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Management and Conservation

Stable Isotopes to Detect Food-Conditioned Bears and to Evaluate Human-Bear Management

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ABSTRACT We used genetic and stable isotope analysis of hair from free-ranging black bears (*Ursus americanus*) in Yosemite National Park, California, USA to: 1) identify bears that consume human food, 2) estimate the diets of these bears, and 3) evaluate the Yosemite human–bear management program. Specifically, we analyzed the isotopic composition of hair from bears known *a priori* to be food-conditioned or non-food-conditioned and used these data to predict whether bears with an unknown management status were food-conditioned (FC) or non-food-conditioned (NFC). We used a stable isotope mixing model to estimate the proportional contribution of natural foods (plants and animals) versus human food in the diets of FC bears. We then used results from both analyses to evaluate proactive (population-level) and reactive (individual-level) human–bear management, and discussed new metrics to evaluate the overall human–bear management program in Yosemite. Our results indicated that 19 out of 145 (13%) unknown bears sampled from 2005 to 2007 were food-conditioned. The proportion of human food in the diets of known FC bears likely declined from 2001–2003 to 2005–2007, suggesting proactive management was successful in reducing the amount of human food available to bears. In contrast, reactive management was not successful in changing the management status of known FC bears to NFC bears, or in reducing the contribution of human food to the diets of FC bears. Nine known FC bears were recaptured on 14 occasions from 2001 to 2007; all bears were classified as FC during subsequent recaptures, and human–bear management did not reduce the amount of human food in the diets of FC bears. Based on our results, we suggest Yosemite continue implementing proactive human–bear management, reevaluate reactive management, and consider removing problem bears (those involved in repeated bear incidents) from the population.

KEY WORDS black bear, carbon isotope, hair, human–bear management, IsotopeR, mixing model, nitrogen isotope, noninvasive sampling, stable isotope, *Ursus americanus*, Yosemite National Park.

Thousands of black bear (*Ursus americanus*) incidents (definition in Hopkins et al. 2010) have been reported in Yosemite National Park (hereafter Yosemite) over the past decade (Yosemite, unpublished data). Most of these incidents occurred in Yosemite Valley (hereafter the Valley); an area that comprises <1% of Yosemite National Park, California, USA (hereafter Yosemite; Keay and Webb 1989). In 1998, Yosemite experienced a record number of bear incidents (Table 1) from food-conditioned bears (FC; definition in Hopkins et al. 2010). The following year, Yosemite began receiving an annual congressional appropriation of $500,000 to fund their Valley-focused proactive (population-level management) and reactive (individual-level management) human–bear management program. Reported bear incidents decreased in Yosemite since 1998; however, hundreds of incidents are still reported each year (Table 1).

Bear incident reports are used to evaluate the human–bear management program in Yosemite. Each year, program managers report the percent increase or decrease of incidents compared to the previous year and to 1998, with a decrease in incidents as an indicator of success. Greenleaf et al. (2009) provided an alternative metric for evaluating the human–bear management program. They compared the percent volume of human food in bear scats from the Valley in 2001 and 2002 (6%; Greenleaf et al. 2009) to scats collected in the mid-1970s (21%; Graber 1981). Their results suggested that the human–bear management program reduced the amount of human food available to bears in the Valley; however, they did not investigate the diets of bears in other developed areas or the wilderness (the latter being approx. 95% of Yosemite).

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Table 1. Reported bear incidents and property damage (in US dollars) in Yosemite National Park, California, USA, 1998, 2005–2007.

Year	Valley	Outside valley (non-wilderness)	Wilderness	Human injuries	Bears hit by vehicles	Total
1998						
Incidents	1,369	150	65	7	3	1,594
Property damage	593,270	61,685	4,614			659,569
2005						
Incidents	344	53	48	3	3	451
Property damage	98,133	15,381	4,882			118,396
2006						
Incidents	354	14	32	3	6	409
Property damage	84,081	364	2,495			86,940
2007						
Incidents	417	51	32	1	5	506
Property damage	71,249	11,969	4,608			87,826
Total (2005–2007)	1,115	118	112	7	14	1,366
	253,463	27,714	11,985			293,162

Outside the Valley, bears are rarely outfitted with tags or radio-collars (Greenleaf 2005); therefore, it is difficult to assign bears in the Yosemite wilderness to a management status (e.g., FC bear) and monitor their activities. Instead, managers rely on reported bear incidents to monitor problem bears (those involved in repeated bear incidents; Hopkins et al. 2010) in the wilderness. McCurdy and Martin (2007) showed that only 1 of 4 bear incidents in the Yosemite wilderness is reported, suggesting the magnitude and severity of incidents in the wilderness are under-represented.

Stable isotope analysis of bear hair was proposed as a method to investigate the diets of bears throughout Yosemite (Greenleaf 2005). Isotopic analysis of hair is particularly useful because hair integrates assimilated protein, fat, and carbohydrates (Ayliffe et al. 2004, Mowat and Heard 2006) and preserves this dietary information within inert keratin (Michael et al. 2003). Hair is also useful because it can be collected noninvasively (Mowat and Heard 2006), analyzed to determine average diet during the period of hair growth (i.e., whole hair analysis), or sub-sampled to examine temporal variation in diet (e.g., Ayliffe et al. 2004, Mizukami et al. 2005).

Stable carbon and nitrogen isotope analysis of bear hair can be used to predict the management status of bears. Corn and sugar cane (C_4 plants) are enriched in ^{13}C relative to C_3 plants; thus, bears with elevated carbon isotope values ($\delta^{13}C$) in a C_3 ecosystem such as Yosemite may be feeding on human food. Bears may be ^{13}C-enriched as a result of directly feeding on corn (e.g., from agricultural fields) or indirectly consuming sugar cane and corn products (including corn-fed livestock) via human foods (Koch 2007, Chesson et al. 2008). Hobson et al. (2000) and Mizukami et al. (2005) showed that bears that posed a management problem or were trapped close to human habitation had elevated $\delta^{13}C$ values for their hair compared to conspecifics.

Because ^{15}N concentration increases with trophic level in food webs, bears with greater nitrogen isotope values ($\delta^{15}N$) may be feeding on meat-rich, human food or animal tissues via natural pathways. Hobson et al. (2000) showed that management grizzly bears (*Ursus arctos*) had greater $\delta^{15}N$ values (hair) than non-management grizzly bears, indicating a greater proportion of human food or livestock in their diets. In addition, Mizukami et al. (2005) examined the diets of Asiatic black bears (*Ursus thibetanus*) by analyzing whole hairs and hair segments. They found high $\delta^{15}N$ values for bears (whole hair) that fed on garbage, and high $\delta^{15}N$ values for hair segments that corresponded to the time of year when individuals were a management problem. Lastly, Greenleaf (2005) showed that $\delta^{15}N$ values for bear hair are useful for predicting the management status of bears in Yosemite because these bears are primarily herbivorous (Graber and White 1983, Greenleaf et al. 2009).

