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Featured Article Due Nov 19

Consumption of Intentional Food Subsidies by a Hunted Carnivore

REBECCA KIRBY,[1] *Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*

DAVID M. MACFARLAND, *Wisconsin Department of Natural Resources, 107 Sutliff Avenue, Rhinelander, WI 54501, USA*

JONATHAN N. PAULI, *Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*

ABSTRACT Wildlife consumption of human foods is common and these subsidies can alter a species' behavior, demography, and interspecific interactions, and lead to conflicts with humans. Intentional food subsidies, including feeding or baiting of wildlife for viewing or hunting, can represent a large energy source. We studied consumption of bait for an American black bear (*Ursus americanus*) population in northern Wisconsin. Given the state's liberal baiting regulations, we hypothesized that bear baits would be highly available, and that bears would readily consume such baits within a hunting season. We documented the abundance of bear bait on forestlands, and quantified the diets of harvested black bears using stable isotopes and Bayesian mixing models to determine the relative contribution of human foods to individual and population diets. Baits occurred at $\geq$0.25 bait stations/km^2 on public lands, and bears ($n = 180$) were subsidized by these baits, which contributed to >40% of their diet. Our analysis of multiple tissue types with different turnover rates revealed that harvested bears were relying on subsidies throughout their lifetimes. Patterns of bait consumption were primarily influenced by age-sex class; adult males were the most reliant on human foods, followed by adult females. We found a high level of food subsidization in this bear population. We posit that the high density of bears in northern Wisconsin may be partly due to subsidies. Our results reveal how baits used for hunting can become an important resource for free-ranging bears and highlight the importance of considering potential consequences when bait is used in harvest management. © 2017 The Wildlife Society.

KEY WORDS anthropogenic effects, bait, black bears, foraging, stable isotopes, supplemental food, *Ursus americanus*.

Food subsidies for wildlife from human sources are a near-global phenomenon (Oro et al. 2013). The high availability and predictability of calorically rich subsidies can affect many aspects of an animal's biology: behavior (Yirga et al. 2012, Newsome et al. 2015), space use (Newsome et al. 2013), survival (Oro et al. 2008), population densities (Fedriani et al. 2001), interspecific interactions (Rodewald et al. 2011), and even community structure (Newsome et al. 2014*b*). Research has focused on human foods that are available to wildlife unintentionally, in the form of refuse and agricultural crops. The effects of intentional food subsidies have been less studied.

Supplemental feeding has been used to support declining or endangered populations (Ewen et al. 2014), reduce conflict with humans (diversionary feeding; Kubasiewicz et al. 2016), or enhance hunting or viewing of wildlife (Maljković and Côté 2011). In relatively intact landscapes, intentional subsidies principally take the form of baiting, a common method to increase success and selectivity of hunting game species (Putnam and Staines 2004). In the United States an estimated 2.8×10^{12} metric tons of bait is used each year in hunting (Oro et al. 2013). Because baiting can enhance reproduction (Ballari et al. 2015), increase human-wildlife conflicts (Steyaert et al. 2014), and spillover to non-target species (Bowman et al. 2015), understanding how a population responds to bait can be important for conservation and management.

American black bears (*Ursus americanus*) are opportunistic omnivores that readily use human foods (Merkle et al. 2013, Kirby et al. 2016). Reliance on subsidies, predominantly from refuse and crops, tends to increase in years of low natural food production (Baruch-Mordo et al. 2014, Johnson et al. 2015), mitigating food shortage effects and enhancing fecundity, but subsidies can also lead to increased conflict with humans and elevated adult mortality from lethal removal as nuisance bears (Beckmann and Lackey 2008). Black bears are hunted in 30 states in the United States, 12 of which allow baiting as a primary hunting method (Table S1, available online in Supporting Information). Typically, baits are high-caloric

