy cover, while a second observer was responsible for recording observations.

To confirm the presence of bears at middens and squirrels on the railway, we installed remote cameras (PC800 and PC900, RECONYX, Holmen, WI, USA) at 12 primary middens near the railway that had high rates of squirrel activity and nearby locations on the railway with a goal of confirming bear visitation to middens and squirrel visitation to the railway.

From October 8th to 21st 2014, we revisited the active primary middens we found during our first visit to sample them for agricultural seeds and record new bear activity associated with them. During this period there was not yet snow on the ground and we expected that squirrels would have completed caching cones, but bears would not yet be in hibernation (Kendall 1983). First, we recorded any new bear activity associated with the midden. Then, we used a post-hole digger ($\varnothing$=10 cm) to sample the contents up to 20 cm deep in middens by collecting five samples from small middens (4–20 m²), 10 samples from medium-sized middens (21–40 m²) and 15 samples from large middens (41–60 m²). Samples were taken from areas of the midden that contained the highest level of hoarding activity, categorized by large piles of stored food items, and areas of the midden that had recent squirrel digging. When possible, even numbers of samples were taken from areas with and without evidence of recent squirrel digging. We recorded the number of midden samples with agricultural seeds, as well as the type of seeds found in each midden. During this second visit, we went back to the sites in approximately the same order as the first visit, to maintain consistent time between visits. We placed each midden sample on a bright blue corrugated plastic board, and then systematically examined small subsets of the sample for grain presence until the whole sample had been visually examined. The blue colour of the board contrasted with the midden contents, so the contents within the sample were more easily distinguishable. We recorded the number of samples from a midden that contained grain, as well as grain type.

We revisited the active primary middens for a third time from September 18th to 20th 2015 to record new bear signs. During this visit, we also measured altitude at three points along the railway at each site, at approximately parallel locations to the start, middle and end points of the transects. Altitude was measured for its potential effect on food availability for squirrels and bears.

To overcome potential differences in our ability to detect active primary middens with increasing distance from the transect line, we fitted detection functions. During the first visit, a GPS point was taken at the edge of each midden closest to the transect line. We calculated the distance of the primary middens from transect line in ArcGIS 10.3.1 (ESRI 2015). Using the Distance package (Miller 2016) in R (version 3.2.3, R Core Development Team, Boston, MA, USA), we fit a detection function of the midden locations from the transect lines, and calculated the goodness-of-fit.

For the statistical analysis, we assessed the significance of each predictor variable alone and each combination of two predictor variables in a series of models for each response variable. In models with two predictor variables, we added an interaction term. To assess the significance of models in relation to one another, we used corrected Akaike's Information Criterion (AIC_C) values and average coefficients of the models. For each model set, we performed an analysis of variance (ANOVA) between the model with the lowest AIC_C value to the null model. Each model series used one response variable, these were squirrel sightings, active primary midden density, all (active and inactive) primary midden density, secondary midden density, agricultural seeds in middens, and bear digging in middens. In each series of models, transect location (near or far) was included as one of the predictor variables. Variance inflation factors (VIF) were used to test if there were correlated predictor variables (VIF > 5).

For squirrel sightings, active primary midden density, all primary midden density and secondary midden density, we used multiple generalized linear mixed models (GLMM), with site as a random effect. The squirrel sightings and active primary midden density were run with a poisson distribution, all primary midden density with a negative binomial distribution and secondary middens with a normal distribution. To obtain normally distributed residuals, we transformed the secondary midden counts by taking the natural log. For squirrel sightings and primary midden density, we included transect location, canopy cover and altitude as potential predictor variables. Visual squirrel sightings were only used for squirrel detections, owing to their correlation with acoustic detections (Kendall's tau = 0.42, P = 0.014). Red squirrels are common and have high detectability, so false zeros for visual sightings would likely be due to the shortness of the survey period relative to their temporary absence during home-range movements (Dénes et al. 2015). For secondary middens, we used size of active primary middens, as well as transect location, canopy cover and altitude.

For agricultural seed presence and bear digging in middens, we used a logistic regression. For agricultural seeds in middens, the potential predictor variables included in the models were transect location, canopy cover and altitude. For bear digging in middens, transect location, the proportion of samples with agricultural seeds detected and altitude were used as potential predictor variables. All analyses were performed in R using the packages Distance (Miller 2016), glmmADMB (Skaug et al. 2015) and lme4 (Bates et al. 2015).

Results

Among the 14 pairs of transects parallel to the railway, we detected a total of 221 primary middens and 9566 secondary middens with similar densities near and far from the rail (Table 1). Size of active primary middens and altitude with their interaction best predicted the number of secondary middens detected (χ^2 = 21.9, df = 3, P < 0.001). Despite a trend toward higher prevalence near the railway (Table 1), active primary middens were best predicted by their positive relationship with forest cover

Table 1. Mean ± SD of squirrel sightings, middens, midden samples containing agricultural products, middens with evidence of bear activity, and forest cover measured on 14 pairs of 500 m transects positioned near (< 50 m) and far (≈ 200 m) from the rail in Banff and Yoho National Parks in 2014. The differences between transect means are reported as ([near – far] / far * 100) with their significance assessed via generalized linear models using the best-fitting distribution with transect location as the single predictor variable.

