USE OF STABLE ISOTOPES TO INVESTIGATE BLACK BEAR DIETS AND TO EVALUATE THE HUMAN-BEAR MANAGEMENT PROGRAM AT YOSEMITE NATIONAL PARK, CA

by

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DEDICATION

I dedicate this dissertation to my family and closest friends. Thank for your love and support over the years.

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ABSTRACT

Yosemite has applied extraordinary effort to manage people and bears over the past century. For the past decade, human-bear management has implemented both proactive (population-level) and reactive (individual-level) management to prevent bear incidents; however, incidents continue to occur at high frequency even though the program has received $500,000 in congressional funding each year since 1999. For this study, we developed a new method to detect human food-conditioned (FC) bears throughout the Park using isotopic data and used these results and dietary estimates for these bears to evaluate the effectiveness of the human-bear management program. In the first chapter, we proposed 40 definitions for terms and concepts common to human-bear management. In the second chapter, we provide details on a stable isotope mixing model designed to accurately estimate dietary parameters in the remaining two chapters. In these last chapters, we collected tissues (bone and hair) from contemporary and historic bears with known and unknown management statuses (FC or non-food-conditioned [NFC]) and analyzed them for their stable isotopic composition. In chapter 3, we used these isotopic data to predict the management status of unknown bears using a logistic regression model. For chapters 3 and 4, we used isotopic data for FC bears and stoichiometric data for their food sources to estimate the proportional dietary contributions to bear diets through time using our mixing model. Results from chapter 3 show a small proportion (~13%) of the unknown sampled population (n = 145) is currently FC, and chapter 4 results showed the proportion of human food in food-conditioned bear diets increased before the park began implementing a rigorous proactive human-bear management strategy in 1999. Since then, the amount of human food in known FC bear diets has decreased dramatically. We conclude that proactive human-bear management was effective at reducing the amount of human food available to bears since 1999. In contrast, evidence suggests reactive human-bear management was not effective at eliminating or reducing the amount of human food in individual bear diets. We suggest the Park reevaluate the effectiveness of their reactive human-bear management strategy, reduce problem bears from the population, and continue proactive management. Supplemental tables for chapters 3-5 (Hopkins_S3.pdf, Hopkins_S4.pdf, Hopkins_S5.pdf) are available electronically at UMI and on CD in Special Collections at the Montana State University Library.

INTRODUCTION

Human-bear management strategies have varied over the past century in Yosemite National Park (YNP) as human attitudes towards black bears (*Ursus americanus*) have changed. In the early 1900s, black bears, like other carnivores, were being extirpated across their range in North America because they were considered nuisance animals. However, by the 1920s, their instrumental value changed in the National Parks. In particular, bear viewing increased visitation in National Parks such as YNP and Yellowstone, which resulted in a campaign to establish convenient locations where people could watch bears feed. In YNP, park staff allowed bears to feed in open-pit garbage dumps (i.e., bear pits) and intentionally fed bears at feeding platforms (locations where Park staff would regularly feed bears food scraps). By the 1940s, human-bear interactions increased to intolerable levels in these areas, resulting in high levels of human injuries. In response, YNP closed the feeding areas and began phasing out bear pits. In addition, the Park began relocating bears out of Yosemite Valley. This reactive (individual-level) human-bear management strategy provided temporary relief from known problem bears; however, new bears filled vacant niches. Because the current proactive (population-level) human-bear management was not yet implemented, new bears likely became human food-conditioned (FC) in Yosemite Valley, increasing the human-bear management problem in YNP. By the 1960s, the Park changed their management practices once again. Management staff learned that most problem bears would return to Yosemite Valley after relocation; therefore, they decided to remove these animals from the population altogether. High numbers of management-induced mortalities (i.e., >200 bears killed from 1960-70) eventually led to public outcry in the

1970s and the resulting Human-Bear Management Plan (1975). Although this plan laid out a program for reducing bear incidents by concentrating on proactive management, it was not effective because resources were not available to carry out its elements. As a result, ~1,600 bear incidents were reported in 1998. Since 1999, the human-bear management program has received an annual congressional appropriation of $500,000 to implement both proactive and reactive management to mitigate bear incidents. Currently, an interdivisional Bear-Team implements proactive management in visitor-use areas and Wildlife Management responds to individual problem bears (i.e., reactive management). Despite this ample funding source, bear incidents continue to occur at relatively high levels in YNP.

For this study, we evaluate the human-bear management program over the past century using new quantitative methods. Specifically, we conducted isotopic analysis on bear tissues collected throughout time and space to detect FC bears. We then used these results and dietary estimates to evaluate the program's effectiveness at reducing the amount of anthropogenic food available to bears. First, we sampled bears park-wide and provided measures that can be used to evaluate the overall human-bear program each year. Next, we evaluated proactive (Interdivisional Bear-Team management) and reactive management (Wildlife Management) separately using dietary estimates for FC bears sampled from 1915–2007 and 2001–2007, respectively. For this project we assume that the average amount of anthropogenic food in FC bear diets is an index for the amount of these food sources available to bears. Therefore, we suggest that a reduction in the amount of human food in bear diets over time suggests human-bear management was effective at reducing the amount of human food available to bears.

Contribution of Author and Co-Authors

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A proposed lexicon of terms and concepts for human–bear management in North America

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Abstract: We believe that communication within and among agency personnel in the United States and Canada about the successes and failures of their human–bear (Ursidae) management programs will increase the effectiveness of these programs and of bear research. To communicate more effectively, we suggest agencies clearly define terms and concepts used in human–bear management and use them in a consistent manner. We constructed a human–bear management lexicon of terms and concepts using a modified Delphi method to provide a resource that facilitates more effective communication among human–bear management agencies. Specifically, we defined 40 terms and concepts in human–bear management and suggest definitions based on discussions with 13 other professionals from the United States and Canada. Although new terms and concepts will emerge in the future and definitions will evolve as we learn more about bear behavior and ecology, our purpose is to suggest working definitions for terms and concepts to help guide human–bear management and research activities in North America. Applications or revisions of these definitions may be useful outside of North America.

Key words: bear incidents, definitions, food conditioning, habituation, human–bear conflict, human–bear interactions, human–bear management, *Ursus americanus*, *Ursus arctos*, *Ursus maritimus*

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Bear (Ursidae) population management includes four main objectives: conservation, sustained yield harvest, predator or depredation control (Miller 1990), and human–bear management (Fig. 1). Although methods to achieve these goals discussed by Miller (1996) may vary within and among agencies, management programs often use similar strategies to meet their objectives. In contrast, the strategies used by agencies to manage bear incidents can vary greatly.

Over the past several decades, human–bear management strategies evolved throughout the United States and Canada as proactive management methods emerged to face challenges of mitigating bear incidents (Witmer and Whittaker 2001). This evolution in management resulted in divergent strategies (site- and agency-specific) despite common program goals to prevent bear incidents. Because various human–bear management methods and strategies are used throughout the United States and Canada, we believe it is important for agencies to share information about program successes and failures to learn what methods and strategies are effective.

Currently, there are numerous terms and concepts used in human–bear management; however, some programs have different definitions for the same terms and concepts. We suggest agencies clearly define the terms and concepts they use in their programs (Whittaker and Knight 1998) and use them in a consistent manner. We also feel a common human–bear management language would improve communication among human–bear management professionals in the United States and Canada and may be applicable to human–bear management programs worldwide.

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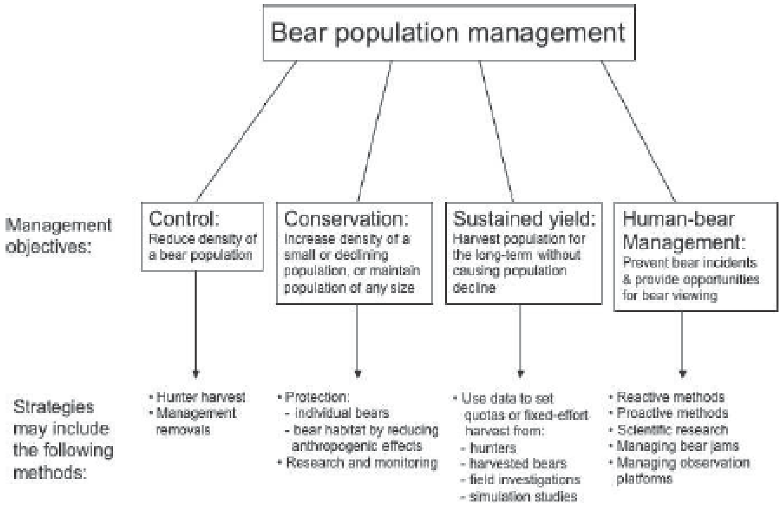

Fig. 1. **The four bear population management objectives and examples of their strategies and methods.**

Standardized definitions for terms and concepts could benefit human–bear management programs in three ways. First, they would enhance site-specific and intra-agency bear conservation efforts. For example, Yellowstone (Gunther et al. 2004), Glacier (Gniadek and Kendall 1998), Yosemite (V. Seher, Yosemite National Park, California, USA, personal communication, 2009), and several Alaskan national parks (Wilder et al. 2007) developed human–bear management databases. Although each database contains similar information, terminology and definitions for the data differ. If the U.S. National Park Service (NPS) adopted the same terms and definitions and collected the same data, an intra-agency meta-analysis could be conducted. Such an analysis would benefit each park and could provide insight regarding the successes and failures of human–bear management programs throughout the NPS, facilitating a general NPS management strategy.

Second, universal definitions would also promote interagency bear conservation efforts. For example, in the Greater Yellowstone Ecosystem (GYE), records of bear incidents prior to 1992 varied in level of detail, criteria, and definition, depending on which of the 13 state and federal land management agencies had jurisdiction over the site where the incident occurred (Gunther et al. 2004). Consequently, these inconsistencies contributed to delayed prediction, evaluation, correction, and prevention of incidents between humans and grizzly bears (*Ursus arctos*) in the GYE.

Lastly, a common language would benefit human–bear management by defining terms and concepts to researchers who study and evaluate these methods and programs. Definitions would be useful to researchers when designing projects, documenting and discussing study results, and making recommendations.

Here, we propose working definitions for terms and concepts currently used in human–bear management and research. We understand that new terms and concepts will need to be addressed as they emerge in the future, and that definitions for terms and concepts will evolve as we learn more about bear behavior and ecology. The main purpose of this paper, however, is to provide bear population management programs a resource to help guide their human–bear management and research activities.

Methods

We constructed the lexicon in two stages. First, we reviewed peer-reviewed and unpublished human–bear management literature from the United States and Canada and assembled a list of commonly used management terms. We then either extracted or inferred definitions for these terms from the literature, or constructed new definitions for these terms.

In addition, we developed and defined terms and concepts that are not common in the literature, but that we believe are important to human–bear management. Each term defined in the lexicon (Table 1) is italicized the first time it is described in Discussion.

Next, we asked 25 professionals (federal, state, or provincial managers, researchers, and a private consultant) engaged in human–bear management and research in the United States and Canada to review the lexicon and the original manuscript. We used a modified Delphi method (Linstone and Turoff 1975) to incorporate professional opinions in defining terms and concepts. Specifically, we reviewed comments, addressed remarks by correspondence, and modified the lexicon until there was consensus among co-authors.

Results

In addition to co-authors, a total of 13 professionals (see Acknowledgements) reviewed the original manuscript and 40 human–bear management terms and concepts were defined (Table 1), and discussed in four sections. We used Fig. 1 and Fig. 2 to describe bear population management objectives, strategies, and methods as well as illustrate the management status of bears, respectively. We also developed a flow chart (Fig. 3) and dichotomous key (Table 2) to assist managers with documenting bear sightings and bear incidents.

Discussion

Human–bear management strategies

The focus of bear population management in the United States and Canada has evolved over more than 100 years as the perception and extrinsic value of bears has changed. In the late 19th and early 20th centuries, bears were considered vermin, and bear population management reduced or eliminated bears from large regions (Miller 1990, Schwartz et al. 2003). By the 1920s, bears were classified as game animals in many areas throughout the United States and Canada, which ultimately restricted indiscriminate killing and set the stage for modern bear harvest management (Miller 1990). Currently, a common goal of bear population management is to ensure the long-term viability of the species. Most bear population management plans include a program to address the human role in bear management. Adding the word human to bear management (*human–bear management*) reflects an increasing focus in bear population management: to mitigate bear incidents, and in some cases, to provide people with opportunities for enjoying bears through managed viewing (Fig. 1).

Human–bear management uses one or more of the following management strategies: reactive, proactive, and adaptive management. *Reactive human–bear management* is a strategy that responds to individual bears involved in bear incidents through immediate and direct action (Thompson and McCurdy 1995), or increases the harvest of a local population of bears in an attempt to reduce bear incidents. The goal of reactive management is to prevent future conflicts or other incidents with specific bears, or to reduce the local population if a specific individual cannot be identified. Under this strategy, management staff generally deal with bears on a case-by-case basis. Reactive human–bear management includes, but is not limited to, the following management methods: capture (often including immobilization, handling, and marking bears), monitoring, management removal (lethal or non-lethal), translocation, relocation, on-site release, hazing, aversive conditioning treatments, and closing areas to human access (and posting warning signs, or both) where there have been human–bear conflicts.

Proactive human–bear management is a population-level management strategy that aims to deter or prevent individual bears not previously or currently involved in bear incidents from being involved in incidents. This often involves the application of management measures to people and human-use areas where conflicts and other bear incidents occurred or may occur. Proactive methods such as management of edible waste, implementing food storage regulations, exclusion (e.g., fencing), public education, closing bear management areas, and other techniques are now common in human–bear management programs in the United States and Canada.

Implementing preventative methods has reduced the amount of human injury, bear removals and translocations, and incidents of bears obtaining *anthropogenic food* (e.g., agricultural and garden crops, barbeque grill scraps, compost, fish from hatcheries, fruit from orchards or vineyards, grease and lubricants, honey from apiaries, *human food*, hunter-killed carcasses, livestock or pets, pet food or birdseed, sanitary waste, trash) and incidents of

Table 1. Lexicon of terms and concepts for human–bear management. Italicized terms are included in the lexicon.

Definitions for terms and concepts
aggressive behavior: bear behavior (defensive or offensive) that is threatening to people
aggressive bear: a bear that has displayed *aggressive behavior* and is a public safety concern
defensive-aggressive bear: a bear that may be a public safety concern because it exhibited *aggressive behavior* in response to being *provoked*
offensive-aggressive bear: a bear that may be a public safety concern because evidence suggests the bear exhibited aggressive behavior and was not provoked
anthropogenic food: foods or attractants having a human origin
aversive conditioning: a learning process in which deterrents are continually and consistently administered to a bear to reduce the frequency of an undesirable behavior
aversive conditioning treatment (or trial): a management method that attempts to use the *aversive conditioning* learning process to modify bear behavior for the long-term
bear attack: intentional contact by a bear resulting in human injury (verbatim from Smith et al. 2005)
bear deterrent: aversive agent administered to bears to cause pain, avoidance, or irritation
bear incident: an occurrence that involved a *human–bear conflict* or episodes where bears caused property damage, obtained anthropogenic food, killed or attempted to kill livestock or pets, or were involved in vehicle collisions (Gunther 1994, Schirokauer and Boyd 1998, Gunther et al. 2004, Wilder et al. 2007)
bear jam: an instance when people slow or stop their vehicles to view or photograph bears, causing traffic congestion (Gunther and Biel 1999)
bear sighting: an observation when a bear was seemingly unaware of the person observing it (not a *human–bear interaction*), had no observable stress-related response to the person during an *interaction* (Smith et al. 2005, Wilder et al. 2007), or responded to the person (who did not take extreme *evasive action*) by taking *evasive action*
bear that tolerates people: a bear that does not take *evasive* or *aggressive* action when in the presence of people (*habituated* or innately tolerant)
conditioning: learning involved in receiving a reward or punishment for a given response (behavioral act) to a given stimulus (verbatim from McCullough 1982)
evasive action of bears or humans: when a bear or person responds to a *human–bear interaction* by escape or avoidance
food-conditioned bear: a bear that has learned to associate people (or the smell of people), human activities, human-use areas, or food storage receptacles with *anthropogenic food* (Herrero et al. 2005)
habituation: the waning of a response (or muted response) when a reward or punishment is discontinued (verbatim from McCullough 1982)
habituated bear: a bear that shows little to no *overt reaction* to people (Herrero et al. 2005) as a result of being repeatedly exposed to anthropogenic stimuli without substantial consequence
hard release: a hazing method where *deterrents* are administered to a bear as it exits a trap
hazing: a technique where *deterrents* are administered to a bear to immediately modify the bear's undesirable behavior (Schirokauer and Boyd 1998)
human–bear conflict: when a bear exhibited stress-related or curious behavior, causing a person to take extreme evasive action (Schirokauer and Boyd 1998), made physical contact with a person or exhibited clear predatory behavior, or was intentionally harmed or killed (not including legal harvests) by a person
human food: *anthropogenic foods* that only include human foodstuff and food waste
human–bear interaction: an occurrence when a person and bear are mutually aware of each other (Smith et al. 2005)
human–bear management: a bear population management program that focuses on mitigating *bear incidents* and providing bear viewing opportunities
management bear: a bear that may be monitored for management purposes because it is individually identifiable
management closure: when management staff restrict or prevent human access to an area because of the increased potential for *human–bear conflict*
management removal: lethal or non-lethal removal of a bear from the population by or at the direction of management personnel
management status: a classification assigned to each management bear of *habituated* (not food-conditioned), *food-conditioned* (not habituated), habituated and food-conditioned, *aggressive*, *predatory*, *unknown*, or *unmanaged*
on-site release: a management method that consists of capturing and releasing a bear at the site of capture (Gunther et al. 2000, Clark et al. 2002)
overt reaction distance (ORD): the distance at which a bear visibly responds to people (Herrero et al. 2005) during a *human–bear interaction*
predatory bear: a bear that preyed or attempted to prey on people (Herrero and Higgins 2003)
proactive human–bear management: a population-level management strategy that aims to deter or prevent individual bears not previously or currently involved in *bear incidents* from being involved in incidents
problem bear: a bear involved in repeated *bear incidents*
provoked bear: when a person enters a bear's *ORD*
reactive human–bear management: a management strategy that responds to individual bears involved in *bear incidents* through immediate and direct action (Thompson and McCurdy 1995) or increases the harvest of a local population of bears in an attempt to reduce bear incidents

Table 1. Continued.

Definitions for terms and concepts

relocation: the capture and subsequent transport of a bear from the site of capture to a location within its likely home range often in an attempt to temporarily mitigate *bear incidents*

stress-related behaviors: observed bear response when provoked during a *human–bear interaction* (Herrero et al. 2005)

translocation: the capture and subsequent transport of a bear from the site of capture to a location outside its presumed home range often in an attempt to permanently mitigate *bear incidents* or augment a population

unknown bear: a bear that has an unknown management status and will be monitored in the future

unmanaged bear: a bear that will not be monitored in the foreseeable future because it has not been observed interacting with people or suspected of being involved in any *bear incidents*

property damage (Herrero 1985, Gunther 1994, Thompson and McCurdy 1995, Gniadek and Kendall 1998, Honeyman 2008; L.M. Ciarniello, 1997, Reducing bear–human conflicts: Solutions through better management of non-natural foods, Westworth, Brusnyk and Associates, Edmonton, Alberta, Canada). Although we realize that preventing an individual bear from being involved in an incident may seem proactive, we believe that responding to any individual bear should be considered reactive human–bear management.

Implementing reactive and proactive human–bear management allows managers to prevent or reduce conflict as well as respond to incidents as they occur. The choice of various combinations of proactive and reactive management methods is often based on a manager's qualitative analysis of past experiences (KAG, unpublished data) and is not typically based on data collected to answer a particular management-related question. Although managers' decisions often result in fewer human–bear incidents, the effectiveness or success of each method is often unclear because they are not scientifically evaluated.

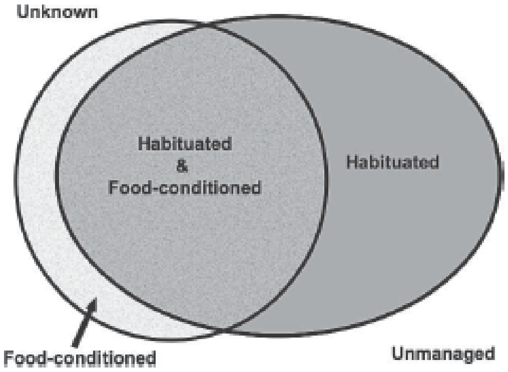

Fig. 2. Venn diagram illustrating the management status of bears: food-conditioned (not habituated), habituated (not food-conditioned), habituated and food-conditioned, unknown, unmanaged. The management status aggressive bear and predatory bear are not included in the diagram, but may be designated simultaneously or following assignment to a classification.

Research is used to evaluate current management methods and program success, justify the use of new untested methods, predict the efficacy of future strategies, and investigate bear ecology. A dynamic management strategy, which adjusts according to new information from management and research, is referred to as adaptive management (Walters 1986). Adaptive human–bear management typically employs both reactive and proactive management methods, and we believe is the most effective human–bear management strategy because management direction shifts according to previous successes, failures, and research findings.

Management methods

A *management removal* is the lethal or non-lethal removal of a bear from the population by, or at the direction of, management personnel. Non-lethal removals include sending bears to zoos, rehabilitation facilities, or other ecosystems, whereas lethal removals involve intentionally or unintentionally killing bears during management actions (Gunther 1994). Examples of management removals include killing predatory or aggressive bears or augmenting another population.

Following Ciarniello (unpublished report 1997), we propose defining *translocation* as the capture and subsequent transport of a bear from the site of capture to a location outside its presumed home range (often a remote area) in an attempt to permanently mitigate bear incidents or augment a population. The term *relocation* is often used synonymously (Landriault et al. 2009); however,

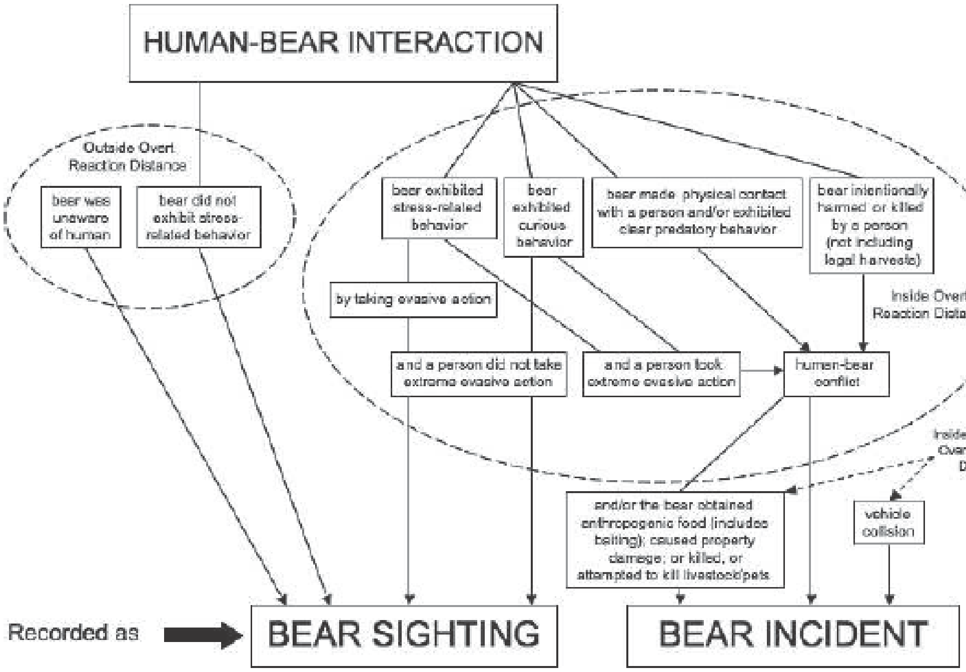

Fig. 3. Flow chart illustrating whether a human–bear interaction or other episode involving a bear should be documented as a bear sighting or bear incident given the suggested definitions for these terms.

we propose defining relocation as moving a bear within its likely home range (often in an attempt to temporarily mitigate bear incidents). Unlike relocated bears, translocated bears are transported to sites outside their home ranges to increase the probability that the individual will establish a home range elsewhere and not return to the capture area. Although some agencies continue to perform this reactive management method, many have discontinued translocations because most such bears return to the capture area (Miller and Ballard 1982, Knight et al. 1988, Meagher and Fowler 1989, Blanchard and Knight 1995, Beckmann and Lackey 2004). However, relocations are used in some situations where short-term removal from an immediate conflict situation may eliminate the conflict over a longer period. Relocation of polar bears (*U. maritimus*) from Churchill, Manitoba to remote areas near the forming sea ice has been successful in reducing incidents (D. Hedman, Manitoba Conservation,

Table 2. Dichotomous key to determine whether a human–bear interaction should be documented as a bear sighting or bear incident.

Question	Response
1. Did the bear make physical contact with you or did you intentionally harm or kill the bear?	yes, document as a *incident* no, go to question 2
2. Did the bear act as if it was aware of you?	yes, go to question 3 no, document as a *sighting*
3. Did you take extreme evasive action (e.g. ran away, climbed a tree, played dead, fired bear deterrent spray, discharged ammunition from a firearm) in response to feeling threatened by the bear's behavior?	yes, document as a *incident* no, document as a *sighting*

Thompson, Manitoba, Canada, personal communication, 2009). Likewise, Parks Canada relocated grizzly bears and American black bears (*U. americanus*) (H. Morrison, Parks Canada, Field, British Columbia, Canada, personal communication, 2009) and Montana Fish, Wildlife, and Parks relocated grizzly bears (M. Madel, Montana Fish, Wildlife and Parks, Great Falls, Montana, personal communication, 2009) that were observed near human-use areas. These grizzly and black bears were moved to locations where natural foods were abundant as a short-term measure to reduce conflicts.

An *on-site release* consists of capturing—and in some cases immobilizing, handling, and marking—and releasing a bear at the site of capture (Gunther et al. 2000, Clark et al. 2002). Capturing and handling bears may provide individual bears a negative stimulus, reinforcing its avoidance of people and deterring it from returning to areas where is was captured (Brady and Maehr 1982; Wooding et al. 1988; Shull 1994; Clark 1999; Clark et al. 2002, 2003). Therefore, under certain circumstances, an on-site release could be used as a form of hazing, but is not a form of translocation or relocation because the bear is not transported from the capture site. A *hard release* (in a hazing context) is a method where *bear deterrents*—defined as aversive agents administered to bears to cause pain, avoidance, or irritation (e.g., projectiles such as rubber buckshot, batons, bean bags)—are administered to a bear as it exits a trap (Beckmann et al. 2004; Brabyn, N., L. Homstol, and T. Hamilton. 2005, Unpublished progress report 2005. Whistler black bear aversive conditioning and monitoring project. Whistler, British Columbia, Canada).

Hazing is a technique where deterrents are administered (independently, simultaneously, or consecutively) to a bear to immediately modify the bear's undesirable behavior (e.g., bear entering a campground; Schirokauer and Boyd 1998). Hazing is usually not intended to alter undesirable bear behavior for the long-term. Instead, it is the primary reactive management technique to disperse management bears from human-use areas on a case-by-case basis. Hazing may, however, prove effective at modifying undesirable behavior of unmanaged bears or of bears that are in the initial stages of food conditioning (Mazur 2010). Hazing is also currently used to describe the action of applying deterrents to bears during aversive conditioning treatments (Hunt 2003, Honeyman 2008, Mazur 2010) and should not be confused with the learning process, aversive conditioning.

