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Changes in black bear diets in Yosemite
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The changing anthropogenic diets of American black bears over the past century in Yosemite National Park

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We used carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes derived from the tissues of American black bears (*Ursus americanus*) to estimate the proportion of human-derived foodstuffs and food waste (“human foods”) in the diets of human food-conditioned bears over the past century in Yosemite National Park, located in central-eastern California. Our goal was to understand how the foraging ecology of bears responded to changing management strategies. We found that the proportion of human foods increased in bear diets when park personnel and visitors fed bears intentionally in 1923–1971, remained relatively high and constant after artificial feeding areas were closed, and declined drastically in 1999–2007, following a \$500 000 annual government appropriation used to mitigate human–bear conflicts in the park. This reduction in the amount of human foods in bear diets suggests that Yosemite managers have been successful in reducing the availability of human foods to bears. Yosemite bears currently consume human foods in the same proportion as they did in 1915–1919. This result indicates a notable management achievement in the park, considering that thousands of people visited Yosemite annually in the early 1900s while about four million people visit each year today.

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Synanthropization – the adaptation of wildlife populations to humans and human-impacted environments – is a subject of increasing interest to ecologists. Synanthropic species exhibit ecological and behavioral plasticity and microevolutionary changes in response to anthropogenic pressure (Luniak 2004), which can result in expanded ranges or increased populations (Francis and Chadwick 2012). Understanding how synanthropes respond to human-induced impacts is critical when developing conservation and management strategies for human-dominated ecosystems, or even human-use areas (hereafter, developed areas), given that these species are often in conflict with humans (Parker and Nilon 2012).

Synanthropic generalist species can adapt to a wide variety of urban conditions (Shochat *et al.* 2006). For example, mammals such as foxes (*Vulpes* spp), coyotes (*Canis latrans*), and American black bears (*Ursus americanus*) alter their foraging patterns to seek out human foodstuffs and food waste (hereafter, human foods) because such foods are high in calories and protein (Gehrt 2007; Beckmann and Lackey 2008; Newsome *et al.* 2010). The ecological costs of wildlife foraging for human foods or securing other resources in

developed areas can be substantial (Parker and Nilon 2008).

Yosemite National Park is one of the highest profile sites of human–bear conflict in North America. Large numbers of people visiting developed areas, such as Yosemite Valley, result in an influx of human foods into the Yosemite ecosystem. Many bears seek out these foods on a daily basis, often resulting in human–bear conflicts. For instance, in the past two decades, black bears in Yosemite were involved in more than 12 000 reported incidents, injuring nearly 50 people and causing \$3.7 million of property damage (Hopkins and Kalinowski 2013). In addition, the killing of individual “problem” bears by wildlife managers and the presence of human foods may have altered the reproductive rates of Yosemite bears, with potential population- and ecosystem-level consequences (Graber 1982). In response to the public’s criticism of killing bears, Yosemite developed a human–bear management plan in 1975. Since 1999, the US Congress has appropriated approximately \$7.5 million to mitigate human–bear conflicts in Yosemite.

Developing management strategies to prevent wildlife, especially naïve individuals, from foraging for anthropogenic foods (which include human foods as well as other foods or attractants associated with humans) is important for species conservation. Besides lethal control methods, the most effective strategy for preventing wildlife from foraging for anthropogenic foods is to eliminate such foods from the landscape. Unfortunately, this goal is often unrealistic in places such as national parks. Instead, wildlife managers, such as the bear management personnel in Yosemite, use different strategies to try to reduce or control the amount of anthropogenic foods available to wildlife. These strategies often include animal-proofing solid waste receptacles, haz-

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ing animals in an attempt to modify their foraging behavior, or transporting animals to other locations where anthropogenic sources are absent (Hopkins and Kalinowski 2013).

The goal of this study was to understand how the foraging ecology of black bears responded to changing human–bear management strategies in Yosemite. Our main objective was to use stable isotope analysis (Panel 1) to estimate the proportion of anthropogenic foods, specifically human foods and non-native trout, in the diets of black bears during four different time periods in the past century (Panel 2). We estimated proportional contributions of food sources (Panel 3) to the diets of bears using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes derived primarily from bone (collected by museums between 1915 and 1985) and hair (collected from the field in 2001–2007) samples.

Evaluating management strategies is vital to improving the performance of species conservation programs (Kleiman *et al.* 2001). For this purpose, we compared estimated dietary contributions to evaluate Yosemite’s most recent (1999–2007), primarily nonlethal, human–bear management program (Panel 2). We assumed that the average proportion of anthropogenic foods in the diets of bears was a proxy for the availability of these foods to the bear population. We considered a decrease of human foods in the diets of bears between time periods as an indicator that management had reduced the amount of human foods available to bears.