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[1] *E-mail: kirbyr@gmail.com*

foods, which may include meat or fish, but are often high-sugar foods, such as cookies, donuts, and candies. Baiting regulations vary by state, but bear baits are deployed on average 23 days prior to the bear hunting season, and in 7 states hunters are limited in the number of baits they can deploy and maintain (e.g., 3 baits/hunter in Minnesota; Table S1). Wisconsin is unique, however, in its extended 145 days of baiting prior to the 35-day hunting season, from mid-April through early October, spanning virtually the entire active period for bears. Also, the state restricts bait to non-animal products. The Wisconsin Department of Natural Resources (WDNR) estimates >15 million L of bear bait is deployed throughout the state annually (Rees et al. 2014). In addition to bait piles intended for bears, shelled corn for deer baiting (Bowman et al. 2015) is also accessible to bears in the fall, but how much bears rely on either form of bait is unknown. It is unclear if the high availability of subsidies could be affecting individual behavior and the size of Wisconsin's bear population (Johnson 2007). In northern Wisconsin, the bear population is large (estimated population size = 20,400); it has grown on average 3.4% annually since 1988, although the growth rate has slowed in the last few years in response to increased harvest. Current bear density is estimated to be twice that of northeastern Minnesota or the Upper Peninsula of Michigan (Fig. 1; Garshelis and Tri 2015, Rolley et al. 2015, Michigan Department of Natural Resources 2016), both of which also use bear baiting, although have more restrictive baiting regulations.

We explored baiting effects as potentially contributing to the high population density of bears in northern Wisconsin. Given the duration and scale of baiting, we hypothesized that bait would be a substantial portion of bear diet, and that bait would be broadly consumed by bears within a season. To quantify the importance of bait, we estimated the density of baits on public lands and used stable isotope analysis of tissues from black bears in northern Wisconsin collected during the 2011–2013 hunting seasons to determine the extent that bears consume bait, and temporal variations in bear diet.