Aversive conditioning of bears is a learning process in which deterrents are continually and consistently administered to a bear to reduce the frequency of an undesirable behavior (Brush 1971, McCullough 1982). An *aversive conditioning treatment* (*or trial*) is a management method that attempts to use the aversive conditioning learning process to modify undesirable bear behavior for the long-term. Many studies investigated aversive conditioning of bears by examining the effects on bears that have undergone aversive conditioning treatments in a natural setting (e.g., Gillin et al. 1994, Ternent and Garshelis 1999, Beckmann et al. 2004, Leigh and Chamberlain 2008, Mazur 2010). In some aversive conditioning studies, bears were not continually monitored during treatments, which may have led to inconsistent reinforcement. A pilot study in Yosemite National Park investigated the effects of aversive conditioning treatments on black bears by continually and consistently administering deterrents to them. This was achieved by applying deterrents to 4 highly habituated and food-conditioned bears nearly every time they approached a human-use area, for an average of 168 consecutive hours/treatment. Findings suggested that these aversive conditioning treatments were unsuccessful at deterring highly food-conditioned bears from approaching human-use areas (V. Seher, Yosemite National Park, California, unpublished data, 2005). Many human–bear management programs haze bears routinely, but few programs continually and consistently apply deterrents to bears so that aversive conditioning has occurred.

A *management closure* restricts or prevents human access to an area because of increased potential for human–bear conflict. Typically areas are closed by management personnel reactively in response to human conflict with aggressive bears, female grizzly bears with cubs, injured bears, or bears guarding a carcass. Management closures are also used to reduce the likelihood of conflict due to the availability of high-quality food sources (e.g., ungulate or livestock carcasses, spawning streams, calving areas, ungulate winter ranges, berry patches). For example, Yellowstone National Park closes rental cabins, campgrounds, and backcountry trails and campsites in areas containing high quality bear foods. These proactive seasonal management closures are designed to (1) minimize human–bear interactions that may lead to habituation of bears to people, (2) prevent human-caused displacement of bears from prime food sources, and (3) decrease the risk of bear-inflicted human injury in areas with high levels of bear activity (Gunther 1994). Denali National Park, Alaska closes one of their campgrounds when moose (*Alces alces*) calve in or near the campground and attract grizzly bears. Once calving is over, the campground is re-opened (RTS, unpublished data).

Management status

A *management bear* is a bear that may be monitored for management purposes because it is individually identifiable (i.e., with a visual tag, radio-collar, lip tattoo, microchip, or a distinct morphological characteristic). Management bears are often involved in bear incidents or are sighted regularly, typically captured in human-use areas, and may have a known or unknown management status. A bear's *management status* is a classification assigned to each management bear: (1) habituated (not food-conditioned), (2) food-conditioned (not habituated), (3) habituated and food-conditioned, (4) aggressive, (5) predatory, (6) unknown, or (7) unmanaged (Fig. 2).

Habituation and conditioning. Habituation and conditioning are commonly but erroneously used interchangeably, and may be the two most complex and misapplied terms in human–bear management. According to McCullough (1982:28), who summarized the concepts of learning behavior and applied them to bear behavior, *habituation* "is the waning of a response [or muted response] (whether learned by conditioning or otherwise) when a reward or punishment is discontinued. It is not the learning or formation of a habit as it is sometimes appears in the wildlife literature," and *conditioning* "is learning involved in receiving a reward or punishment for a given response (behavioral act) to a given stimulus." We believe these terms are often confused when applied to human–bear management because the process of human food conditioning can lead to rapid habituation, and the process of habituation may lead to more opportunities for bears to become positively conditioned by human food rewards.

Habituated bear. We define a *habituated bear* as a bear that shows little to no overt reaction to people (Herrero et al. 2005) as a result of being repeatedly exposed to anthropogenic stimuli (e.g., people, human scent, human structures) without substantial consequence. The lack of an overt reaction from a bear may be a mild response by the bear but not detectable to observers.

Herrero et al. (2005) and Smith et al. (2005) examined the complexities of the behavioral response habituation, using the term *overt reaction distance* (ORD) to describe the distance at which a bear visibly responds to people during a human–bear interaction (Herrero et al. 2005). A bear's behavioral response may vary from being undetected (e.g., salivating and posturing), to mild (e.g., cessation of feeding or looking at the source of the stimulus), to obviously stress-related. Examples of *stress-related behaviors* include fleeing the area, climbing a tree, intense staring, bluff-charging, jaw or lip-popping, front leg stomping, standing on hind legs, loud vocalizations (e.g., huffing, woofing, growling, gulping, moaning), and defensive non-predatory *attack* (Herrero et al. 2005). Correct interpretation of these behaviors depends on a broader understanding of the context of the interaction. For instance, a bear approaching or circling may be displaying signs of curiosity or predatory behavior, and may not be stress-related.

In addition to habituation, there are many factors that can influence the distance at which bears tolerate people. These include human-related factors (e.g., person's activity at time of encounter, group size, person's behavior in response to encountering a bear), environment-related factors (e.g., season, time, presence of conspecifics), and bear-related factors (e.g., species, sex–age class, previous experience with people; Herrero et al. 2005). Therefore, each individual bear's ORD varies depending on the factors involved in the human–bear interaction.

There is considerable confusion between the terms tolerance and habituation. Nisbet (2000:315) defines tolerance as "the intensity of disturbance that an individual tolerates without responding in a defined way." We believe a *bear that tolerates people* does not take evasive or aggressive action when in the presence of people. Smith et al. (2005) stated that confusion often arises because both bears habituated to people and bears innately tolerant of people (i.e., not learned) have little to no response when close to people. To clarify, habituated bears are tolerant of people to some degree; however, some bears that are tolerant of people may not have undergone the learning process of habituation (pathways of habituation described below) but instead may be inherently tolerant of people. Tolerant bears have shorter ORDs than intolerant or non-habituated bears.

Smith et al. (2005) distinguished between three types of habituation: bear-to-bear, bear-to-human, and human-to-bear. Bear-to-bear habituation usually occurs when bears frequently interact (e.g., aggregations of bears feeding on salmon [*Oncorhynchus* spp.] in spawning streams, or at a garbage dump; Egbert 1978, Jope 1983, Craighead et al. 1995). As a result, bears in these situations have very short ORDs with each other, which may lead to increased habituation to people (Herrero et al. 2005). Bear-to-human habituation occurs when bears tolerate the presence of people as a result of frequent and benign contact (McCullough 1982; Jope 1983, 1985; Smith et al. 2005). For example, bear-to-human habituation may take place in areas such as Yellowstone National Park, where bear density is relatively low and human visitation is high. Although Jope (1985) found that habituated bears were less likely to injure people than non-habituated bears, increased human use in bear habitat leads to more frequent (and potentially dangerous) interactions between people and bears and may increase the tolerance bears have for people, decreasing their ORDs (Jope 1983, Herrero et al. 2005, KAG unpublished data). Alternatively, Smith et al. (2005) considered that bear-to-human habituation is more common in high-density bear areas where bear-to-bear habituation is high. Bear-to-bear and bear-to-human habituation results in bears expending less energy reacting to people, therefore benefiting bears by allowing individuals to adapt to local circumstances (Jope 1983, Smith et al. 2005). The final type of habituation, human-to-bear, occurs when human avoidance response declines as a result of bears not reacting aggressively (offensive or defensive) when close to people. This type of habituation is a concern because people become increasingly casual around bears (e.g., viewing bear on salmon spawning streams in Alaska), increasing the potential for human–bear conflict (Schullery 2001, Smith et al. 2005).

The process of habituation is one of the most important influences on bears' ORDs (Smith et al. 2005), but a more complete understanding of habituation must also incorporate other factors influencing ORD (Herrero et al. 2005). Although we recognize that bears habituated to people and bears innately tolerant of people exhibit similar behaviors, and that the pathways and factors involved in their tolerance of people are difficult to determine, we proposed our modified definition of a habituated bear (see beginning of section). When managing individual bears, we suggest that managers consider (1) the potential pathways that led to the bear's habituation (i.e., bear-to-bear or bear-to-human), (2) factors influencing a bear's ORD, and (3) that the observed bear may be tolerant of people and not habituated.

For example, imagine that a bear initially classified as habituated is reported at a roadside viewing area. When management personnel arrive, they observe the bear near people (therefore tolerating them to a certain degree) at the parking lot bathroom. When approached to 25 meters, the bear escapes into the timber. A few days later, they see the bear has entered the bathroom, and in response, they haze the bear from the area using various deterrents. Following the incident, they inspect the bathroom and find a non-bear-proof garbage can inside and learn the door does not close properly; they suspect the bear received a human food reward during a previous visit. A day later, the can is removed, the door is fixed, and the pullout is closed for 2 weeks to mitigate the potential for conflict. After a week of observing the bear near the bathroom, the bear is never seen again. Staff determined the primary factor influencing the bear's ORD was the non-bear-proof garbage can in the bathroom. For this case study, we believe the bear was tolerant of people and in the process of being food conditioned, which likely led to the animal's bear–human habituation.

We provide another scenario to illustrate bear tolerance. Two fishermen were fishing for salmon on a remote section of river in Alaska. After a few hours of fishing, a large bear emerged from the willows (*Salix* spp.) 25 meters away and startled the anglers. In response to their presence, the bear ambled downstream 50 meters and began fishing for salmon in the middle of the river. As a result of this benign interaction, the fishermen continued to fish in the same area while also viewing the bear. Although it is unknown if the bear was tolerant of the fisherman due to previous interactions with humans or other bears, the animal should be described as having tolerance for people and classified as an unmanaged bear.

Habituation often occurs in human-use areas that contain high-quality bear foods. For example, some bears in the Rocky Mountain national parks of Canada and U.S. have learned to graze on the green vegetation adjacent to roads, ignoring nearby traffic and onlookers. In this case, habituation may extend the available feeding habitat and allow bears to use habitat otherwise not available. Because habituated bears are often near people when using these habitats, their potential to be exposed to human food is higher than that of conspecifics that use more remote areas. A habituated bear in a human-use area is often the greatest management concern because of the individual's susceptibility to becoming food-conditioned. As a result, it is often advisable to monitor and manage people in human-use areas or haze such bears from these areas.

Clearly, further research on habituation is needed to advance the term's use. Nisbet (2000), in reference to colonial waterbirds, suggested such study would require the examination of repeated measures of response on individuals subjected to controlled repetition of the same stimulus. Until research results can provide new insight on how to classify habituated bears, we suggest using the modified Herrero et al. (2005) definition for this complex term.

Food-conditioned bear. A *food-conditioned bear* has learned to associate people (or the smell of people), human activities, human-use areas, or food storage receptacles (e.g., bear-lockers, trashcans, dumpsters, backpacks, vehicles) with anthropogenic food (Herrero et al. 2005).

Food-conditioned bears have varying levels of food-conditioned behavior, and as a result some individuals are more tolerant of people than others. The level to which a bear is food-conditioned seems to be associated with factors such as natural and anthropogenic food availability (Mattson 1990, Gunther et al. 2004), natural tolerance of people (Mattson 1990, Herrero et al. 2005, Smith et al. 2005), and perhaps reproductive status (Clark et al. 2002). For instance, a bear that patrols campgrounds from spring through fall, receives food rewards on a daily basis, and continues food-conditioned behavior when repeatedly hazed is an example of a highly food-conditioned bear. Alternatively, a bear that only scavenges human food in a few unoccupied campsites at night, during a season when natural foods are scarce, is an example of a bear that has a low level of food-conditioned behavior.

Although many food-conditioned bears are also habituated to people, there is evidence suggesting bears can be food-conditioned but not habituated. In Yellowstone and Great Smoky Mountains national parks, there have been reports and observations of bears routinely entering empty campsites at night to scavenge human food discarded during the day. The observations suggest that these bears are food-conditioned but not habituated because they purposefully scour the campsite for food when people are absent, presumably to reduce the chance of conflict. Following each episode, the bears leave evidence (digging in campfire rings, tracks, or scats in camp), but are rarely observed (KAG, unpublished data; E.K. DeLozier, Smoky Mountains National Park, Gatlinburg, Tennessee, personal communication, 2009). In addition, bears that consume some agricultural foods (e.g., corn, apples, livestock) may not be tolerant of people or interested in seeking out food around human habitations.

Classifying a bear as food-conditioned or habituated. We believe a source of confusion for classifying bears as food-conditioned or habituated stems from the fact that human food conditioning and habituation are complicated behavioral concepts that are not fully understood (Whittaker and Knight 1998, Herrero et al. 2005, Smith et al. 2005). Herrero's (1985) popular description of a 'food-conditioned bear' has been cited differently in the literature, adding to the complication of understanding these management classifications. For example, Gunther (1994:551) interpreted Herrero's definition as "bears that have learned to identify humans or human developments as a source of foods due to a prior food reward,'' while Smith et al. (2005:2) provided what we suggest is a more accurate definition: "such a bear forms a simple association between people and food.'' In contrast to these definitions, Mattson et al. (1987:261) suggested food-conditioned bears are also habituated: "habituated bears that characteristically associated feeding opportunities with human facilities." Although Herrero (1985:51) discussed the association between habituation and food conditioning, he suggested that food-conditioned bears are not always habituated: "…the food-conditioned bear is almost always somewhat habituated to the smell or sight of people.''

Using the term habituation to describe a food-conditioned bear has resulted in the misquoted term 'food-habituated' (Smith et al. 2005). We suggest discontinuing this term's use because habituation and food conditioning are not always simultaneously acquired (Gilbert 1989, Fig. 2). In addition, the term 'food-habituated' is self-contradictory because bears that are habituated to people and are food-conditioned are, by definition, not habituated to human food. Instead, they have a desire to seek human food and have become habituated to people in the process.

Bears that are food-conditioned (but not habituated) behave differently than bears that are habituated (but not food conditioned). Food-conditioned bears seek out anthropogenic stimuli (e.g., people, human scent, waste containers, human-use areas) and often obtain a human food reward in the process. This positive conditioning reinforces the attraction to the stimuli, thus perpetuating food-conditioned behavior. In contrast, habituated bears have a neutral response to anthropogenic stimuli and have a reduced ORD to people. Because human food conditioning and habituation are different processes in animal behavior, managers should evaluate them independently when classifying management bears and implementing management responses.

Our final distinction between a food-conditioned and a habituated bear is that a bear can be habituated but not food-conditioned (a food reward is not necessary for habituation), whereas food-conditioned bears often show signs of habituation (Fig. 2; Herrero 1985). Bears that are food-conditioned, habituated, or both habituated and food-conditioned are usually classified after direct observation. However, food-conditioned bears may also be identified via stable isotope methods (Hobson et al. 2000; Greenleaf 2005; Mizukami et al. 2005; JBH, unpublished data; RTS, unpublished data), trans fatty acids (Thieman et al. 2008), and body size (i.e., skeletal size and body weights normalized for season; RTS, unpublished data).

Habituated and food-conditioned bear. Many food-conditioned bears are habituated, and many habituated bears become food-conditioned. Therefore, there is a need for a management term that describes a bear that is both habituated and food-conditioned. Until another term is presented, we suggest classifying a bear that is habituated and receives anthropogenic food as habituated and food-conditioned (Fig. 2).

Aggressive and predatory bears. Bears may threaten people by exhibiting *aggressive behavior* (e.g., direct approaches to humans, bluff-charging, jaw or lip-popping, front leg stomping, loud vocalizations, circling, intense staring, salivating, non-predatory attack) during human–bear interactions. These behaviors may be stress-related and displayed defensively (e.g., protect young, ensure safety) in response to being *provoked*, or may be exhibited offensively (e.g., predatory attack, asserting dominance, taking food from people). In a management classification context, an *aggressive bear* displays aggressive behavior (defensive or offensive) and is a public safety concern. Under some circumstances it may be difficult to ascertain if a bear's aggressive behavior should be classified as a public safety concern. In situations such as these, it is important for management personnel to accurately document the bear's behavior (often on multiple occasions), and to analyze the context of the incidents. This information could aid managers in deciding whether the bear should be classified aggressive.

Although *offensive-aggressive* animals are often classified aggressive and subsequently removed from the population, *defensive-aggressive* bears may be removed as well. For instance, a female with cubs repeatedly bluff-charged trail users and eventually attacked a person in the outskirts of Anchorage in 2008. After the first incident it was clear the bear displayed aggressive behavior; however, it was unclear if the bear was acting offensively or defensively. In this case, the bear was not originally classified as an aggressive bear, but the repetition of similar defensive-aggressive incidents resulted in her being classified aggressive and lethally removed (R. Sinnott, Alaska Department of Fish and Game, Anchorage, Alaska, USA, personal communication, 2009). In contrast, a female black bear with cubs bluff-charged a person from 100 yards away in an open meadow and was never observed again that year. In this scenario, the bear was likely provoked and therefore responded with defensive-aggressive behavior to protect young and ensure safety. Given the bear's behavior and context of the incident, this bear should not be classified an aggressive bear (i.e., considered a public safety concern). We suggest classifying a bear aggressive if and only if the evidence is convincing (i.e., the behavior and incident are well documented, and typically repeated), because a bear classified aggressive is often removed from the population. *Predatory bears* are also typically removed from the population and are defined as bears that preyed or attempted to prey on people. Predatory bears were reported as displaying the following behaviors: "searching, following or testing, attacking (capturing), killing, dragging a person, burying, and feeding upon a person" (Herrero and Higgins 2003:46).

Unknown and unmanaged bears. The term 'wild bear' is commonly used to describe both a bear not contained in captivity (i.e., free-ranging) as well as a bear that flees during human–bear interactions. A bear considered neither habituated nor food-conditioned after monitoring is often referred to as 'wild', 'wary', or 'naïve'. However, a bear termed 'wild' in this way may have been classified habituated or another management status if observed under differing conditions (i.e., if influences on a bear's ORD were different). For example, a bear may have been originally classified 'wild' because it fled a remote area when approached unexpectedly, but may not have shown signs of avoidance if the interaction were less surprising or occurred along a road. In the latter situations it would have been classified as habituated. Thus, designating a bear 'wild' for management purposes is subjective; instead, we suggest classifying the bear as having an *unknown* management status. We also suggest classifying a bear as unknown when it has not been monitored, but will be in the future.

Many reviewers suggested we include a management classification for a bear that will not be monitored in the foreseeable future because it has not been observed interacting with people or suspected of being involved in any bear incidents. We suggest personnel refer to such bears as *unmanaged*. The term 'non-food-conditioned' typically implies the animal is habituated or unmanaged. To be confident the bear is not food-conditioned, the animal is monitored. If the manager is unsure whether the bear consumes human food, we suggest classifying the animal unknown and continue monitoring. If a monitored bear's management status is unclear, we suggest that it be classified unknown until empirical evidence suggests otherwise.

Bear sightings and incidents

A *bear sighting* has occurred when the bear (1) was seemingly unaware of the person observing it (i.e., not a human–bear interaction; Smith et al. 2005, Wilder et al. 2007), (2) had no observable stress-related response to the person during an interaction, or (3) responded to the person by taking *evasive action* (e.g., walked or ran away, climbed a tree; Fig. 3). The person involved in the latter type of sighting did not take extreme evasive action (e.g., ran away, climbed a tree, played dead, fired capsicum spray [bear deterrent spray], discharged ammunition from a firearm; Schirokauer and Boyd 1998) (Fig. 3). A *human–bear interaction* (or 'encounter,' Wilder et al. 2007) occurs when a person and bear are mutually aware of each other (Smith et al. 2005). During interactions with humans, bears either tolerate people (typically outside the bear's ORD), allowing people to observe them at a distance (documented as a bear sighting), or respond to humans inside their ORD with behavior that may or may not lead to human–bear conflict (Fig. 3). A *bear jam* is an instance when people slow or stop their vehicles to view or photograph bears, causing traffic congestion. We suggest documenting most bear jams as bear sightings. However, if a human–bear conflict transpired during the bear jam or the bear obtained anthropogenic food or caused property damage, we suggest recording the bear jam as a bear incident (Fig. 3).

A *human–bear conflict* has occurred when a bear has (1) exhibited stress-related or curious behavior, causing a person to take extreme evasive action (Schirokauer and Boyd 1998), (2) made physical contact with a person (e.g., to assert dominance, while acting defensively or taking human food) or exhibited clear predatory behavior, or (3) was intentionally harmed or killed (not including legal harvests) by a person (e.g., poached, wounded/killed in defense of life or property; Fig. 3). We agree that bears often respond to interactions with people by exhibiting aggressive behaviors to warn people to increase or maintain their distance. Although these behaviors are threatening, they are often a defense mechanism. Regardless of the reason bears exhibit these aggressive behaviors, we suggest documenting these human–bear interactions as human–bear conflicts if and only if the person took extreme evasive action (Schirokauer and Boyd 1998) (Fig. 3). We assume that if a bear caused a person to take extreme evasive action, the person must have felt threatened by the bear's behavior. Under this scenario, we believe the bear was involved in a conflict with the person. In addition to documenting evasive actions of bears and people during human–bear interactions, it is important to document the stress-related behavior bears exhibit during these interactions to better understand the dynamics of human–bear conflict.

A *bear incident* is an occurrence that involved (1) a human–bear conflict; or episodes where bears (2) caused property damage, (3) obtained anthropogenic food (includes being baited), (4) killed or attempted to kill livestock or pets, or (5) were involved in vehicle collisions (Fig. 3) (Gunther 1994, Schirokauer and Boyd 1998, Gunther et al. 2004, Wilder et al. 2007). Currently, some human–bear management programs use variants of the term conflict (e.g., bear–human conflict, human–bear conflict, human conflict) instead of our term, bear incident. We suggest that managers make the distinction between episodes with and without direct conflict between people and bears. Specifically, we suggest recording all episodes involving bears and people (or their property) as bear incidents, while documenting any human–bear conflict (a subset of bear incidents) that transpired during the incident (Fig. 3, Table 2). For example, an incident occurred where a bear made physical contact with a person to acquire human food. In this case, we suggest recording the bear incident as a human–bear conflict where a bear also received human food. Another example: a bear broke a window of an unoccupied vehicle in a parking lot to obtain human food. We suggest recording this episode as a bear incident (but not as a human–bear conflict) where the bear obtained human food and caused property damage. Since it is often difficult to determine whether a human–bear interaction should be documented as a bear incident or a bear sighting, our flow chart (Fig. 3) and dichotomous key (Table 2) may aid in making a more objective decision.

Failing to remove anthropogenic food sources from bear habitat sometimes leads to undesirable human–bear interactions, resulting in conflict or other bear incidents. Regardless of whether the bear incident is human or bear-induced, the bear may be removed from the population (McCullough 1982). The term nuisance bear is commonly used to describe habituated bears or bears involved in human–bear conflict or other bear incidents. Generally speaking, managers consider nuisance bears to be pests. We believe referring to habituated bears as a nuisance does not accurately categorize these individuals. For example, a habituated bear that is commonly observed near the roadside foraging is typically not a nuisance to people. In fact, people enjoy observing them and these sightings often lead to opportunities to better educate visitors about bear behavior and food storage (KAG, unpublished data). In addition, a bear involved in incidents is not always a nuisance, especially if the bear was never involved in human–bear conflicts. We suggest using the general term *problem bear* to describe a bear involved in repeated incidents, regardless if they are a nuisance to people or not.

Management implications

Human–bear management strategies will continue to evolve as our knowledge of bear behavior and ecology increases. The most effective way to continue to improve methods to prevent bear incidents is for agencies to evaluate their programs using well defined terms and concepts, and communicate the successes and failures of their programs internally and externally. Bridging gaps in communication within and among agencies will ultimately improve site-specific, intra- and interagency bear conservation efforts, and bear research in the United States and Canada. In addition, effective communication may eventually lead to a clear definition for 'management success,' a term that is frequently used, but hardly ever defined, as well as a human–bear management database that can be used for meta-analysis.

We hope our suggestions will be used by wildlife management agencies with bear population management programs, as well as other wildlife professionals, to provide clarification of terms and concepts in human–bear management. We hope this document will foster discussion on establishing a common human–bear management language and provide direction to human–bear management programs and researchers.

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The rapid development of estimating assimilated diet using stable isotopes and an improved Bayesian mixing model

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ABSTRACT

Using stable isotope mixing models (SIMMs) as a tool to investigate ecological questions is gaining popularity among researchers. As a result, statistical methods are rapidly evolving and numerous models have been produced—each with benefits and limitations. When estimating the assimilated (the conversion of nutrient into tissues by the processes of digestion and absorption) diets of animals, the decision of which SIMM to use is contingent on factors such as the consumer of interest, its food sources, sample size, the familiarity a user has with a particular framework for statistical analysis, or the level of inference the researcher desires to make (e.g., population or individual-level). The purpose of this paper is to provide researchers a review on current SIMM models as well as describe a new SIMM, IsotopeR. We believe our model will be useful to ecologists because it incorporates all recognized and quantifiable SIMM features. We used data collected in Yosemite National Park to demonstrate IsotopeR's ability to estimate dietary parameters. We then examined the importance of each feature in the model and compared our results to inferences from commonly used SIMMs. This comparative analysis suggests that IsotopeR should be used as the foundation for future SIMM development.

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INTRODUCTION

Stable isotopes were first used to investigate the feeding ecology of animals in the 1970s [1–5]. Such early studies used stable isotope analysis (SIA) to determine the relative importance of food sources in animal diets by comparing distributions of isotope ratios (expressed as isotope values; derived below) for animal tissues to the foods they consume after corrected for fractionation (the sorting of isotopes during natural biochemical processes)—a technique primarily used when food sources had distinctly different isotope values (e.g., C_3 and C_4 plants, or prey that differ in trophic level) [2,6]. Isotope values (e.g., ™*X,* ™*Y*) are expressed in delta (™) notation as per mil (‰) units (or parts per thousand):

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) * 1000$$

where R is the ratio of heavy to light isotopes (e.g., $^{13}C/^{12}C$ or $^{15}N/^{14}N$) in the sample and the standard [7]. Samples with a lower ratio of heavy isotopes relative to the standard will yield a negative value and samples with higher ratios will have a positive value.

For the past few decades, SIA has gained popularity among ecologists [e.g., 8–13]. In particular, stable isotope mixture models (commonly referred to as “mixing” models, and hereafter, SIMMs) are commonly used to estimate the relative contribution of assimilated dietary sources to animal tissues, and if certain assumptions are met (Table 1), animal diets. Euclidian distance formulas were used in some early studies [e.g., 14–18], however these methods did not provide correct solutions for observed [18] and simulated data [19]. Specifically, these Euclidean distance models failed to preserve mass balance, an application of the law of conservation of mass which states that the proportional assimilated dietary contributions (mass) flowing into an organism or population are constrained to sum to one. Recently, variants of mass-balance models have developed rapidly [19, 20]. Although the profusion of SIMMs (many of which are discussed in this paper) indicates the importance of this field to ecologists, current models require researchers to make tradeoffs (e.g. some do not address SIMM assumptions; Table 1) when choosing one model over another.