Our study had 3 objectives. First, we classified bears with an unknown management status as FC or as non-food-conditioned (NFC) based on the isotopic composition of their hair. To accomplish this objective, we sampled bears during management actions (primarily chemical immobilizations in the Valley) and throughout Yosemite via hair-snare (hereafter hair-snare bears). Next, we estimated the diets of FC bears using a stable isotope mixing model, IsotopeR (Hopkins and Ferguson 2012). Lastly, we used these dietary estimates to evaluate the effectiveness of proactive and reactive human–bear management since 2001.

STUDY AREA

Only a small portion of Yosemite is prime black bear habitat (Fig. 1). Bears in Yosemite tend to forage in the spring at lower elevations (e.g., the Valley) and follow snowmelt and sprouting vegetation upslope in June; bears then return to lower elevations in September for acorns (*Quercus* spp.) and berries (Graber 1981). In general, as elevation increases in Yosemite, forage quality and quantity decrease (Fig. 1; Graber and White 1983). During the early 1900s black bears were rarely seen above 2,500 m (Grinnell and Storer 1924), but are now commonly sighted at 3,100 m. Studies conducted in the 1970s suggest that bears increased occupation of these higher elevations to commandeer human food (Graber 1981, Keay and van Wagtendonk 1983).

METHODS

Sampling

Management bears.—We used hair sampled from bears captured in Yosemite for management purposes (e.g.,

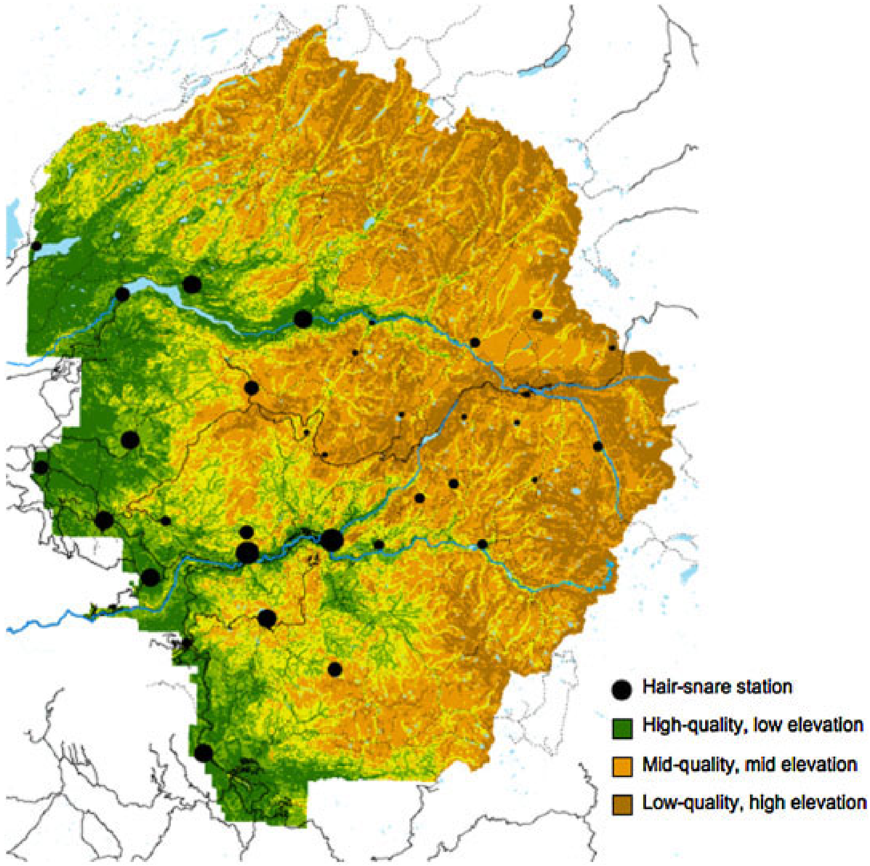

Figure 1. Hair-snare stations used to sample bear hair in Yosemite National Park, California, USA, 2006–2007. The relative proportion of bears detected via hair-snare denoted by black dot at each hair-snare location (details in Table S2). Figure provided by G. Reed.

tag and radio-collar, euthanize, translocate) from August 2005 to September 2007. All bears were trapped by Yosemite Wildlife Management (hereafter Wildlife Management) and processed according to Wildlife Management protocol.

We used isotopic data for bears known to be FC (hereafter known FC bears) from Greenleaf (2005) and from bears that we identified as known FC to develop an isotopic method to discriminate between FC and NFC bears. Greenleaf (2005) captured bears in the Valley, fitted them with radio-collars, and monitored these individuals from July 2001 to November 2003. Greenleaf (2005) used location data as well as a qualitative assessment (e.g., bear was observed consuming human food) of each bear's foraging behavior to classify bears as known FC ($n = 14$; Table 2A) or known NFC ($n = 9$; Table S1, available online at www.onlinelibrary.wiley.com). From 2005–2007, we designated known FC bears in a similar manner as Greenleaf (2005); however, resources limited us from classifying bears as known NFC. Therefore, we classified management bears not designated FC, as unknown. Isotope values for known NFC bears from Greenleaf (2005), allowed us to develop an isotopic baseline for bears that do not consume human food.

Hair-snare bears.—We used a modified method for noninvasive hair-snare sampling described by Woods et al. (1999) to collect bear hair. We strung a maximum of 100 feet of 4-barbed, 2-strand wire around ≥ 3 trees, approximately 40 cm above the ground to reduce the probability of capturing individuals <2 years of age. Excluding young animals is necessary because nursing confounds the isotopic signature in the tissues of bears (Polischuk et al. 2001).

We installed 35 hair-snare stations throughout Yosemite from March to July 2006; these included 31 of the 35 general locations where bear incidents have occurred repeatedly (V. Seher and S. Thompson, Yosemite National Park, personal communication). In addition, we installed 4 stations at locations where bear incidents had not been recorded (i.e., remote locations). We installed stations at sites that were convenient for sampling and did not use a random design because we were interested in maximizing captures of FC bears. In the end, we divided hair-snare stations into 5 groups (Table S2, available online at www.onlinelibrary.wiley.com): frontcountry campgrounds (i.e., campgrounds accessible by car; $n = 11$), wilderness campgrounds ($n = 6$), wilderness campsites ($n = 10$), residential neighborhoods ($n = 4$), and remote locations ($n = 4$).

We installed each hair-snare station (as soon as the site was free of snow) ≥ 300 m from human-use areas in the best black bear habitat available. We positioned stations along game trails and other travel corridors to maximize captures. We baited stations with cow blood or anise oil by pouring the liquid over decaying logs centered in the trap. We visited snares from March to October 2006 and May to October 2007 at 2- to 3-week intervals (sessions) to collect samples

Table 2. Isotopic data ($\delta^{13}C$ and $\delta^{15}N$), probability food-conditioned (P-FC), and proportional dietary estimates (95% credible intervals) of known and predicted FC bears sampled in Yosemite National Park, California, USA, 2001–2007. Diet-year represents the year the diet is cataloged in the hair for all bears except known FC bears sampled during 2001–2003 (A; Greenleaf 2005); for these bears, diet-year denotes the year the bear was captured. P-FC was calculated by entering $\delta^{15}N$ values for bear hair into a logistic regression model (Figure S1). IsotopeR calculated proportional dietary estimates (plants and animals, human food) for known (A and B; $n = 36$) and predicted (C and D; $n = 19$) FC bear samples. Bear IDs with a † indicate bears that were recaptured in 2005–2007. Bear IDs with a § denote bears originally classified as known NFC (Greenleaf 2005; Table S1). Bear 3566 was originally captured as an unknown management bear (Table S7).