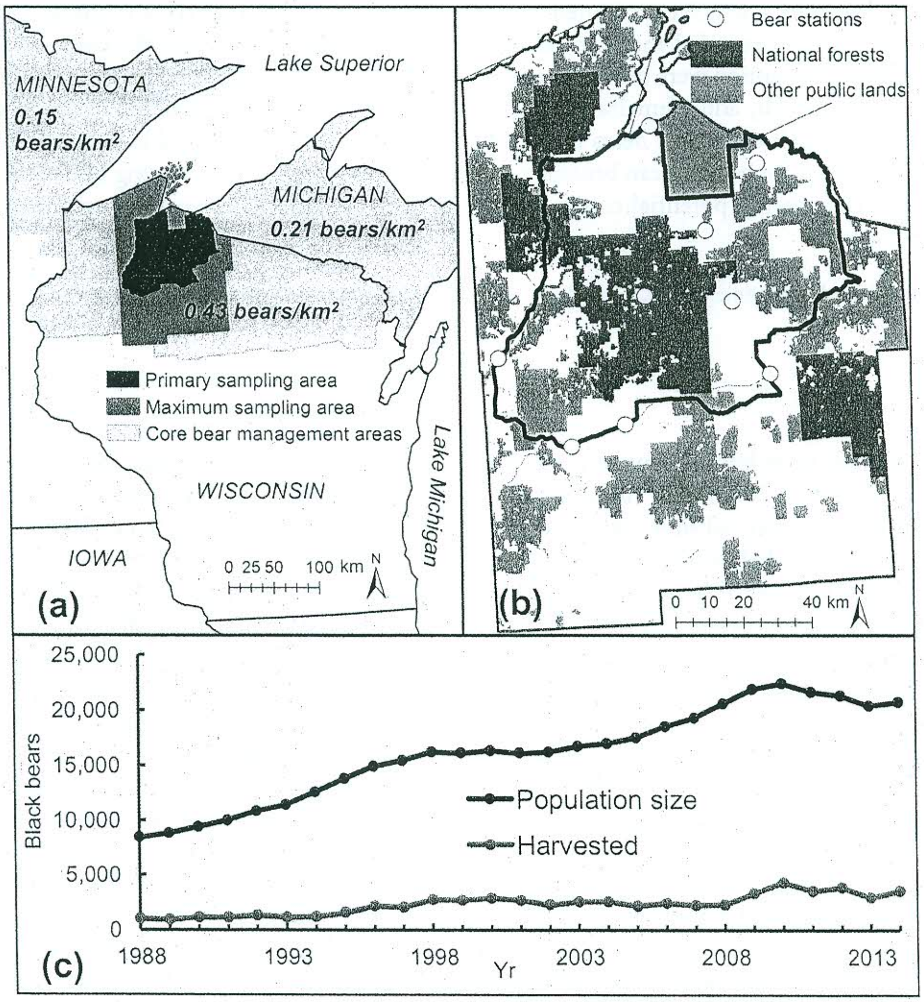

Figure 1. a) Regional bear density estimates for core black bear management areas in northeastern Minnesota, the Upper Peninsula of Michigan, and northern Wisconsin, USA, 2015. We derived crude densities from recent population size estimates determined by state natural resource agencies (MN: Garshelis and Tri [2015], MI: Michigan Department of Natural Resources [2016], WI: Rolley et al. [2015]), divided by area (MN: the defined core bear range, MI: the Upper Peninsula of Michigan, WI: northern Wisconsin bear management units). b) Study area with public lands and bear hunting registration stations used for sample collection. Bears were typically harvested within the primary sampling area (game management units) outlined in black. c) Northern Wisconsin black bear population size estimates and harvest numbers from 1988 to 2014 (Rolley et al. 2015).

STUDY AREA

We investigated black bear diets in north-central Wisconsin, USA principally on national forest lands of the Chequamegon-Nicolet National Forest (Fig. 1b). We restricted our core study area to game management units that were forested (60%) and had minimal crop cover (<5% crop cover from the 2006 National Land Cover Database) and were $\geq$50% publicly owned. Other cover types included wetlands (23%), shrubland (4%), hay and pasture (3%), and developed (3%). Dominant tree species included sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), aspen (*Populus* spp.), basswood (*Tilia americana*), and oak (*Quercus* spp.), with scattered conifer stands of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), hemlock (*Tsuga canadensis*), red pine (*Pinus resinosa*), and white pine (*Pinus strobus*; Sadeghpour and Ginnett 2011). Important natural bear foods included raspberries and blackberries (*Rubus* spp.), chokecherries (*Prunus virginiana*), black cherry (*Prunus serotina*), red osier dogwood (*Cornus stolonifera*), and oak acorns (*Quercus* spp.). Bears also preyed on or scavenged white-tailed deer (*Odocoileus virginianus*) and ants (Payne et al. 1998). Estimated white-tailed deer densities were 3–18 deer/km^2 after the 2014 fall hunting season (Rolley 2015). In addition to black bears, bobcats (*Lynx rufus*), wolves (*Canis lupus*), and coyotes (*Canis latrans*) were present in the area. Mean annual precipitation was 77.3 cm and mean annual temperature was 6.98°C (Midwestern Regional Climate Center [MRCC] 2017). Although there were minimal differences among yearly precipitation in northern Wisconsin, 2011–2013 anecdotal evidence suggested that 2012 was a good mast year for acorns.

METHODS

Food Availability

We sampled native bear foods (Noyce et al. 1997, Payne et al. 1998) monthly on public lands from May to September 2012 for isotopic analyses. We collected a minimum of 5 different plants per sampled genus opportunistically throughout the study area. Native forage included known bear foods grouped broadly into vegetation ($n = 122$; 60 berries, 12 acorns, 29 grasses and sedges, 21 other herbaceous plants) and animal matter ($n = 34$; 18 white-tailed deer, 16 ant mounds). We also sampled bear baits throughout the forest ($n = 27$). Although we sampled only diet sources during the primary year of the study, we would not expect substantial yearly differences in bulk isotopic signatures of forage or prey in the same locations (Ben-David and Flaherty 2012).

We also estimated the amount of available bait in late August 2012, 1 week prior to the start of the bear hunting season, by searching 15, 5-km forest road transects for bait stations. We designated transects by overlaying a 2.5 × 2.5-km grid onto forest lands, then randomly selecting 15 grids, a random point within each grid, and the road nearest to the point as the starting locations for the transects. We drove primary forest roads, and walked non-drivable secondary roads, along each transect searching for well-worn foot trails. Although we designed our study area to minimize crop cover, to corroborate our assumption that the sampled bears would have minimal access to crops in the area, we also estimated the amount of agricultural corn that bears could access by examining 2012 United States Department of Agriculture Census of Agriculture field crop data for the 6 counties surrounding the core sampling area (Ashland, Bayfield, Iron, Price, Rusk, Sawyer) combined with corn damage reports from the Wisconsin Department of Natural Resources. Because deer bait was not deployed until mid-September, we did not sample these baits.