All models discussed in this paper use the same basic methodology for estimating proportional source contributions to animal diets. For example, a duel element (X, Y), three-source, mass-balance, linear mixing model is described by the following equations [20]:

$$\begin{aligned} \delta X_m &= f_1 \delta X_1 + f_2 \delta X_2 + f_3 \delta X_3 \\ \delta Y_m &= f_1 \delta Y_1 + f_2 \delta Y_2 + f_3 \delta Y_3 \\ 1 &= f_1 + f_2 + f_3 \end{aligned} \tag{1}$$

This system of three equations yields three unknown proportional source contributions (f_1, f_2, f_3) for a mixture (m) when ™X and ™Y values are known for mixtures and sources.

In the following sections, we discuss the SIMMs commonly used to estimate assimilated contributions to animal diets and follow this review with details about our SIMM, IsotopeR.

Frequentist SIMMs

IsoError

Phillips and Gregg [21] refined the application of linear mass-balance procedures (equation set 1) with IsoError. This SIMM can be applied to systems where the number of sources do not exceed $n + 1$ (n = number of isotope systems); when sources do exceed $n + 1$, the system of equations is underdetermined and no unique solutions for the source contributions exist. IsoError calculates deterministic solutions and allows an informed user the ability to incorporate process error of each source or mixture(s), isotopic correlation, and measurement error (definitions in Table 1). We note that measurement error associated with mass spectrometry is not typically calculated and explicitly incorporated into the IsoError mixing model equations. Instead, it is included (often unknowingly) in the source and mixture standard deviations when they are calculated from the isotopic data.

Isoerror does not address many of the assumptions (Table 1) that may be violated when estimating diets using SIMMs [e.g., 19,22,23]. In addition, neither IsoError nor the mass balance equations (equation set 1) are constrained to yield proportional source contributions (f variables in equation set 1) in the interval (0,1). Therefore, when data fall outside the isotope mixing space (the area or volume contained in the space formed by lines connecting the sources in multivariate isotope space) because an important food source was overlooked, the wrong discrimination factor (discussed in Process and discrimination error) was applied to a source, or a mixing model assumption was violated [24], nonsensical negative proportional contributions are calculated.

IsoConc

Most stable isotope mixing models assume that the relative contribution of dietary sources to a consumer's diet is identical for all elements (e.g., C, N). Although this assumption is valid for many carnivore and herbivores, it is often violated for omnivores who feed on multiple dietary sources and trophic levels [24]. IsoConc was developed to estimate the contribution of each source to an animal's diet by assuming a source's contribution is proportional to the assimilated biomass of the source multiplied by the elemental concentration (e.g., % C, % N) in the source [24]. This model was the first to transform a polygonal mixing space to a curved polygon [24]. In a comment on the paper, Robbins et al. [25] pointed out the need to consider digestibility when determining the elemental concentrations of potential sources; standard linear mixing models and the examples presented in Phillips and Koch [24] assumed that all sources are equally digestible. Koch and Phillips [26] presented a method for calculating the digestibility of macronutrients in food sources and included the corrected elemental contributions of these sources in their diet estimation. By incorporating "concentration-dependence" and explicitly considering digestibility, this SIMM made a significant stride towards making more accurate inferences on animal diets [26]. However, unlike IsoError, IsoConc did not allow the user to incorporate various sources of error.

IsoSource

IsoSource was developed to calculate the frequency and range of potential source contributions in situations where the number of sources exceeds $n + 1$ [27]. Using the standard linear mixing model, IsoSource systematically creates each combination of possible source contributions (that sum to 1.0) by a certain increment (e.g., 0.01). Next, the model calculates predicted mixture isotope values for each combination using estimated source isotope values (means). If these predicted values fall within a certain designated mass balance tolerance (e.g., ±0.1‰; which accounts for the error associated with measurement and source variability) then the combination is considered a feasible solution. Instead of calculating parameter estimates (e.g., mean proportional contributions), Phillips and Gregg [27] suggest reporting the distribution of feasible solutions.

This model can be helpful at inferring diet composition when a unique solution is impossible to calculate, but has limits when investigating many ecological questions [28]. In particular, each feasible solution is no more probable than another; therefore, the results are difficult to interpret—especially when the range of certain source proportions (minimum and maximum values selected from the solution set for a particular source) is wide (e.g., 0.1 – 0.9).

Bayesian SIMMs

Bayesian SIMMs allow ecologists to fit probability models to isotopic data more directly by including various sources of error, greater than $n + 1$ sources, prior information, and a hierarchical structure in a flexible and intuitive estimation framework. Specifically, Bayesian models allow users to efficiently estimate numerous parameters while avoiding calculation of multidimensional derivatives, as in likelihood methods. Current Bayesian models calculate the proportional contributions of dietary sources in animal diets and incorporate sources of isotopic uncertainty. These models assume that model inputs for food sources (sample means and standard deviations) are used to calculate the contribution of sources to animal diets are known.

Several Bayesian SIMMs have been used to estimate diet composition at the population- [29,30] and individual-level [31], and incorporate different sources of uncertainty. The earliest model, MixSIR (v.1.0.4) [29], estimates the joint posterior probability of sources used by animals (reported as marginal distributions for each dietary source contribution) by importance sampling (less efficient sampling method than Markov chain Monte Carlo sampling; described below) and incorporates the following isotopic information in the model: (1) source mean and standard deviation, (2) tissue-diet discrimination factor mean and standard deviation, (3) mixture data (single consumer or sample of the population), and (4) a Dirichlet prior on the proportional estimators (recommended by Jackson et al. [32] and incorporated in Semmens et al. [31]). Although the model may provide reasonable estimates of the proportional contribution of sources to a mixture (especially when sources are $\leq n + 1$), MixSIR's credible intervals may be too narrow in some cases because they do not account for variation among individuals and other sources of error (Table 1).

In addition to MixSIR, two novel Bayesian SIMMs were developed [31,30]. Semmens et al. [31] built the first hierarchical Bayesian model to account for demographic variability among individuals when estimating a population's diet (herein referred to as Semmens et al. model). This model is very useful because it allows researchers to estimate diets at both the population- and individual-level. In general, hierarchical models are used to make such individual-level inference possible; however, difficulties may persist when estimating individual diets. Specifically, these hierarchical models use information from the population-level to estimate individual diets; therefore, when the population sample size is large, individual estimates will be pulled to the population mean [33]. Currently, it is unknown what the ideal sample size is for individuals when making individual-level inference. However, it is certain that the population has a major influence on individual diet estimates and repeated measures for individuals will improve inference [33].

Another model, the SIAR model [30]—originally developed as an R package [34] and first described by Jackson et al. [32]—allows a user to incorporate unequal elemental concentrations in sources and estimates assimilated diets at the population-level. Although these new Bayesian models provide reasonable estimates for proportional dietary contributions, all SIMM features (i.e., components of the model expressed in mathematical terms) should be combined into a single SIMM model.

Here we combine SIMM features and explore the assumptions associated with SIMM analysis to develop new features for our comprehensive SIMM model called IsotopeR. We use the hierarchical model structure of the Semmens et al. model and the concentration-dependence formulation originally developed by Phillips & Koch [24] as the foundation for our model while incorporating several features to more accurately infer proportional diet composition (Table 1). In addition, unlike other Bayesian SIMM models the features (Table 1) are jointly estimated in a fully Bayesian framework. Joint estimation is useful when estimating multiple dependent quantities because it accounts for the inherent uncertainty associated with the joint estimation process (e.g., the normal distribution changes to a Student's *t*-distribution when jointly estimating the mean and variance). Not accounting for this uncertainty can lead to overly precise credible intervals.

We validated the applicability of IsotopeR by estimating the relative contribution of sources in the diets of food-conditioned black bears (i.e., bears that have learned to associate people, human activities, human-use areas, or food storage receptacles with anthropogenic food) [35] sampled in Yosemite National Park (YNP). We chose black bears because we also aim to provide users a framework for estimating omnivores' diets using SIMM analysis (i.e., estimating dietary parameters for animals with mixed diets). We then examine each feature's effect on inference by systematically removing each feature independently. Lastly, we compare IsotopeR estimates to those from other frequently used models.

METHODS

Study area

The eastern side of Yosemite Valley (YV) is one of the premier sites in North America to investigate the effects of anthropogenic impacts (e.g., human food availability) on bear behavior. This is primarily due to bears and humans coexisting in high densities. Consequently, this broad human-bear interface is responsible for 80% of the 1,100 reported bear incidents during 2005 – 2007 [YNP 2005 – 2007]. As a result, wildlife management focuses most of their effort mitigating bear incidents in eastern YV. We concentrated our sampling effort in eastern YV because management staff routinely capture and monitor food-conditioned bears in this area.

Sampling

Mixtures

Yosemite National Park Wildlife Management staff live-captured FC bears primarily in YV for management purposes from March 2006 through June 2008 (Table S1). They captured bears in culvert traps according to Park Service protocol and immobilized them using 2mg of Telezol (Fort Dodge Animal Health, Fort Dodge Iowa, USA) for every estimated pound of body weight. They classified bears as food-conditioned (FC) if bears were positively identified feeding on human food more than once.

They collected bear tissues in accordance to Wildlife Management protocol. For hair, they collected ten or more full-length guard hairs from along bears' spines or upper limbs during March–June, or from the lower limbs or flanks in September–November. Hair collected during spring months were grown the previous year, whereas hair collected in the fall was produced during the current year [37]. Bear hair collected from March through June of 2006–2008 therefore represented bear diets in 2005–2007, respectively. Hair collected from September through November of 2006 and 2007 represented the diet in those years.

Sources

We collected the following bear foods opportunistically in 2007 because they were identified by previous fecal analysis studies as being important natural food sources for bears throughout YNP [38, 39]: acorns (*Quercus kelloggii, Quercus wislizenii*), manzanita berries (*Arctostaphylos* spp.), grass (*Agrostis* spp.), forbs (*Trifolium* spp., *Lupinus* spp., *Montia* spp.), and animals [ants (Formicida), wasps (Vespidae), bees (Apidae), termites (Isoptera), and mule deer (*Odocoileus hemionus*)](Table S2). SIA of these foods yielded isotope values used to estimate 100% plant and 100% animal diet for FC black bears in YNP.

We collected human hair samples in 2009 from floor clippings at two salons and one barbershop in St. Louis, MO (*n* = 20; Table S3). Collecting human hair from the garbage did not require an ethics permit. Results from 2009 were compared to results from a 2004 nation-wide survey of human hair (*n* = 52) [40], and samples were statistically indistinguishable [2004: mean $\delta^{13}C$ (Suess corrected, see below) = -16.9, SD = 0.8, mean $\delta^{15}N$ = 8.8, SD = 0.5; 2009: Table S3; t = -0.79, df = 71.62, P = 0.43]. Therefore, samples were pooled to form the human food aggregate (Fig. 2, Table 2A). We assume that bears on 100% human food diet would be isotopically similar to humans because both humans and bears are monogastric omnivores; therefore, it is likely that they discriminate against ^{14}N and ^{12}C by a similar magnitude.

We estimated the elemental concentration ([C] and [N]) of the average human diet in the United States by analyzing nutrient data from the USDA National Nutrient Database (NDB: http://www.nal.usda.gov/fnic/foodcomp/search/; Table S4). First, we calculated the mean and 1 SD of digestible C and N of samples from each food group ($n \geq 3$ food items), then we weighed the food group mean and SD based on the fractional contributions of these food groups to human diets provided in Nakamura et al. [41]. Lastly, the weighted means and SDs were used to estimate the average digestible [C] and [N] for human foods (Table S4). These estimates were used to construct the isotopic mixing space used in our diet analysis of FC bears, and unlike the plant and animal aggregate, this aggregate was not estimated using Bayesian methods.

Sample preparation, analysis, and Suess effect correction

We rinsed guard hairs with a 2:1 chloroform-methanol solution to remove surface oils. We oven-dried plants and homogenized each sample. We then weighed all samples into tin cups (4 x 6 mm). The Stable Isotope Laboratory at University of California, Santa Cruz, CA analyzed samples for their carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopic composition by continuous flow methods using a Carlo-Erba elemental analyzer interfaced with an Optima gas source mass spectrometer.

All tissues were corrected for the Suess effect (Table S1 and S2), which is defined as the global decrease of ^{13}C in Earth's atmospheric CO_2, primarily due to fossil fuel burning over the past 150 years [42– 44]. Based on ice core records [45], a time-dependent correction of -0.022‰ per year [46] to 2009 was applied to all isotope values for samples, except 2009 human hair.

IsotopeR's model features

Unlike other SIMM models we incorporate all features currently used in SIMM analysis as well as other important features currently not included in SIMM analysis (Table 1). Figure 1 is used to describe model features, to illustrate how features interrelate, and to define prior distributions. For those interested, we also provide the model likelihood in Appendix A. IsotopeR's structure is hierarchical (similar to the Semmens et al. model, such that an individual's estimate is conditional on the group or population's distribution. The hierarchical structure of the model allows us to make statistical inference on each individual in the population, even though we only have one observation for each individual. Although we calculate individual estimates using only one observation in this analysis, the structure of our model allows for repeated observations of the same individual. Including repeated measures for each individual consumer would result in less influence from the population-level and more accurate individual-level estimates.

Whereas current SIMMs consider input parameters as known quantities, IsotopeR considers them random variables. These variables are estimated using a fully Bayesian approach, which incorporates all the uncertainty associated with the joint estimation process. In our analysis we jointly estimated 75 parameters using the full IsotopeR model. Incorporating the uncertainty associated with estimating multiple parameters leads to more accurate intervals [47] for sources and their concentrations. We report credible intervals, as well as mean and standard deviations to illustrate (Fig. 2) and statistically summarize (Table 1B) our isotopic mixing space. In addition to defining our mixing space, we simultaneously estimate the joint posterior probability distribution of the sampled population's dietary source contributions (Fig. 3, Table S5). In the end, marginal distributions of each food source in each sampled bear's diet were reported (Fig. 4, Table S6).

We follow the transformational procedure described by Semmens et al. [31] to estimate proportional diet contributions using Markov chain Monte Carlo (MCMC). This approach assumes that the observed isotopic distribution $M_{i,e}$ of an individual i and element e is a mixture distribution where the isotopic distribution of each source s, $X_{s,e}$ is weighted by the individual's assimilated diet proportion, $f_{s,e,i}$ of each element. For a study with n food sources, the individual's observed isotopic distribution is given by

$$M_{i,e} = \sum_{s=1}^{n} f_{s,e,i} X_{s,e}\,, \tag{2}$$

where the vector of diet proportions for each element sums to 1, such that

$$\sum_{s=1}^{n} \left| f_{s,e,i} \right| = 1. \tag{3}$$

Specifically, we assume that the vector of $\underline{f_s}$'s in equation 2 are random variables distributed using the centered log-ratio (CLR) transformation described by Semmens et al. [31]. This transformation allows us to use MCMC on random variables (i.e., the proportions in equation 3) on the continuous real line, and then transform results to the interval [0,1], resulting in estimators of proportions. Due to low acceptance rates, approaches such as importance sampling (used in the estimation of proportions in the MixSIR model) are difficult to apply when estimating numerous parameters. Therefore, we choose to use an MCMC algorithm similar to Semmens et al. [31] and Parnell et al. [30].

Isotopic correlation

Isotope ratios for different elements are often assumed to be independent because independent biochemical and ecological processes are ultimately responsible for their fractionation [24]. Although the processes explaining most of the variation in different elements may be different (e.g., photosynthetic pathway for carbon vs. trophic enrichment for nitrogen), secondary factors can lead to coupling between isotopic ratios of different elements [e.g., 27,40,48,49]. For example, some bear studies that use SIA provide evidence that the nutritional pathways of carbon and nitrogen may be linked and the strength of correlation may increase with trophic level [e.g., 13,50,51].

Ignoring correlations in a model's covariance structure can have effects on both point estimates [52] and their intervals [53]. IsoError is currently the only model that considers isotopic correlation in mixing model calculations [21]. Similar to IsoError, we estimate correlation of sources and the mixture however we use a different approach. IsoError calculates the correlation coefficient (*r*) of the sources and the mixture and applies these values to correct the variance estimates. In contrast, we estimate *r* for all sources using Bayesian methods and included these estimates as terms in the covariance matrix (Fig. 1, #6).

Measurement Error

Measurement error was estimated and applied to each observation (i.e., sampled sources and mixtures) in this study. Error was estimated from calibration runs used to ensure the mass spectrometer's accuracy. Because these calibrations are run on standards (samples with known isotope values), we are able to jointly estimate the instrument’s measurement error along with the remaining model parameters (Figure 1, #1-3). It is important to note that the calibration runs represent a source of data independent of the mixture data.

Residual Error

We include a residual error term in our model to account for the error otherwise unaccounted for in the mixture (e.g., a population of bears). Our use of an error term (Fig. 1, #15, 25, 26) is consistent with standard linear regression models and is similar to other SIMMs [e.g., 31, 30]. This term takes into account unexplained variation, that is, variation not included in sources, discrimination processes, sub-sampling error, or measurement error.

Process and discrimination error

Differences between the isotope ratios in consumer’s tissues and their dietary sources are the result of fractionation and stoichiometric effects (i.e., isotopic routing) [54]. In general, animal tissues are ^{15}N- and ^{13}C-enriched relative to diet because lighter isotopes (^{14}N, ^{12}C) are preferentially eliminated from the animal via waste [6] and respiration [2], respectively, allowing heavier isotopes (^{15}N, ^{13}C) to be assimilated into animal tissues. These differences are commonly referred to as the source’s “discrimination factor” and values will vary depending on factors such as the taxon and tissue analyzed [55], a consumer’s nutritional status [e.g., 56,57], sex [58], and the macromolecular composition of diet (e.g., 12,23,59–61). Discrimination factors of food sources are often estimated (mean and SD) from results from controlled diet studies or from controlled studies on free-ranging animals, and are used to shift food sources to consumers in an isotopic mixing space. These corrections are critical to estimating animal dietary contributions using SIMMs [23].

Discrimination factors extracted from the literature are assumed to be true and predicted correctly from regression models fitted to controlled diet data [55]. Using these fixed values can result in erroneous results when estimating wild animals' mixed diets using SIMMs [62]. Recent research suggests that some controlled studies have used invalid procedures to predict discrimination factors [58,61,63]. For example, studies that fed captive bears controlled diets [e.g., 50,64] regressed tissue isotope values on food isotope values. The predicted discrimination factors for foods were calculated from the difference between the isotope value of the sampled food source and the predicted isotope value for the tissue, which was calculated from the regression equation. Robbins et al. [61] note that regression coefficients calculated by such methods are biased at estimating discrimination factors because tissue (i.e., tissue isotope value = diet isotope value + discrimination factor) and diet isotope values are necessarily autocorrelated. As a result, using these covariates (diet and tissue isotope values) in regression equations to predict discrimination factors yield spurious results; discrimination factors obtained by such methods should not be used to estimate diet using SIMM analysis. Furthermore, results from recent controlled diet studies using Sprague-Dawley rats suggest that correlations between discrimination factors and dietary isotope values are artifacts of the association between discrimination and biologically significant characteristics of diet (e.g., %N, % protein) that correlate with dietary isotope values. Therefore, if a regression approach is used, discrimination factors should be regressed on biologically significant characteristics of food, rather than its isotope values.

In addition to using an invalid method for estimating discrimination factors, many controlled diet studies do not keep animals on experimental diets long enough for their tissues to equilibrate, thus confounding estimation of discrimination factors [58]. Such studies also suggest isotope values are similar among most tissues; however, if tissues were not equilibrated to the diet, results may be an artifact of another process.

We used regression models developed by Kurle [58] to predict the tissue-diet discrimination factors of each sampled bear food. The discrimination factor was defined in this study as the difference in isotope values ($\delta^{13}C$ and $\delta^{15}N$) of a bear food and bear hair and is expressed with Δ notation: $\Delta X_{tissue\text{-}diet} = \delta X_{tissue} - \delta X_{diet}$. Kurle [58] fitted regression models to data collected from a controlled diet study where omnivorous rats were fed various diets that equilibrated to their tissues. Because rats are often used as proxies for wild omnivores, we used the regression equations developed in Kurle [58] to predict discrimination factors for the hair of male bears on different % protein diets. Specifically, we entered the estimated % protein (x) of plant and animal foods—determined by multiplying %N of sampled foods by 6.25, or calculated from the NDB# (acorns only)—into the regression equations ($\Delta^{13}C = -0.14x + 7.43$; $\Delta^{15}N = 0.14x - 2.10$) provided by Kurle [58] to predict $\Delta^{13}C$ and $\Delta^{15}N$ values for each observation (i.e., each sample collected for each species). Each sample's Δ value was then added to each sample's measured isotope value. Ultimately, the process error of the aggregate includes the inherent error associated with the isotopic variation of the samples in the aggregate and the variation of discrimination factors associated with each sample in the aggregate.

Current Bayesian models and some frequentist models allow users to apply fixed discrimination factors (predicted from regression equations, or extracted or inferred from the literature) and the associated uncertainty of each source to estimate dietary parameters. It is common for researchers to use discrimination factors from the literature instead of performing a complementary controlled experiment on their species of interest. Often researchers either use discrimination values from a controlled study that investigated discrimination in a similar species or taxon, or researchers use an average discrimination value (and SD) calculated from multiple studies (e.g., a duck study may calculate the mean discrimination factor from various controlled studies on birds). In addition to calculating predicted discrimination factors for each plant and animal sample collected, we calculated the error associated with the regression models used to predict these discrimination factors. Because we include the variation of predicted discrimination factors associated with each sample when we estimate the plant and animal source, and include a "discrimination error" term as a parameter in our model (Fig. 1, #4) when estimating these sources, all known error associated with the discrimination process is accounted for in the model.

Concentration-dependence

SIMMs that fail to account for the stoichiometry of dietary sources may distort assimilated dietary estimates [26]. Including unequal elemental concentrations of sources when calculating dietary estimates using SIMMs will alter the polygonal isotopic mixing space, and in some cases, include mixtures that may have been previously outside the mixing space [24]. Similar to IsoConc [24] and SIAR [30], we stray from the assumption that concentrations are equal among sources. Specifically, IsotopeR jointly estimates the concentration of C and N for each aggregate (Table 2B) and incorporates the assimilation efficiency (i.e., digestibility) of different foods (Fig. 1, #10 – 14) in each aggregate because previous studies [25,26] suggest it is important to consider when applying concentration dependence to mixing model calculations. Digestible [C] and [N] of human and bear foods were estimated by analyzing nutritional data from the NDB (Table S4) and sampled bear foods (Table S2), respectively. Calculations are described in Koch and Phillips [26] and in Table S2 and S4.

Aggregating plants and animals

We aggregated sampled bear foods into 3 sources: 100% plant diet, 100% animal diet, and 100% human food diet. Acorns (*n* = 15), berries (*n* = 9), grass (n = 9), and forbs (*n* = 15) were grouped into a plant aggregate (*n* = 48), and deer (*n* = 5) and insect species (*n* = 24) into an animal aggregate (*n* = 29)(Table 2 and S3). We aggregated these natural food source groups [38,39] because they were biologically similar [65] and isotopically different (Table S2).

The three aggregated sources were then used to estimate a joint probability distribution of proportional dietary source contributions for each individual bear and for the population as a whole. These distributions only provide inference to the foods (combined as aggregates) that we include in the model and will likely be biased, considering YNP black bears' omnivorous diets (i.e., they eat other plant and animal foods besides the species included in the analysis); however, we include the major contributors to bear diets based on previous diet studies [38,39].

Prior distributions

The effect the prior distribution has on inference is an important issue to address in Bayesian analysis. The prior can be especially influential when sample sizes are low; in such cases, using prior distributions derived from past results can improve inference [66]. Noninformative prior distributions (distributions that play a minimal role in the posterior distribution), also referred to as vague, flat, diffuse, or uninformative, are used in Bayesian analysis "to let the data speak for themselves, so that inferences are unaffected by information external to the current data" [66:61].

When conducting such Bayesian analyses it is important to ascertain the influence of the prior on the posterior distribution. Likelihood methods such as data cloning may be used to examine such influence [67]. For each of the multivariate normal distributions in this study, we used a normal distribution prior to estimate mean parameters and gamma distributions on variance parameters. We assessed the effect priors had on inference by conducting a data cloning procedure described by Lele et al. [67]. For this procedure, we replicated the dataset (n = 10) and used these copies to swamp the posterior distribution, effectively minimizing the influence of the prior distribution [67]. Data cloning procedures yield estimator output that are asymptotically equivalent to maximum likelihood estimators. We evaluated the influence of prior distributions on our analysis by comparing the data cloning estimates to IsotopeR's estimates.

Model comparisons

We estimated the sampled population's relative source contributions (means, medians, and 95% credible intervals) from the data using the full IsotopeR model and compared these estimates to those when IsotopeR model features were independently removed from the model. In addition, we compared IsotopeR estimates to estimates calculated by commonly used SIMMs (Fig. 3, Table S5). Summary statistics were calculated from the data for source aggregates and used as input parameters in all models except IsotopeR, which estimates most of these parameters in our fully Bayesian framework (Table 2A and 2C). Lastly, we compared individual food-conditioned bears' dietary estimates calculated by IsotopeR and the Semmens et al. model (Fig. 4).

Different Bayesian models have different convergence properties; therefore, we ran each model using a different number of iterations. Specifically, we ran a burnin of 5 x 10^5 iterations for all IsotopeR models, followed by 1.5 x 10^6 iterations of MCMC. We thinned our resulting chain by every 1,000th draw due to strong autocorrelation in some parameters. The MixSIR models was run at a burnin of 5 x 10^3 draws followed by 3 x 10^4 iterations, whereas the Semmens et al. model used a burnin of 15 x 10^3 draws followed 1.5 x 10^5 iterations of MCMC that were thinned by every 100 draws. SIAR was run at a burnin of 4 x 10^5 draws ran at 1 x 10^6 iterations with a thinning of every 300 draws.

RESULTS

SIA results and diet analysis

Eleven male FC bears were sampled and hair isotope values were corrected for the Suess effect (Table S1). The protein content of sampled plants and animals were outside the bounds of the protein content in rat diets [58]; therefore, we extrapolated our predicted discrimination factors in this study. Specifically, the estimated protein content of sampled plants (range = 2.5–23.1%) was less than rat diets (range = 30–40%) and the estimated protein content of sampled animals (60.5–98.1%) was greater than rat diets (Table S2). Each sample's predicted discrimination factor was added to the Suess-corrected isotope value for each sample (Table S2). Adjusted plant and animal samples were then used to estimate plant and animal source aggregates, respectively (Table 2B and S3). All three source aggregates were estimated by IsotopeR (Table 2B) and illustrated in bivariate isotope space (Fig. 2). The frequentist summary statistics generated from the data for sources (Table 2A and 2C) and the Bayesian IsotopeR estimates for sources (Table 2B) were essentially equivalent.

Measurement error (mean of SDs: $\delta^{13}C = 0.34$; $\delta^{15}N = 0.12$) was estimated using IsotopeR and applied to each observation in the IsotopeR analysis. In addition, the discrimination factor variability associated with each controlled diet from Kurle [58] was used to determine the overall discrimination factor variation among diets (discrimination error: $\Delta^{13}C = 1.96$; $\Delta^{15}N = 0.37$). Isotopic correlation was calculated for use in IsoError (Table 2A), and estimated by IsotopeR to infer bear diets (Fig. 5, Table 2B). Animal and human $\delta^{13}C$ and $\delta^{15}N$ values were highly correlated based on estimates from IsotopeR (Figs. 5B and C, Table 2B) and all source correlations were similar to estimates calculated from the data (Figs. 5A and B, Table 2A and 2B). We found that estimation of correlation in the residual error term was unnecessary because the correlation in the bear population ($r = 0.17$) was accounted for by the correlation in the sources.