							Plant and animal proportions			Human food proportions		
							95% credible interval			95% credible interval		
Bear ID	**Sex**	**Capture site**	**Diet-year**	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**P-FC**	**0.025**	**0.50**	**0.975**	**0.025**	**0.50**	**0.975**
A. Known FC bears 2001–2003 ($n = 14$)												
1278	M	East Valley	2003	5.4	−21.1	1.000	0.66	0.79	0.89	0.11	0.21	0.34
2251	M	East Valley	2003	3.5	−22.6	0.638	0.83	0.91	0.97	0.03	0.09	0.17
2255[†]	M	East Valley	2003	6.7	−21.4	1.000	0.52	0.67	0.81	0.19	0.33	0.48
3552	M	East Valley	2003	6.7	−19.9	1.000	0.49	0.65	0.79	0.21	0.35	0.51
2297[†]	M	East Valley	2001	5.3	−21.0	1.000	0.67	0.80	0.90	0.10	0.20	0.33
2297[†]	M	East Valley	2002	5.1	−20.6	0.999	0.69	0.81	0.91	0.09	0.19	0.31
2312	M	East Valley	2003	5.4	−21.3	1.000	0.67	0.79	0.90	0.10	0.21	0.33
2391[†]	F	East Valley	2003	3.8	−20.0	0.849	0.80	0.89	0.96	0.04	0.11	0.20
2394[§]	F	East Valley	2001	4.0	−21.2	0.919	0.79	0.89	0.96	0.04	0.11	0.21
3049	F	East Valley	2003	6.6	−20.4	1.000	0.50	0.66	0.80	0.20	0.34	0.50
2283	F	East Valley	2003	2.9	−20.4	0.124	0.85	0.93	0.97	0.03	0.07	0.15
3558[†]	F	East Valley	2003	3.5	−21.0	0.657	0.82	0.91	0.96	0.04	0.09	0.18
3821[†]	F	East Valley	2003	5.3	−20.9	1.000	0.67	0.79	0.90	0.10	0.21	0.33
3820	F	East Valley	2003	4.9	−20.5	0.998	0.70	0.82	0.92	0.08	0.18	0.30
Mean				4.9	−20.9							
1 SD				1.2	0.7							
B. Known FC bears 2005–2007 ($n = 22$)												
2255	M	East Valley	2005	4.6	−20.6	0.993	0.74	0.85	0.93	0.08	0.18	0.30
2255[†]	M	East Valley	2006	5.9	−20.9	1.000	0.61	0.75	0.87	0.07	0.15	0.26
3602	M	Foresta	2005	3.9	−22.4	0.895	0.81	0.90	0.96	0.13	0.25	0.39
3602[†]	M	Foresta	2006	4.8	−22.9	0.997	0.74	0.85	0.93	0.04	0.10	0.19
3566[†]	M	White Wolf	2006	3.5	−22.1	0.569	0.83	0.91	0.97	0.07	0.15	0.26
2297	M	East Valley	2005	4.0	−20.8	0.922	0.79	0.89	0.95	0.03	0.09	0.17
2297[†]	M	May Lake	2007	3.7	−20.4	0.814	0.80	0.90	0.96	0.05	0.11	0.21
3012	M	East Valley	2005	4.9	−20.8	0.998	0.71	0.83	0.92	0.04	0.10	0.20
3254[§]	M	East Valley	2005	4.6	−22.1	0.928	0.80	0.89	0.96	0.08	0.17	0.29
3254[†]	M	East Valley	2007	4.0	−22.2	0.994	0.75	0.85	0.94	0.04	0.11	0.20
3055	M	East Valley	2006	4.2	−22.4	0.968	0.79	0.88	0.95	0.06	0.15	0.25
3821	F	East Valley	2005	4.1	−20.6	0.958	0.78	0.88	0.95	0.05	0.12	0.21
3821[†]	F	East Valley	2006	5.6	−20.2	1.000	0.63	0.76	0.88	0.05	0.12	0.22
2391	F	East Valley	2006	4.4	−20.2	0.982	0.76	0.86	0.94	0.12	0.24	0.37
2259	F	East Valley	2006	3.5	−21.7	0.667	0.82	0.91	0.97	0.06	0.14	0.24
2394[§]	F	East Valley	2006	4.7	−20.7	0.995	0.74	0.84	0.93	0.03	0.09	0.18
3558	F	East Valley	2005	3.9	−21.1	0.891	0.80	0.89	0.96	0.07	0.16	0.26
3558[†]	F	East Valley	2007	4.3	−20.6	0.978	0.76	0.87	0.95	0.04	0.11	0.20
3569	F	East Valley	2005	4.7	−22.0	0.996	0.74	0.85	0.93	0.05	0.13	0.24
3899	F	East Valley	2006	4.2	−21.3	0.973	0.77	0.87	0.95	0.07	0.15	0.26
3899[†]	F	East Valley	2007	4.8	−21.9	0.996	0.74	0.85	0.93	0.05	0.13	0.23
3057	F	East Valley	2007	4.3	−22.5	0.980	0.78	0.88	0.95	0.07	0.15	0.26
Mean				4.4	−21.4							
1 SD				0.6	0.8							
C. Unknown management bears predicted FC, 2005–2007 ($n = 4$)												
3573	M	East Valley	2006	3.9	−22.8	0.898	0.81	0.90	0.96	0.04	0.10	0.19
3097	M	East Valley	2005	3.6	−22.3	0.728	0.82	0.91	0.96	0.04	0.09	0.18
3097[†]	M	East Valley	2006	3.9	−21.8	0.878	0.81	0.90	0.96	0.04	0.10	0.19
134550	M	Merced Lake	2007	6.3	−22.0	1.000	0.58	0.72	0.85	0.15	0.28	0.42
Mean				4.4	−22.2							
1 SD				1.3	0.5							
D. Unknown hair-snare bears predicted FC, 2005–2007 ($n = 15$)												
130155	M	Foresta	2006	4.8	−22.2	0.997	0.74	0.85	0.93	0.07	0.15	0.26
198732	M	Aspen Valley	2006	4.1	−20.7	0.947	0.78	0.88	0.95	0.05	0.12	0.22
117799	M	Crane Flat	2005	3.5	−23.0	0.648	0.83	0.91	0.97	0.03	0.09	0.17
130069	M	Hogdon	2007	3.8	−23.1	0.849	0.82	0.90	0.96	0.04	0.10	0.18
130062	M	Foresta	2006	3.6	−22.8	0.751	0.83	0.91	0.97	0.03	0.09	0.17
125599	M	Yosemite Creek	2007	3.6	−21.6	0.719	0.82	0.91	0.96	0.04	0.09	0.18
125849	M	Crane Flat	2007	3.6	−22.9	0.667	0.83	0.91	0.97	0.03	0.09	0.17
130142	M	Mono Pass	2007	3.5	−21.5	0.657	0.83	0.91	0.96	0.04	0.09	0.17
163347	M	Foresta	2006	3.6	−22.2	0.736	0.82	0.91	0.96	0.04	0.09	0.18
198847	M	West Valley	2006	3.6	−20.3	0.728	0.81	0.90	0.96	0.04	0.10	0.19
138675	M	Cloud's Rest	2006	3.5	−20.4	0.590	0.82	0.91	0.97	0.03	0.09	0.18