■ Materials and methods

Black bear bone and hair samples

Historical specimens (1915–1985)

We used the Mammal Networked Information System (<http://manisnet.org>) and the Yosemite Museum database to locate federal, state, and university museum collections that contain black bear tissues (bone from skulls and hair from pelts) from Yosemite National Park. On the basis of historical records, we inferred that all sampled bears foraged for human foods. We sampled < 1 gram of nasal turbinate from the nasal cavity of adult bear skulls ($n = 52$) and plucked > 10 guard hairs from each adult bear pelt ($n = 7$) at the Museum of Vertebrate Zoology in Berkeley, California, and the Yosemite Museum in Yosemite National Park, California (WebTable 1). We collected both bone and hair for six of these bears (WebTable 1). We used the mean difference in isotope values between bear bone collagen and bear hair ($\Delta^{13}\text{C}_{\text{collagen-hair}}$: $\bar{x} = 0.7\text{‰}$; $\Delta^{15}\text{N}_{\text{collagen-hair}}$: $\bar{x} = 0.3\text{‰}$; $n = 6$) from museum specimens to adjust isotope values for bear bone collagen to bear hair (WebTable 1). This procedure allowed us to compare dietary parameters for bears between periods 1–3 (bone and hair) and period 4 (hair).

Contemporary specimens (2001–2007)

We used isotopic data derived from hair of bears that foraged for human foods in Yosemite in 2001–2007 ($n = 55$; WebTable 1; see Hopkins *et al.* 2012). We considered

recaptured bears as independent if their hair contained isotopes from a subsequent year (ie isotopes in hair collected in spring and fall represent the previous and current year’s diet, respectively). Management personnel immobilized or euthanized some of these bears in 2001–2003 ($n = 14$) and in 2005–2007 ($n = 22$; Hopkins *et al.* 2012). Management staff observed these bears consuming human foods on multiple occasions, which resulted in bears being classified as human food-conditioned. Hopkins *et al.* (2012) used a logistic regression model to predict 19 bears (18 individuals, as one was recaptured) as human food-conditioned, based on the $\delta^{15}\text{N}$ values of their hair. The authors collected hair from those bears during management actions ($n = 4$) in 2005–2007 and from hair-snares ($n = 15$) distributed throughout Yosemite in May–September 2006 and 2007.

Estimated isotopic mixing spaces

We estimated an “isotopic mixing space” (the area or volume contained in the space formed by lines connecting the sources in a multivariate isotope space; Panel 1) for each time period because we assumed that the availability of anthropogenic dietary sources and their isotopic compositions (hereafter, isotopic “endmembers”: vertices in an isotopic mixing space; Panel 3) changed over the past century (WebTable 2). We used endmembers for plants and animals, non-native trout, and human foods, and the relative difference between their digestible C and N concentrations ([C] and [N]), to estimate the shape of each mixing space (Panels 1 and 3).

Sample preparation and stable isotope analysis

We rinsed bear hair samples with a 2:1 chloroform-methanol solution to remove surface oils. We cleaned bone (from bear skulls and trout fins) of tissue and demineralized specimens in 0.5 M HCl for 72 hours at 5°C. We washed the resulting bone collagen repeatedly in petroleum ether to remove lipids, then rinsed and freeze-dried all samples. We weighed bone collagen and hair in tin cups (4 × 6 mm; number 041070, Costech Analytical Technologies Inc, Valencia, CA) and analyzed samples for their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using a Carlo Erba 1108 elemental analyzer interfaced to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer at the University of California, Santa Cruz. Stable isotope ratios are expressed in delta (δ) notation as parts per thousand or per mil (‰). Stable isotope analyses are reported and defined as:

$$\delta^i\text{X} = \frac{(^i\text{X}/^j\text{X})_{\text{sample}}}{(^i\text{X}/^j\text{X})_{\text{standard}}} - 1 \quad (\text{Equation 1})$$

where ^iX is the heavier isotope (^{13}C , ^{15}N) and ^jX is the lighter isotope (^{12}C , ^{14}N) in the analytical sample (numerator) and international measurement standard (denominator; Bond and Hobson 2012); reference standards are