Estimated elemental concentrations among food sources were non-constant, causing the lines that connect the sources in the isotopic mixing space to be curvilinear (Fig. 2). Specifically, the isotopic data for animal matter had a higher [N] than sampled plants ($t = 47.40$, $df = 47.12$, $P = <0.001$), regardless of whether digestibility corrections were included in the estimation (Table S5; non-digest: $t = 6.98$, $df = 47$, $P = <0.001$;

digest $t = 9.96$, $df = 47.12$, $P = <0.001$). As expected, ignoring the effect of concentration-dependence among sources had a considerable effect on inference (Fig. 3, Table S5).

IsotopeR feature comparison

We removed each feature from the model independently and compared inference to the full IsotopeR model (Fig. 3, Table S5). Removal of correlation and measurement error independently may have had some effect on proportional dietary source estimates (especially for human food) although differences are near the range of sampling error present (Monte Carlo error ~3%). Removal of the residual error term and discrimination error (larger effect) also had some effect on dietary estimates and increased the size of the credible intervals (Fig. 3, Table S5). Independently eliminating digestibility, concentration dependence, and all features from the full model had large influences on dietary estimates (Fig. 3, Table S5).

Bayesian and frequentist SIMMs

IsotopeR, SIAR, and IsoConc population estimates were different than other model estimates because they include concentration dependence. The digestibility and non-digestibility population estimates for these models were different within and among models (Table S5). Results from the Semmens et al. model, MixSIR, IsoError, and IsotopeR (without other IsotopeR features) were all similar (Fig. 3, Table S5); we note that all models except IsoError (confidence interval) report credible intervals. MixSIR's population estimates were nearly identical to estimates by the Semmens et al. model (Fig. 3, Table S5). However, small differences were due to error associated with MCMC sampling in Semmens et al. [31] and because the model includes individual-level estimation. Estimates by SIAR's were different than IsotopeR's estimates. This was likely due to IsotopeR estimating dietary proportions at the individual-level, including isotopic correlation when estimating the mixing space, accounting for the error associated with the joint estimation process, and the measurement error applied to each observation in the study. Including these features will increase the accuracy of credible interval estimates.

IsotopeR interval estimates for individual bears were wider than estimates calculated by the Semmens et al. model (Fig. 4, Table S6). Although the mean estimates for human food were similar between these models, plant and animal proportions were higher when estimated by IsotopeR and the Semmens et al. model, respectively (Fig. 4, Table S6). This discrepancy was likely due to the fact that Semmens et. al. model did not include concentration dependence, measurement error, and joint estimation in their calculation. Furthermore, their model estimates were essentially the same for each individual (Fig. 4, Table 6) and therefore provided little dietary information at the individual-level (Table S6), whereas IsotopeR estimated greater variability at the individual level.

IsoError and IsoSource (tolerance of 0.05) point estimates were essentially identical although IsoError provided confidence intervals and IsoSource did not. It is important to note that mean estimates for these models were similar to all other models that did not include concentration dependence in their calculations.

Influence of prior distributions

We used the data cloning procedure to examine the influence of priors on our mean dietary contribution point estimates. We found that cloning led to little change in estimator values (<3%)(Fig. 3, Table S5); therefore, priors had little influence on our proportional dietary source estimates. We further tested the influence of the priors by changing all prior distributions to be uniformly distributed, which led to essentially no change (<3%) in our estimated population- or individual-level estimators (Fig. 3, Table S5). Given the Monte Carlo error present (~3%) these results suggest that inferences are robust when using uninformative priors.

DISCUSSION

IsotopeR includes all features used in current SIMM analysis and includes other important features to consider when using SIMMs. This hierarchical, fully Bayesian model is capable of inferring animal diets at the population-, group-, and individual-level, while incorporating error associated with the input parameters. We demonstrated IsotopeR's performance by using real isotopic data to infer the assimilated diets of 11 black bears sampled in YNP using all SIMMs (Fig. 3, Table S5).

Although credible intervals generated by IsotopeR were generally wider than other models (Fig. 3, Table S5 and S6), the model calculates more accurate parameter estimates because the analysis includes all recognized and quantifiable SIMM features, such as measurement error, concentration dependence (including digestibility), isotopic correlation, individual-level estimation, and a fully Bayesian calculation. Together these model features can affect credible interval estimates significantly when compared to current models (Figs. 3 and 4, Tables S5 and S6)—an important consideration when using SIMMs for wildlife conservation and management.

Based on the analysis of our dataset, the Semmens et al. model, MixSIR, and IsoError, all generated very similar solutions (Fig. 3, Table S5). These models provide invalid estimates when elemental concentrations are nonconstant. Although IsoConc incorporates concentration dependence and had mean estimates similar to SIAR, like IsoSource it does not calculate interval estimates and should be used with caution. SIAR provides reasonable parameter estimates however it does not incorporate the sources of error and other important features IsotopeR includes in its model design.

Measurement error, isotopic correlation, and residual error

We suggest SIMM users include measurement error in their diet calculations because it always exists in SIA (and can be estimated from isotope values of standards) and it can affect proportional dietary estimates (Fig. 3, Table S5). Previous studies have shown that not including measurement error may lead to biased parameter estimates and can also lead to a loss of statistical power [68]. We also found that accounting for measurement error and discrimination error changed our correlation coefficient estimators, increasing the magnitude of correlation in sources.

Ignoring measurement error may reduce correlation coefficient estimates. Not accounting for this error in measurements may effectively 'wash out' dependencies between variables. It is important to account for correlation of isotope values in sources because they affect the shape of mixing space and posterior probability distributions (Figs. 2 and 5). Determining the proper shape of the isotopic mixing space is crucial when inferring diets for animals. Although there may not always be enough measurements for source isotope values to accurately estimate correlation coefficients, our results suggest that including these estimates may be important when estimating dietary proportions. Evidence from our analysis suggests that correlation of the population was explained by correlation in sources; however, future studies should determine if accounting for source correlations fully explain the mixture data.

Discrimination error

Isotopic discrimination is often mentioned briefly in studies that use SIMMs because currently the discrimination process is difficult to accurately measure [23]. As a result, many researchers assume discrimination factors in the published literature are estimated correctly, regardless of the methods used to calculate such values. In this study, we presented a novel method to potentially improve discrimination-corrected source estimation of mixed diets by correcting for dietary protein complementation [61]. Specifically, we corrected each sample's isotope value using a predicted discrimination factor and included the variability of these predictions in the estimation of source aggregates. In addition, we estimated sources using a discrimination error term, which represents the uncertainty associated with the regression models used to predict discrimination factors. Although our predicted discrimination factors are outside the regression range provided by Kurle [58] and are therefore unreliable (especially because many Δ values were predicted to be < 0), we assume interpolated predictions are valid and suggest researchers adjust each sample in their study in such a manner if feasible. We recommend sampling prey items to determine their nutrient compositions before designing the range of biologically significant diets (e.g. protein quantity and/or quality) to feed animals in a complementary controlled study. This will ensure regression models are useful in predicting discrimination factors for consumer's dietary sources. We used the adjusted isotope values for sources calculated by the method proposed in this study because they provided us reasonable estimates for sources given our bears' isotope values

(Fig. 2). It is important to note that the actual discrimination factors used to correct isotope values used in this study are irrelevant (as long as bears fall in the isotopic mixing space) because our purpose is to accurately estimate bears' assimilated diets given the data provided. In addition, we provided a potential method to consider when estimating sources in mixed diets, and used these same data to calculate parameter estimates for all SIMMs evaluated in this study.

In this study, we assumed rats, bears, and humans have similar discrimination factors for the same tissues because all omnivorous species have similar digestive physiologies. Although this assumption is reasonable (i.e., rats are commonly used as a proxy for humans in controlled experiments), more controlled studies need to be conducted to determine if discrimination variation is negligible among omnivores on different protein quality diets; and regardless of whether this assumption holds, it would be valuable to feed captive omnivores food with similar macromolecular content as the foods bears consume in the wild. Unfortunately, this would be impossible to do for all foods consumed by bears given captive omnivores nutrient requirements (i.e., low protein diets would likely lead to negative nitrogen balance in captive animals, leading to their death before food could equilibrate in their tissues). Therefore, a new model needs to be developed to predict these theoretical discrimination factors [61].

Estimating source aggregates and concentration-dependence

The standard assumption that elemental concentrations among sources are constant was violated (i.e., YNP black bear dietary sources had nonconstant elemental concentrations) and addressed by IsotopeR. Specifically, IsotopeR corrected the isotopic mixing space (Fig. 2) by accounting for different estimated digestible [C] and [N] values for each food source. When excluding this feature from the model, dietary estimates changed (Table S5) because a linear relationship between sources (inlay in Fig. 2) will overestimate sources with higher N concentrations. Similar to other models that incorporate concentration dependence (i.e., SIAR and IsoConc), our full model estimates for plants increased considerably while animals and human food decreased. This occurred because estimated N concentrations were higher for animals and human food when compared to plants (Table 2). Correcting for differences in sources' digestible C and N concentrations curved the lines that connected the isotopic endpoints and pinched the bottom of the mixing space. This decrease in area proximate to the plant aggregate increased the estimated proportion of plants to bear diets (Fig. 2). Although we believe estimates are not reliable without taking concentration dependence (with digestibility corrections) into consideration (especially for omnivorous species), the effects of concentration dependence on inference using SIMMs have not been evaluated using captive animals. Therefore, in addition to including concentration dependence in SIMM calculations it may be important to exclude it and report all results.

Aggregates were composed of species that were biologically significant and important to bears diets [38,39]. We believe it is not necessary to group species based on their within-aggregate statistical similarity as suggested by Phillips et al. [65] if species between aggregates do not overlap and the between-aggregate disparity is statistically significant. Although we believe we use a reasonable method for estimating each source aggregate, methods for estimating sources for omnivores need to be developed further and tested. In addition, SIMMs such as IsotopeR must undergo more rigorous validation procedures in controlled environments [62] in order to determine how accurately they infer the diets of free-ranging animals, especially those of omnivores.

Similar to previous work by Parnell et al. [30], IsotopeR's estimator coverage will decrease as the number of sources increase. This is due to the inability of the model to always estimate unique solutions when the number of sources is greater than the number degrees of freedom (n+1). Therefore, we recommend reducing the amount of inherent variation in SIMM analysis by having $\leq n + 1$ sources. This can be accomplished by aggregating sources when they exceed $n + 1$, adding dimensionality by including additional isotopes in the analysis, or eliminating sources that do not significantly contribute to animal diets as suggested by previous diet studies. Without taking one of these appropriate steps, a user will often calculate confounding results (i.e., inconsistent or bimodal posterior probability distributions). For example, a wolf population was partitioned into three groups and a Bayesian SIMM was used to make inference to group and individual diets [31]. For the mainland group, the sampled salmon population fell in the middle of the wolf distribution and directly between the deer and marine mammal distributions, confounding the estimation process. Adding another isotope (e.g., δ^{34}S) or eliminating marine mammals from the analysis—only if they were shown in other studies to not significantly contribute to wolf diets on the mainland—would have likely remedied this problem.

For omnivores, plant and animals may be aggregated into more groups (i.e., more sources to estimate) if a user increases the number of isotopes used to make inference (e.g., including δ^{34}S in the SIMM analysis to estimate fish contribution in bear diets in

Alaska). This would increase the predictive power of the model [30], especially if sources were ≤ *n* + 1. It is important to put great effort in using other studies (e.g., scat, gut content analysis, behavioral studies) to determine the complete list of food sources used in a SIMM analysis, to conduct SIA on these sources, and to aggregate them appropriately to construct an isotopic mixing space that will produce unique and biologically significant solutions. In addition, such studies are also important when defining prior distributions in Bayesian SIMM analysis.

Influence of prior distributions

Estimating all parameters of the model simultaneously (i.e., fully Bayesian approach) is most useful when consumer sample size is low, however the influence of priors on inference must be examined. When sample sizes increase, estimation error decreases, and parameter estimates will effectively become constants. Despite our small sample size (*n* = 11), the data cloning estimates were similar (<3%, Table S5) to our model estimates suggesting the prior had little influenced on IsotopeR's estimates. These results suggest that IsotopeR inference is robust to the distribution of the prior used.

CONCLUSION

The purpose of this project was to offer SIMM users a comprehensive guide to current SIMM analysis and build an improved SIMM. In particular, our goal was to build a Bayesian model capable of including various sources of error and other important features to make more accurate inference at various demographic levels (population-, group-, individual-level). Although we are confident that our model has provided more accurate inference compared to other models, our purpose was not to accurately estimate YNP bear diets. In addition to the challenge of accurately predicting discrimination factors for low- and high-protein diets, the data we used for the analyses in this paper were based on an incomplete collection of the plant foods bears consume in YNP; therefore, our inference to YNP bear diets is inherently incorrect. However, we do believe IsotopeR estimates seem reasonable given what we know about FC bear diets (i.e. dietary sources included in the analysis were identified from previous scat studies as major contributors to YNP black bear food habits) in YNP and bears' nutrient requirements. In particular, we believe it is reasonable for bears that regularly consume human food (18–43%), which is high in protein [41], to eat less animal matter (0–19%) than bears that do not consume human food. This is especially the case for YNP black bears since most of the animal matter in their diets is composed of insects [38,39]. In addition, vegetation is clearly the largest natural contributor to YNP bear diets as suggested by several diet studies [38,39], which is consistent with our model results (Fig 3, Table S5 and S6).

SIMMs are evolving rapidly and we believe this expeditious process will result in the abandonment of many models currently used to infer assimilated animal diets and the creation of new models (e.g., isotopic routing and time-series models). Because IsotopeR includes all features used in current models as well as other new features, we believe it will be the model of choice for many ecologists interested in using isotopic and nutrient data to estimate animal diets. In addition, the model could be used as the foundation for future SIMM development. We also believe the model is applicable for use in archeological, anthropological, and forensic studies as well as estimating pollution inputs. The R code and directions for "Isotopers" (researchers who use stable isotopes) are currently available as supplementary material (Appendix B) and the R package "IsotopeR" is available on CRAN with a straightforward user interface.

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APPENDIX A. Likelihood used in the IsotopeR model.

$$L(\theta \mid X) = \prod_{j}\prod_{s} \frac{1}{(2\pi)^{k/2}\left|\Sigma_j + \Sigma_{res} + \Sigma_Z\right|} \exp\left(\frac{1}{2}\left(m_j - \sum_{s} \frac{\mu_{D,s} i_{j,s}}{\sum_{s'} \mu_{D,s'} i_{j,s'}} \right)^T \left(\Sigma_j + \Sigma_{res} + \Sigma_Z\right)^{-1} \left(m_j - \sum_{s} \frac{\mu_{D,s} i_{j,s}}{\sum_{s'} \mu_{D,s'} i_{j,s'}} \right) \right) \times$$

(1)

$$\prod_{j}\prod_{s} CLR\left(\frac{1}{(2\pi)^{k/2}\left|\Sigma_{j,s}\right|^{1/2}} \exp\left(-\frac{1}{2}\left(i_{j,s} - f_s\right)^T \Sigma_{j,s}^{-1}\left(i_{j,s} - f_s\right) \right) \right) \times \qquad (2)$$

$$\prod_{s} CLR\left(\frac{1}{(2\pi)^{k/2}\left|\Sigma_{f,s}\right|^{1/2}} \exp\left(-\frac{1}{2}\left(f_s - \mu\right)^T \Sigma_{f,s}\left(f_s - \mu\right) \right) \right) \times \qquad (3)$$

$$\prod_{s} \frac{1}{(2\pi)^{k/2}\left|\Sigma_{D,s}\right|^{1/2}} \exp\left(-\frac{1}{2}\left(\varepsilon_s d_s - \mu_{D,s}\right)^T \Sigma_{D,s}^{-1}\left(\varepsilon_s d_s - \mu_{D,s}\right) \right) \times \qquad (4)$$

$$\prod_{s} \left(\frac{1}{(2\pi)^{k/2}\left|\Sigma_s + \Sigma_{disc} + \Sigma_Z\right|^{1/2}} \exp\left(-\frac{1}{2}\left(x_s - \mu_s\right)^T \left(\Sigma_s + \Sigma_{disc} + \Sigma_Z\right)^{-1}\left(x_s - \mu_s\right) \right) \right) \times \qquad (5)$$

$$\left(\frac{1}{(2\pi)^{k/2}\left|\Sigma_Z\right|^{1/2}} \exp\left(-\frac{1}{2}\left(z - 0\right)^T \Sigma_Z^{-1}\left(z - 0\right) \right) \right) \qquad (6)$$

Each line in the likelihood equation corresponds to a section in our model diagram (Fig. 1). Lines 1 – 3 correspond to the likelihood of the Mixtures section: line 1 gives the distribution of the observed mixtures, line 2 is the distribution of diet proportions for individuals, and line 3 is the distribution of the population diet proportions. The CLR function on lines 2 and 3 is the transformation of the random variable $\underline{X}$ and is given by $e^{x_i} / \sum_{i=1}^{n} e^{x_i}$. This expression is used to transform numbers on the continuous real line to the interval (0,1), constraining the sum of those variables to 1. Line 4, 5, and 6 correspond to the Source Concentrations section, Source Isotope Values section, and Measurement Error section, respectively.

APPENDIX B. Directions for running IsotopeR model in R.

1. Install JAGS from http://sourceforge.net/projects/mcmc-jags/
   (IsotopeR was tested on JAGS v2.2.0, 2.1.0 and 1.0.4)

2. Install the all R package dependencies using the R command: install.packages (c("R2jags","plotrix"),dep=T) or by using the graphical interface to install the following packages: *coda, lattice, rjags, R2jags, R2WinBUGS, plotrix*.

3. Setup data input files (underlined below) in the same format as the example data provided. Each data file name can be modified, but must match the R code (line 10–15). All input files must be saved as .csv files, not .xls files.

   Mixtures (consumer data, line 10): The first *n* columns in this data input file are the isotope values associated with each individual (i.e., consumer), where *n* is the number of isotopes used in the analysis. The last two columns designate the group and individual assignments. If there is no group structure, then column *n* + 1 will contain "1" for all individuals. If designating multiple groups, the group identity will be determined by the variable in the column. Individuals in the first group should be designated as "1," the second group as "2," etc. The last column identifies each individual. If you have no repeated isotopic measures for individuals then each individual will be designated by a unique integer (e.g., 1, 2, 3…). If you have repeated measures for an individual then individuals with repeated measures will have the same number (e.g., 1, 1, 1, 2, 2, 2…).

   Sources (line 11): Each source is a sample of a consumer's dietary items (may be a sample of the same species or aggregate of species). The first *n* columns in this data input file are the isotope values associated with each sampled dietary item, where *n* is the number of isotopes used in the analysis. Isotope values need to be in the same order as the mixture data file (e.g., column 1 in Mixtures and Sources contain δ^{13}C values). The next column (i.e., *n* + 1) identifies the source to which the sampled dietary item belongs. All entries for samples belonging to the first source should be denoted with integer "1", the second source as "2", etc. The last column identifies which species or taxon (i.e., sub-source) the sampled dietary item belongs within each source. This feature assigns equal weight to each sub-source.

   SourceCD (concentration-dependence data, line 12): The first *n* columns in this data input file are the concentration data for each sample, where *n* is the number of elemental concentrations used in the analysis (e.g., [C], [N]). Columns with elemental concentrations need to match Sources and Mixtures (e.g., column 1 in *SourceCD* and *Sources* files contain [C] and δ^{13}C values, respectively). Column *n* + 1 identifies the source in which the set of concentrations belong. All concentrations belonging to the first source should be denoted with integer "1", the second source as "2", etc. The last column links sampled dietary item concentrations to each sub-source. This feature assigns equal weight to each sub-source's elemental concentrations.

MeasurementError (error associated with mass spectrometry, line 13): This data input file contains all isotopic measurements for standards. Isotope values need to be in the same order as other data files (e.g., column 1 in *MeasurementError, Mixtures,* and *Sources* files contain $\delta^{13}C$ values).

DiscrimSD (discrimination data, line 14): This data input file contains the standard deviations associated with estimated discrimination factors measured in a controlled diet study. The first *n* columns in the data file are the standard deviations associated with each controlled diet isotope. The last column gives the source identification of the discrimination factors.

Digest (digestibility corrections, line 15): This data file contains the digestibility of different sub-sources. The first *n* columns contain the digestibility for *n* source isotopes. The next column is the source identification code defined in *Sources*. The final column is the sub-source identification code.

4. Change control parameters (defined below) for an MCMC run in IsotopeR.R (lines 21-24).
   mcmc.chains: The number of independent markov chains to be run.
   mcmc.burn: The length of the chain discarded at the beginning of the run. This is interpreted as the length of time it takes for the MCMC to stabilize.
   mcmc.chainLength: The total number of iterations run per chain (includes burnin)
   mcmc.thin: Reduces the sample size to every *n*th iteration; used to reduce autocorrelation in the chain.

5. Run model by pasting all code into the R console or type *source('IsotopeR.R')* into the command line of R (Note: the working directory in R needs to be the same folder as the code unless you have changed the paths of the input files in IsotopeR.R).

6. Results will be saved to an R image file and a .txt file named “output.name” (line 18). Files can then be imported as a .csv file into Excel or OpenOffice. Files are formatted in a matrix with rows given by the parameter names (defined in table below) and columns denoting the following values. The first two columns are the mean value, and the standard deviation. Quantiles (2.5%, 25%, 50%, 75%, 97.5%) are reported, followed by the Rhat values (a metric of convergence that should be less than 1.2 or the model should be rerun with a longer MCMC chain [71]) and n.eff, the effective sample size (an adjusted estimate of sample size that accounts for autocorrelation).

Estimated IsotopeR output parameters and definitions

Parameter	Definition
mu.conc[y,z]	Mean concentration for element y, source z.
mu.mix[x,z]	Isotopic mixture value for individual x, source z (note: these are joint estimation values that include all sources of error).
mu.source[y,z]	Mean isotope value for isotope y, source z.
p[x,z]	Individual-level proportional dietary contribution for individual x, source z.
p.pop[x,z]	Population-level proportional dietary contribution for individual x, source z.
rho.source[z]	Correlation values between isotopes in source z.
sd.conc[i, z]	Concentration standard deviations for concentrations i, source z.
sd.me[i]	Measurement error standard deviations for isotope i.
sd.res [i]	Standard deviations of the residual error term for isotope i.
sd.source[i,z]	Source standard deviation for isotope i, source z.

A user may receive several warnings during a model run. These errors are associated with JAGS and are not well documented by the package maintainers. Generally, these errors are related to the model not converging. Therefore, rerun the model with longer chains (and may also need a higher thinning rate).

Further details on the JAGS program can be found in the JAGS manual, available for download at http://sourceforge.net/projects/mcmc-jags/. JAGS model syntax is compatible with the BUGS language. Users unfamiliar with the BUGS language can find many tutorials at the WinBUGS site http://www.mrc-bsu.cam.ac.uk/bugs/

Table 1. A comparison of SIMM features among commonly used SIMMs. A. Four mixing model assumptions (italics) commonly violated when estimating the proportional dietary contribution of sources in an animal diet, and the model feature that addresses each violated assumption. B. A list of other features included in SIMMs and their definitions. “X” denotes the model addresses the assumption and/or includes the feature, and Y indicates the feature is not explicitly included in the model (i.e., model may account for error using an arbitrary tolerance measure). MCMC (Markov chain Monte Carlo), SIR (sequential importance resampling), and ML (maximum likelihood) denotes sampling method used when estimating parameters. “X^a” denotes that the model provides solutions when sources exceed *n* + 1, but solutions are not comparable to other models (i.e., output lists ranges of potential solutions, not parameter estimates).

Models	IsotopeR	SIAR	Semmens et al. 2009	MixSIR	IsoConc	IsoError	IsoSource
A. SIMM assumptions:							
Elemental concentration (e.g., [C] and [N]) of all dietary items are equal							
• Different source concentrations for dietary sources	X	X			X		
Elements are assimilated with the same efficiency							
• Different assimilation efficiencies for dietary sources	X						

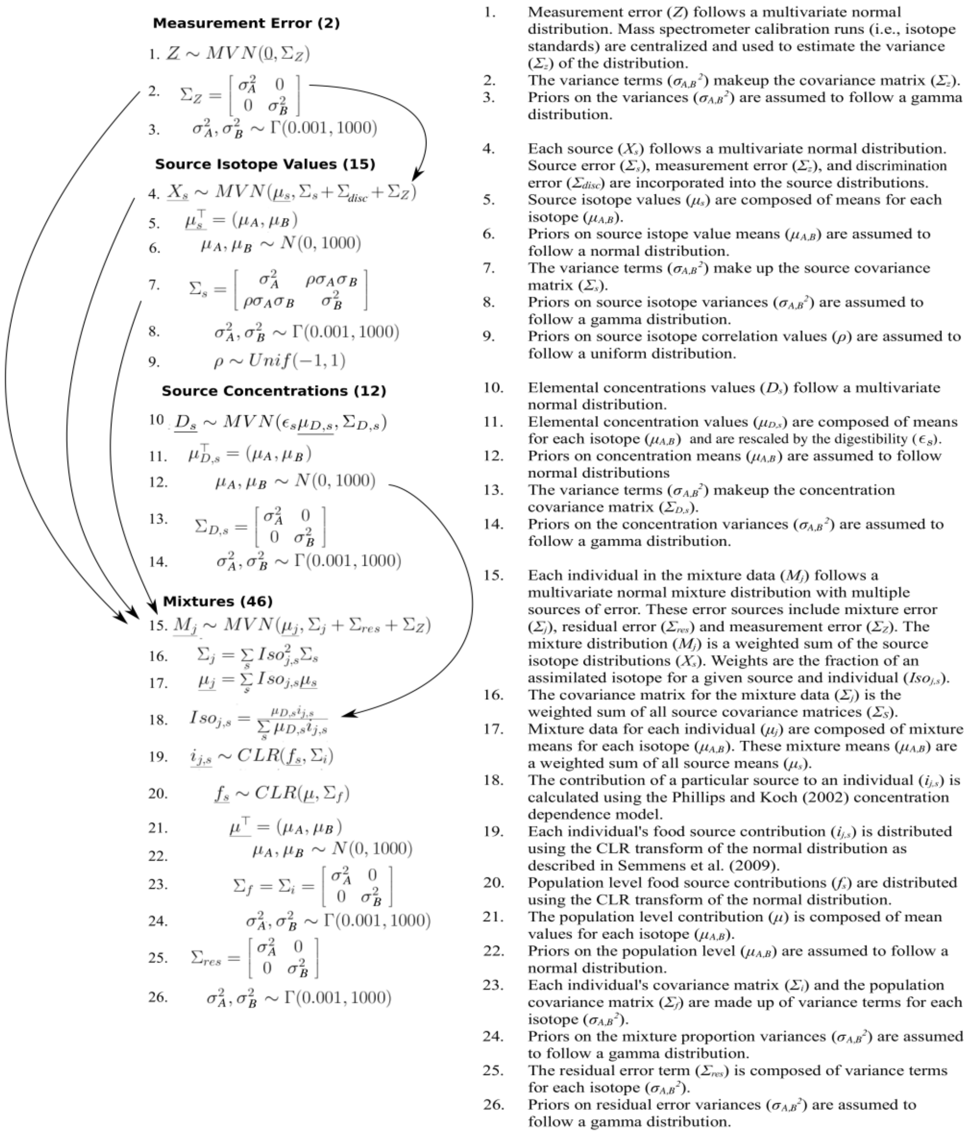
No tissue-diet discrimination							
• Variation associated with predicted discrimination factors	X	X	X	X			
• Includes a fixed “discrimination error” term (calculated *a priori*) - error associated with the regression line used to predict discrimination factors	X						
No isotopic routing							
• Differential allocation of isotopically distinct dietary sources to different tissues							
B. Other SIMM features:							
• Uses a Bayesian analytical framework	X	X	X	X			
• Sampling procedure used to estimate parameters	MCMC	MCMC	MCMC	SIR	ML	ML	ML
• Joint estimation of proportional source contributions	X	X	X	X			
• Uses raw data (not parameter estimates of raw data) to simultaneously estimate parameters (random variables): dietary sources (including isotopic correlation, variation), measurement error, proportional source contributions at the population- and individual-level	X						

• Measurement error – variation associated with SIA: sample preparation error and error during mass spectrometry; applied to each observation in the study	X					Y
• Source process error – inherent isotopic variation of the sampled source (i.e., within and between individual plants and animals of the same species or taxa)	X	X	X	X	X	Y
• Mixture process error – inherent isotopic variation in a sub-sampled tissue (e.g., non-homogenized hairs, feathers, claws from the same individual) and/or sample of mixtures (e.g., population)	X	X	X	X	X	X
• Correlation of isotope values in sources – accounts for the linear relationship among isotope values for different elements	X				X	
• A residual error term	X	X		X		
• Individual-level proportional dietary source estimation	X		X			
• Prior information associated with sources (e.g., source proportions, distribution of isotope values, elemental concentrations) and mixtures (e.g., measurement error)	X	X	X	X		
• Calculates proportional dietary source estimates when > n + 1 sources	X	X	X	X		X[a]

Table 2. Bear food aggregates. (A) Discrimination factor-corrected plant (*n* = 48), animal (*n* = 29), and human food (*n* = 72) aggregates are calculated from the sample data and used in frequentist models (see also Supplemental Table 3). (B) Plant and animal aggregates are estimated by IsotopeR using the sample data, whereas the human food aggregate was estimated as in A. (C) Non-fractionated isotope values and discrimination factors are used in IsoSource and all Bayesian models except IsotopeR. Means and (1 SD) are reported.