Table 2. (*continued*)

Bear ID	Sex	Capture site	Diet-year	δ^{15}N (‰)	δ^{13}C (‰)	P-FC	Plant and animal proportions			Human food proportions		
							95% credible interval			95% credible interval		
							0.025	0.50	0.975	0.025	0.50	0.975
130188	F	LYV	2006	4.1	−19.4	0.960	0.77	0.87	0.95	0.05	0.13	0.23
198706	F	East Valley	2006	3.6	−22.1	0.685	0.82	0.91	0.97	0.03	0.09	0.18
117749	F	White Wolf	2007	4.3	−21.9	0.978	0.77	0.87	0.95	0.05	0.13	0.23
162801	F	Pate Valley	2006	4.5	−22.5	0.991	0.76	0.87	0.94	0.06	0.13	0.24
Mean				3.9	−21.8							
1 SD				0.4	1.1							
Total mean				4.4	−21.4							
1 SD				0.9	0.9							

and to add new lure. At inspection, each barb with hair was considered a separate sample and was inserted into a paper envelope, labeled, and stored in a desiccant chamber.

Hair samples represented the diets of bears from 2005 to 2007, and as with management bears, full-length guard hair collected during spring and fall months were assumed to be representative of the previous and current year's diet, respectively; we tested isotopic differences among years using analysis of variance (ANOVA; $\alpha = 0.05$). Similar to Hobson et al. (2000), we considered isotopic values for hair from the same individuals in successive years (hereafter recaptured bears) as independent in our analysis.

Plants and animals.—We collected plant and animal foods (Table S3, available online at www.onlinelibrary.wiley.com) identified in previous fecal analysis studies (Graber and White 1983, Greenleaf 2005) in 2007 to measure their elemental compositions in order to estimate digestible [C] and [N]. We used these concentrations (Tables S3 and S4, available online at www.onlinelibrary.wiley.com) to construct the isotopic mixing space (Koch and Phillips 2002) used to estimate the diets of FC bears. These foods include herbage (i.e., grasses, forbs), reproductive plant parts, and animals (Tables S3 and S4). Instead of conducting isotopic analyses on bear foods and accounting for isotopic discrimination (a correction used to account for metabolic fractionation and stoichiometric effects during the formation of bear hair), we used isotope values for hair of NFC bears to define the 100% plant and animal dietary source.

Human sampling.—We collected human hair samples from floor clippings at two salons and one barbershop in St. Louis, Missouri in 2009 ($n = 20$; Table S5, available online at www.onlinelibrary.wiley.com); collecting human hair from the garbage did not require an ethics permit. We combined the isotopic data for these hair samples (Table S5) with isotopic data from a 2004 nation-wide survey of human hair ($n = 52$; δ^{13}C [corrected for Suess effect; described below] $\bar{x} = -16.9$, SD = 0.8; δ^{15}N: $\bar{x} = 8.8$, SD = 0.5; Bowen et al. 2009) because they were statistically indistinguishable ($t_{71.62} = -0.79$, $P = 0.43$); these data collectively defined the 100% human food dietary source. We assumed that the isotopic signature of hair for bears on 100% human food diet would be similar to the isotopic signature of human hair. Both humans and bears are monogastric omnivores; therefore, they likely discriminate against ^{14}N and ^{12}C by a similar magnitude.

We estimated the digestible elemental concentrations ([C] = 52.8, SD = 2.5; [N] = 6.9, SD = 1.1; Table S6, available online at www.onlinelibrary.wiley.com) for the average (weighted) human diet in the United States using nutrient data from the United States Department of Agriculture National Nutrient Database (NDB; http://www.nal.usda.gov/fnic/foodcomp/search/). We used these estimates, as well as estimates of plant and animal digestible [C] and [N] (Tables S3 and S4), to define the isotopic mixing space used in our diet analysis.

Genetic Analysis

We conducted DNA analysis to identify individuals. We sub-selected hair samples from each session to maximize the ratio of individuals identified to cost of genetic analysis, based on the following criteria: 1) ≥10 guard hairs, 2) sample on wire not adjacent to other samples, and 3) largest sample of adjacent homogeneous (in color) samples. Exceptions included: 1) adjacent samples that varied in color, 2) samples with <10 guard hairs were only available for collection during the session, or 3) no guard hair was available, only underfur. We sent samples to Wildlife Genetics International (WGI; Nelson, British Columbia, Canada) for DNA analysis.

WGI extracted DNA using QIAGEN's DNeasy Tissue kits (Qiagen, Mississiauga, Ontario, Canada), following the manufacturer's instructions. They used at least 10 guard hair roots when possible to reduce the probability of genotyping errors (Gossens et al. 1998); in one case, they combined small samples from adjacent barbs. WGI used eight microsatellite loci (*G10J*, *G10H*, *G10X*, *G10U*, *G10P*, *G10B*, *CPH9*, *CXX110*) to identify individuals (Paetkau and Strobeck 1994, GenBank accession numbers UAU 22084-95; Ostrander et al. 1993). They determined genotyping error by searching for pairs of genotypes that were similar enough to raise concerns; they reanalyzed genotypes that mismatched at only 1 or 2 markers (1MM-pairs and 2MM-pairs; Paetkau 2003). Lastly, WGI determined bear gender by length polymorphism in the amelogenin gene (Ennis and Gallagher 1994).

Sample Preparation and Stable Isotope Analysis

We rinsed hairs with a 2:1 chloroform–methanol solution to remove surface oils and then air-dried the samples. For plants, we oven-dried samples and powdered them for sub-sampling. We weighed samples into tin capsules

(4 mm × 6 mm; no. 041070, Costech Analytical Technologies, Inc., Valencia, CA). The Stable Isotope Laboratory at University of California, Santa Cruz analyzed samples for their carbon and nitrogen isotope composition by continuous flow methods using a Carlo-Erba elemental analyzer coupled to an isotope ratio-monitoring mass spectrometer (Delta-XP IR-MS, Thermo-Scientific, Waltham, MA). Stable isotope ratios are expressed in delta (δ) notation as parts per thousand or per mil (‰):

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1,000,$$

where δX is $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio of heavy-to-light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in the sample or the standard; reference standards are V-PDB for carbon and atmospheric N_2 for nitrogen. We estimated measurement error using isotope values from reference standards, calculated by our mixing model; we applied this error to each sample.

We corrected $\delta^{13}C$ values for the Suess effect, the global decrease in ^{13}C in Earth's atmospheric CO_2 due to fossil fuel burning over the past 150 years (Peng and Freyer 1986, Francey et al. 1999). Following Chamberlain et al. (2005), we applied a time-dependent correction (to 2009) of −0.022‰ per year to all samples except 2009 human hair.