Panel 1. Stable isotope analysis to estimate animal diets

Stable isotope analysis emerged as a useful tool for animal ecologists over three decades ago, but applications such as elucidating the trophic structure of food webs and reconstructing the diets of consumers have increased markedly over the past decade. Stable isotopes do not undergo radioactive decay, which simplifies their use (and safety) as tracers in food chains. Many elements have several naturally occurring stable isotopes, each with different masses. For example, the most common isotope of nitrogen, ^{14}N , has a rare and heavier counterpart, ^{15}N , with one additional neutron in its nucleus. Stable isotope ratios (eg $^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) derived from consumers' tissues reflect the isotopic composition of their dietary sources. Metabolic and digestive processes lead to small offsets between diet and animal tissues, which are quantified as "discrimination factors". Consumer tissues either turn over (ie cells die and are replaced) at different rates or are metabolically inert. Therefore, different animal tissues contain different abundances of isotopes from foods previously consumed, with each tissue offering a different temporal window on past diet. For instance, new plasma replaces old plasma in a few days, whereas bone undergoes slow continuous turnover; these tissues therefore contain isotopes derived from animal diets from days to years, respectively. Claws and hair, on the other hand, incorporate isotopes into their keratin structure as the tissue is synthesized, encapsulating dietary information permanently during the time the tissue grew.

Ecologists must carry out three steps to estimate the diets of animals. First, they attempt to sample food items during the same time frame that these foods are ingested and assimilated by consumers. For instance, hairs molted in spring/summer are typically representative of the previous year's diet; therefore, ideally, foods need to be collected during year x and hair collected in spring/summer of year $x + 1$. Second, ecologists must construct an accurate isotopic mixing space. To create this space, they must estimate the isotopic composition of a consumer's tissue when feeding on each food source exclusively, producing endmembers for the isotopic mixing space. Such an exercise is performed in two ways: (i) often, ecologists use captive animals to estimate discrimination factors by feeding test subjects a range of diets with different biological importance (eg different protein quantity or quality). Through time, isotopes from each diet will equilibrate in the tissues of each study animal (Figure 1a). The difference in isotope values of the animal tissue once equilibrated and the diet consumed is the discrimination factor for that particular diet. Researchers then model the relationship between discrimination factors for different diets and their biological importance (Figure 1b). These biologically important factors are then measured in foods collected from the field, and discrimination factors are interpolated from regression functions. Discrimination factors are then added to isotope values for foods sampled in the field (Figure 1c); these adjusted isotope values for food sources define endmembers in the isotopic mixing space (Figure 1d). (ii) Ecologists can also build isotopic mixing spaces by using tissues from animals known to forage for certain foods exclusively. As demonstrated in this study, we used both hair from bears that ate plants and animals exclusively and hair from humans, which we used as a proxy for bears with a diet consisting of 100% human foods, as endmembers in our isotopic mixing spaces (Figure 3). Third, ecologists rely on the principle of mass balance to estimate the contribution of food sources to the diets of animals. Dietary parameters are estimated using frequentist or Bayesian approaches. See Hopkins and Ferguson (2012) for a comprehensive review of current models used to estimate the diets of animals.

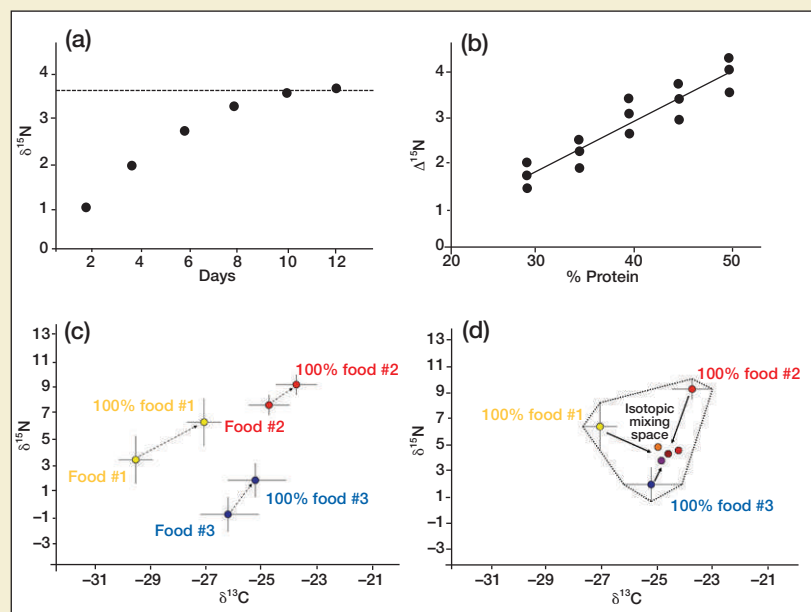


Figure 1. An example of estimating discrimination factors for captive animals (a and b) to build an isotopic mixing space for free-ranging animals (c and d). "100% food" denotes the estimated isotopic composition of animal tissue when feeding on the food exclusively.