Aggregate	δ^{13}**C** (‰)	δ^{15}**N** (‰)	***r***	Δ^{13}**C** (‰)	Δ^{15}**N** (‰)	**% C**	**% N**	**Digest [C]**	**Digest [N]**
A. Frequentist models	discrimination included:								
Plants	-21.5 (2.83)	-1.48 (1.61)	-0.29			45.41 (3.92)	1.57 (1.03)	47.29 (3.43)	3.51 (3.09)
Animal	-27.4 (1.82)	11.71 (1.74)	-0.83			48.26 (3.81)	12.17 (1.69)	51.50 (0)	12.17 (1.69)
Human	-16.9 (0.79)	8.78 (0.47)	0.58					52.83 (2.54)	6.88 (1.10)
Bear	-21.6 (0.88)	4.37 (0.68)	0.17						
B. IsotopeR estimates	discrimination included:								
Plant	-21.72 (2.66)	-1.42 (1.61)	-0.28			45.45 (3.94)	1.57 (1.03)	47.28 (3.91)	3.42 (2.28)
Animal	-27.43 (1.61)	11.69 (0.29)	-0.91			48.28 (3.86)	12.14 (1.70)	51.50 (0.06)	12.18 (1.63)

Human	-16.95 (0.29)	8.78 (0.27)	0.69			Fixed estimates (same as A)			
C. Other Bayesian models	discrimination separate:								
Plants	-27.53 (2.25)	-0.75 (1.19)		6.06 (0.90)	-0.73 (0.90)	45.41 (3.92)	1.57 (1.03)	47.29 (3.43)	3.51 (3.09)
Animals	-24.23 (0.71)	3.16 (1.00)		-3.22 (1.48)	8.55 (1.48)	48.26 (3.81)	12.17 (1.69)	51.50 (0)	12.17 (1.69)
Humans	-16.94 (0.79)	8.78 (0.47)		Discrimination included		Fixed estimates (same as A)			



Measurement Error (2)

1. $Z \sim MVN(\underline{0}, \Sigma_Z)$
2. $\Sigma_Z = \begin{bmatrix} \sigma_A^2 & 0 \\ 0 & \sigma_B^2 \end{bmatrix}$
3. $\sigma_A^2, \sigma_B^2 \sim \Gamma(0.001, 1000)$

Source Isotope Values (15)

4. $\underline{X_s} \sim MVN(\underline{\mu_s}, \Sigma_s + \Sigma_{disc} + \Sigma_Z)$
5. $\underline{\mu_s}^\top = (\mu_A, \mu_B)$
6. $\mu_A, \mu_B \sim N(0, 1000)$
7. $\Sigma_s = \begin{bmatrix} \sigma_A^2 & \rho\sigma_A\sigma_B \\ \rho\sigma_A\sigma_B & \sigma_B^2 \end{bmatrix}$
8. $\sigma_A^2, \sigma_B^2 \sim \Gamma(0.001, 1000)$
9. $\rho \sim Unif(-1, 1)$

Source Concentrations (12)

10 $\underline{D_s} \sim MVN(\epsilon_s \underline{\mu_{D,s}}, \Sigma_{D,s})$

11. $\mu_{D,s}^\top = (\mu_A, \mu_B)$
12. $\mu_A, \mu_B \sim N(0, 1000)$
13. $\Sigma_{D,s} = \begin{bmatrix} \sigma_A^2 & 0 \\ 0 & \sigma_B^2 \end{bmatrix}$
14. $\sigma_A^2, \sigma_B^2 \sim \Gamma(0.001, 1000)$

Mixtures (46)

15. $\underline{M_j} \sim MVN(\underline{\mu_j}, \Sigma_j + \Sigma_{res} + \Sigma_Z)$
16. $\Sigma_j = \sum_s Iso_{j,s}^2 \Sigma_s$
17. $\underline{\mu_j} = \sum_s Iso_{j,s} \underline{\mu_s}$
18. $Iso_{j,s} = \frac{\mu_{D,s} i_{j,s}}{\sum_s \mu_{D,s} i_{j,s}}$
19. $\underline{i_{j,s}} \sim CLR(\underline{f_s}, \Sigma_i)$
20. $\underline{f_s} \sim CLR(\underline{\mu}, \Sigma_f)$
21. $\underline{\mu}^\top = (\mu_A, \mu_B)$
22. $\mu_A, \mu_B \sim N(0, 1000)$
23. $\Sigma_f = \Sigma_i = \begin{bmatrix} \sigma_A^2 & 0 \\ 0 & \sigma_B^2 \end{bmatrix}$
24. $\sigma_A^2, \sigma_B^2 \sim \Gamma(0.001, 1000)$
25. $\Sigma_{res} = \begin{bmatrix} \sigma_A^2 & 0 \\ 0 & \sigma_B^2 \end{bmatrix}$
26. $\sigma_A^2, \sigma_B^2 \sim \Gamma(0.001, 1000)$

1. Measurement error (Z) follows a multivariate normal distribution. Mass spectrometer calibration runs (i.e., isotope standards) are centralized and used to estimate the variance (Σ_z) of the distribution.
2. The variance terms ($\sigma_{A,B}{}^2$) makeup the covariance matrix (Σ_z).
3. Priors on the variances ($\sigma_{A,B}{}^2$) are assumed to follow a gamma distribution.

4. Each source (X_s) follows a multivariate normal distribution. Source error (Σ_s), measurement error (Σ_z), and discrimination error (Σ_{disc}) are incorporated into the source distributions.
5. Source isotope values (μ_s) are composed of means for each isotope ($\mu_{A,B}$).
6. Priors on source istope value means ($\mu_{A,B}$) are assumed to follow a normal distribution.
7. The variance terms ($\sigma_{A,B}{}^2$) make up the source covariance matrix (Σ_s).
8. Priors on source isotope variances ($\sigma_{A,B}{}^2$) are assumed to follow a gamma distribution.
9. Priors on source isotope correlation values (ρ) are assumed to follow a uniform distribution.

10. Elemental concentrations values (D_s) follow a multivariate normal distribution.
11. Elemental concentration values ($\mu_{D,s}$) are composed of means for each isotope ($\mu_{A,B}$) and are rescaled by the digestibility (ϵ_S).
12. Priors on concentration means ($\mu_{A,B}$) are assumed to follow normal distributions
13. The variance terms ($\sigma_{A,B}{}^2$) makeup the concentration covariance matrix ($\Sigma_{D,s}$).
14. Priors on the concentration variances ($\sigma_{A,B}{}^2$) are assumed to follow a gamma distribution.

15. Each individual in the mixture data (M_j) follows a multivariate normal mixture distribution with multiple sources of error. These error sources include mixture error (Σ_j), residual error (Σ_{res}) and measurement error (Σ_Z). The mixture distribution (M_j) is a weighted sum of the source isotope distributions (X_s). Weights are the fraction of an assimilated isotope for a given source and individual ($Iso_{j,s}$).
16. The covariance matrix for the mixture data (Σ_j) is the weighted sum of all source covariance matrices (Σ_S).
17. Mixture data for each individual (μ_j) are composed of mixture means for each isotope ($\mu_{A,B}$). These mixture means ($\mu_{A,B}$) are a weighted sum of all source means (μ_s).
18. The contribution of a particular source to an individual ($i_{j,s}$) is calculated using the Phillips and Koch (2002) concentration dependence model.
19. Each individual's food source contribution ($i_{j,s}$) is distributed using the CLR transform of the normal distribution as described in Semmens et al. (2009).
20. Population level food source contributions (f_s) are distributed using the CLR transform of the normal distribution.
21. The population level contribution (μ) is composed of mean values for each isotope ($\mu_{A,B}$).
22. Priors on the population level ($\mu_{A,B}$) are assumed to follow a normal distribution.
23. Each individual's covariance matrix (Σ_i) and the population covariance matrix (Σ_f) are made up of variance terms for each isotope ($\sigma_{A,B}{}^2$).
24. Priors on the mixture proportion variances ($\sigma_{A,B}{}^2$) are assumed to follow a gamma distribution.
25. The residual error term (Σ_{res}) is composed of variance terms for each isotope ($\sigma_{A,B}{}^2$).
26. Priors on residual error variances ($\sigma_{A,B}{}^2$) are assumed to follow a gamma distribution.

Figure 1. IsotopeR (full model) operational schematic. Indented formulas on the left side denote terms and prior distributions associated with random variables. The right side provides a description of each formula. Sub-section titles are followed by the number of parameters estimated (in parentheses), and arrows denote hierarchical dependencies among random variables.

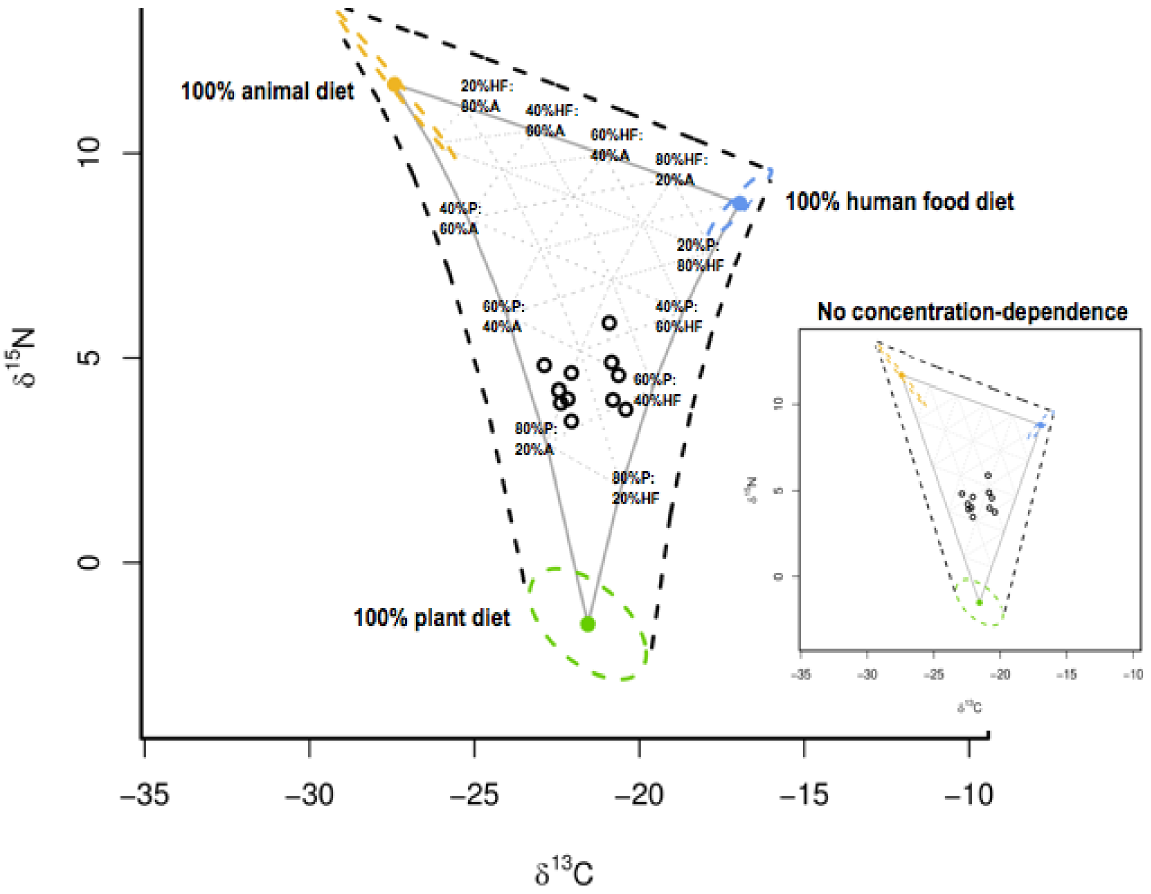


Figure 2. Isotopic mixing space. Isotope values (δ^{13}C and δ^{15}N) for male bears (○) captured in YNP and their estimated food source aggregates provided. Estimated means for source aggregates (100% plant diet ●, 100% animal diet ●, 100% human food diet ●) and process error (1 SD; dashed colored ovals) were estimated by IsotopeR and defined the vertices of the dietary mixing triangle; the shape of each source aggregate illustrates the degree of estimated isotopic correlation of observations used to define each aggregate. Variations in dietary contributions (%) of plants (P), animals (A), and human

food (HF) are shown along the edge of the mixing triangle (solid gray line) that connects estimated source means; labels denote the contribution of diet when consumers lie at the intersection of the mixing triangle edge and gray dashed iso-diet lines (within the triangle). The black dashed triangle illustrates the approximate total mixing space at 1 SD. Measurement error (not shown) was also estimated by IsotopeR and applied to each source observation when estimating source aggregates and to each bear in the mixing space. The inset illustrates the isotopic mixing space if concentration dependence was not included in the analysis.

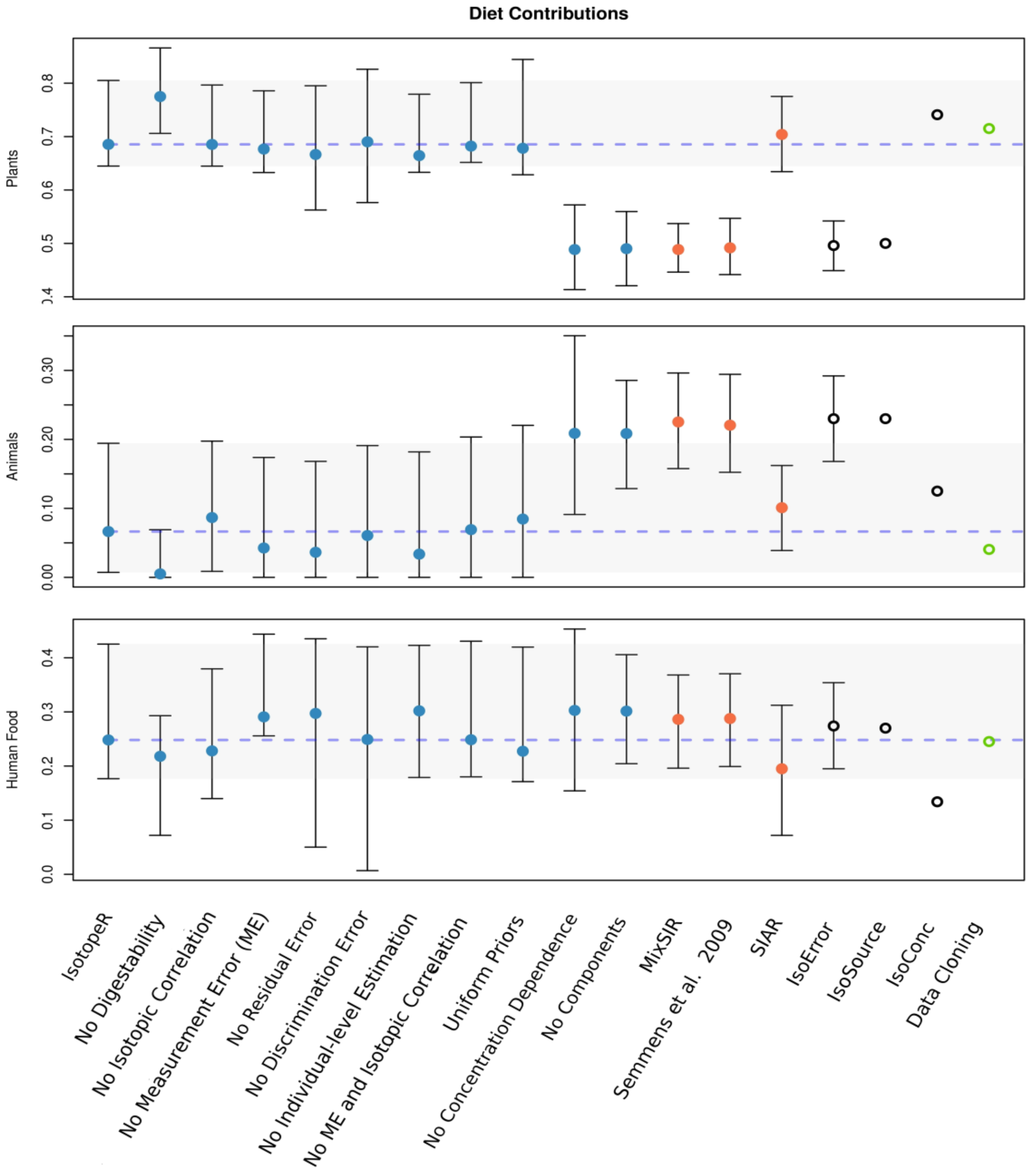


Figure 3. Model comparisons. Mean and 95% credible intervals (error bars) calculated by IsotopeR (●) and other Bayesian (●) models, as well as frequentist (○; confidence intervals reported), and data cloning models (○). Blue dashed line and gray bar is the estimated mean and 95% credible interval for IsotopeR, respectively.

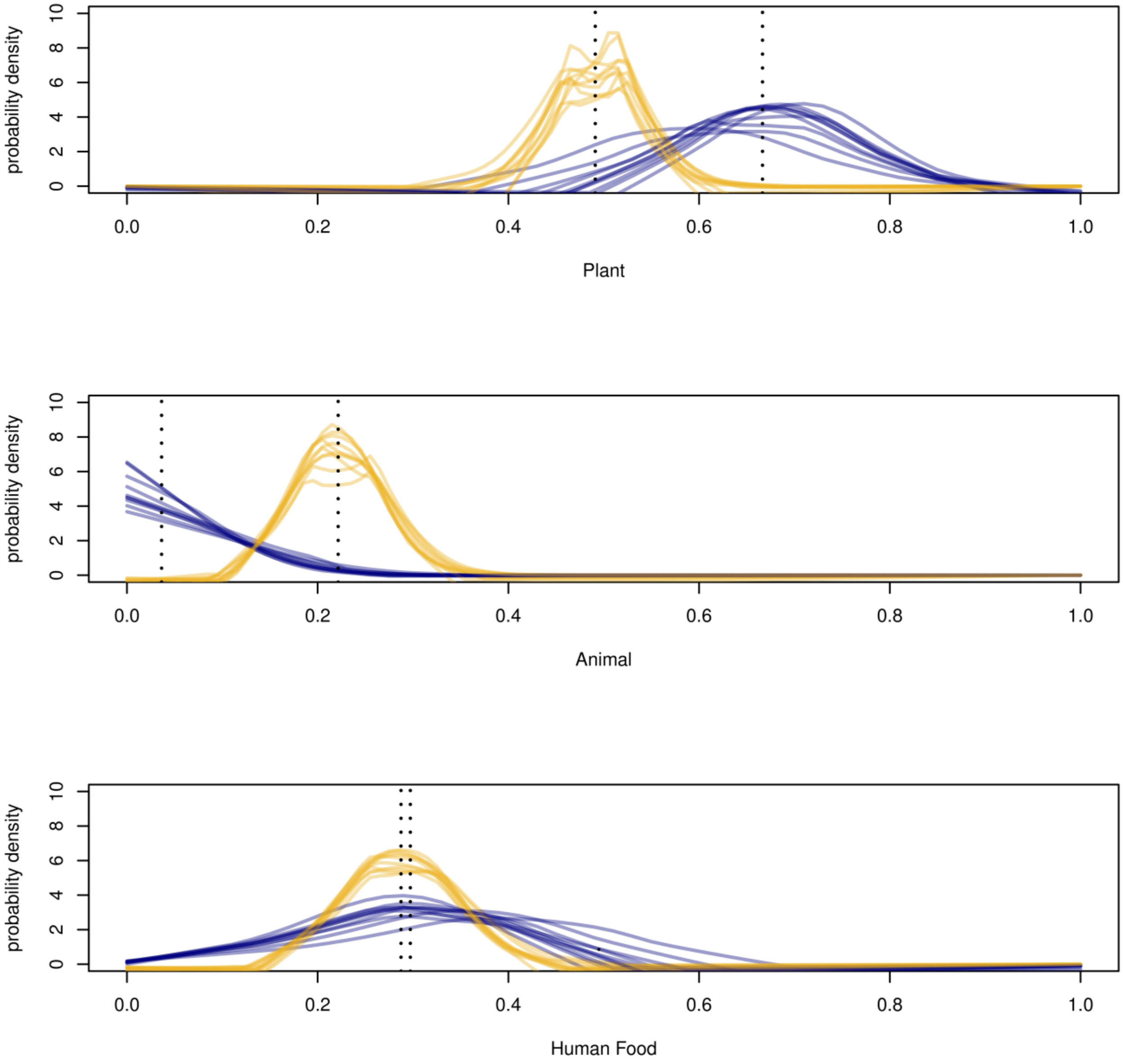


Figure 4. Model comparison diet estimates for 11 food-conditioned bears. Posterior probability distributions of individual dietary estimates for IsotopeR (—) and Semmens et al. model (—).

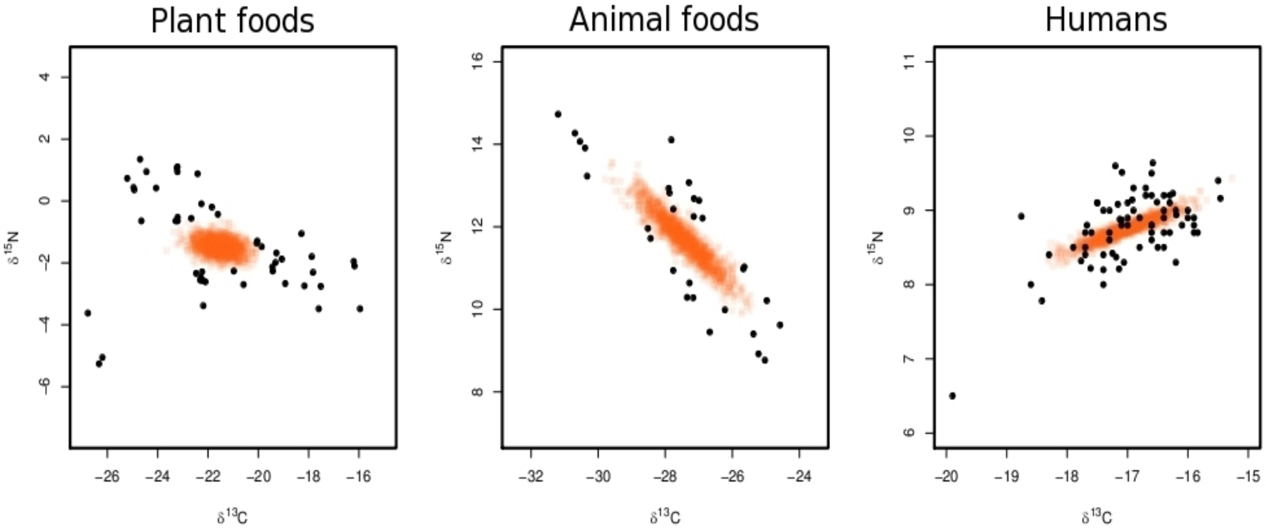


Figure 5. Isotopic correlation of δ^{13}C and δ^{15}N in aggregated sources. The IsotopeR MCMC chains (each accepted draw denoted by ●) used to estimate the source isotope mean parameters are compared to observed values (●) of each isotopic source. Source estimates denote weakly correlated data at the low trophic level (Plants) and highly correlated data at higher trophic levels (Animals and Humans).

Contribution of Author and Co-Authors

Manuscript in Chapter 4

Chapter 4:

Author: John B. Hopkins III

Contributions: conceived the study and figures, designed methods, collected data, and wrote the manuscript.

Co-author: Paul L. Koch

Contributions: provided expertise on stable isotope analyses, provided lab support, discussed results and implications, and commented on the manuscript.

Co-author: Jake M. Ferguson

Contributions: designed model code for statistical analyses and for figures, discussed results and implications, and commented on the manuscript.

Co-author: Charles C. Schwartz

Contributions: provided feedback on study design, statistical analyses, and commented on the manuscript.

Co-author: Steven T. Kalinowski

Contributions: provided feedback on study design, statistical analyses, and commented on the manuscript.

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Stable isotopes to detect food-conditioned bears and 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*) to identify food-conditioned (FC; bears that consume human food) bears throughout Yosemite National Park, USA and to evaluate the Park's human-bear management program. Specifically, we analyzed hair from bears known *a priori* to be FC or non-FC (NFC) and used these isotopic data to predict whether bears with an unknown management status are FC or NFC. We also used a stable isotope mixing model to estimate the proportional contribution of two dietary sources (plants and animals, and human food) to FC bear diets. We then used results from both analyses to evaluate the

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program's proactive (population-level management) and reactive management (individual-level management) strategies, and provided a new metric to evaluate overall human-bear management. The logistic model predicted that 19 out of 145 (13%) bears sampled from 2005–2007 were FC. In addition, the proportion of human food in known FC bear diets (*n* = 36) likely declined between time periods (2001–2003 and 2005–2007), suggesting proactive management was successful in reducing the amount of human food available to bears since 2001. In contrast, evidence suggests reactive management was not successful in changing known FC bears management status to NFC or reducing the contribution of human food in FC bear diets. Specifically, 9 known FC bears were recaptured on 14 occasions between 2001 and 2007; all bears were classified as FC during subsequent recaptures, and human-bear management may have been successful at reducing the amount of human food in one bear's diet. Based on our results, we suggest YNP continue implementing their proactive human-bear management strategy, reevaluate reactive management, and remove problem bears from the population.

