



Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing



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Prey consumption forms a large part of prey-handling time, and knowledge of where prey is ingested can inform management of predator–prey systems. Safeguarding habitats that promote prey consumption could enhance populations of facultative or obligate carnivores of conservation concern. We investigated habitat characteristics at 124 sites where radiocollared adult grizzly bears, *Ursus arctos* ($N = 9$) consumed ungulates, and we contrasted these sites with paired random sites. We developed a priori models incorporating the potential effects of ungulate and plant food distribution as well as risks of detection by humans and other carnivores on consumption site choice, and evaluated which factors best explain grizzly bear food-caching behaviour. Ungulates were consumed in forested areas, close to edges, and where horizontal cover was high, whereby vegetation impeded visibility of the ungulate carcass. Distance to roads had no effect on the distribution of prey consumption sites, but carcasses were further from trails than expected. Models incorporating presence/absence of key non-ungulate bear foods had little weight of evidence ($w_i \leq 0.01$). Food-caching behaviour did not appear to be related to variation in resource availability or risk of food spoilage but was significantly influenced by prey size. Although bears chose sites that minimized detection risk, spent more time at larger carcasses and cached 75.9% of ungulates, 50% of consumption sites had other carnivore sign, which was more likely to be present at large carcasses.

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To avoid food shortage and store food securely, some animals have developed caching as an evolutionary strategy integral to foraging behaviour (Smith & Reichman, 1984). In mammals, caching has been documented for various species, such as Arctic fox, *Vulpes lagopus* (Careau, Giroux, & Berteaux, 2007; Careau et al., 2008), badger, *Taxidea taxus* (Michener, 2000), otter, *Lutra lutra* (Lanszki, Molnar, & Molnar, 2006) and wolverine, *Gulo gulo* (Wright & Ernst, 2004). In theory, caching should preserve food for later use while minimizing detection by competitors. In the case of food caching by predators, scavenging by other carnivores probably diminishes the future reward of food caching, and other aspects could also affect the benefits of caching.

One explanation for the occurrence of caching behaviour relates to food consumption time, stating that caching is more likely for resources that take a long time to consume (Careau et al., 2007). Alternative explanations consider caching to be a strategy used for securing food during resource pulses (Careau et al., 2008) or during

harsh environmental conditions associated with food shortage (Lanszki et al., 2006). On the other hand, animals may cache food to avoid food spoilage, which is more likely when ambient temperatures and humidity are high, such as at low elevations and on moist sites (Bischoff-Mattson & Mattson 2009). Investigations on determinants of caching as well as caching effectiveness have seldom been performed, particularly for large carnivores in forested environments where direct observations are difficult. Moreover, basic knowledge about the choice of habitat where meat is consumed and the duration of prey consumption is also scarce for large carnivores because of their wide-ranging patterns, and because of monitoring and safety challenges.

Because human activities have the potential to alter animal behaviour profoundly (Caro & Sherman, 2012), researchers working at the interface of behaviour and conservation often want to know if and how wildlife behaviour is affected by humans (Blumstein & Fernández-Juricic, 2004). When large carnivores are among the wildlife potentially affected, understanding their behaviour is necessary to mitigate risk of conflict with humans. For example, if prey consumption by carnivores is lengthy and occurs in areas with human access, it could lead to conflict with people, which is more likely for carnivores that defend carcasses such as African lions,

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Panthera leo (Kissui, 2008) or grizzly bears, *Ursus arctos* (Quigley & Herrero, 2005). Although carnivores can adjust behaviourally to reduce risk of encounters with humans (Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012), longer consumption times for solitary predators such as cougars, *Puma concolor* (Knopff, Knopff, Warren, & Boyce, 2009) may set these animals/individuals more at risk of conflict at the consumption site than group-living carnivores that have shorter consumption times (Webb, Hebblewhite, & Merrill, 2008). Improved knowledge of habitats where carnivores consume prey along with prey consumption times can be used proactively to prevent dangerous encounters, such as by implementing restrictions on human access.

Being an essential component of predator–prey relationships, prey consumption time (kill handling time/time spent at kill) is also important theoretically (Holling, 1959; Merrill et al., 2010), allowing parameterization of optimal foraging and patch residency models for carnivores. Technological advancements enable straightforward estimation of consumption time from GPS radio-telemetry (Merrill et al., 2010). Studies that employ this technology can decrease the bias associated with documenting prey consumption time by direct observations in open environments or during daytime only (Knopff et al., 2009; Webb et al., 2008).

Because of wide-ranging movements, seasonal habitat requirements, low reproductive rates and risk of conflict with people (Mattson & Merrill, 2002; Weaver, Paquet, & Ruggiero, 1996), the grizzly bear has declined throughout much of its range. In west-central Alberta, grizzly bears are designated as threatened and persist at low densities at the interface between largely pristine mountainous areas and heavily developed foothills. Similar to other interior populations of grizzly bears (Jacoby et al., 1999; Mowat & Heard, 2006; Zager & Beecham, 2006), ungulates form an important part of the diet of Alberta bears in late spring and early summer, during ungulate calving and fawning (Munro, Nielsen, Price, Stenhouse, & Boyce, 2006), with ungulate consumption occurring throughout the active season (outside denning) (Mattson, 1997; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003).