Vienna Peedee Belemnite for C and atmospheric N_2 for N. IsotopeR (the stable isotope mixing model) estimated measurement error ($\delta^{13}\text{C} = 0.35\text{‰}$, $\delta^{15}\text{N} = 0.12\text{‰}$) from the isotope values of reference standards (Hopkins and Ferguson 2012). IsotopeR simultaneously estimated these parameters and applied the error to each observation when estimating dietary parameters (Hopkins and Ferguson 2012).

We corrected all isotopic data to account for the global decrease of ^{13}C concentration in Earth surface C reservoirs, primarily due to fossil-fuel combustion in the past

150 years (Francey *et al.* 1999). Following Chamberlain *et al.* (2005), we applied a time-dependent correction of -0.005‰ per year and -0.022‰ per year to all isotope values for samples collected from 1915 to 1959 and from 1960 to 2009, respectively.

Statistical analyses

We used t tests ($\alpha = 0.05$) to compare isotope values for bears between time periods (WebTable 3). Using

Panel 2. Time periods**Period 1 (1890–1922; bear sample: 1915–1919)**

In 1890, when Yosemite National Park was established, black bear abundance was relatively low in the park (Grinnell and Storer 1924). Bears accessed human foods (eg food waste from hotels) at garbage dumps located near park concessions in Yosemite Valley. Management personnel killed many of the bears that were habituated to these “bear pits” because the park considered them a nuisance (Runte 1990).

In 1895–1914 and 1917–1928, the Wawona Fish Hatchery raised primarily non-native salmonids (*Oncorhynchus aguabonita*, *Salvelinus fontinalis*, *Salmo trutta*, *Oncorhynchus clarkii*, *Salvelinus malma*, *Thymallus arcticus*), which were stocked in lakes, rivers, and streams throughout Yosemite (Evans and Wallis 1949; Greene 1987).

Period 2 (1923–1971; bear sample: 1928–1939)

In 1923, Yosemite opened artificial “feeding areas” to free-ranging bears in the park (Figure 2). Feeding areas were meant to draw bears away from developed areas and allowed visitors to observe bears more easily (Greene 1987). Lighted feeding platforms were used to entertain visitors during evening bear shows until 1940 (Figure 2). The last feeding area closed in 1971 (Graber and White 1983).

The California Fish and Game Commission operated Happy Isles Fish Hatchery in Yosemite Valley in 1927–1956. The hatchery raised over one million non-native trout annually (Greene 1987); hatchery personnel reported that bears consumed fish directly from their holding tanks.

Period 3 (1972–1998; bear sample: 1975–1985)

This period followed the closure of the last feeding area. In response, displaced bears returned to concession properties and campgrounds to seek out human foods (Graber and White 1978). An increase in incidents and property damage led to the development of a human–bear management plan in 1975 and to a comprehensive black bear ecology study conducted in 1974–1978 (Graber 1982). This plan outlined the steps necessary to reduce bear incidents and property damage in the park by implementing a proactive management strategy that prevents bears from accessing human foods. Unfortunately, due to limited resources, most management activities were not put into practice during this time period. In 1998, Yosemite documented a record high of nearly 1600 bear incidents in the park (Hopkins *et al.* 2012).

Period 4 (1999–2007; bear sample: 2001–2007)

Beginning in 1999, Congress has appropriated \$500 000 annually to Yosemite to address the human–bear management problem. Since then, the park has focused management efforts on preventing the bear population from accessing human foods, while managing individual “problem” bears (Hopkins *et al.* 2012). Yosemite installed food storage receptacles throughout the park, implemented a comprehensive interpretation and education program aimed at preventing bears from acquiring human foods, and carried out a rigorous hazing program for problem bears in Yosemite Valley (Hopkins *et al.* 2012).



Figure 2. Artificial feeding areas, including lighted feeding platforms (bottom), in Yosemite National Park.

IsotopeR, we estimated the endmembers (Panel 3; WebTable 2) of each isotopic mixing space for each time period and estimated dietary contributions (means \pm 1 standard deviation [SD] of mean marginal posterior distributions, and 95% credible intervals) at the population and individual level (Hopkins and Ferguson 2012).

We compared (1) estimated contributions of human foods in the diets of bears between time periods; (2) estimated trout contributions for the first two time periods; and (3) the total anthropogenic contribution (human foods + trout) for period 2 to the estimated contribution of human foods in period 3. We calculated the probability that the diets of bears were similar for each pair of time periods. This Bayesian test allowed us to use the entire posterior distribution without resorting to transformations, because these distributions are non-normal (see WebFigure 1; for details about calculating probabilities, contact the authors).