Statistical Analyses

Predicting the management status of bears using isotopic data.—We used a logistic regression model to determine the probability of known FC and known NFC bears being classified as FC or as NFC using isotope values of their hair as covariates. We then used this model to predict the management status of unknown bear samples ($n = 145$; Table S7, available online at www.onlinelibrary.wiley.com). We found that known FC bear samples ($n = 36$; 14 samples from Greenleaf (2005) and 22 samples collected during this study; Table 2A and B) and known NFC bear samples ($n = 9$; Table S1) had significantly different $\delta^{15}N$ values ($t_{31.3} = 6.9$, $P < 0.001$; FC: $\bar{x} = 4.6 \pm 0.9‰$; NFC: $\bar{x} = 3.2 \pm 0.4‰$), but similar $\delta^{13}C$ values ($t_{15.8} = -0.8$, $P = 0.42$; FC: $\bar{x} = -21.2 \pm 0.8‰$; NFC: $\bar{x} = -21.0 \pm 0.6‰$; Fig. 2). As a result, we used $\delta^{15}N$ as the predictor in our logistic regression model to classify unknown bears. We used model selection to confirm our modeling strategy. We used $\delta^{15}N + \delta^{13}C$ + Year as our full model and compared it ($AIC_c = 26.66$) to a model with $\delta^{15}N$ as the sole covariate ($AIC_c = 25.58$, $P = 0.005$). We found that $\delta^{15}N$ ($P = 0.02$) was a significant predictor of management status, whereas $\delta^{13}C$ ($P = 0.89$) and Year ($P = 0.21$) were not significant predictors. We also tested our assumption of a logit link function against a log–log model ($AIC_c = 26.49$) and probit model ($AIC_c = 25.75$).

We then used a Receiver Operating Characteristic (ROC) curve to determine the probability threshold for classifying unknown bears as either FC or NFC. We identified the probability threshold for classifying a FC bear by selecting the point on the ROC curve that maximized our ability to predict known FC bears correctly (true positive rate), while minimizing FC bear misclassifications (false positive rate).

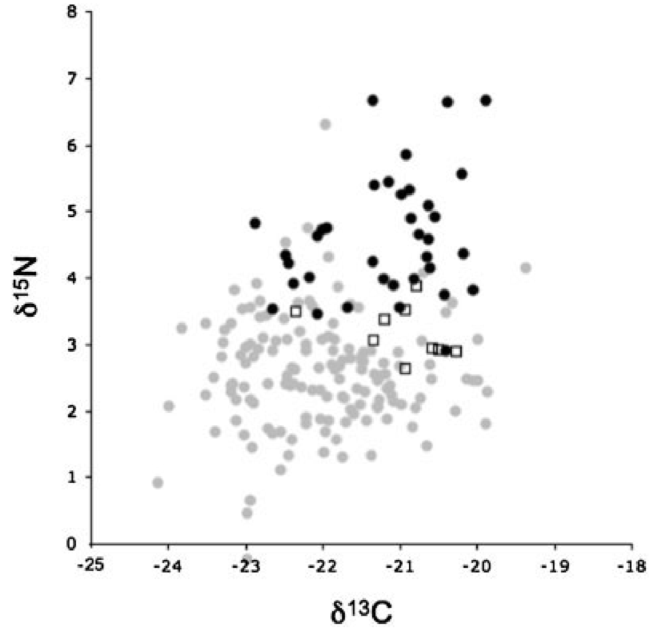

Figure 2. Isotope values ($\delta^{13}C$ and $\delta^{15}N$) for bear hair sampled in Yosemite National Park, California, USA, 2001–2007. Isotope values for known food-conditioned (FC) bears captured from 2006 to 2007 (this study) and known FC bears captured from 2001 to 2003 (Greenleaf 2005) were pooled to form the FC bear group (●). We used known non-food-conditioned (NFC; □) bear isotope values (Greenleaf 2005) and known FC bear isotope values to predict the management status (FC or NFC) of unknown bears (●) using a logistic regression model (Fig. S1).

We were willing to misclassify some NFC bears as FC because we believe it is an acceptable management response to implement proactive management in areas where these misclassified bears were captured; the benefit of this strategy was correctly classifying real FC bears as FC. In the end, we classified unknown bears as FC if the probability of being FC was greater than or equal to the threshold value; otherwise, we classified bears as NFC.

Estimating the diets of FC bears.—To estimate the diets of FC bears, we first estimated the isotopic mixing space. We used a ROC curve to maximize our ability to predict NFC bears, while minimizing NFC bear misclassifications. We then pooled data from predicted NFC bears and known NFC bears (Greenleaf 2005) and used this isotopic distribution as the 100% plant and animal dietary source. We defined the human food source using isotope values for human hair (Table S5) and the average (weighted) digestible [C] and [N] for the human diet (Table S6). The relative difference in [C] and [N] between the 2 sources determined the shape of the line that connected the 2 isotopic end points (i.e., dietary sources: 100% plants and animals, 100% human food). IsotopeR estimated this isotopic mixing space by estimating the sources (and their isotopic correlation) and the [C] and [N] of plants and animals from the data. In addition, IsotopeR simultaneously estimated measurement error and applied it to each observation in this study while estimating the proportional dietary contributions of the population and each individual (Hopkins and Ferguson 2012). Similar to other Bayesian mixing models, IsotopeR provides marginal posterior probability distributions for dietary parameters rather than point estimates or confidence intervals; in this study, we report the mean or median, 1 standard deviation, and 95% credible interval for the marginal posterior distributions.

Evaluating the human–bear management program.—We evaluated both proactive and reactive human–bear management in Yosemite and provided new metrics (reported incidents/FC bear, dollars of property damage/FC bear) for evaluating the overall program. We did not evaluate each proactive (e.g., food storage, interpretation, law enforcement) and reactive management technique (e.g., hazing, translocations, management-induced mortalities) independently. Instead, we determined whether management was successful at reducing the amount of human food available to the bear population by comparing estimated proportions of human food in the diets of known FC bears in 2001–2003 and 2005–2007. Since known FC bears consistently seek out human food, we consider the proportion of human food in the diets of these bears as an index for the amount of human food available to the population. We also evaluated reactive human–bear management by comparing the contribution of human food to the diet of each known FC bear through time (collectively, these bears are a sub-set of all known FC bears). A reduction in the amount of human food in the diet of a FC bear through time suggests management was successful at reducing the amount of human food available to the bear. We examined differences in individual dietary estimates using *t*-tests. A P-value <0.05 suggests management was successful at reducing the amount of human food available to a FC bear.

RESULTS

Bear Hair Samples

We collected 1,093 samples from hair-snares (2006: $n = 588$; 2007: $n = 505$) during 350 trap-sessions (2006: $n = 199$; 2007: $n = 151$). We submitted 375 of these hair-snare samples (2006: $n = 184$; 2007: $n = 191$) and hair from 42 management bears (2005: $n = 3$; 2006: $n = 24$; 2007: $n = 15$) to WGI for genotyping. The lab genotyped 298 (79%) hair-snare samples (2006: $n = 146$; 2007: $n = 152$) and all management bears (except 1 captured in 2007: No. 3057) using 8 microsatellite loci ($\bar{x}$: $H_E = 0.70$, $H_o = 0.69$). Twenty-nine of the 224 genotyped bears were recaptured; therefore, a total of 195 different genotyped bears (including young bears) were captured from 2005 to 2007. Undetected genotyping error was unlikely for the 8-locus marker system as the lab observed no 1MM-pairs and obtained consistent genotypes for the 7 2MM-pairs. In addition to a low false-match probability, the lab unknowingly assigned 6 hair samples to the correct individuals (i.e., blind samples). Kendall et al. (2009) reported that the same lab was 100% successful at genotyping 653 blind samples of grizzly bear hair.