KEY WORDS black bear, carbon isotope, hair, human-bear management, IsotopeR, nitrogen isotope, mixing model, stable isotopes, *Ursus americanus*, Yosemite National Park

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Wildlife Management staff at Yosemite National Park (YNP) have evaluated the human-bear management (Table 1) program over the past decade by comparing annual bear incident (Table 1) reports (i.e., tallies of incidents) collected park-wide. Most reports are collected in Yosemite Valley (here after referred to as the Valley), an area that comprises

<1% of the park, but receives 90% (Key and Webb 1989) of the nearly four million visitors each year (National Park Service Public Use Statistics Office: http://www.nature.nps.gov/stats/). In fact, from 2005 to 2007, ~83% of the reported bear incidents (1,084; not including 7 injuries because their locations are unknown) occurred in the Valley (Yosemite National Park, unpublished data). As a result, the Park has historically concentrated its human-bear management efforts in this high quality black bear habitat. Although this Valley-focused human-bear management program may seem warranted because of the concentrated visitor use, this centralized management may reduce the program's ability to provide effective management park-wide. As a result, over 99% of YNP, including >1,000 front country campsites and wilderness (277,000 ha), currently receive less management attention compared to the Valley.

Monitoring bears in remote areas of YNP is difficult with the methods currently employed (Greenleaf 2005). Managers rely heavily on bear incident reports to monitor food-conditioned (FC) bears (Table 1) in the backcountry. Reports usually detail the incident (e.g., "a medium size bear broke into my bear canister"), however they often fail to include useful information that can be used to monitor the bear in the future. Unlike monitored bears in the Valley, bears involved in incidents in the backcountry rarely have discernible identification (e.g., tags) or devices (e.g., radio collars) for monitoring them. As a result, it is difficult for personnel to assign such bears a management status (Table 1), link bears to specific incidents, and monitor these bears over time.

Past research suggests the magnitude and severity of incidents in the backcountry are under-represented (McCurdy and Martin 2007). A study by McCurdy and Martin (2007) showed that only one of four bear incidents was reported in YNP wilderness, and despite a 97% compliance rate for bear canister use in the wilderness, only 62% of backpackers were able to store all their food, trash, and scented toiletries in their canisters. Based on these results, we estimated that ~428 incidents (from 107 annual incident reports) occurred outside the Valley from 2005 to 2007 (Yosemite National Park, unpublished data); therefore, ~321 incidents went unreported. If this estimate is valid, approximately how many unknown (UNKN) bears (Table 1) are responsible for incidents outside of Yosemite Valley? Also, has human-bear management been effective at reducing the amount of human food available to bears during this time period when compared to previous years (2001–2003)?

This study had three objectives. First, we classified bears with UNKN management statuses as FC or non-food-conditioned (NFC; Table 1) based on stable isotopic composition of their hair (see Stable isotope analysis below). To accomplish this goal, we sampled bears during management actions (i.e., chemical immobilizations primarily in the Valley) and throughout YNP via hair-snare (hereafter referred to as hair-snare bears). We then identified individual bears by conducting DNA analysis on bear hair; these individuals then underwent whole hair nitrogen stable isotope analysis. We used $\delta^{15}N$ values to predict the management status for UNKN bears using logistic regression. Next, we estimated assimilated diets of FC bears using a stable isotope mixing model, IsotopeR (Hopkins et al. 2011). We used hair from predicted NFC bears (Table 1) and humans to isotopically define the natural food source (i.e., plants and animals) and human food (Table 1) source, respectively. We then used these isotopic distributions and plant and animal elemental concentrations ([C] and [N]) to build the isotopic mixing space (i.e., bears estimated isotopic distribution if their fed on a source 100% of the time) used to estimate bear diets. Our final goal was to provide useful indices for evaluating the human-bear management program in YNP and specifically evaluate the effectiveness of both proactive (Table 1) and reactive human-bear management (Table 1).

Stable isotope analysis

Stable isotope analysis emerged as an ecological tool in the late 1970s to infer animal diets, reveal trophic structure, and elucidate food web linkages (Fry 2006). In particular, stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios have been used in an extensive range of ecological applications (Peterson and Fry 1987, Lajtha and Michener 1994, Kelly 2000, Fry 2006). In general, the carbon isotopes of consumer tissues elucidates the photosynthetic pathway of food sources (i.e., C_3 versus C_4 plants; DeNiro and Epstein 1978, Ramsay and Hobson 1991, Hobson and Welch 1992), while nitrogen isotopes reveal the trophic position of consumers in the food chain (i.e., ^{15}N is enriched relative to ^{14}N with each trophic shift) (DeNiro and Epstein 1981, Minagawa and Wada 1984, Hobson and Welch 1992).

Animal tissues have different growth rates and isotopic turnover rates; the later defined as the time required for stable isotopes in the tissue to equilibrate to isotopes derived by the diet. Therefore, each tissue provides a different temporal window of dietary information (Hilderbrand et al. 1996). For example, bone collagen yield isotope ratios (expressed as $\delta^{13}C$ and $\delta^{15}N$ values) that may represent much of the lifetime diet of the organism due to the tissue's slow, continuous turnover rate (Chisholm and Schwarcz

1982, Tieszen et al. 1989, Hobson and Montevecchi 1991), whereas breath has rapid turnover (begins within ~3 hr) and more clearly reflects exogenous dietary sources recently ingested by the animal (Ayliffe et al. 2004).

Conducting isotopic analysis on hair is particularly useful because hair integrates assimilated carbohydrates, protein, and fat (i.e., endogenous and exogenous resources) (Ayliffe et al. 2004, Mowat and Heard 2006) and preserves dietary information within inert hair keratin (Michael et al. 2003). Hair is useful when reconstructing wild animal diets because it can be collected using noninvasive methods (Mowat and Heard 2006), analyzed to determine average diet during the period of hair growth (whole hair stable isotope analysis), or used to examine temporal variation in diet by sub-sampling the hair (Ayliffe et al. 2004, Mizukami et al. 2005).

Carbon isotopes in bears.— Hobson et al. (2000) and Mizukami et al. (2005) showed that bears that posed a management problem or trapped close to human habitation had elevated $\delta^{13}C$ values (in hair) compared to other bears. Carbon pools in bears may be enriched in ^{13}C 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). Corn and sugar cane (C_4 plants) are enriched in ^{13}C relative to C_3 plants, and because YNP is a C_3 ecosystem, bears with elevated $\delta^{13}C$ values relative to conspecifics may be feeding on human food.

Nitrogen isotopes in bears.— Bear populations that consume more dietary meat (Hilderbrand et al. 1996, 1999, Mowat and Heald 2006) or are a management concern (Hobson et al. 2000, Greenleaf 2005, Mizukami et al. 2005) have elevated $\delta^{15}N$ values.

Hobson et al. (2000) showed that management grizzly bears (*Ursus arctos*; Table 1) had higher $\delta^{15}N$ values in their hair when compared to research grizzly bears (i.e., not management bears), indicating a higher proportion of human food or livestock in their diets (Greenleaf 2005). In addition, Mizukami et al. (2005) examined the average and temporal variation in Asiatic black bear (*Ursus thibetanus*) diets by analyzing whole hairs and hair segments. Their study demonstrated high $\delta^{15}N$ values in whole hair for nuisance bears (bears that fed on garbage), and high $\delta^{15}N$ values for hair segments that corresponded to the time of year individuals were a management problem. Lastly, a study by Greenleaf (2005) showed that $\delta^{15}N$ values for bear hair are useful for predicting the management status of bears in YNP.

STUDY AREA

We sampled bears throughout Yosemite National Park (Fig. 1; see Sampling) for isotopic analysis; however only a small portion of YNP (Fig. 1) is prime habitat for bears. As elevation increases, forage quality and quantity decreases (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. Results from studies conducted in the 1970s suggest that bears occupy these higher elevations to commandeer human food (Graber 1981, Keay and van Wagtendonk 1983). Generally, bears tend to forage in the spring at lower elevations, such as the Valley, and follow snowmelt and sprouting vegetation upslope in June; they return to lower elevations in September for acorns and berries (Graber 1981).

Vegetation in the central Sierra Nevada Mountains is generally arranged in belt-like elevation zones that are strongly influenced by topography. Graber and White (1983) described five major vegetation types in Yosemite. The first is located in the western, low elevation margin of the Park and consists of chaparral and foothill woodland. This prime bear habitat comprises 2% of the Park and is composed of primarily oaks (*Quercus* spp.), manzanita (*Arctostaphylos* spp.), and ceanothus (*Ceanothus* spp.). The second vegetation type, the mixed conifer forest (1,000–2,100 m), includes the prevalent ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and 3 groves of giant sequoia (*Sequoiadendron giganteum*) and occupies 21% of the Park. In addition, this type also includes California black oak (*Quercus kelloggii*), moist meadows, and a complex shrub understory. The red fir (*Abies magnifica*) (2,000–2,600 m) and lodgepole pine (*Pinus contorta*) subalpine zones (2,400–3,200 m) make up the most extensive vegetation types (23% and 40%, respectively); the latter type consists of nearly pure lodgepole pine stands and subalpine meadows comprised of primarily sedges (*Carex* spp.) and several grasses. The remaining 14% (44,000 ha) of the Park is above timberline at 3,200 m.

METHODS

Terminology

Inconsistent definitions for the terms and concepts used in human-bear management may lead to miscommunications among wildlife professionals, adding to the complexity of the already daunting task of managing humans and bears (Hopkins et al. 2010). Therefore, we listed definitions for terms and concepts frequently used in this paper in Table 1.

Sampling

Management bears.— We live-captured bears in YNP (primarily in the Valley) for management purposes (e.g., to tag and radio-collar, euthanized, translocate) from August, 2005 through September, 2007. We sampled bear hair from live-captured bears and management induced mortalities. We captured bears in culvert traps and immobilized them using Telezol (Fort Dodge Animal Health, Fort Dodge Iowa, USA) at a dose of 2 mg/2.2kg body weight. All bears were processed according to the Park's Wildlife Management protocol. Bears received a subcutaneous PIT tag for subsequent identification (Avid Power Tracker II Multi Mode Reader, Norco, California, USA), were weighed, blood- and hair-sampled, aged by teeth using a dichotomous key, and standard morphological measurements were documented.

Black bears in Yosemite typically begin molting in the spring (Graber 1981). During this time (early molt), hair from the previous year is shed, and darker guard hairs begin to grow and appear on the lower limbs and around the eyes (Graber 1981). By mid-molt, previous hair is replaced on the limbs, down the flanks, as well as the remainder of the face (Graber 1981). Molt finally terminates (post-molt) 20–60 days later along the spine (Graber 1981). We characterized bears as being in the pre-molt, early molt, mid-molt, or post-molt stage upon capture. Greater than 10 full-length guard hairs were collected from either along the spine or from the upper limbs during March–July (usually pre- to mid-molt), or from the lower limbs or flanks from August–September. Full-length guard hair collected during spring months grew the previous year, whereas hair collected in the fall grew during the current year. Generally, full-length hair collected from fall 2005–2007 was representative of bear diets from 2005–2007.

We used isotopic values for bears from Greenleaf (2005) and bears that we identified as FC to develop an isotopic method to discriminate between FC and NFC bears. In a study by Greenleaf (2005), bears were captured in the Valley, fitted with radio-collars, and monitored from July 2001 to November 2003. Location data and a qualitative assessment (e.g., bear was observed consuming human food) of each foraging bear's behavior (suggested by management staff) were used in concordance to classify bears as known FC (n = 14; Table 1) or known NFC (n = 9; Table 1, S1). In this study, we designated known FC in a similar manner as Greenleaf (2005), however resources limited staff from classifying bears as known NFC. Therefore, we classified management bears not designated FC as UNKN. Isotope values for known NFC bears from Greenleaf (2005), allowed us to develop an isotopic baseline for bears that do not consume human food. We used these values in conjunction with known FC bears isotope values from both studies to predict the management status of UNKN bears using a logistic regression model (see analysis 1).

Hair-snare bears.— We used a modified method for noninvasive hair snare sampling described by Woods et al. (1999) to collect bear hair. This sampling design used a maximum of 100 feet of 4-barbed, 2-strand wire strung around ≥ 3 trees, approximately 40 cm above the ground to target adults and reduce the probability of capturing individuals <2 years of age; isotopes in tissues of young bears are affected by mother's milk, thus confounding results (Polischuk et al. 2001).

We installed hair-snares stations a minimum of 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 all stations with cow blood or anise oil by pouring the liquid over decaying logs, centered in the trap. We visited snares from March–October 2006, and May–October 2007, at 2–3 week intervals (sessions) to collect hair samples and add new lure; collectively, these hair samples represented bear diets from 2005–2007, and similar to management bears, full length guard hair collected during spring and fall months were representative of the previous and current year's diet, respectively. When snares were inspected, each barb with hair was considered a separate sample and was therefore inserted into an individual paper coin envelope, labeled, and stored in a desiccant chamber.

We installed 35 hair-snare stations throughout YNP from March–July 2006 (Fig. 1); each station was installed as soon as the site was free of snow. We categorized hair-snare stations into 5 groups (Table S2): frontcountry campgrounds (i.e., accessible by car; n = 11), backcountry campgrounds (n = 6), backcountry campsites (n = 10), residential neighborhoods (n = 4), and remote locations (n = 4). We installed 31 stations at locations where human-bear incidents have occurred historically; we selected these sites after examining bear incident reports and interviewing wildlife staff (V. Seher and S. Thompson, Yosemite National Park, personal communication). In addition, we installed 4 stations at locations in YNP where human-bear interactions had not been recorded (i.e., remote locations); the candidate list for these locations was recommended by wilderness management staff and were selected by choosing sites distant from human-use areas and were convenient for sampling.

Plants and animals.— We collected plant and animal foods identified in previous fecal analysis studies (Graber and White 1983; Greenleaf 2005) in 2007 to estimate their elemental compositions (digestible [C] and [N]). We used these concentrations (Table S3, S4) to construct the isotopic mixing space (Koch and Phillips 2003, Hopkins and Ferguson 2011) and accurately estimate FC bear diets. These foods include herbage (i.e., grasses, forbs), reproductive plant parts (RPP), and animals (Table S3, S4). Plant-derived foods (herbage, RPP) were sampled seasonally throughout the park and include grasses (*Agrostis* spp., *Poa* spp*., Avena* spp.), forbs (*Trifolium* spp., *Montia* spp., *Perideridia parishii*, *Lupinus* spp., *Equisetum* spp.), and RPPs from *Arctostaphylos* spp, *Quercus* spp., *Malus* spp., *Pyrus* sp*., Prunus subcordata, Pinus* spp., *Prunus emarginata, Cornus sericea, Cornus nuttallii, Prunus demisse, Sambucus mexicanus, Ribes roezlii, Ribes nevadense, Rubus discolor, Rubus leucodermis, Rubus parviflourus, Rhamnus* spp., *Amelanchier* spp., *Vaccinum* spp., *Symphoricarpos* spp., and *Rosa californica*. Animal-derived foods included insects (*Apidae*, *Campanotus* spp., *Lasius* spp., *Isoptera, Hymenoptera, Vespula* spp*,*) and mule deer (*Odocoileus hemionus*). We kept all food items frozen until dried and analyzed. Finally, instead of conducting isotopic analyses on bear foods and then accounting for discrimination factors (to adjust for metabolic fractionation and stoichiometric effects during the formation of bear hair), we used isotope values of NFC bears to define the plant and animal dietary source.

Human sampling.— We collected 20 human hair samples in 2009 and combined them with hair samples collected by Bowen et al. (2009) in 2004 because they were statistically similar (Hopkins and Ferguson 2011). We assume that bears on 100% human food diet would be isotopically similar to humans because both humans and bears are monogastric omnivores; therefore, it is likely that they discriminate against ^{14}N and ^{12}C by a similar magnitude (Hopkins and Ferguson 2011).

Hopkins and Ferguson (2011) estimated the digestible elemental concentrations ([C] = 52.8, SD = 2.5; [N] = 6.9, SD = 1.1) for the average (weighted) human diet in the United States by analyzing nutrient data from the USDA 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] (Table S3, S4) to define the isotopic mixing space used in our diet analysis (see analysis 2).

Genetic analysis

We conducted DNA analysis to identify individuals for isotopic analysis. We sub-selected hair samples from each session at the end of each field season in order to maximize the ratio of individuals identified to cost of genetic analysis/session. We sub-sampled based on the following criteria: (1) ≥10 guard hairs, (2) sample on barb or 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) only samples with <10 guard hairs were available for collection during the session, or (3) no guard hair was available, only underfur. We sent sub-selected samples to Wildlife Genetics International (WGI; Nelson, British Columbia, Canada) for DNA analysis.

DNA was extracted using QIAGEN's DNeasy Tissue kits (Qiagen, Mississiauga, Ontario, Canada), following the manufacturer's instructions. WGI 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 & 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 adult bear guard hairs with a 2:1 chloroform-methanol solution to remove surface oils; we then air-dried all samples. For plants, we oven-dried all samples and powdered them for sub-sampling. We weighed all samples and packaged them in tin cups (4 x 6 mm). The Stable Isotope Laboratory at University of California, Santa Cruz, CA analyzed samples for their carbon and nitrogen stable isotopic composition by continuous flow methods using a Carlo-Erba elemental analyzer interfaced with an Optima gas source mass spectrometer. Stable isotope ratios are expressed in delta (δ) notation as "per mil" (‰):

$$\delta X = ((R_{sample}/R_{\mathrm{standard}}) - 1) * 1000,$$

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 Vienna Peedee-Belemnite for carbon and atmospheric N_2 for nitrogen. We estimated stable isotope analysis measurement error using isotope values from reference standards, calculated by our mixing model; we applied this error to each sample collected in this study.

We corrected carbon isotope 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, Quay et al. 1992, Sonnerup et al. 1999). Based on ice core records (Francey et al. 1999), we applied a time-dependent correction (to 2009) of -0.022‰ per year (Chamberlain et al. 2005) to all sample isotope values, except 2009 human hair.

Statistical analyses

Analysis 1.— We built a logistic regression model to determine the probability of known bears (FC and NFC) being classified as FC using isotope values of their hair as covariates. This model was then used to predict the management status of UNKN bears (n = 145; Table S5). Prior to our analysis, we used ANOVA and found that known FC bears (n = 36; 14 bears from Greenleaf (2005) and 22 bears collected for this study; Table 2) and known NFC bears (n = 9; Table S1) had significantly different $\delta^{15}N$ values (FC: $\bar{x}$ = 4.6‰, SD = 0.9; NFC: $\bar{x}$ = 3.2‰, SD = 0.4; $P < 0.001$, df = 44), but similar $\delta^{13}C$ values (FC: $\bar{x}$ = -21.2‰, SD = 0.8; NFC: $\bar{x}$ = -21.0, SD = 0.6; P = 0.48, df = 44) (Fig. 2). As a result, we used $\delta^{15}N$ as the predictor in our logistic regression model to classify UNKN bears as either FC or NFC; we note that mean $\delta^{15}N$ values of known FC bear were not significantly different between sexes (males: $\bar{x}$ = 4.8, SD = 1.0, *n* = 18; females: $\bar{x}$ = 4.4, SD = 0.9, *n* = 18; t = 1.2, *df* = 33.4, *P* = 0.25).

We then determined the probability threshold for classifying UNKN bears as either FC or NFC by using a Receiver Operating Characteristic (ROC) curve. 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; i.e., probability of FC bears correctly classified), while minimizing FC bear misclassifications (false positive rate; i.e., probability of classifying NFC bears as FC bears). We were willing to misclassify some FC bears 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 classifying nearly all FC bears that were truly FC. In the end, we classified UNKN bears as FC if the probability of being FC was greater than or equal to the threshold value; otherwise, bears were classified as NFC.

Analysis 2.— 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 predicted NFC bears and known NFC bears (Greenleaf 2005); this isotopic distribution was used as the plant and animal dietary source used in our mixing space. We defined the human food source by using isotope values of human hair and digestible C and N concentrations (expressed as [C] and [N]) for human diet calculated by Hopkins and Ferguson (2011). The relative difference in [C] and [N] between the 2 sources determined the shape of the line that connected the two isotopic end points (i.e., dietary sources: 100% plants and animals, 100% human diet). IsotopeR estimated isotopic measurement error associated with each observation in this study, the sources (and their isotopic correlation), and the [C] and [N] of plants and animals to define our isotopic mixing space. Unlike other mixing models, IsotopeR uses isotopic measurement error and the actual sample data (not parameter estimates of sampled distributions) as model inputs to simultaneously estimate the mixing space and proportional dietary contributions at the population- and individual-level using a hierarchical framework (Hopkins and Ferguson 2011). Similar to other Bayesian mixing models, IsotopeR provides marginal posterior probability distributions for the parameters of interest rather than point estimates or confidence intervals; in this study, we report the mean, 1 SD, and 95% credible interval for the marginal posterior distributions.

Analysis 3.— We evaluated YNP's proactive and reactive human-bear management strategies and provided metrics (reported incidents/FC bear, dollars in property damage/FC bear) for evaluating the overall human-bear management program in the future. We evaluated proactive human-bear management (1) by calculating the proportion of predicted FC bears from UNKN bears sampled park-wide, (2) by providing a minimum count of NFC bears that became FC, and by (3) comparing estimated proportions of human food in known FC bear diets between time periods (2001–2003 and 2005–2007). Because FC bears persistently seek out human food sources in YNP, we assumed the average proportional human food contribution to FC bear diets can be used as an index for the amount of human food available to bears in YNP. In addition, we evaluated reactive human-bear management by comparing human food contributions in each known FC bear's diet through time. We examined differences in dietary estimates using t-tests.

RESULTS

Bear hair samples

We collected 58 hair samples from management captures and dead bears (2005: $n = 2$; 2006: $n = 36$; 2007: $n = 20$), and 1,093 samples from hair-snares (2006: $n = 588$; 2007: $n = 505$) during 350 sessions (2006: $n = 199$; 2007: $n = 151$). We sub-sampled 375 hair-snare samples (2006: $n = 184$; 2007: $n = 191$) and all management bears for genotyping. Our lab successfully genotyped 298 (79%) hair-snare samples (2006: $n = 146$; 2007: $n = 152$) and 52 management bears (2005: $n = 2$; 2006: $n = 31$; 2007: $n = 19$) using 8 microsatellite loci ($\bar{x}$: $H_E = 0.69$, $H_o = 0.73$; $n = 348$). These genotypes defined 109 and 115 unique individuals in 2006 and 2007, respectively. Twenty-nine (11 management bears were captured via hair-snare) of these 224 bears were captured in both 2006 and 2007; therefore, a total of 195 different bears were captured during this study. Undetected genotyping error was unlikely for the 8-locus marker system given no 1MM-pairs and consistent results from replicating 7 2MM-pairs. In addition to a low false-match probability, the lab unknowingly assigned 6 bear hair samples to the correct individuals (i.e., blind samples); we also note a study by Kendall et al. (2009) reported that the same lab was 100% successful at genotyping 653 blind bear hair samples.

We determine the stable isotopic composition of available guard hair from adult management bears [known FC = 22, Table 2; UNKN = 11, Table S5] and from hair-snare bears (n = 134) (Fig. 2, Table S5). In 33 cases we used isotope values for the same individuals in successive years, but considered them independent in our analyses.

Statistical analyses

Analysis 1.— We used isotopic data from known FC and NFC bears to build a logistic regression model ($\log it(y) = -13.975 + 4.132\delta^{15}N$; Appendix A). 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 bears as FC and 126 as NFC (Fig. 4B). It is likely that 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 identifying FC bears using bear hair δ^{15}N values.

Analysis 2.— We used the same probability threshold of 0.569 to classify NFC bears (n = 126) from UNKN bears using the nitrogen isotopic composition of their hair (Fig. 4). We determined this threshold by selecting a true positive rate of 0.67 (NFC bears correctly classified) and a false positive rate of 0.03 from the ROC curve (NFC bears misclassified; Fig. 3B); a low false positive rate suggests few UNKN 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 nitrogen stable isotope values.

We estimated measurement error ($\bar{x}$ SD: ™^{13}C = 0.3, ™^{15}N = 0.1) and applied this error to all mixture and source observations when estimating the isotopic mixing space.

Specifically, we estimated the 100% plant and animal source (i.e., all NFC bears; *n* = 135)(™^{13}C: $\bar{x}$ = -22.0 ± 0.9‰, ™^{15}N: $\bar{x}$ = 2.4 ± 0.8‰) and 100% human food source (™^{13}C: $\bar{x}$ = -17.0 ± 0.8‰, ™^{15}N: $\bar{x}$ = 8.8 ± 0.7‰); we also estimated the isotopic correlation of sources (plants and animals: *r* = 0.12, human food: *r* = 0.64) and digestible elemental concentrations of the plant and animal source ([C]: $\bar{x}$ = 47.4 ± 3.5, [N]: $\bar{x}$ = 2.6 ± 3.0). The relative difference between the estimated [C] and [N] for plants (*n* = 134) and animals (*n* = 29) (Table S3, S4) and the fixed concentrations for human food caused the mixing line to bend in a convex fashion between the two sources in the isotopic mixing space (Fig. 5). We simultaneously estimated FC bear diets at the population- (plants and animals: $\bar{x}$ = 87, CI = 83–91%; human food: $\bar{x}$ = 13, CI = 9–17%) and individual-level (Table 2, 3) using IsotopeR.

Analysis 3.— The logistic model predicted 19 FC bears (Table 2) from 145 UNKN bears (~13% of sample including one recapture; Table S5). The mean proportion of human food in known FC bear diets likely declined (*t* = 2.00, *df* = 16.27, *P* = 0.06) between time periods (2001–2003: $\bar{x}$ = 20 ± 9%, range = 8–36%, *n* = 14; 2005–2007: $\bar{x}$ = 14%, SD = 4%, range = 9–25%, *n* = 22). Of the 33 recaptured bears, 7 NFC bears (3 known, 4 predicted) became FC (4 known, 3 predicted) on subsequent captures (Table 2, S1, S5) and 11 bears originally predicted as NFC remained NFC (Table S5). We recaptured 9 known FC bears [management bears originally captured by Greenleaf (2005) or from 2005–2007] on 14 occasions (Table 3); all bears were classified as FC during subsequent recaptures, and human-bear management may have been successful at reducing the amount of human food in one bear's diet (#2297; Table 3). Finally, we classified one UNKN management bear as FC originally and on recapture (#3097; Table 2).

DISCUSSION

Our study is the first to use noninvasive genetic sampling and stable isotope analysis to predict bear management statuses (analysis 1), to conduct a park-wide investigation of FC bear diets (analysis 2), and to use such results to evaluate a human-bear management program (analysis 3).

Analysis 1

We used conservative true positive/false positive rates from the ROC curve (Fig. 3A) to select our threshold value (Fig. 4) for predicting the management status of UNKN bears (i.e., to discriminate between FC and NFC bears). We used this approach because our main goal was to classify most FC bears in our sample even though it came at a cost of falsely classifying a few FC bears (i.e., NFC bears falsely predicted FC). Although we could have used a true positive rate of 1.0 (i.e., correctly classifying all FC bears) it would have resulted in potentially classifying a large proportion (~89% instead of ~33%) of NFC bears as FC bears.