Results**Changing isotopes through time**

The isotopic composition of bear tissues has changed over time due to bears consuming different amounts of anthropogenic foods (Figure 3). The $\delta^{15}\text{N}$ values for bears increased significantly from 1915 to 1939 – when artificial feeding areas and fish hatcheries were in operation (period 1 versus 2) – then decreased significantly through time (period 2 versus 3 versus 4; Figure 3; WebTable 3). The bears' $\delta^{13}\text{C}$ values did not change when human foods and non-native trout were available (period 1 versus 2), but increased significantly after the feeding areas and hatcheries closed (period 2 versus 3; Figure 3; WebTable 3). In the 1970s and early 1980s (period 3), isotope values collapsed along the isotopic mixing line (connecting the two remaining endmembers), and in recent years, $\delta^{13}\text{C}$ values have also

Panel 3. Dietary sources as isotopic endmembers

Natural foods

Bears that consumed human foods had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than bears that did not (WebTable 3). We used isotope values derived from hair of bears that do not forage for human foods ($n = 135$; Hopkins *et al.* 2012) to estimate the isotopic endmember of bears on a 100% plant and animal diet (ie natural foods). This strategy circumvented the need to predict discrimination factors for a suite of plants and animals. We also used digestible [C] and [N] for plants ($n = 134$) and animals ($n = 29$) from Hopkins *et al.* (2012) to help estimate an isotopic mixing space for each time period.

Trout

We sampled a pelvic fin from eight trout specimens (*Salvelinus fontinalis*, $n = 2$; *Oncorhynchus clarkii*, $n = 1$; *Salmo trutta*, $n = 5$) from the California Academy of Sciences (WebTable 4). These samples were collected in Yosemite from 1921–1926. We corrected isotope values for trout bone collagen to estimate the isotopic endmember for bears (hair) on a 100% trout diet during periods 1 and 2. We did not include a trout endmember for periods 3 and 4 because trout were not available to bears during these time periods. We calculated the tissue–diet discrimination factor by first correcting trout bone collagen to trout muscle. We calculated the difference between muscle and bone collagen discrimination ($\Delta^{13}\text{C}_{\text{muscle-bone}} = \delta^{13}\text{C}_{\text{muscle}} - \delta^{13}\text{C}_{\text{bone}}$; $\Delta^{15}\text{N}_{\text{muscle-bone}} = \delta^{15}\text{N}_{\text{muscle}} - \delta^{15}\text{N}_{\text{bone}}$) using isotope values for muscle and bone collagen of anchovies and roundherring ($\delta^{13}\text{C}$: $\bar{x} = -1.4\text{‰}$; $\delta^{15}\text{N}$: $\bar{x} = 2.4\text{‰}$; Sholto-Douglas *et al.* 1991; WebTable 4) and then added these corrections to isotope values for trout bone collagen (WebTable 4). Next, we calculated the mean hair–diet discrimination factor for mammals ($\Delta^{13}\text{C}_{\text{hair-diet}}$: $\bar{x} = 2.5\text{‰}$; $\Delta^{15}\text{N}_{\text{hair-diet}}$: $\bar{x} = 3.4\text{‰}$; Caut *et al.* 2009) and added these discrimination values to isotope values for trout muscle to estimate the isotopic endmember for the hair of bears on a 100% trout diet (WebTable 4). We also included error for $\Delta^{13}\text{C}_{\text{hair-diet}}$ and $\Delta^{15}\text{N}_{\text{hair-diet}}$ values (1 SD of 0.9‰ and 1.2‰, respectively; both from Caut *et al.* 2009) to account for the variation in estimating Δ values from controlled studies (Hopkins and Ferguson 2012). Lastly, we estimated digestible [C] and [N] by analyzing nutrient data for trout from the USDA National Nutrient Database (www.nal.usda.gov/fnic/foodcomp/search) (WebTable 5).

Human foods

We used human hair sampled from four time periods to estimate the endmembers for bears on an exclusive diet of human foods. Similar to Hopkins *et al.* (2012), we assumed that the isotopic composition of hair for bears on a 100% human food diet would be similar to the isotopic composition of human hair. A Wilson (University of Bradford) conducted stable C and N isotope analysis on human hair collected in the US in 1940 (Trotter Collection, National Museum of Natural History, Smithsonian Institution) (WebTable 6), analyzing the hair of 10 individuals twice. We averaged each set of these isotope values (WebTable 6) and used these hairs to define isotopic endmember for bears on a 100% human food diet during periods 1 and 2. We also used isotope values for human hair collected from 1982–1983 (Schoeller *et al.* 1986) as well as 2004 (Bowen *et al.* 2009) and 2009 (Hopkins *et al.* 2012) to define isotopic endmembers for bears on a 100% human food diet during periods 3 and 4, respectively. Similar to Hopkins *et al.* (2012), we grouped the 2004 and 2009 hair samples because they were isotopically similar.

decreased (period 3 versus 4; Figure 3; WebTable 3).