We determined the isotopic composition of guard hair samples collected from both adult management bears (known FC bears = 22, Table 2B; unknown management bears = 11, Table S7) and from hair-snare bears ($n = 134$; Tables S2 and S7). In 23 cases (known FC bears = 8, Table 2B; unknown management bears = 2 and hair-snare bears = 13, 13, Table S7), we used isotope values for recaptured bears; therefore, we analyzed the isotopic composition of hair from 144 individual bears sampled from 2005 to 2007 (Tables 2B–D and S7). We did not observe differences in isotope values among years (δ^{13}C: $P = 0.653$; δ^{15}N: $P = 0.825$).

Statistical Analyses

Predicting the management status of bears using isotopic data.—We used isotopic data from known FC and known NFC bear samples to build a logistic regression model ($\log\mathrm{it}(y) = -13.975 + 4.132\delta^{15}\mathrm{N}$; Fig. S1). We then selected a point on a ROC curve (true positive rate of 0.97, and false positive rate of 0.33; Fig. 3A) to determine the discrimination threshold (0.569) for assigning bears as FC (Fig. 4A). Using this threshold value, we classified 19 bear samples (18 individuals; Table 2C and D) as FC and 126 as NFC (Fig. 4B, Table S7). It is likely we correctly classified nearly all FC bears at a cost of misclassifying a few individuals who were actually NFC. Our model had a large area under the ROC curve (0.95), suggesting it had a high predictive capacity for correctly classifying FC bears using δ^{15}N as a predictor.

Estimating the diets of FC bears.—We used the same probability threshold of 0.569 to classify NFC bears ($n = 126$ samples) from unknown bears using the nitrogen isotope composition of their hair (Fig. 4). We determined this threshold by selecting a true positive rate of 0.67 and a false positive rate of 0.03 from the ROC curve (Fig. 3B); a low false positive rate suggests few unknown bears that were predicted NFC were misclassified. Our model had a large area under the ROC curve (0.95), suggesting the same logistic regression model had high predictive capacity for correctly classifying NFC bears using δ^{15}N as a predictor.

We estimated measurement error ($\bar{x}$ SD: δ^{13}C = 0.3, δ^{15}N = 0.1) using IsotopeR and applied this error to all mixture and source observations when estimating the isotopic mixing space. We estimated the 100% plant and animal source (i.e., includes 9 NFC bears from Greenleaf (2005); $n = 135$; δ^{13}C: $\bar{x} = -22.0 \pm 0.9$‰, δ^{15}N: $\bar{x} = 2.4 \pm 0.8$‰) and the 100% human food source (i.e., human hair, $n = 72$; δ^{13}C: $\bar{x} = -17.0 \pm 0.8$‰, δ^{15}N: $\bar{x} = 8.8 \pm 0.7$‰); we also estimated the isotopic correlation of sources (plants and animals: $r = 0.12$, human food: $r = 0.64$) and the digestible elemental concentrations of the plant and animal source ([C]: $\bar{x} = 47.4 \pm 3.5$, [N]: $\bar{x} = 2.6 \pm 3.0$). The relative difference between the estimated [C] and [N] for plants ($n = 134$) and animals ($n = 29$; Tables S3 and S4) and the fixed concentrations for human food caused the mixing line to bend in a convex fashion between the 2 sources in the isotopic mixing space (Fig. 5). We simultaneously estimated the diets of FC bears at the population- (plants and animals: $\bar{x} = 87\%$, CI = 83–91%; human food: $\bar{x} = 13\%$, CI = 9–17%) and individual-level (Tables 2 and 3) using IsotopeR.

Evaluating the human–bear management program.—Human–bear management was likely successful at reducing

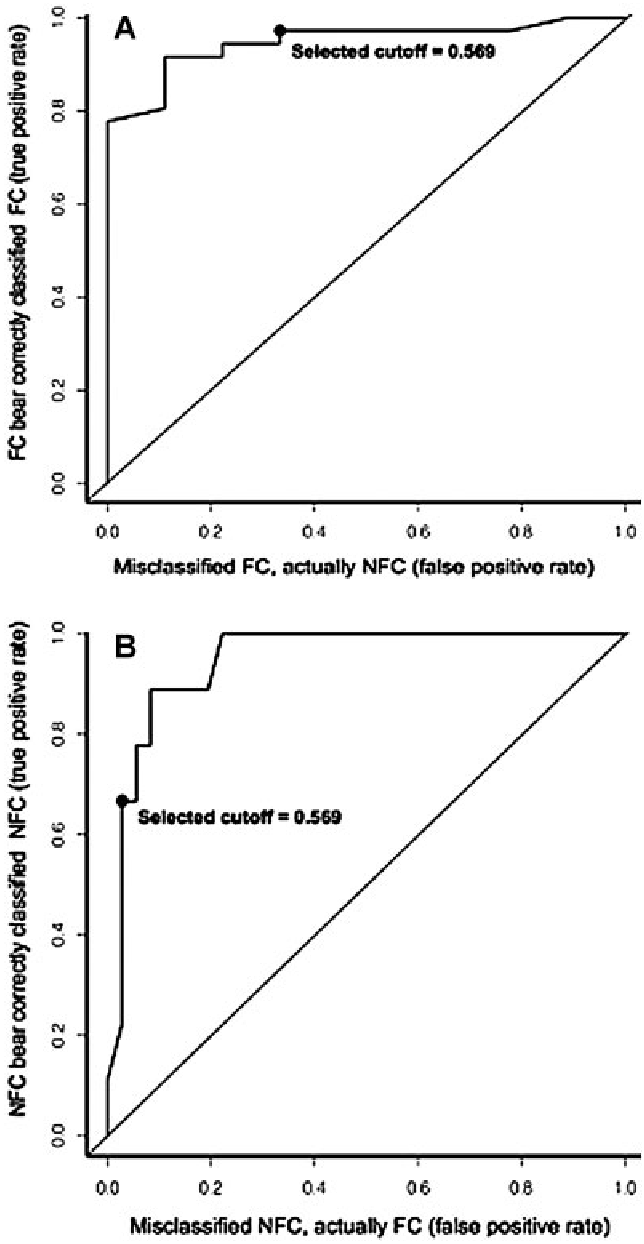

Figure 3. Receiver Operating Characteristic (ROC) curves used to determine the threshold value for classifying the management status of unknown bears sampled in Yosemite National Park, California, USA, 2005–2007. A: The point (●) on the ROC curve represents the true positive and false positive rates selected to determine the threshold value used to classify food-conditioned (FC) bears using $\delta^{15}N$ values for bear hair. B: The point (●) on the ROC curve represents the true positive and false positive rates selected to determine the threshold value used to classify non-food-conditioned (NFC) bears using $\delta^{15}N$ values for bear hair.

the amount of human food available to bears from 2001–2003 to 2005–2007. The mean proportion of human food in the diets of known FC bears likely declined ($t_{16.27} = 2.00$, $P = 0.06$) between time periods (2001–2003: $\bar{x} = 20 \pm 9\%$, range = 8–36%, $n = 14$; 2005–2007: $\bar{x} = 14 \pm 4\%$, range = 9–25%, $n = 22$; Table 2A and B).