Black Bear Diet Reconstruction

We sampled hair, blood, and bone from hunter-harvested black bears at hunting registration stations during the 5-week fall hunting seasons of 2011 (pilot study, $n = 11$), 2012 ($n = 129$), and 2013 ($n = 40$). To maximize efficiency, we chose stations scattered throughout the study area with high numbers of harvested bears. We recorded sex of the individual, and determined age from counts of cementum annuli (Matson's Lab, Milltown, MT, USA). Because corn and cane-sugar dominated foods (i.e., human foods) are enriched in ^{13}C relative to C$_3$ native plant base (Jahren et al. 2006, Jahren and Kraft 2008), stable isotope analysis has been previously used to reconstruct human food contributions to bear diets (Hopkins et al. 2014, Kirby et al. 2016). Hair growth in black bears occurs from the spring through fall, and isotopic signatures represent assimilated diets (Hilderbrand et al. 1996, Jacoby et al. 1999). Whole blood represents recent bear diets (the previous 1–2 months), whereas bone constantly assimilates diet (Hobson and Montevecchi 1991, Loken et al. 1992), representing several prior years to sampling, and generally, the lifetime diet for the bear (Hilderbrand et al. 1996). By comparing tissue types, we could compare the diet of the current year to that in previous years and lifetime diets. Though there is some overlap in the periods captured by each tissue, we refer to spring-summer, fall, and lifetime for hair ($n = 159$), blood ($n = 158$), and bone ($n = 43$), respectively. We randomly selected the subset of bones analyzed from among the samples, stratified by age class. Most of the bears were aged $\leq$7 years (range = 1–21 yr).

We rinsed bear hair and animal prey (i.e., deer hair) samples 3 times with a 2:1 chloroform-methanol solution to remove surface oils, then homogenized them with surgical scissors, and dried them for 72 hours at 56°C (Pauli et al. 2009). We dried whole bear blood samples, vegetation and bear bait at 56°C for a minimum of 72 hours and homogenized samples with a spatula or in a ball mill (Mixer Mill MM200, Restch, Newton, PA, USA). We extracted collagen from rib bone by decalcifying samples with hydrogen chloride and extracting lipids with 2:1 chloroform-methanol (Ambrose 1990). We weighed all samples (>50% in duplicate) into tin capsules for δ^{13}C and δ^{15}N analysis at the University of Wyoming's Stable Isotope Facility using a Costech 4010 and Carlo Erba 1110 Elemental Analyzer (Costech, Valencia, CA, USA) attached to a Thermo Finnigan Delta Plus XP Continuous Flow Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, MA, USA); we analyzed bone collagen at University of New Mexico's Center for Stable Isotopes. Results are provided as per mil (‰) ratios relative to the international standards of Vienna Peedee Belemnite for C and atmospheric N_2 for N, with calibrated internal laboratory standards.

We tested the isotopic difference for biologically distinct diet groups: native vegetation, animal matter, bear bait, and corn bait (Fig. 2a and Table S2; corn signatures from Ditmer et al. 2016) with a K nearest-neighbor randomization test (KNN; Rosing et al. 1998). Because we selected a study area to minimize the presence of agriculturally derived foods (crop corn), we assumed the corn signature was from feed corn bait. We estimated proportional importance of each forage group with Bayesian mixing models in Stable Isotope Analysis in R package (SIAR; Parnell et al. 2010). Because samples did not differ isotopically among years (multivariate analysis of variance [MANOVA], Wilk's $\lambda = 0.99$, $P = 0.41$), we pooled them. To test age and sex differences in bait use by bears, we compared 3 groups: adult male, adult female, and subadults (1–2 yr). We ran 2 sets of mixing models to estimate bear diet for each tissue type. In the first set, we used an informative prior probability for animal matter estimated from previous studies in Minnesota and Wisconsin (Payne et al. 1998, Ditmer et al. 2016). Because black bears in the upper Midwest consume minimal animal matter, we chose a prior estimate of 10% (with a standard deviation of 0.05), which is greater than the maximum animal matter expected in a black bear's diet (Payne et al. 1998, Ditmer et al. 2016), thus restricting the model from overinflating the contribution of animal matter. We kept the remaining priors flat (uniformly distributed across the 3 groups, with the same standard deviations) because there was no prior information on expected bait contribution to further parametrize the model. In the second model set, we used uninformative priors (uniform across all groups) to explore the potential influence of our prior probability on diet estimates. All models included trophic discrimination and concentration dependence. We corrected each diet group with concentration dependence estimated from mean digestible elemental concentrations (Hopkins and Ferguson 2012; Table S3). We applied hair and blood discrimination factors developed for omnivorous mammals (Kurle et al. 2014). Because discrimination of bone collagen is similar to that of hair (Hilderbrand et al. 1996), we corrected bone samples to hair by adding 0.7 $\delta^{13}C$ and 0.3 $\delta^{15}N$ (Hopkins et al. 2014), and analyzed the samples within the hair mixing space. We report medians of the probability density functions with 95% credible intervals (CI), which represent each forage group's likely contribution to bear diet (Parnell et al. 2010). We also examined tissue-specific differences in the raw isotopic signatures with a repeated measures MANOVA. We present all 3 tissue types, but we focus on spring-summer diets because hair is the most commonly examined tissue in isotopic bear studies and was the largest sample in this study.