Changing dietary contributions through time

We found that the proportion of human foods in bear diets (1) increased when people fed bears intentionally in 1923–1971; (2) remained relatively high and constant after feeding areas closed; and (3) declined substantially following government intervention, beginning in 1999 (Figure 4; WebFigure 1; Table 1; WebTable 1). In the past century, mean dietary contributions for individual bears ranged from 31% to 92% for plants and animals, from 2% to 11% for trout, and from 7% to 69% for human foods (Table 1; WebTable 1). Human foods increased in the diets of bears during period 2, while trout contributions remained constant (period 1 versus 2; Figure 4; WebFigure 1; Table 1; WebTable 1). During period 3, some bears were consuming more human foods than at any other time period over the past century (Table 1; WebTable 1); however, human food contributions for periods 2 and 3 were similar (WebFigure 1). The mean dietary contribution in period 3 (35%) was similar to the total contribution of anthropogenic foods prior to the

closure of feeding areas and hatcheries (period 2: 27% human foods + 4% trout = 31%; probability of similarity = 69%; Figure 4); this was not the case for bears that currently forage for human foods (13% during period 4; Table 1; WebTable 1). During period 4, the contribution of human foods decreased in bear diets (period 3 versus 4; Figure 4; WebFigure 1), although some bears continued to consume a relatively large amount of human foods (Table 1; WebTable 1).

Conclusions

Our isotopic analysis suggests that black bears that consume anthropogenic foods in Yosemite National Park have highly flexible diets (Figure 3). The relatively high isotope values among bears that consume human foods are attributable to the diet of humans in North America being meat- (Schoeller *et al.* 1986) and corn-rich (from corn products such as corn syrup and corn-fed livestock; Koch 2007; Chesson *et al.* 2008). When compared to local animals and C_3 plants, meat and corn products are high in ^{15}N and ^{13}C , respectively. The tissues of bears that consume human foods therefore have high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