Variable		Transect (Mean ± SD)		Difference (%)	χ^2	P
		Near	Far			
Squirrel density (per ha)	Sightings	1.86 ± 1.29	0.79 ± 0.80	135.4	6.26	0.012
Midden density (per ha)	Primary	8.78 ± 5.83	7.00 ± 6.11	25.4	2.83	0.432
	Primary - Active	1.71 ± 1.54	1.29 ± 1.20	32.6	0.86	0.408
	Primary - Inactive	7.07 ± 5.20	5.71 ± 5.90	23.8	2.02	0.523
	Secondary	394.21 ± 812.85	288.86 ± 546.79	36.5	1.81	0.36
Agricultural seeds in middens	Proportion of middens with seeds	0.58 ± 0.50	0.06 ± 0.24	866.7	14.42	<0.001
	Proportion of samples / midden with seeds	0.19 ± 0.23	0.02 ± 0.09	850	28.49	0.003
Bear activity at middens	All signs	0.29 ± 0.46	0.06 ± 0.24	383.3	4.2	0.04
	Digging	0.21 ± 0.41	0.00 ± 0.00	NA	6.1	0.014
	Digging and agricultural seeds	0.17 ± 0.38	0.00 ± 0.00	NA	4.79	0.029
	Bedding	0.00 ± 0.00	0.06 ± 0.24	NA	1.73	0.189
	Digging at inactive middens	0.09 ± 0.29	0.01 ± 0.11	800	6.06	0.014
Ecological variables	Forest cover	68.21 ± 12.1	71.96 ± 9.04	-5.2	98.75	0.354

(χ^2 = 10.1, df = 1, P = 0.002), whereas the sum of active and inactive primary middens was best predicted by the combination of forest cover and transect location (χ^2 = 10.1, df = 2, P = 0.006). Our overall ability to detect primary middens was very high (0.99 ± 0.16) with no evidence that detectability was affected by distance to the transect line (Kolmogorov-Smirnov test, χ^2 = 0.13, P = 0.477). Consequently, we did not include detectability in our model of midden abundance. Squirrel sightings were more prevalent near the railway (135.4% higher; Table 1), and best predicted by the combination of transect location and altitude (χ^2 = 11.9, df = 2, P = 0.003).

Of the 15 middens in which we detected one or more types of agricultural seeds or their sprouted plants, 14 were on transects near the railway and only 1 was located far from the railway (Table 1). The best predictors of agricultural seed presence in middens was transect location and forest cover (χ^2 = 16.9, df = 2, p < 0.001). These middens revealed a wide variety of seed types, primarily canola (*Brassica* spp.) and wheat (*Triticum aestivum*), but also including sprouted wheat, soybean (*Glycine max*), canary seed (*Phalaris canariensis*) and sulfur pellets. Agricultural seeds were found in 18.6% of midden samples (n = 180) near the railway, and only 2.2% of midden samples (n = 135) far from the railway.

We detected evidence of bear activity at seven active middens in 2014, six of which were on transects near the railway (Table 1; for video evidence see Suppl. material 1).

Of the active middens near the railway with bear signs of any sort, five showed evidence of bear digging, which reached up to 1m in depth (Figure 1C). Four of these middens contained agricultural products when the midden samples were taken (Figure 1D). The midden near the railway with non-digging bear signs exhibited a bear scat on its surface containing wheat and sulfur pellets. The single active midden with bear signs far from the railway was a bedding site, and no agricultural seeds were observed. The proportion of samples with agricultural seeds in middens and transect location best predicted digging by bears (χ^2 = 10.7, df = 2, P = 0.005). Remote cameras at squirrel middens confirmed that grizzly bears excavated the middens (see video in Suppl. material 1). When we revisited previously active middens in 2015, we found evidence of bear activity at two middens, one near the railway (where there was digging and sprouted canola) and one far from the railway (which had been used for bedding).

Discussion

The purpose of this study was to determine whether caching of agricultural seeds by red squirrels could potentially contribute, via food conditioning, to the risk of train strikes on grizzly bears foraging for spilled grain on a railway. Our results suggest it might. Red squirrels were 2.4 times more prevalent near than far from the railway, and 14 of the 15 middens where we detected agricultural seeds were located on the near transects. Squirrels on the railway were observed harvesting grain, and we recorded digging by grizzly bears only at middens near the railway where they appeared to target agricultural seeds.

The higher density of red squirrels visually detected near the railway was likely caused by the food supplement afforded by spilled agricultural seeds. Caching behaviour is generally responsive to habitat conditions (Dally et al. 2004, Tsurim and Abramsky 2004), and supplemental food typically results in an increase in population density (Boutin 1990). Supplemental food can increase the density of red squirrels by 3-4 times, in turn, increasing recruitment (Sullivan 1990). Unlike squirrel sightings, primary midden density was not statistically different between the transect locations. An explanation for this could be that the transect area near the railway was closer to the forest edge than where high densities of primary middens occurred. In our study, secondary middens were 36% more prevalent near than far from the railway, which might have been an adaptation to reduce losses to pilfering by bears or conspecifics, or a response to greater food availability. Smaller caches and scatter-hoarding appear to reduce the rate of pilfering in both birds (Brodin and Ekman 1994) and mammals (Daly et al. 1992, Geluso 2005). Previous studies have found scatter-hoarding rodents, including squirrels, also maintain smaller caches when food is more abundant (Moore et al. 2007), which was not supported in our study.