It is unlikely that many UNKN bears predicted to be FC bears were misclassified as NFC because known FC bears had higher $\delta^{15}N$ values (except one which may have been misclassified; Fig. 4A) than known NFC bears (Fig. 2). However, we note that because we conducted a whole hair analysis, relatively high $\delta^{15}N$ values in small sections (representing short time periods or events where bears may have consumed human food) of UNKN bear hair may have been diluted in the analysis, resulting in relatively low whole hair $\delta^{15}N$ values. To remedy this problem, growth segment analysis (i.e., isotopic analysis of hair segments; Mizukami et al. 2005) 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 $\delta^{15}N$ was useful in predicting the management status of bears in YNP and $\delta^{13}C$ was not. Although $\delta^{13}C$ values were similar for known FC and known NFC bears, we suggest YNP managers collect more isotopic data for known NFC bears and include $\delta^{13}C$ (and potentially other isotopes such as $\delta^{34}S$) as isotopic predictors in a revised logistic regression model. The isotopic mixing space illustrates our rational 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 greater than ~15% (median) human food tend to have $\delta^{13}C$ values higher than the average NFC bear, and as the human food contribution increases in bear diets, the correlation between $\delta^{15}N$ and $\delta^{13}C$ increases.

The correlation of carbon and nitrogen isotope values of FC bears may be the result of bears indirectly consuming sugar cane and corn products (including corn-fed livestock) via human foods (Koch 2007, Chesson et al. 2008). Hobson et al. (2000) showed 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 are coupled (i.e., they correspond to dietary protein intake; both ^{12}C and ^{14}N are discriminated against elevating $\delta^{13}C$ and $\delta^{15}N$ values). However, they found a weak isotopic relationship for bears primarily foraging on plant foods. Similarly, our results suggest that YNP bears with relatively high and correlated $\delta^{13}C$ and $\delta^{15}N$ values consumed human food instead of a largely plant-based diet (Fig. 5).

Analysis 2

Several known NFC bears from Greenleaf (2005) may have been originally misclassified (Fig. 4A). However, removing these misclassified bears (i.e., NFC bears actually FC) from the analysis had no effect on the threshold value used to discriminate between FC and NFC bears. Also, removing these three bears from the NFC bear group (i.e., plant and animal source; *n* = 135) had a negligible effect on the isotopic distribution of this source and proportional dietary estimates.

Typically researchers add discrimination factors to isotope values of sampled sources in order to estimate consumer diets using isotopic mixing models. These critical factors are either estimated from a complementary experiment where individuals from the species of interest are fed controlled diets, or more commonly, these corrections are calculated from regression models or extracted from the literature (Hopkins and Ferguson 2011). When using the latter method, discrimination factors for a particular tissue are often averaged across multiple species fed similar diets (e.g., 10 mammal species fed fish). As a result, using such values to estimate animal diets may bias parameter estimates, especially if the errors associated with the regression model and the average (i.e., process error) are not applied to each source when estimating animal diets. In addition, discrimination factors are assumed to be true and predicted correctly; however, recent research suggests that some controlled studies use invalid procedures to predict discrimination factors (Caut et al. 2008, Kurle 2008, Robbins et al. 2010). In this study, we did not need to apply such values to either dietary source, which increased our ability to accurately estimate dietary parameters. Although using human hair isotope values to define the human food source was an effective method, we assumed this source was equivalent to bears on a 100% human food diet. Although not ideal, this method is the only option because we believe feeding bears a 100% human food diet is unethical given personal observations of FC bear teeth (i.e., rotten, presumably from human food; Yosemite National Park, unpublished data).

Another limitation to our estimation procedure was that IsotopeR did not estimate digestible [C] and [N] for human foods (unlike the plant and animal source). Instead we used a reasonable weighted average (fixed parameter) for digestible [C] and [N] (Hopkins and Ferguson 2011). Preferably, we would have used IsotopeR to calculate digestible [C] and [N] for each human food; however, this would have required a human diet study, which was outside the scope of this project.

Analysis 3

A total of 145 different UNKN bears were classified to a management status, of which 19 of were predicted to be FC. Since the number of incidents and property damage is likely a function of the number of FC bears in the Park, the total number of FC bears (known and predicted) could be used in the future to standardize the number of annual bear incidents and property damage recorded each year; these metrics (i.e., reported incidents/FC bear, dollars in property damage/FC bear) could be used to evaluate the overall human-bear management program. For instance, we predicted 18 individual bears as FC and knew 15 different individual bears were FC (Table 2). During the time period (2005–2007) these 33 individual bears were sampled (Table 2), the Park recorded 1,300 bear incidents and $268,292 in property damage. Therefore, each bear on average was involved in ~40 reported incidents and ~$8,130 in property damage; however, we note that these figures may be high if additional FC bears exist or too low if predicted FC bears were misclassified. In addition, we detected 15 FC bears (1 known FC bear from White Wolf, 1 predicted FC management bear, and 13 predicted FC hair-snare bears; Table 2) outside the Valley. Therefore, each of these bears may have been involved in as many as 28.5 estimated incidents on average.

We suggest YNP replicate the methods used in this study to evaluate proactive and reactive management in the future. Specifically, such measures as percent predicted FC bears, number of incidents and damage per predicted FC bear, number of new FC bears, and average proportion of human food in known (and predicted) FC bear diets may be valid measures to evaluate YNP's proactive human-bear management strategy. We propose YNP estimate known FC bear diets in the more distant past (i.e., by analyzing tissues from museum specimens) and future and compare these estimates to the estimates provided in this study. Like our results, a decrease in the proportion of human food in known FC bears diets over time may suggest successful proactive management. In contrast to proactive management results, reactive management (i.e., Wildlife Management's primary strategy) did not change known FC bear management status to NFC and was also unsuccessful at reducing the amount of human food in individual FC bear diets through time. Based on our results, we suggest YNP continue implementing their proactive human-bear management strategy, reevaluate the effectiveness of reactive human-bear management, and remove problem bears from the population.

Implementing proactive and reactive management methods concurrently allows managers to reduce or prevent conflict and respond to incidents as they occur (Hopkins et al. 2010). Therefore, it is important to apply proactive management to areas that receive relatively high bear activity to prevent future bear incidents as well as to reactively manage individual FC bears. Evidence from this study suggests that the YNP human-bear management program is focusing efforts in an area (i.e., East Valley) where the highest proportion of FC bears are active (Table 2, S2); however, results also suggest that other locations may require more proactive effort to prevent bears from becoming FC (Table S2). For instance, 8 different bears were captured in both Bridalveil and Crane Flat Campgrounds (Table S2), and two of these bears (from Crane Flat) were predicted to be FC based on the stable isotopic composition of their hair (Table 2). In addition, other campgrounds (frontcountry and backcountry) and neighborhoods (e.g., Foresta: 3 predicted FC bears and 1 known FC bear; Table 2) could benefit from proactive and potentially reactive management in the future. Although we sampled all areas of the park that receive high annual visitation, we were unable to sample all human-use areas (e.g., backcountry campsites). Therefore, there may be other sites in the park that need human-bear management.

MANAGEMENT IMPLICATIONS

Human-bear management success is a term frequently used, but rarely defined (Hopkins et al. 2010). In this study, we provide definitions for proactive and reactive human-bear management success and new quantitative methods that can be used to evaluate human-bear management. We suggest YNP construct a bear management status database to organize the data used for such evaluations. Such a database could also be used to link individual bears to specific bear incidents and to monitor bears park-wide over the long-term. Other management programs outside Yosemite may also benefit from building and maintaining such a database.

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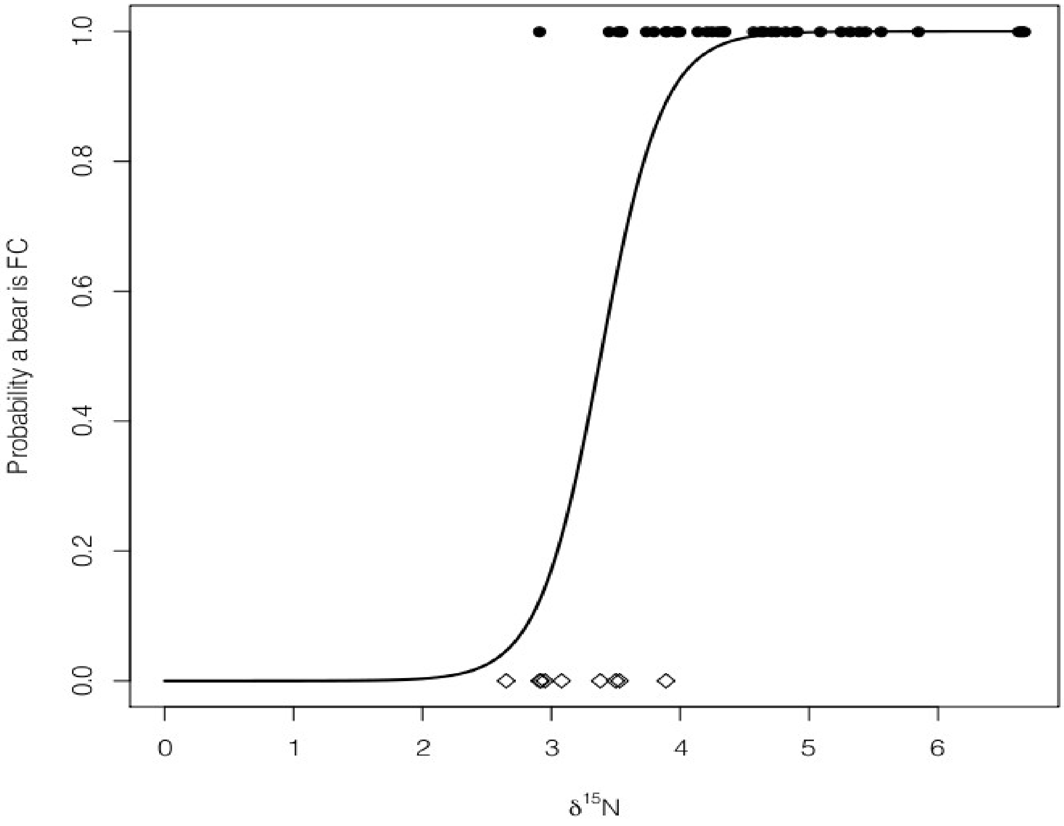

APPENDIX A. Logistic regression model used to predicted UNKN bear management statuses (2005–2007) in Yosemite National Park, CA, USA. We used the logistic curve to predict UNKN bear management statuses based on $\delta^{15}N$ values of known FC (●) and known NFC (◊) bears. We used the threshold value (0.569; horizontal line in figure) for analysis 1 and 2; we determined this value by selecting points on ROC curves (Figure 3A and 3B).

Table 1. Terms and definitions used in human–bear management. Important human-bear management terms are cited in the text the first time they are used. We extracted definitions verbatim from the lexicon in [a]Hopkins et al. (2010); terms without a footnote were defined for use in this study.

Definitions for terms and concepts

bear incident[a]: an occurrence that involved a human–bear conflict or episodes where bears caused property damage, obtained anthropogenic food, killed or attempted to kill livestock or pets, or were involved in vehicle collisions (Gunther 1994, Schirokauer and Boyd 1998, Gunther et al. 2004, Wilder et al. 2007)

food-conditioned (FC) bear[a]: a bear that has learned to associate people (or the smell of people), human activities, human-use areas, or food storage receptacles as sources of anthropogenic food (Herrero et al. 2005)

  known FC bear: a bear classified food-conditioned based on location data and a qualitative assessment of the bear's behavior as suggested by human-bear management staff

  predicted FC bear: a bear predicted to have a food-conditioned management status based on results from logistic regression

human food[a]: anthropogenic foods that only include human foodstuff and food waste

human–bear management[a]: a bear population management program that focuses on mitigating bear incidents and providing bear viewing opportunities management bear[a]: a bear that may be monitored for management purposes because it is individually identifiable

management status[a]: a classification assigned to each management bear of habituated (not Food-conditioned), food-conditioned (not habituated), habituated and food-conditioned, aggressive, predatory, unknown, or unmanaged

non-food-conditioned (NFC) bear: a bear that does not seek out people (or the smell of people), human activities, human-use areas, or food storage receptacles as sources of anthropogenic food

known NFC bear: a bear that has been extensively monitored and is believed not to be a food-conditioned bear

predicted NFC bear: a bear predicted to have a non-food-conditioned management status based on results from logistic regression

proactive human–bear management[a]: a population-level management strategy that aims to deter or prevent individual bears not previously or currently involved in bear incidents from being involved in incidents

proactive human–bear management success: when the proportion of predicted FC bears park-wide is relatively small, few FC bears are new to the bear population, or the average estimated proportion of human food in known FC bear diets decrease through time

reactive human–bear management[a]: a management strategy that responds to individual bears involved in bear incidents through immediate and direct action (Thompson and McCurdy 1995) or increases the harvest of a local population of bears in an attempt to reduce bear incidents

reactive human–bear management success: when the management status of a FC bear changes to NFC or the amount of human food in the bear's diet decreases through time

unknown (UNKN) bear[a]: a bear that has an unknown management status and will be monitored in the future

Table 2. Isotopic data ($\delta^{13}C$ and $\delta^{15}N$), probability FC, and proportional dietary estimates of known and predicted FC bears sampled in Yosemite National Park, CA, USA, 2001–2007. Diet-year represents the year the diet is cataloged in the hair (e.g., hair collected in the spring represents the previous year's diet) for all bears except known FC bears (2001–2003); for these bears, diet-year denotes the year the bear was captured. The probability of being FC (P-FC) was calculated by entering $\delta^{15}N$ values from bear hair into a logistic regression model. IsotopeR calculated proportional dietary estimates (plants and animals, human food) for known (n = 36) and predicted (n = 19) FC bears. Italicized IDs denote bear was originally classified NFC in 2001–2003 (Table S1).

							Plants and animals			**Human food**		
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**
Known FC bears 2005–2007 (*n* = 22; individuals = 15)												
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	East Valley	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
3889	F	East Valley	2006	4.2	-21.3	0.973	0.77	0.87	0.95	0.07	0.15	0.26
3889	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							
Known FC bears 2001–2003 (*n* = 14; individuals = 13; individuals different than 2005 – 2007 = 4)												
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

2283	F	East Valley	2003	2.9	-20.4	0.124	0.85	0.93	0.97	0.03	0.07	0.15
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
3552	M	East Valley	2003	6.7	-19.9	1.000	0.49	0.65	0.79	0.21	0.35	0.51
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							
UNKN management bears predicted FC, 2006–2007 (*n* = 4; individuals = 3)												
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							
UNKN hair-snare bears predicted FC, 2006–2007 (*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
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
138675	M	Cloud’s Rest	2006	3.5	-20.4	0.590	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							

Table 3. Reactive human-bear management success in Yosemite National Park, CA, USA, 2001–2007. Nine known FC bears were captured on 23 occasions. IsotopeR estimated the marginal posterior distributions for human food contributions (expressed as $\bar{x}$ proportion and $\bar{x}$ of 1 SD of the proportion) to bear diets. A probability <0.5 suggests management may have been successful (+) at reducing the contribution of human food to a FC bear's diet. The first *P*-value is the result of comparing mean contributions from consecutive years and the second *P*-value compares first and last captures. A bold and italicized *P*-value suggests the bear's human food contribution may have decreased over time. Italicized IDs denote the bear was originally captured from 2001–2003 (Greenleaf 2005); all other bears were captured in 2005–2007. An asterisk indicates a bear was captured via hair-snare, but known to consume human food that year.

ID	**Sex**	**Year**	**Human Food ($\bar{x}$)**	**SD ($\bar{x}$)**	**Success**	**P-value**
2255	M	2003	0.33	0.07		
		2005	0.15	0.05	+	0.28
		2006	0.26	0.07	–	0.42, 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	–	
		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	–	
3821	F	2003	0.21	0.06		
		2005	0.13	0.04	+	0.47
		2006	0.24	0.06	–	0.40, 0.78
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	–

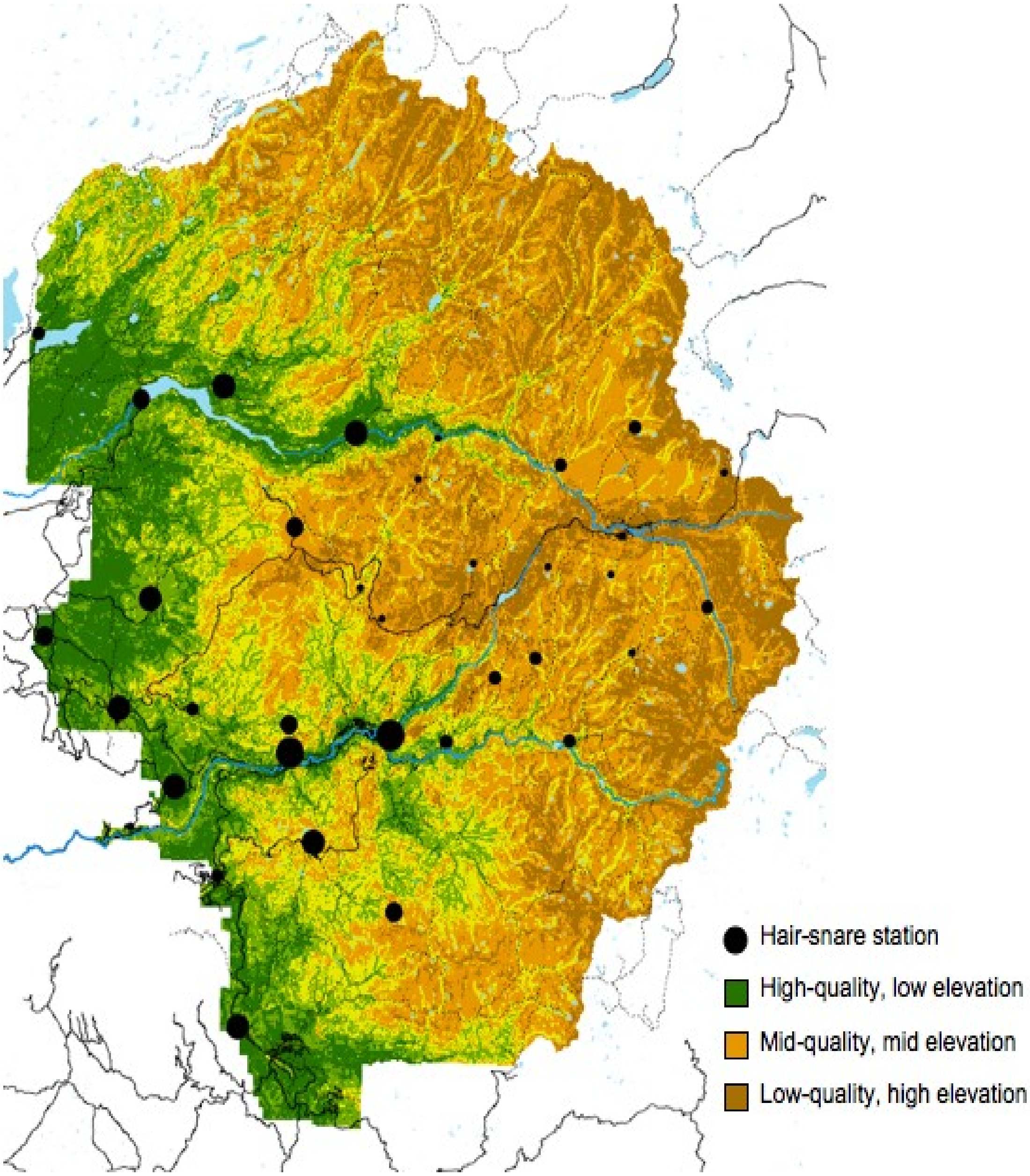

Figure 1. Hair-snare station locations in Yosemite National Park, CA, USA, 2006–2007. Habitat quality and relative proportion of total individual bears captured via hair-snare denoted by black dot at each hair-snare location (details in Table S2).

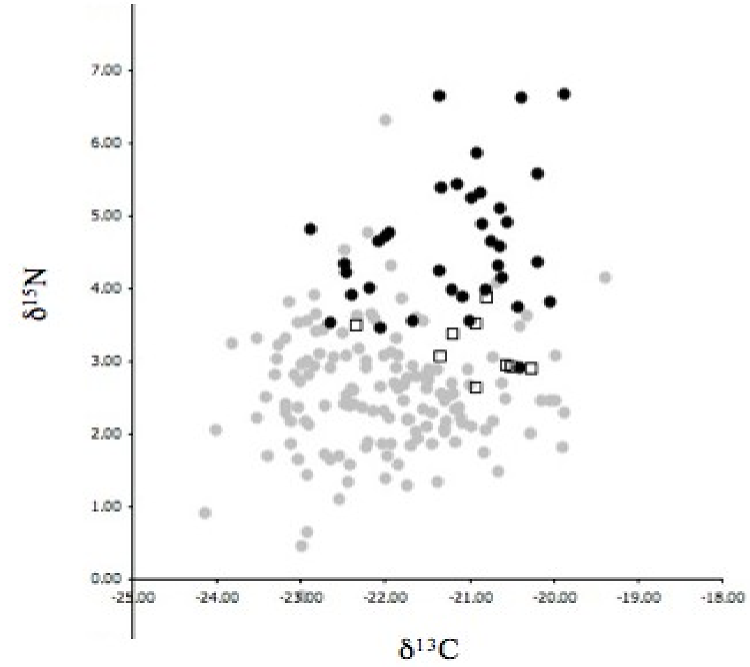

Figure 2. Isotope values ($\delta^{13}C$ and $\delta^{15}N$) for bear hair sampled in Yosemite National Park, CA, USA, 2001–2007. Isotope values for known FC bears captured from 2006–2007 (this study) and known FC bears captured 2001–2003 (Greenleaf 2005) were similar; therefore, we pooled their isotope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

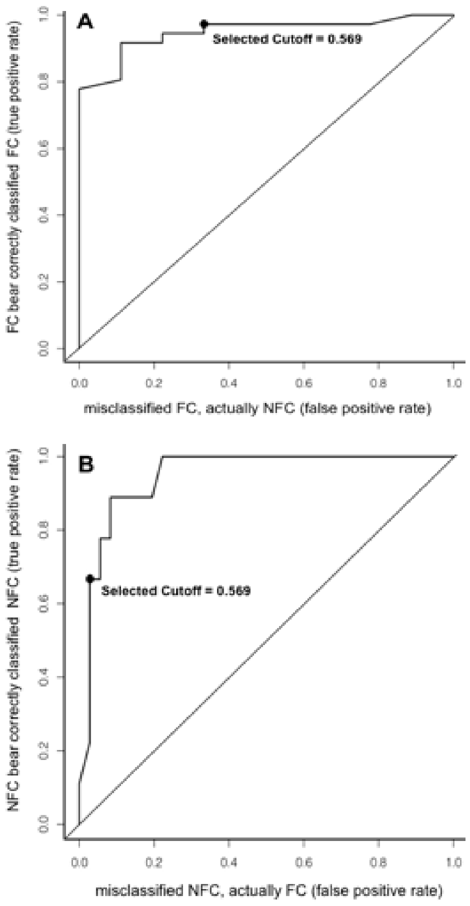

Figure 3. ROC curves used to determine the threshold value for classifying UNKN bears sampled in Yosemite National Park, CA, USA, 2005–2007. A. Point (●) on ROC curve represents the true positive and false positive rates selected to determine the threshold value used to maximize the ability of the regression model to correctly classify FC bears and minimize misclassifications based on bear hair $\delta^{15}N$ values (analysis 1). B. Point (●) on ROC curve represents the true positive and false positive rates selected to determine the threshold value used to maximize the ability of the regression model to correctly classify NFC bears and minimize misclassifications based bear hair $\delta^{15}N$ values (analysis 2).

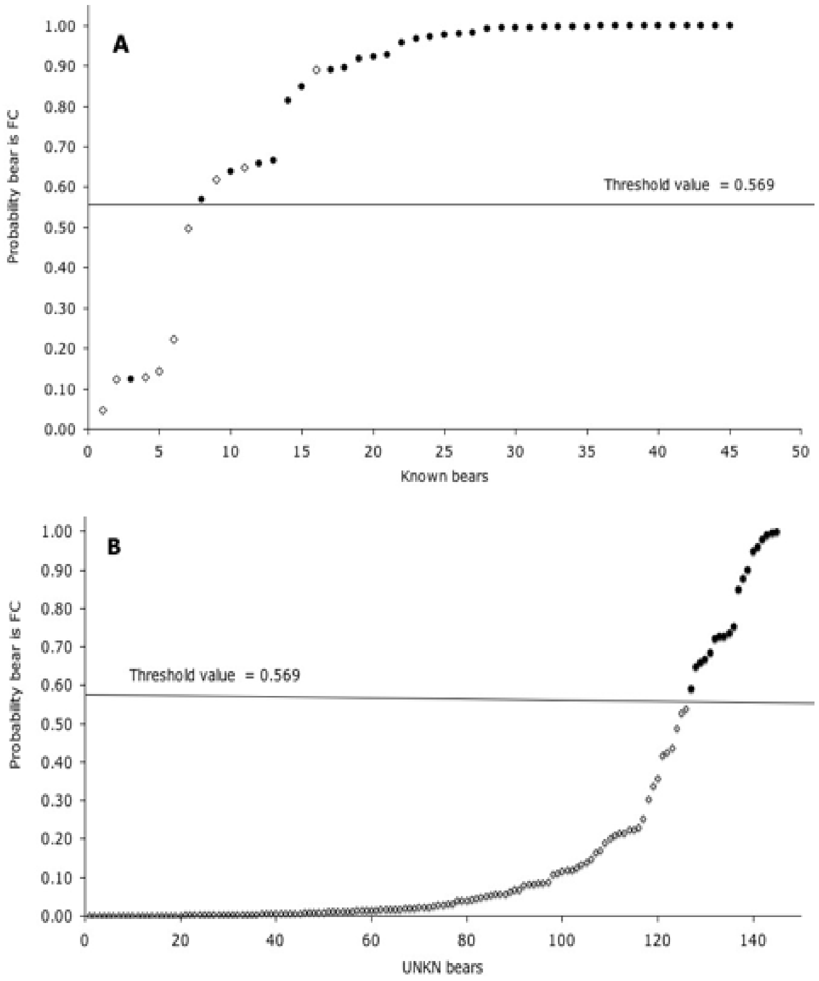

Figure 4. Probability bears are FC based on δ^{15}N values of their hair. A. Probability that known FC bears (●) (*n* = 36) and known NFC bears (◊) (*n* = 9) are FC based on δ^{15}N values of their hair calculated by a logistic regression model. B. Probability that UNKN bears (*n* = 145) are FC (●) (*n* = 19) or NFC (*n* = 136) based on δ^{15}N values of their hair calculated by a logistic regression model.