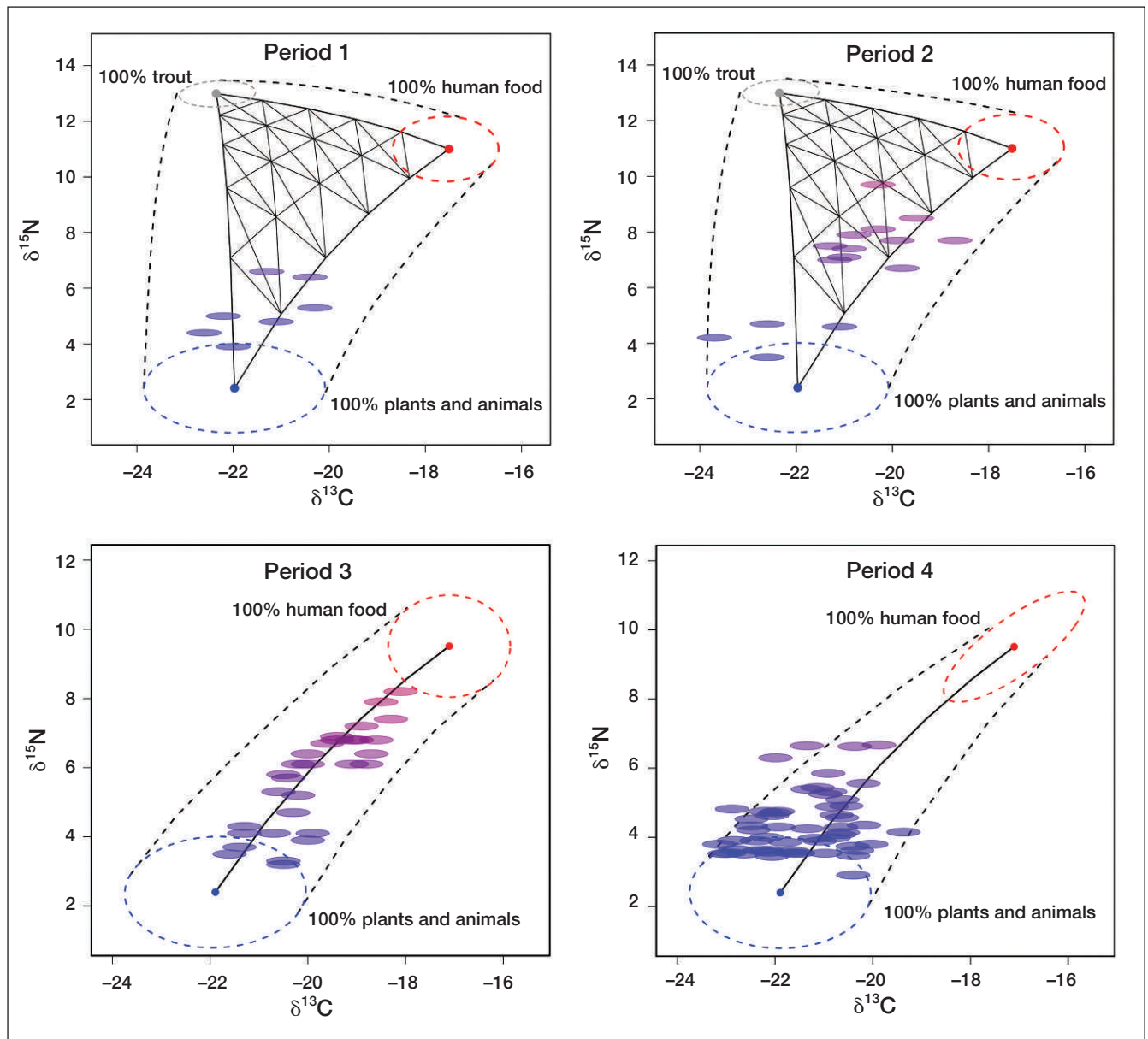


Figure 3. Estimated isotopic mixing spaces and isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) for black bears (small ovals illustrate the approximate measurement error applied to each observation) that forage for anthropogenic foods in Yosemite National Park, 1915–2007. Bears were killed, captured, or hair-snared during the following years: 1915–1919 (period 1), 1928–1939 (period 2), 1975–1985 (period 3), and 2001–2007 (period 4). Each estimated endmember (circles = \bar{x} ; ovals = 2 SD) represents the estimated isotopic composition of bear hair when bears feed on the dietary source exclusively (Panels 1 and 3). The shape of each endmember illustrates the degree of estimated correlation among isotope values for each dietary source. The curvature of each side of the mixing triangle results from the relative differences in concentrations of digestible C and N between endmembers (Phillips and Koch 2002). Black iso-diet lines (lines within the mixing triangle) illustrate how dietary proportions are estimated by the mixing model, IsotopeR (Hopkins and Ferguson 2012).

The contribution of anthropogenic foods to bear diets varied over the past hundred years, as a result of changing management strategies. Bears that foraged for human foods likely fed on more of these foods as they gained access to feeding areas (period 1 versus 2). Certain individuals in the population therefore adapted behaviorally to foraging for this new food source, leading to more heterogeneous, human food-based diets. Although the average proportion of human foods in bear diets was similar during the years following the closure of feeding areas and

hatcheries (periods 2 versus 3), the amount of human foods in bear diets increased from the early part of the century (periods 1 versus 3; Figure 4; WebFigure 1). In addition, some individual bears consumed a greater proportion of human foods during period 3 (Figure 3; Table 1; WebTable 1). Our results also imply that the proportion of anthropogenic foods was similar before and after feeding areas and hatcheries closed (period 2 versus 3). As with the closure of garbage dumps in the early 1970s in Yellowstone National Park (Gunther 1994), removing

artificial feeding areas in Yosemite National Park caused bears to disperse from their routine feeding areas to seek out human foods in other locations, such as campgrounds and hotels (Graber and White 1978). Isotopic collapse (eg Layman *et al.* 2007) along the mixing line that connects endmembers for human and natural foods indicates that trout were no longer a dietary component more than 35 years after hatcheries closed in Yosemite (period 2 versus 3; Figure 3).

We found that the proportion of human foods in the diets of bears recently decreased by 63% (period 3 versus 4; Figure 4), indicating that Yosemite reduced the amount of human foods available to bears during period 4. Furthermore, the variation in isotope values was relatively high for bears during period 4, indicating that individuals currently have more heterogeneous diets of plants and animals (Figure 3). Finally, there is a 97% probability that the diets of bears living in Yosemite today are currently similar to the diets of bears in the early 1900s (period 1 versus 4; Figure 4; WebFigure 1). Although it is unclear how many bears foraged for human foods in the early 1900s, this result implies that similar amounts of human foods were available to bears in 1915–1919 and 2001–2007. This finding signifies a notable management achievement in Yosemite, as the park received an average of 32 625 visitors each year in 1906–1922 (range: 5414 – 100 506) and about four million visitors each year today (Yosemite National Park, www.nature.nps.gov/stats/viewReport.cfm).