RESULTS

Subsidy Availability

We encountered active bear bait stations (i.e., filled with bait) during the first week of July 2012 on United States Forest Service lands, though we found remnant stations (previously established but currently empty) as early as May. Northern Wisconsin public lands have a high road density of 0.98 km/km^2. During the peak of baiting just prior to the hunting season in September, we encountered 42 bait stations along transects, 19 of which were filled at the time with a mixture of items (e.g., donuts, cookies, candies, cereals, and frosting; Table S3). Based on the road density, this reflected $\geq$1 active bear bait station (plus 2 currently inactive stations) every 4 km^2. In Wisconsin, the average female bear home range is 17 km^2, and the average male home range is 85 km^2 (Johnson 2007, Sadeghpour and Ginnett 2011). This would suggest an average female bear would encounter 4–13 bear baits and the average male would encounter 21–63 bear baits/year.

Agricultural corn in 2012 constituted only 0.67% of the landcover within the 6 counties surrounding our study area. Bear damage reports confirmed that only 0.7% of that crop (or 0.85 km^2) was damaged by bears in 2012, suggesting low consumption of agricultural corn in our study area. These results support that most corn present in the diet of bears was derived from intentionally deployed bait, either for hunting bears or possibly deer.

Black Bear Diet

Potential foods for bears were isotopically distinct, and bear signatures varied throughout the mixing space and by age-sex class (Fig. 2a, Table 1). Spring-summer diet of black bears as a population consisted of just over 50% native foods (44% vegetation, 13% animal matter) and somewhat less of human foods (29% bear bait, 13% corn bait; Table 2). Hair samples from adult males were significantly enriched in ^{13}C and ^{15}N compared to adult females or subadults (MANOVA, Wilk's $\lambda = 0.78$ $P < 0.001$; Table 1), indicating this group consumed the most human subsidies. Although consumption of bear bait by adult males was similar (31% of diet) compared to adult females and subadults (30% and 28% of diet, respectively), adult males consumed more corn bait (23% of diet; Fig. 2b). Adult females consumed more corn bait than subadults. Adult males consumed slightly more animal matter than other age-sex classes and substantially less native vegetation during the spring-summer (Fig. 2b and Table S4). Both model sets yielded similar median estimates for population diet, with the informed model primarily reducing estimates of variability (95% CI), particularly for bear bait and animal matter. When comparing age-sex classes, the informative model median estimate for adult males did have slightly higher estimates of bear bait and lower estimates of animal matter than the uninformed model; however, the credible intervals substantially overlapped (Table S4).

Tissue samples were more similar within individuals than across tissue types (repeated measures MANOVA, Pillai's trace, $F_{4,168} = 0.88$, $P < 0.001$), indicating changes in diet were consistent across individuals, and that an individual enriched in ^{13}C and ^{15}N in current seasons was likely to be enriched throughout its lifetime. Diet changed minimally across time analyzed, with consistently high consumption of bait subsidies regardless of tissue analyzed (Table 2). The