Wildlife Management was unsuccessful at reducing the amount of human food in the diets of known FC bears (Table 3). We recaptured 9 known FC bears on 14 occasions; all these bears were classified as FC during subsequent recaptures, and the contribution of human food to the diets of these bears did not decrease through time (Table 3).

DISCUSSION

Wildlife Management classified 15 individual bears as FC from 2005 to 2007, and we detected an additional 18 FC individuals from bears sampled throughout Yosemite. It is likely that we classified most FC bears correctly because known FC bears had greater $\delta^{15}N$ values than most known NFC bears (Fig. 2). Several known NFC bears and one known FC bear may have been misclassified by Greenleaf (2005; Fig. 4A); however, removing these bears from the analysis had no effect on the discrimination of FC and NFC bears. Because we conducted whole hair analysis, relatively high $\delta^{15}N$ values in small sections (representing short time periods when bears consumed human food) of unknown bear hair may have been diluted in the analysis, resulting in relatively low whole hair $\delta^{15}N$ values. To address this problem, isotopic analysis of hair segments could be conducted in the future to identify bears that receive human food during short time periods or at low levels.

Similar to Greenleaf (2005), we found that $\delta^{15}N$ values for bear hair were useful in predicting the management status of bears in Yosemite, whereas $\delta^{13}C$ was not. Although $\delta^{13}C$ values were similar for known FC and known NFC bears, we suggest Yosemite managers collect more isotopic data for known NFC bears and include $\delta^{13}C$ and potentially other isotopes (e.g., $\delta^{34}S$) as predictors in a revised logistic regression model. The isotopic mixing space illustrates our rationale for including $\delta^{13}C$ as a covariate (Fig. 5). Specifically, bears are distributed along a curvilinear line that connects sources in the isotopic mixing space (Fig. 5); therefore, $\delta^{13}C$ has less influence in predicting FC bears when bears consume relatively low amounts of human food. In contrast, FC bears with an estimated diet including more than 15% human food (Table 2) tend to have $\delta^{13}C$ values greater than the average NFC bear, and as the human food contribution increases in the diets of bears, the correlation between $\delta^{15}N$ and $\delta^{13}C$ increases (Fig. 5).

This isotopic correlation at greater $\delta^{15}N$ values may be the result of bears indirectly consuming sugar cane and corn products (including corn-fed livestock) via meat-rich human foods (Chesson et al. 2008). Hobson et al. (2000) detected a strong positive correlation between $\delta^{13}C$ and $\delta^{15}N$ values of bears likely consuming meat, suggesting that the nutritional pathways of carbon and nitrogen were coupled. However, they found a weak isotopic relationship for bears primarily foraging on plant foods. Similarly, our results suggest that Yosemite bears with relatively high and correlated $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 5) consumed human food at a relatively high proportion compared to bears on a largely plant-based diet.

Evaluating the Human–Bear Management Program

Proactive management was evaluated by comparing the proportional contributions of human food to the diets of known FC bears at the population-level during two time periods

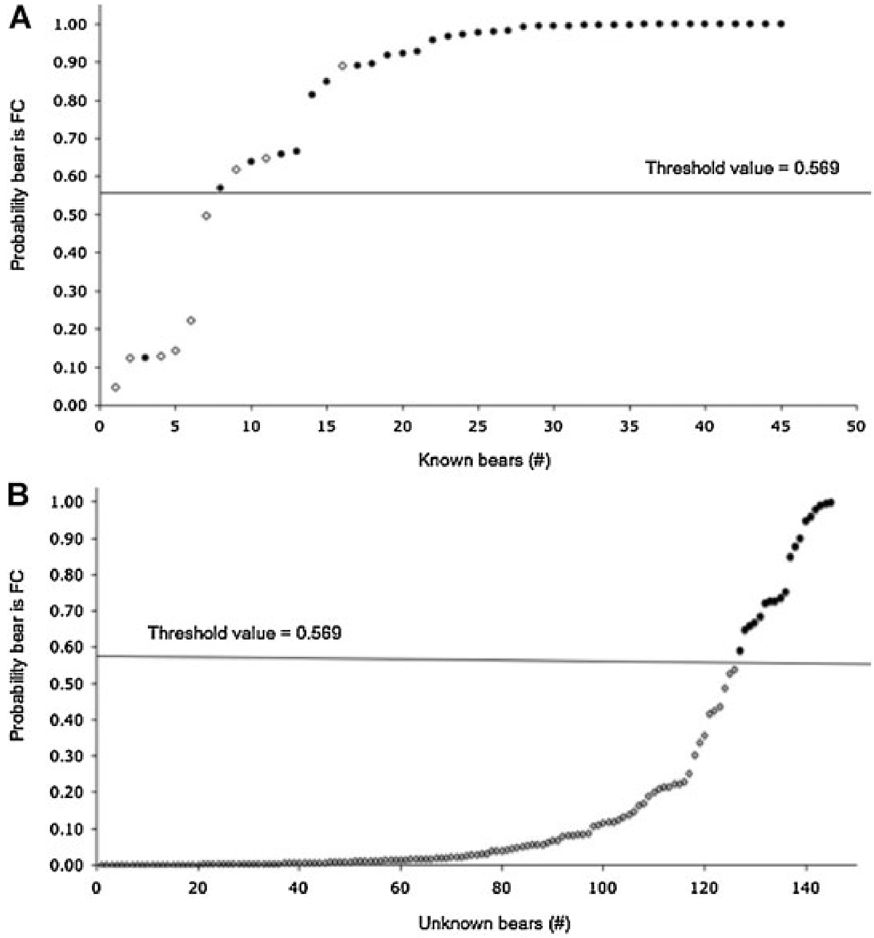

Figure 4. Probability that bears are food-conditioned (FC) based on $\delta^{15}N$ values for their hair sampled in Yosemite National Park, California, USA, 2005–2007. A: Probability that known FC bears (●; $n = 36$) and known non-food-conditioned (NFC) bears (◇; $n = 9$) are FC based on $\delta^{15}N$ values for their hair (calculated by a logistic regression model; Fig. S1). B: Probability that unknown bears (FC [●] = 19; NFC [◇] = 126) are FC based on $\delta^{15}N$ values for their hair (calculated by a logistic regression model; Fig. S1).

over the past decade. In addition to replicating this study in the future and comparing results, we propose that Yosemite estimate the diets of known FC bears in the more distant past by analyzing tissues from museum specimens; these estimates could be used to evaluate the past and current human-bear management program. Specifically, a significant decrease in the proportion of human food in the diets of known FC bears since 1998 would suggest successful proactive management. Such an analysis would demonstrate if government funding was effective in proactively reducing the amount of human food available to the bear population. We also note that proactive human–bear management could be evaluated in the future by estimating the number of new FC bears in the population or in a given location (e.g., the Valley) using the methods provided in this study.