Evidence from this study suggests that black bears are a conduit for anthropogenic nutrients in the Yosemite ecosystem. Yet, the magnitude and impact of this enhanced nutrient flux and other effects related to anthropogenically subsidized bears on the Yosemite ecosystem are difficult to estimate because bear population density was not tracked over the past century. There are reasons, however, to suspect these impacts could be important. Bears that forage for human foods in Yosemite are, on average, larger, have higher annual reproductive rates and litter sizes (Graber 1982), and have a lower breeding age as compared with conspecifics that forage for plants and animals exclusively (Keay 1995). In addition, management staff eventually kill many bears conditioned to seek out human foods in Yosemite (Hopkins and Kalinowski 2013). Larger bears with greater dietary plasticity and the anthropogenic nutrients they broadcasted to the ecosystem may have bolstered the population's role in maintaining food-web stability or destabilized the system (Rosenzweig 1971). Future research in Yosemite and other ecosystems should

quantify the effects of human-derived nutrients on food-web stability. In particular, longitudinal studies that examine the foraging ecology of synanthropes in human-altered landscapes as well as ecosystem processes (eg primary pro-

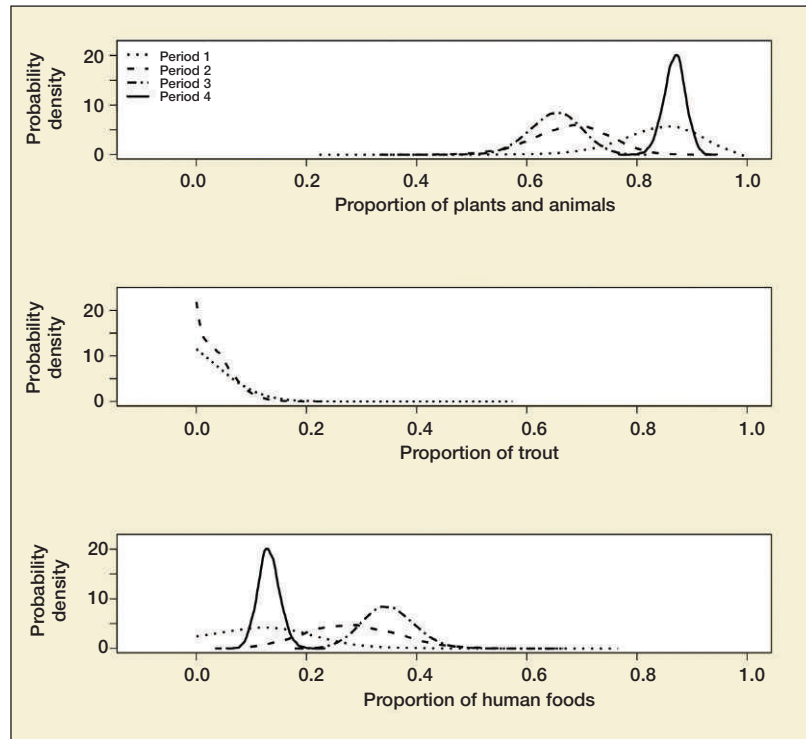


Figure 4. Proportional dietary contributions (expressed as marginal posterior distributions) estimated at the population level for black bears that forage for anthropogenic foods in Yosemite National Park, 1915–2007. IsotopeR estimated all dietary parameters (for model details, see Hopkins and Ferguson [2012]). Bears were killed, captured, or hair-snared during the following years: 1915–1919 (period 1), 1928–1939 (period 2), 1975–1985 (period 3), and 2001–2007 (period 4).

Table 1. Estimated dietary contributions for bears that foraged for human foods in Yosemite National Park, 1915–2007

Dietary source	Time period	E[p]	S[p]	Population credible interval (95%), median			Range for individuals
				0.025	0.500	0.975	
Plants and animals	1	0.83	0.07	0.69	0.84	0.94	0.73–0.90
	2	0.69	0.07	0.55	0.69	0.81	0.39–0.91
	3	0.65	0.05	0.56	0.65	0.74	0.31–0.87
	4	0.87	0.02	0.83	0.87	0.91	0.64–0.92
Trout	1	0.03	0.04	0	0.02	0.13	0.02–0.06
	2	0.04	0.03	0	0.04	0.11	0.02–0.11
Human foods	1	0.13	0.08	0	0.13	0.30	0.08–0.22
	2	0.27	0.07	0.14	0.26	0.42	0.07–0.49
	3	0.35	0.05	0.26	0.35	0.44	0.13–0.69
	4	0.13	0.02	0.09	0.13	0.17	0.08–0.36

Notes: IsotopeR estimated proportional dietary contributions for bears at the population and individual level during each time period. Dietary contributions for period 4 are from Hopkins *et al.* (2012). E[p] and S[p] denote the mean and SD of the posterior density distribution of each proportional dietary contribution, respectively.

duction, seed dispersal, and nutrient cycling) may reveal that human-derived nutrients alter the stability of food webs, the ecological functions of healthy ecosystems, and the goods and services they provide.

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