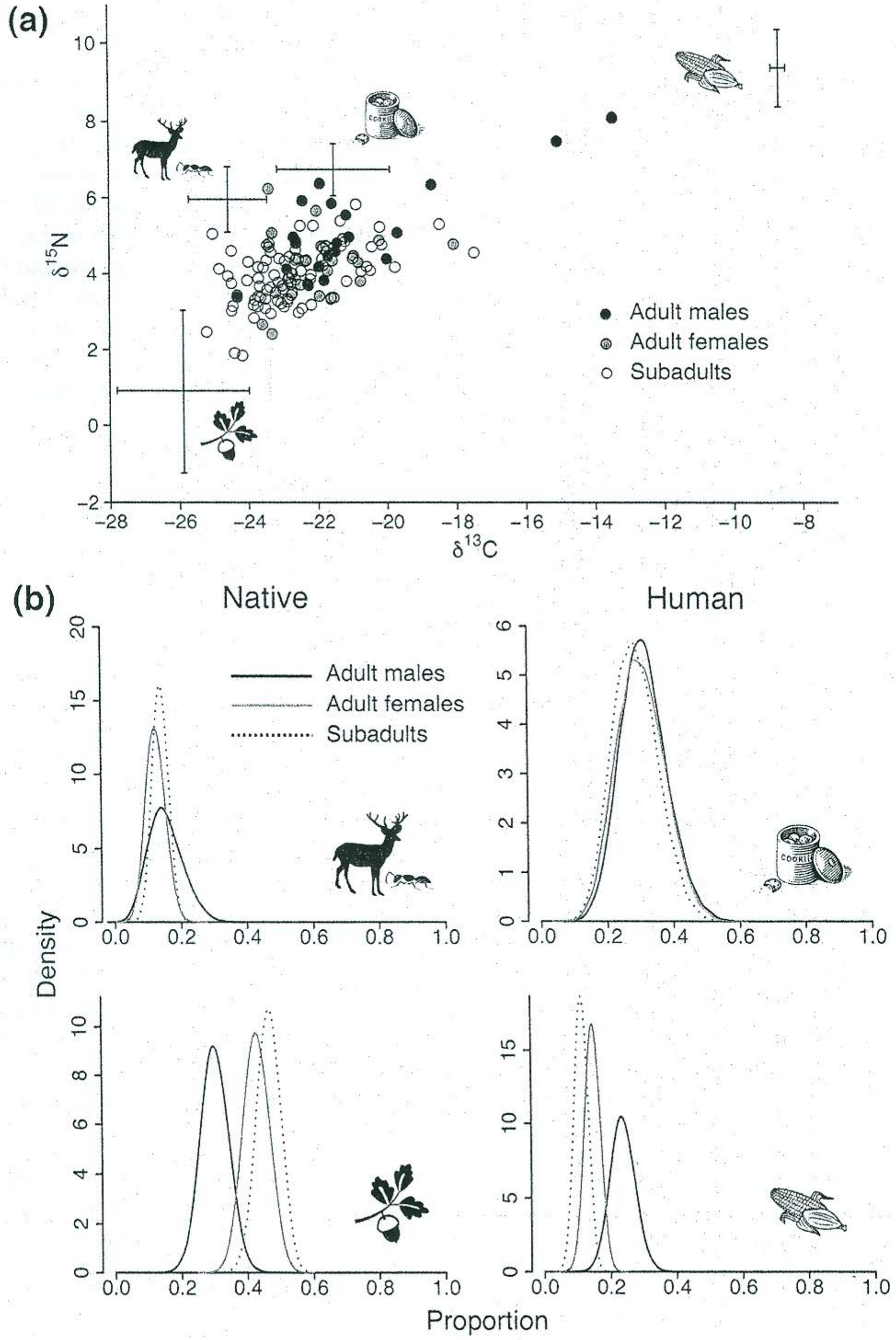

Figure 2. a) Isotopic signatures of potential forage groups and black bear hair samples from northern Wisconsin, USA, 2011–2013. Diet groups include native vegetation ($n = 122$), animal matter ($n = 34$), bear bait ($n = 27$), and corn bait ($n = 24$). b) Assimilated dietary estimates shown as proportional density distributions for summer-fall bear diet, and grouped by age-sex class (informed model).

isotopic signatures from bone samples suggested bears were consuming subsidies in years prior to the year they were harvested. The forage group with the greatest seasonal variation was animal matter, which showed increased consumption in the fall (for all age-sex classes), although there was substantial overlap with other seasons.

DISCUSSION

We concluded harvested black bears in northern Wisconsin readily used hunting baits. Over 40% of bear diet consisted of subsidies in the form of bait, bear bait and corn bait likely intended for bears or deer. Bear bait is abundant on the landscape throughout active bear season. In other populations, human foods, including refuse, bird feed, fruit trees, and agricultural crops (Merkle et al. 2013) contributed to bear diets. However, our study area is primarily composed of public lands with little agricultural corn, so although such unintentional subsidies might have contributed to the human food signature, they should have been minimal. Because the purpose of baiting is to habituate bears to improve hunting

Table 1. Mean isotopic signatures of black bear tissues sampled from hunter-harvested bears in northern Wisconsin, USA, 2011–2013, separated by age-sex class.