We observed that agricultural seeds were collected from the railway by red squirrels, and we detected them considerably more often in middens that were near the railway (Figure 1B). Scatter-hoarding rodents preferentially cache valuable food items

and transport them farther distances than items of lesser value (Moore et al. 2007). Although red squirrels typically collect items within 10 m of their middens (Hurly and Lourie 1997), the distance between the railway and middens in the near transect was an average of 39.1 m. The single midden that was 200 m from the railway with agricultural seeds may have resulted from intraspecific pilfering.

The fact that we observed digging by grizzly bears in middens only near the railway and almost exclusively where we also detected agricultural seeds suggests that bears smell the seeds and target seed-containing middens. The digging signs we observed were consistent with a targeted search, although at least one observation on transects and several incidentally while doing field work suggest that bears also use middens as bed sites. We found no evidence that bears were affected by the remote cameras set up at middens near the railway, such as photos of bears approaching or manipulating the cameras. Bears are notoriously opportunistic in their foraging habits (Gunther et al. 2014) and quickly adapt to target more abundant resources (Hopkins et al. 2014b), particularly when traditional food sources are rare (Fortin et al. 2013). In our study area, bears rely extensively on Canada buffaloberry (*Shepherdia canadensis*), which exhibits large inter-annual variation in productivity (Hamer and Herrero 1987). Because our data were collected mainly in 2014, which was a particularly poor berry year (Pollock et al., *in review*), bear use of middens may have been unusually high.

Additional evidence suggests that excavating squirrel middens may be a widespread behaviour by bears in this region and potentially other ones. A larger concurrent project, of which this study was a part, recorded extensive use of the forested areas near (< 1000 m) the rail by grizzly bears wearing GPS collars. Site investigations at locations with multiple fixes, detected excavated squirrel middens at 12 / 58 (21%) of these locations in 2014 and 4 / 31 (13%) in 2015, in total representing at least 9 individual bears (unpublished data). The excavated sites were attributed to 9 / 19 (47%) of the collared bears in the study area. Our remote cameras (which were not set up at all middens), captured photos of 2 different grizzly bears (one collared and one uncollared) digging into different middens. Bears in our study area also excavate middens at higher altitudes to obtain whitebark pine seeds (Hamer and Pengelley 2015, Hamer 2017), and that behaviour might easily facilitate foraging at lower altitudes for agricultural seeds. However, it seems likely that there are individual behavioural differences among bears in the region which could vary the degree to which they are food conditioned to consuming grain in squirrel middens.

Our study has identified several topics that could be investigated in future studies. One goal could be to determine whether black bears (*Ursus americanus*) contributed to some of the digging we observed, although this species is less adapted to digging than grizzly bears (Mattson and Reinhart 1997). Another possibility is that bears digging in middens were attempting to catch squirrels or small rodents that might try to pilfer from them, or other available food items. Grizzly bears routinely dig for Columbian ground squirrels (*Urocitellus columbianus*; Munro et al. 2006), and we observed many bear digging sites along the railway in association with ground squirrel burrows. Equal focus could be applied to active and inactive middens, as we observed bear digging at inactive

middens with agricultural products visible during our first visit and through incidental observations (Figure 1E–F). Further investigations could also quantify the potential food value and volume of agricultural seeds obtained by bears from squirrel middens.

Conclusions

In summary, we have shown red squirrels frequent the railway, occur at higher densities along it, and cache several kinds of spilled agricultural seeds in their middens. We documented excavations of squirrel middens by grizzly bears that appear to be targeting agricultural seeds and comparable behaviour was evident in half of the collared bears in our study area. Together, these results suggest that squirrels may contribute, via food conditioning, to the tendency for bears to target grain on the railway, which may subsequently increase their risk of being struck by trains. In addition to conditioning bears to target grain, the caching of agricultural seeds by red squirrels, as well as their consumption by bears and other species, may cause the spread of these agricultural species in Banff and Yoho National Parks. Our study exemplifies the complexity of both food conditioning and vulnerability to train strikes associated with spilled agricultural products on railways. The only feasible mitigation for these effects is likely to reduce spillage from hopper cars via careful attention to loading and gate maintenance.

Acknowledgements

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Supplementary material 1

Video of grizzly bear digging into a red squirrel midden
Authors: Julia Elizabeth Put, Laurens Put, Author, Colleen Cassady St. Clair
Data type: MPG video file

Link: https://doi.org/10.3897/natureconservation.21.12429.suppl1

Supplementary material 2

Data collected along transects
Authors: Julia Elizabeth Put, Laurens Put, Author, Colleen Cassady St. Clair
Data type: specimens data

Link: https://doi.org/10.3897/natureconservation.21.12429.suppl2