Applying proactive management to areas that have high bear activity could prevent bear incidents in the future. Evidence from our study suggests that the Yosemite human–bear management program is focusing efforts in an area (i.e., east Valley) where the highest proportion of FC bears are active (Tables 2 and S2). However, other locations may require more proactive effort to prevent bears from becoming FC (Table S2). For instance, 8 different bears were captured near both Bridalveil and Crane Flat Campgrounds (Table S2), and 2 of these bears (from Crane Flat) were predicted to be FC based on the isotopic composition of their hair (Table 2D). In addition, other campgrounds (front-country and wilderness) and neighborhoods (e.g., Foresta; Table 2B and D) could benefit from proactive, and potentially, reactive management in the future. Although we sampled all areas of Yosemite that receive high annual visitation, we were unable to sample all human-use areas where incidents occurred from 2005 to 2007 (e.g., wilderness campsites). Therefore, other sites in Yosemite might also benefit from proactive human–bear management.

Evidence suggests reactive human–bear management was not successful at changing the management status of known FC bears to NFC or reducing the amount of human food in their diets through time. As a result, we suggest that Wildlife Management reevaluate their reactive human–bear management program by evaluating each reactive management method and discontinue or limit the use of unsuccessful methods.

We also suggest that Wildlife Management evaluate the overall human–bear management program in the future using new metrics standardized to the total number of FC

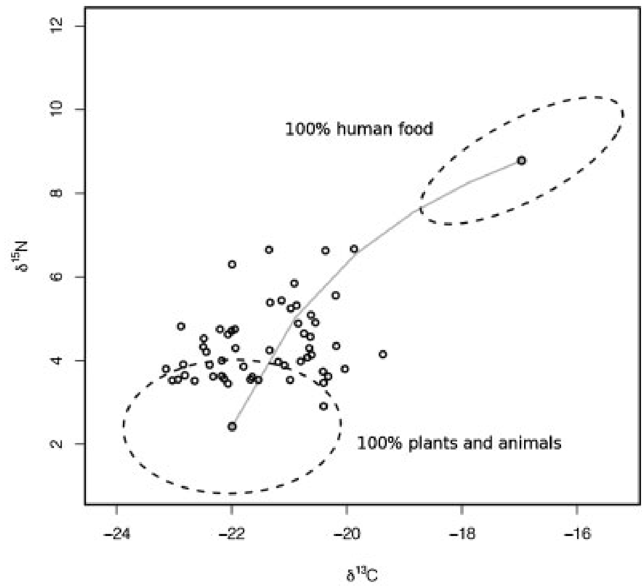

Figure 5. Isotopic mixing space used to estimate the diets of known and predicted food-conditioned (FC) bears sampled in Yosemite National Park, California, USA, 2001–2007. IsotopeR estimated the isotopic distribution ($\bar{x}$ and 2 SD) of each dietary source (100% plants and animals, and 100% human food) and estimated the proportional dietary contributions for the population and each individual bear. IsotopeR estimated measurement error ($\delta^{13}C = 0.3$, $\delta^{15}N = 0.1$), but error bars for bears are not included in the figure.

Table 3. An evaluation of reactive human–bear management in Yosemite National Park, California, USA, 2001–2007. Nine known food-conditioned (FC) bears were captured on 23 occasions (i.e., 14 recaptures). IsotopeR estimated the marginal posterior distributions for human food contributions ($\bar{x}$ proportion, 1 SD) to the diets of bears. A probability >0.05 suggests management was unsuccessful at reducing the contribution of human food to the diet of a FC bear. A *P*-value is provided when mean contributions decrease from consecutive years. *P*-values with a ¥ denote a comparison between first and last captures. Bear identifications (IDs) with a † denote the bear was originally captured from 2001–2003 (Greenleaf 2005); all other bears were captured in 2005–2007. Years with a ‡ indicate a bear was captured via hair-snare and known to consume human food that year.

ID	Sex	Year	Human food ($\bar{x}$, 1 SD)	*P*-value
2255†	M	2003	0.33, 0.07	
		2005	0.15, 0.05	0.28
		2006	0.26, 0.07	0.61¥
3602	M	2005‡	0.11, 0.04	
		2006	0.15, 0.05	
2297†	M	2001	0.20, 0.06	
		2002	0.19, 0.06	0.93
		2005	0.12, 0.04	0.51, 0.47¥
		2007‡	0.11, 0.04	0.89, 0.43¥
3254		2005	0.15, 0.05	
		2007	0.11, 0.04	0.64
3821†	F	2003	0.21, 0.06	
		2005	0.13, 0.04	
		2006	0.24, 0.06	0.47
2391†	F	2003	0.11, 0.04	
		2006	0.14, 0.05	
2394†	F	2001	0.12, 0.04	
		2006	0.16, 0.05	
3558†	F	2003	0.10, 0.04	
		2005	0.11, 0.04	
		2007	0.14, 0.05	
3889	F	2006	0.13, 0.04	
		2007	0.16, 0.05	

bears (known + predicted), such as the number of reported bear incidents per FC bear or dollars of property damage per FC bear. For instance, we predicted 18 individual bears as FC and knew an additional 15 different individual bears were FC (Table 2B–D). During the time period when these 33 individual bears were sampled (2005–2007; Table 2B–D), Yosemite recorded 1,366 bear incidents and $293,162 in property damage (Table 1). Therefore, each bear on average was involved in approximately 41 reported incidents and $8,884 in property damage; we note that these figures may be too high if additional FC bears exist or too low if predicted FC bears were misclassified. Of these 33 FC bears, 18 bears were sampled in the Valley (Table 2B–D), where Wildlife Management recorded 1,115 incidents (not including human injuries and bears hit by vehicles) and $253,463 in property damage. Thus, each Valley FC bear may have been involved in approximately 62 incidents and $14,081 in property damage. Although Wildlife Management will not have the resources to replicate this Park-wide study every year, we suggest they continue to sample bears at the east Valley hair-snare. The total number of FC bears in the east Valley (known and predicted) could then be used each year to standardize the number of incidents and total property damage recorded in the east Valley.

MANAGEMENT IMPLICATIONS

Human–bear management success is a term frequently used, but rarely defined (Hopkins et al. 2010). Here, we offer new methods to evaluate both proactive and reactive human–bear management. In addition, we discuss alternative metrics that can be used to evaluate the overall success of the human–bear management program. We suggest that Yosemite use the quantitative methods provided in this study to evaluate their human–bear management program in the future. We also suggest Yosemite continue implementing proactive human–bear management, reevaluate the effectiveness of reactive human–bear management, and consider removing problem bears from the population. Finally, we suggest Yosemite construct a database for organizing bear profile data (e.g., genotypes, isotopic signatures, management status). Such a database could also be used to evaluate the human–bear management program, to link individual bears to specific incidents, and to monitor bears throughout Yosemite over the long-term. Other wildlife management programs outside Yosemite may also benefit from maintaining such a database and from using the methods in this study to evaluate their programs.

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