			δ^{13}C (‰)		δ^{15}N (‰)	
Tissue type	Age-sex class[a]	n	$\bar{x}$	SD	$\bar{x}$	SD
Hair						
	Adult M	20	−20.90	2.59	5.15	1.23
	Adult F	30	−22.08	1.16	4.14	0.81
	Subadult M	51	−22.50	1.49	4.01	0.88
	Subadult F	31	−22.95	1.33	3.93	0.57
Blood						
	Adult M	20	−23.21	1.73	5.17	0.94
	Adult F	30	−23.66	1.35	4.40	0.88
	Subadult M	51	−23.80	1.67	4.37	0.80
	Subadult F	31	−24.39	1.04	4.00	0.59
Bone						
	Adult M	5	−19.75	1.22	5.59	1.42
	Adult F	15	−20.65	1.39	4.35	0.89
	Subadult M	14	−20.31	1.97	4.33	0.99
	Subadult F	8	−21.63	1.43	4.08	0.83

[a] Adult includes individuals ≥3 years old. Subadult includes individuals 1–2 years old.

success (Bischof et al. 2008), it is not surprising that harvested bears consumed bait. However, the substantial use of subsidies by this population is notable, and even greater than what was historically regarded as one of the most highly food-conditioned black bear populations in North America in Yosemite National Park (35% of bear diet was from human foods, 1975–1985; Hopkins et al. 2014). Our bone analyses revealed that these food subsidies were being consumed in previous years when the bears had not been harvested. These results support our hypothesis that bait contributes substantially to black bear diets in northern Wisconsin and that consumption is not restricted to bears that are harvested in the current season, but rather occurs throughout their lives.

Surprisingly, we did not detect strong inter-annual or inter-seasonal diet differences within this bear population. Bears inhabiting developed landscapes tend to increase use of developed areas according to physiological demands for food (e.g., hyperphagia, natural food shortage years; Baruch-Mordo et al. 2014, Johnson et al. 2015). Black bears artificially fed for tourism in Québec, Canada similarly increased their use of feeding stations in fall, when in hyperphagia (Massé et al. 2014). Because bait is easily accessible and calorically rich, we expected to find similar increased consumption of bait when nutritional demands were high, in fall and in 2013, which appeared to have less mast than 2012. However, we found no temporal differences. This finding corroborates previous work in Wisconsin that similarly found that bears did not alter their bait visitations with changes in natural food phenology over a season (Johnson 2007). Bears can perceive increased risk during hunting seasons (Ordiz et al. 2012), so they may reduce visits to bait in response. Additionally, because our study period did not contain any mast failures, natural food was not likely to be limiting to bears among years. Regularly available bait sources may mitigate natural food limitations for bears in northern Wisconsin. The lack of seasonal differences could have been reinforced by our method of isotopic diet reconstruction. We parameterized each seasonal model with the same diet sources (animal matter, native vegetation, bear bait, corn bait). Bears, however, tend to have more access to animal matter (e.g., ants, deer fawns) in the spring and early summer, and some studies exclude animal matter as a potential source in fall models (Ditmer et al. 2016). A fall model excluding animal matter would have yielded a higher estimate of bear bait consumption (>80%). Although we used tissue-specific discrimination factors, there is temporal overlap in foraging periods in hair and blood samples. Recent work with polar (*Ursus maritimus*) and brown bears (*U. arctos*) reported that whole blood integrates over a longer period (>6 months) than was previously demonstrated in black bears (Rode et al. 2016). Thus, because of the overlap among tissue types, our conservative approach maintained the potential diet sources in all seasonal models. Future work could incorporate segmenting hair samples to provide a finer timescale analysis of diet changes within the same tissue type.

Nevertheless, we found less variability within each individual than among tissue types, suggesting that some bears specialize more on food subsidies than others. As seen in other populations (Merkle et al. 2013, Ditmer et al. 2016), age and sex of the animals primarily influence these differences, with adults and males tending to consume the most subsidies. Adult males typically access the best food sources (Beckmann and Berger 2003*b*) and are also more likely to try unfamiliar diet items (Ditmer et al. 2015). Interestingly, after exposure to novel foods, females will also seek out such resources (Ditmer et al. 2015). Most of the demographic differences in diet contributions appear to be derived from corn bait, rather than bear bait. Adult males may be using deer bait sites of shelled corn, or this corn bait

Table 2. Assimilated dietary estimates and 95% credible intervals (CI) for black bears in northern Wisconsin, USA, 2011–2013 ($n = 180$) across spring-summer, fall, and lifetimes, estimated from isotopic signatures of hair, blood, and bone, respectively, using uninformed and informed Bayesian mixing models.