Despite their importance to the demography of ungulate populations (Middleton et al., 2013), we know very little about the behaviour of brown bears at kill sites, particularly in forested environments. Records of caching by grizzly bears and their Eurasian conspecifics have been opportunistic and sparse. For example, Elgmork (1982) identified 16 meat caching sites by brown bears in Scandinavia, where the bears dug the ground and dragged litter, moss and debris on top of prey. Barker and Derocher (2009) observed two caches of broad whitefish, *Coregonus nasus*, made by grizzly bears in barren habitat in Canada.

Our goals were to (1) evaluate competing hypotheses for explaining the motivation behind caching behaviour, (2) identify habitats conducive to ungulate consumption by grizzly bears, (3) investigate consumption times by grizzly bears and (4) describe inter- and intraspecific ungulate carcass sharing by grizzly bears and other carnivores. We made the following predictions. Bears should (1) be more likely to cache large prey, because a large carcass contains sufficient meat to warrant storage and later consumption (prey size hypothesis), (2) be more likely to cache during the seasonal resource pulse of ungulate calving, because calves are available during a limited period and their storage would enable feeding at later times (resource pulse hypothesis), (3) be less likely to cache at lower elevations, under low vertical cover and on wet sites to avoid spoilage of meat (resource spoilage hypothesis), and (4) preferentially consume ungulates in areas with high probability of presence of ungulates and other bears foods (in high forage areas) but consume carcasses away from roads, trails and habitat edges, and where horizontal cover is high, to minimize detectability by other predators. We also predicted that (5) consumption

time would be longer for larger-bodied ungulates, because more meat intake is generally available from larger carcasses, and (6) cached ungulates would be less likely to be visited by predators other than bears compared to ungulates that were not cached, because caches are presumably difficult to locate; however, larger carcasses should be more likely to be visited by nonbear carnivores, because large prey is difficult to conceal entirely through caching.

METHODS

Study Area

The 3200 km² study area was located in west-central Alberta, Canada at the interface between the eastern slopes of the Rocky Mountains and foothills (Fig. 1). Elevation and ruggedness are greater in the western section, which is mountainous, whereas the eastern section is characterized by rolling hills. The predominant natural land cover is coniferous forest composed of white (*Picea glauca*), black (*Picea mariana*) and Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), balsam (*Abies balsamea*) and subalpine fir (*Abies lasiocarpa*). Mixed and deciduous forests also occur in the study area, primarily at lower elevations and on sunny south facing slopes, and include trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*).

Grizzly bear foods in the study area are diverse (Nielsen, McDermid, Stenhouse, & Boyce, 2010), with the primary foods being sweetvetch roots (*Hedysarum* spp.), a variety of herbaceous plants and berries as well as ungulates, including elk, *Cervus elaphus*, moose, *Alces alces*, white-tailed deer, *Odocoileus virginianus*, mule deer, *O. hemionus*, and bighorn sheep, *Ovis canadensis* (Munro et al., 2006). Grizzly bears coexist with wolves, cougars and American black bears, *Ursus americanus*, as well as mesocarnivores such as coyotes, *Canis latrans*, Canada lynx, *Lynx canadensis*, and red fox, *Vulpes vulpes*.

The eastern side of the study area is primarily Crown (public) land with human activities including extensive recreation (All Terrain Vehicles, hunting, horseback riding, mountain biking, hiking and camping), as well as open-pit coal mining, forest harvesting, oil and gas development. The western side is primarily protected provincially (Whitehorse Wildland Park) and federally (Jasper National Park), with a small amount of Crown lands, two reclaimed coal mines, one operational mine and a cement quarry with employees commuting daily. Only one permanent human settlement (Cadomin) with a population of 60 is present in the study area. Although no data were available on levels of human use, density of linear access features is high (Nielsen, Boyce, Stenhouse, & Munro, 2002), the area receives recreational users from nearby urban centres, and off-highway vehicle use is perceived as unsustainable (McFarlane, Stumpf-Allen, & Watson, 2007). The area is bordered to the north by a major highway, and the Crown lands have a complex network of roads and trails used by recreationists, oil, gas and forestry companies.

Data Collection

During spring/early summer and autumn 2008–2010 we captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on adult grizzly bears. With assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta), we used baited culvert traps, aerial darting from a helicopter and limited leg-hold snaring (Cattet et al., 2008) and attempted to capture bears on reclaimed mines, protected areas (Whitehorse Wildland Park) and Crown lands to reduce bias in sampling bears that might have used only one land designation. All bears were captured and handled according to

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