	Population median (95% CI)	
Diet group and time period	Uninformed model	Informed model
Native vegetation		
Spring-summer	0.44 (0.28–0.58)	0.44 (0.37–0.50)
Fall	0.30 (0.21–0.38)	0.29 (0.24–0.34)
Lifetime	0.43 (0.29–0.57)	0.42 (0.34–0.49)
Animal matter		
Spring-summer	0.13 (0.03–0.22)	0.13 (0.09–0.18)
Fall	0.31 (0.15–0.45)	0.26 (0.18–0.34)
Lifetime	0.10 (0.01–0.18)	0.09 (0.04–0.14)
Bear bait		
Spring-summer	0.30 (0.00–0.63)	0.29 (0.16–0.44)
Fall	0.24 (0.00–0.52)	0.30 (0.16–0.44)
Lifetime	0.28 (0.00–0.54)	0.30 (0.17–0.44)
Corn bait		
Spring-summer	0.13 (0.04–0.20)	0.13 (0.09–0.17)
Fall	0.15 (0.08–0.22)	0.14 (0.10–0.18)
Lifetime	0.20 (0.12–0.27)	0.19 (0.15–0.24)

signature may also come from additional bear bait sites not captured by the sampled isotopic signatures. Deer baiting is not permitted until mid-September, which is already 10 days into the bear hunting season and our sampling period. Bear consumption of deer bait should have been minimal prior to sample collection; however, it could still be important in lifetime consumption. We suspect our sampling of bear baits did not fully capture some of the bait items that are more highly derived from corn (such as candies), and these would be more similar to our corn bait signature (Jahren et al. 2006).

Bears using baits in northern Wisconsin may be contributing to Wisconsin's high population density compared to neighboring states. Female consumption of high caloric food subsidies can increase fecundity (Graber 1982, Beckmann and Berger 2003*a*, Beckmann and Lackey 2008) and can train cubs to seek subsidies (Mazur and Seher 2008). Long-term supplementation can increase a population above its ecological carrying capacity (Gray et al. 2004, Kavčič et al. 2015). Extensive foraging on bear bait could affect individual bear nutrition through increased body sizes and energy requirements (Robbins et al. 2004). Increased energy requirements and habituation may create a dependency on food subsidies; if food subsidies were removed, bear-human conflicts may increase and bears may no longer be able to subsist on natural foods (Gunther et al. 2004, Robbins et al. 2004). High availability of energy-rich food can also alter denning chronology, shortening the denning period (Beckmann and Berger 2003*b*). In northern Wisconsin, humans are influencing the ecosystem not only through top-down forces via hunting (Dorresteijn et al. 2015) but also through bottom-up forces by subsidizing the food base (Newsome et al. 2014*a*).

MANAGEMENT IMPLICATIONS

Our results suggest evaluation of current baiting policies and their effect on bear populations is warranted. Management options are available that could reduce anthropogenic food availability and diet subsidization, including temporal reduction through a reduced baiting period, volume and density reduction through limitations on the number of baits allowed to each hunter, and caloric reduction through bait content restrictions. Similar restrictions are in place in other states (Table S1). If changes are implemented, impacts on bear population trends, harvest rates and changes in diet composition should be monitored. Several non-target species have also been regularly found at bait stations, and examining their use of bait would help evaluate broader ecological consequences of subsidies. The method of isotopic diet analysis used in this study could be implemented for long-term monitoring with hair samples readily obtained from harvested bears and other species. Additionally, management could benefit from the establishment of annual bear food surveys or a qualitative mast index to aid in tracking bear diet. Although our study focuses on Wisconsin, the use of bait in bear hunting is common across jurisdictions. Thus, developing multi-state comparative studies would enhance our understanding of the relationship between baiting policies and bear diet. Our findings emphasize the need to understand what effects conservation and management strategies that feature human subsidies can have on wildlife, particularly how they alter behavior, population sizes, and demographic parameters.

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