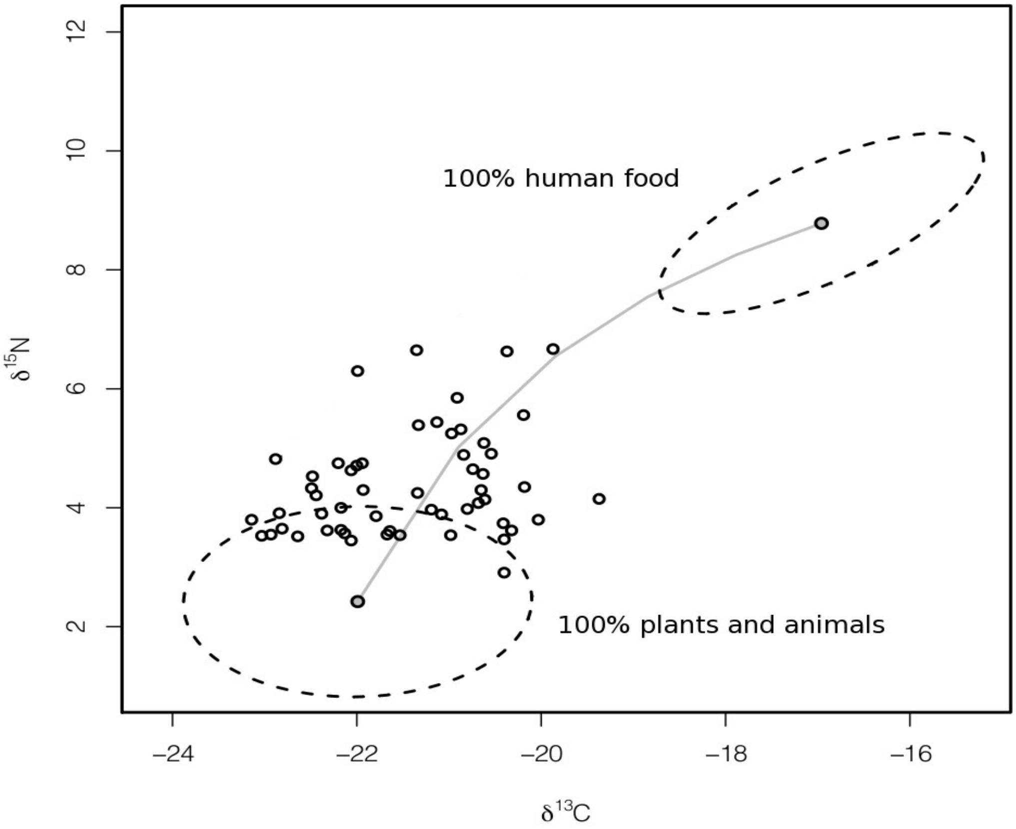

Figure 5. Isotopic mixing space used to determine the diet of known and predicted FC bears sampled in Yosemite National Park, CA, USA, 2001–2007. IsotopeR estimated each dietary source's (100% plants and animals, and 100% human food) isotopic distribution ($\bar{x}$ and 2 SD) and estimated source contributions to bears diets. The curvilinear mixing line illustrates the relative elemental concentrations of sources, which were corrected for digestibility (Table S3, S4). IsotopeR (Hopkins and Ferguson 2011; in review) estimated measurement error ($\delta^{13}C = 0.35$, $\delta^{15}N = 0.12$), but error bars for bears are not included in the figure. Sources and bears' isotope values (with associated error) were used to simultaneously estimate dietary proportions (Mean, 1 SD).

Contribution of Author and Co-Authors

Manuscript in Chapter 5

Chapter 5:

Author: John B. Hopkins III

Contributions: conceived the study and figures, designed methods, collected data, and wrote the manuscript.

Co-author: Jake M. Ferguson

Contributions: designed model code and figures, discussed results and implications, and commented on the manuscript.

Co-author: Paul L. Koch

Contributions: provided expertise on stable isotope analyses, provided lab support, discussed results and implications, and commented on the manuscript.

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Use of stable isotopes to evaluate a century of human-bear management

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ABSTRACT Yosemite National Park (YNP) human-bear management has used various strategies to manage humans and bears for the past century. Few studies have evaluated these human-bear management strategies and no studies have evaluated management throughout Park history. Currently, YNP compares annual black bear incident report summaries (i.e., tallies) to evaluate their program each year. We believe this annual comparison is not the best measure for evaluating the program; therefore, we provide an alternative method and audit Yosemite human-bear management over the past century. We conducted carbon and nitrogen isotopic analysis on bear bone collagen and hair and used these data in conjunction with isotopic and stoichiometric data for dietary sources to estimate bear diets during four human-bear management time periods over the past century. Specifically, we used an isotopic mixing model to estimate dietary parameters and compared proportional contributions of anthropogenic food sources (human food and non-native trout) among these different time periods. We assumed that a proportional decrease in anthropogenic foods in bear diets suggest human-bear management was successful in proactively reducing the amount of anthropogenic food available to bears.

Results show that the isotopic composition of bear tissues changed over time. Human food increased in FC bear diets from period 1 (<1923) to period 2 (1923–1970). Human food comprised more of the diet in period 3 (1971–1998) however the total anthropogenic food contribution was similar between periods 2 (~31%) and 3 (~35%). Since period 3, the contribution of human food has substantially decreased in FC bear diets, suggesting YNP was successful at proactively reducing the proportion of human food in FC bear diets during period 4 (>1998) and may have been successful in reducing the amount of human food available to bears. We suggest that YNP continue their proactive management, reduce problem bears from the population, and use the isotopic methods presented in this study to evaluate the Yosemite human-bear management program in the future. These isotopic methods likely have application to evaluating other wildlife population management programs.

KEYWORDS black bear, bone collagen, carbon isotope, human-bear management, IsotopeR mixing model, nitrogen isotope, stable isotope, *Ursus americanus*, Yosemite National Park

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The most common way to assess the effectiveness of a human-black bear (*Ursus americanus*) management (Table 1) program is to compare annual bear incident report summaries (i.e., tallies of incidents)(Hopkins et al. 2011; in review). However, comparing incident reports may not be the best measure for determining whether a program has been successful over time because (1) a wide variety of resources may have been dedicated to recording these incident data currently that were not available historically, (2) historic incident data are unavailable, and (3) annual incident reports are not standardized (e.g., reported bear incidents/known FC bear) for year-to-year comparisons. Although managers could conduct a retrospective analysis of management success in locations with rich human-bear management histories like Yosemite National Park (YNP)(as suggested in Hopkins et al. 2011), such an analysis may be difficult to conduct prior to the past several decades (V. Seher, National Park Service, personal communication).

Except for a study by Greenleaf et al. (2009), no analysis has been conducted to evaluate the human-bear management program in YNP prior to the past decade. Greenleaf et al. (2009) inferred the relative proportions of different foods in bear diets by examining the contents of bear scats collected in Yosemite Valley (YV) from 2001–2002. Evidence showed a proportional decrease (volume: 21% to 6%) of human food (Table 1) in scats compared to a study by Graber (1981; scats collected from 1974–1978). This result suggests that proactive human-bear management (Table 1) was successful at reducing the availability of human food to bears in YV; however, this study was not a park-wide investigation.

Hopkins et al. (2011) suggested an alternative method to determine if human-bear management was successful at reducing the amount of human food available to bears park-wide. In their study, they measured the stable isotopic composition of bear hair and used these data to detect FC bears throughout YNP using a logistic regression model. In addition to identifying FC bears, they estimated the proportional contribution of dietary sources to FC bear diets and used these parameter estimates to evaluate the Park’s human-bear management program (Hopkins et al. 2011). Specifically, they evaluated the effectiveness of proactive human-bear management by determining the proportion of predicted FC bears in their sample. They also suggested that the total number of predicted and known FC bears could be used to standardize annual incidents and property damage (e.g., dollars of property damage/FC bear), and that these indices could be used to evaluate the overall program. In addition, they compared the estimated proportions of human food consumed by known FC bears (Table 1) during two time periods and suggested that such estimates were an index of the amount of human food available to bears (Hopkins et al. 2011).

In this study, we used the later analytical approach by Hopkins et al. (2011) to evaluate human-bear management's ability to proactively reduce the amount of anthropogenic food (Table 1) available to bears. First, we collected bear tissues (bone and hair) from museum collections and analyzed these samples for their stable isotopic composition. In addition, we also used isotopic data for human hair, trout bone, and bears predicted to be non-food-conditioned (NFC; Table 1) to estimate bear diets using a stable isotope mixing model by Hopkins and Ferguson (2011; in review). Specifically, we applied a series of corrections (i.e., to convert bear and trout bone to bear hair, and the Suess effect; see Methods) to our samples and also used the elemental concentrations ([C], [N]) of sources to construct an isotopic mixing space (i.e., bears estimated isotopic distribution if their fed on a source 100% of the time) used to estimate the proportional contributions of dietary sources (plants and terrestrial animals, trout, and human food) to bear diets. We used the stable isotope mixing model, IsotopeR to simultaneously estimate sources (thus, the isotopic mixing space) and population- and individual-level dietary parameters (Hopkins and Ferguson 2011). Finally, we compared the estimated anthropogenic food contributions among 4 time periods throughout human-bear management history. We assumed that a decrease in anthropogenic food proportions through time suggested that the Park was effect at reducing the availability of these sources to bears (i.e., successful proactive management) and an increase suggests the opposite.

Stable isotope analysis of bear tissues

Stable isotope analysis of tissues can be used to reveal the diet of past and contemporary animals (Koch 2007). As in other organisms, bear tissues have different growth and isotopic turnover rates, defined as the time it takes for stable isotopes in the tissue to equilibrate to isotopes derived by the diet. Therefore, each tissue provides dietary information related to different time periods of a sampled bear's life. For example, isotope ratios (or "isotope values") of blood plasma and red blood cells indicate an animal's assimilated diet ~1 week and ~2–3 months prior to sampling, respectively (Hobson and Clark 1992). In contrast, due to a slower turnover rate, bone collagen represents a nearly lifetime average of the animal's isotope composition (Chisholm and Schwarcz 1982, Tieszen et al. 1989, Hobson and Montevecchi 1991, Hilderbrand et al. 1996).

A controlled feeding study by Hilderbrand et al. (1996) found that isotope values for sampled bear tissues (excluding adipose tissue) were not difference, suggesting tissue-diet discrimination (denoted as $\Delta_{\text{tissue-diet}}$ and defined as the difference between isotope values for animal tissue and animal dietary source) is similar for these tissues; however, many studies did not find similar results (Caut et al. 2009, Crowley et al. 2011). In this study, we conduct stable isotope analysis on bear hair and bear bone collagen. Instead of assuming discrimination was the same for these tissues in bears, we applied a $\Delta_{\text{hair-bone}}$ correction (δ^{13}C: $\bar{x}$ = -0.7‰; δ^{15}N: $\bar{x}$ = -0.3‰; see Sample preparations and stable isotope analysis; Table S1) to bone collagen isotope values. This hair correction allowed us to use bear hair and bone collagen isotope values concurrently in our diet analysis.

Carbon isotope analysis of YNP bears.—Carbon isotope ratios (^{13}C/^{12}C; expressed as δ^{13}C values) are used to identify the photosynthetic pathway of food sources (DeNiro and Epstein 1978, Ramsey and Hobson 1991, Hobson and Welch 1992). Black bear scat (Graber and White 1983, Greenleaf et al. 2009) and stable isotope (Hopkins et al. 2011) studies conducted in YNP suggest NFC black bears, while omnivores, primarily consume native C_3 plants. Bears with relatively high δ^{13}C values likely supplement their diets with plants that fix carbon via the C_4 pathway (or feed on other consumers that feed on a C_4 diet), which have higher δ^{13}C values than C_3 plants (Hopkins et al. 2011). Since YNP black bears are generalists and human food is a reliable, high calorie food source, bears with elevated δ^{13}C values are likely consuming C_4 human-derived foods made of corn, corn-fed livestock, or sugar cane (Mizukami et al. 2005, Koch 2007, Chesson et al. 2008, Hopkins et al. 2011).

Nitrogen isotope analysis of YNP bears.—Nitrogen isotopes ratios (^{15}N/^{14}N; expressed as δ^{15}N) reveal a consumer's trophic position in the food chain (Peterson and Fry 1987, Michener and Schell 1994). Bears with high δ^{15}N values relative to conspecifics typically receive a higher contribution of animal protein to their diets (Mowat and Heard 2006). In addition to consuming animal prey (primarily insects and ungulates; and trout during the first half of the century) in YNP, bears may also receive human-derived nitrogen from human foods, leading to relatively high $\delta^{15}N$ values when compared to bears that do not consume human food (Hopkins et al. 2011). Furthermore, Hobson et al. (2000) and Mizukami et al. (2005) found that bears trapped for management purposes had significantly higher $\delta^{15}N$ values when compared to conspecifics, suggesting these bear likely consume human foods.

METHODS

Time periods

We sorted suspected FC bears (i.e., historic FC bears; Table 1) and known and predicted FC bears (i.e., current bears from Hopkins et al. 2011; Table 1) into 4 groups based on different human-bear management time periods. We clustered historic bears into 3 time periods by “year killed” and we grouped all recently captured or killed bears in time period 4.

Pre-bear-feeding/hatchery (period 1: <1923).— This was the time period prior to YNP opening feeding areas (platforms and other feeding areas where park employees dumped food scraps to attract bears and entertain visitors) to free-ranging bears (Greene 1987). During this time, bears consumed refuse at “bear pits” (i.e., open-pit garbage dumps) and negatively interacted with people (Grinnell and Storer 1924); many bears were destroyed during this time period because they were considered nuisance animals (Runte 1990).

The Wawona Fish Hatchery (1895–1914 and reopened from 1917–1930) was also operating during this time period. During these years, YNP staff introduced native (*Oncorhynchus mykiss*) and nonnative (*Oncorhynchus aguabonita*, *Salvelinus fontinalis*, *Salmo trutta*, *Oncorhynchus clarki*, *Salvelinus malma*, *Thymallus arcticus*) trout into park rivers, lakes, and streams (Willis and Wallis 1941), most of which did not have fish since post Pleistocene glaciation[2].

Bear-feeding/hatchery (period 2: 1923–1970).— The time period when YNP bear pits[3] (last pit closed in 1970) and feeding areas (1923–1940) were used to provide visitors the opportunity to observe bears and to keep bears away from visitor-use areas (Greene 1987); the Park later established such feeding areas in western YV (1935) to mitigate bear incidents in the eastern portion of YV. During this time period, Park Service personnel used reactive management measures such as dogs (to chase bears), trapping and translocating bears (in areas where bear incident-levels were high), killing aggressive bears, and shooting bears with birdshot to keep bears away from hotels and other visitor-use areas (Wright et al. 1932). During one season in the 1930s, over 60 hospital cases were documented where bears caused personal injury to visitors (Parker 1952); this increase in injuries was due to the high frequency of human-bear interactions at bear pits

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[2] No fish lived above 4,000 feet in YNP following the Pleistocene. Precipitous waterfalls thwarted salmonid migration out of the Yosemite and Hetch Hetchy Valleys (Runte 1990; National Park Service, History of Fish Management in Yosemite, Yosemite National Park Research Library).

[3] Yellowstone National Park also opened dumps to free-ranging bears to boost park visitation as well as reduce bear incidents in visitor-use areas (Graber and White 1983); both parks closed their bear pits concurrently as a result of the “Leopold Report” (Leopold et al. 1963) and National Park administrative policy (National Park Service 1967).

and feeding areas (i.e., due to people feeding bears) as well as the roadway. At this time, the Park collected little to no scientific or management data (Graber and White 1978); however, during the end of this time period and beginning of the next time period, management personnel killed a minimum of 94 bears to reduce bear incidents (Harms 1977, Rowell 1974).

A new California State Fish Hatchery (Happy Isles, YV: 1927–1956) also opened in YV during this time period. During the years the hatchery was in operation, the Park raised and released over one million trout into park waters each year (Willis and Wallis 1941); reports suggest FC bears consumed trout from the hatchery[4], from fishermen, and in YNP lakes, rivers, and stream.

Post-bear feeding/post-hatchery (period 3: 1971–1998).— This time period followed the closure of the last bear pit and 15 years following the closure of the YV hatchery. During this era, bears compensated for the loss of food available in the bear pits by scrounging for human food in park campgrounds and residential areas (Graber and White 1978). Bear incidents increased substantially (Harms 1978) resulting in 50 bears being killed (1975–1977) and 373 bears translocated (1974–1976) (Graber and White 1978). Also YNP contracted with the University of California, Davis (1974–1978) to conduct a

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[4] From 1945–1956 Gene Nixon ran hatchery operations in YV and his daughter Lee described FC bear activity as follows: “They’d scrounge first at the dump and then the campgrounds before working their way up to the hatchery. We [at the hatchery] were the dessert stop on the bear cafeteria trail.” She said that her father used electric fencing to keep bears from gorging themselves on the hatchery fish, and stung them with birdshot if they persist. She continued by saying that sometimes, park officials would trap and translocate bears to the high country: "My dad would laugh whenever they did that…the bears would be back (in the valley) before they (the trappers) could make it back" (J. Jardine, “Woman grew up in Yosemite,” Modesto Bee, June 12, 2008).

comprehensive black bear study (Graber 1981) to increase the effectiveness of human-bear management (we note that findings from their diet study suggested that trout were an insignificant food source in bear diets[5]). This study began around the same time the Human-bear Management Plan was initiated (1975), which included various research goals: to investigate bear population dynamics, to record bear morphological characteristics, to determine bear home range size, to evaluate visitor and management activity effects on bear ecology, and to examine bear food habits (Graber 1981). Although the plan recommended implementing proactive human-bear management, the Park did not largely put such activities and methods into practice until the beginning of the current time period.

Current (period 4: >1998).—This period began when YNP received the first congressional appropriation of $500,000 to address human-bear management (Mathews et al. 2006*,* Madison 2008). Since then, the Yosemite interdivisional Bear Team responds and attempts to prevent bear incidents; visitor information and education have been evaluated and improved; food storage receptacles were deployed throughout all frontcountry visitor-use areas and backcountry High Sierra Camps (guest accommodations in canvas wall-tents); bear-resistant food canisters were made mandatory for backcountry use; Wildlife Management implemented a rigorous reactive management strategy for problem bears in YV; and research efforts have been developed to answer questions associated with human-bear management and black bear ecology

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[5] Although researchers observed black bears fishing on two occasions during the study, no salmonid remains were identified in the 1,404 bear scats collected park-wide (Graber 1981).

(Madison 2008). For example, a bear diet study was conducted in YV from 2001–2002; results from analysis of 500 bear scats suggest trout are a trivial dietary component of bear diets (Greenleaf et al. 2009).

Sampling

Suspected FC bears.— We used the Mammal Network Information System (http://manisnet.org/) to locate federal, state, and university museum collections that contain YNP black bear tissues (bone, and hair from pelts). In addition, we queried the Yosemite Museum database for black bear specimens. We identified 87 bears at 5 museums: Museum of Vertebrate Zoology (MVZ; *n =58*), Yosemite Museum (*n =21*), California Academy of Sciences (*n =4*), Smithsonian Institution National Museum of Natural History (*n =3*), and Santa Barbara Museum of Natural History (*n =1*). We collected 84 specimens from 75 of these individuals (4 bears not sampled because they had unknown dates) from the MVZ and the Yosemite Museum (*n* = 79). Specifically, we collected <1 gram of nasal turbinate from each bear's nasal cavity and plucked >10 guard hairs from each bear pelt. We excluded juvenile bear tissues (*n* = 25) from isotopic analysis because the process of tissue-diet discrimination for such bears is different than adults due to the physiological effect of nursing (Polischuk et al. 2001). Therefore, we conducted carbon and nitrogen stable isotope analysis on 52 adult bone samples and 7 adult hair samples (bone and hair was analyzed for 6 of these bears, therefore 53 individual bears were sampled). Bears were killed during the following years within each time period: period 1 (1915–1919; *n* = 7), period 2 (1928–1939; *n* = 15), and period 3 (1975–1985; *n* = 31). We suspected all bears were FC (except one that was illegally killed in 1982; note: we included this bear in our study, but not in our diet analysis) based on historical records.

Current FC bears.— We combined known FC bears (*n* = 36) and predicted FC bears (*n* = 19) from Hopkins et al. (2011) for this group (*n* = 55). Management personnel immobilized or euthanasized known FC bears from 2001–2003 (Greenleaf 2005; *n* = 14) and from 2005–2007 (*n* = 22; Hopkins et al. 2011); management staff observed these bears consuming human food on multiple occasions, which resulted in bears being classified as FC. Hopkins et al. (2011) also used a logistic regression model to predict bears being FC (*n* = 19) based on the $\delta^{15}N$ values of their hair (Hopkins et al. 2011); they collected hair from these bears during management actions (*n* = 4) from 2005–2007 and from hair-snares (*n* = 15) distributed throughout YNP from May–September 2006 and 2007.

Plant and animal diet.— We used isotope values for predicted NFC (Table 1) bear hair (*n* = 126; Hopkins et al. 2011) to define the 100% natural plant and animal diet in the isotopic mixing space. We used this method because predicting discrimination factors for dozens of plants and animals in a mixed diet and applying weights to these foods would likely bias the isotopic distribution of the source and therefore affect proportional dietary estimates. In addition, we used a stable isotope mixing model to re-estimate the digestible [C] and [N] values for plants and animals sampled in Hopkins et al. (2011); we used these parameter estimates, and concentrations for trout and humans (see below), to define the isotopic mixing lines that connect the 100% natural diet (plants and animals source) to the 100% trout and 100% human food sources.

Trout.— We sampled a pelvic fin from eight trout specimens (*Salvelinus fontinalis*, *n* = 2; *Salmo clarkii*, *n* = 1; *Salmo trutta, n* = 5) from the California Academy of Sciences; samples were originally collected in YNP from 1921–1926 (Table S2). The only native species of trout in YNP, *Oncorhynchus mykiss*, was not available for sampling. In order to use trout in our diet analysis, we had to convert trout bone to bear hair. First, we corrected trout bone to trout muscle by applying the mean difference in tissue-diet discrimination factors (Δ) to trout bone ($\Delta^{13}C_{m-b} = \delta^{13}C_{muscle} - \delta^{13}C_{bone}$: $\bar{x}$ = -1.4‰; $\Delta^{13}N_{m-b} = \delta^{13}N_{muscle} - \delta^{13}N_{bone}$: $\bar{x}$ = 2.4‰) (Sholto-Douglas et al. 1991) (Table S2). We then used the mean discrimination factor for hair (Δ^{13}C: $\bar{x}$ = 2.5‰; Δ^{15}N: $\bar{x}$ = 3.4‰) from Caut et al. (2009) to correct trout muscle (i.e., dietary source) to bear hair. We used these corrected values to define the 100% trout source (i.e., bears on a 100% trout diet) used in our diet analysis. We also included discrimination error (Hopkins and Ferguson 2011) for Δ^{13}C (0.9‰) and Δ^{15}N (1.2‰) in order to account for variation in Δ^{15}N and Δ^{13}C values estimated from animals on controlled diets. Specifically, these values represent the variation (1 SD) associated with mean discrimination factors for hair (calculated from Caut et al. 2009). Lastly, we estimated digestible [C] and [N] values by analyzing nutrient data for trout from the USDA National Nutrient Database (NDB: http://www.nal.usda.gov/fnic/foodcomp/search/) (Table S3); we used these parameter estimates, and concentrations for natural sources (plants and animals) and humans (described below) to define the isotopic mixing lines that connect the 100% trout source to the 100% plants and animals source and 100% human food source.

Human food.— Dr. Andrew Wilson from the University of Bradford, UK was issued human hair samples (originally collected in 1940 and catalogued in the Trotter Collection) through a collaboration with Dr. David Hunt (Collections Manager, Physical Anthropology Division) from the Smithsonian Institution, National Museum of Natural History. Dr. Hunt authorized the destructive sampling of hair and Dr. Wilson analyzed the hair samples for their stable isotopic composition. In particular, Dr. Wilson analyzed each individual's hair (n = 10) twice, and we averaged each set of isotope values (Table S4; period 1 and 2). Based on records, individuals were from St. Louis, Missouri; however, they may not have been resident during the entire time-frame cataloged in the hair. In addition, we used human hair isotope values from studies by Schoeller et al. (1986; period 3), Bowen et al. (2009), and Hopkins et al. (2011) to represent human diet in 1982–1983, 2004, and 2009, respectively. We used the 100% human food source for period 4 (samples collected in 2004 and 2009) from Hopkins et al. (2011) because samples were isotopically similar. Finally, we used a fixed estimate for digestible [C] and [N] from Hopkins and Ferguson (2011), and concentration estimates for trout and plants and animals, to define the isotopic mixing lines that connect the 100% human food source to the 100% trout source and 100% plants and animals source.

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 debris 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; we then rinsed and freeze-dried all samples. We weighed bone collagen and hair into tin cups (4 x 6 mm) and analyzed samples for their $\delta^{13}C$ and $\delta^{15}N$ content by continuous flow methods using a Carlo Erba 1108 elemental analyzer interfaced to a ThermoFinningan Delta Plus XP isotope ratio mass spectrometer at University of California, Santa Cruz (we note that 1940 human hair was analyzed at the University of Bradford, UK using the same mass spectrometer and elemental analyzer). Stable isotope ratios are expressed in the following delta (δ) notation as per mil (‰) units (or parts per thousand):

$$\delta X = ((R_{sample}/R_{\mathrm{stan}dard}) - 1) \times 1000$$

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 and the standard; reference standards are Vienna Peedee Belemnite for carbon and atmospheric N_2 for nitrogen. We assume isotopic variation in sub-sampled bone collagen is due to measurement error associated with isotopic analysis since isotopes are homogenized in the sample. Therefore, we analyzed one sub-sample of bone collagen from each historic bear. IsotopeR estimated isotopic measurement error from the isotope values of reference standards (Hopkins and Ferguson 2011).

We corrected the carbon isotope values for fish, humans, and bears for the Suess effect, which is defined as the global decrease of ^{13}C in Earth's atmospheric CO_2, primarily due to fossil fuel burning over the past 150 years (Peng and Freyer 1986, Quay et al. 1992, Sonnerup et al. 1999). Based on ice core records (Francey et al. 1999), we applied a time-dependent correction of -0.005‰ per year to all isotope values for samples collected between 1915 and 1960 and -0.022‰ per year from 1960 to 2009 (Chamberlain et al. 2005).

Analytical procedures

Estimating dietary source contributions.— We calculated the relative contribution of dietary sources (posterior probability estimates reported as credible intervals) to bear diets using the stable isotope mixing model, IsotopeR (Hopkins and Ferguson 2011). We used IsotopeR because the model incorporates all recognized and quantifiable model features to estimate dietary parameters at the population- and individual-level. For instance, IsotopeR is the only Bayesian model that simultaneously estimates correlation between $\delta^{13}C$ and $\delta^{15}N$ in sources and applies this information to calculating estimates for dietary contributions. This relationship is important to consider because these isotopes are often correlated as trophic level increases (e.g., Hilderbrand et al. 1996, Hobson et al. 2000, Mowat and Heard 2006). In the end, we estimated isotopic measurement error, and the isotopic distribution and elemental concentrations (corrected for digestibility) of sources, to accurately define the isotopic mixing space used to estimate proportional source contributions to bear diets (see Hopkins and Ferguson 2011 for model details).

Quantifying management success.— We quantified management success by comparing anthropogenic food contributions (i.e., population-level estimates) to FC bear diets among time periods. First, we compared the estimated anthropogenic-derived diets (i.e., trout and human food) of bears during the first two time periods and human food for the last two time periods. We also compared anthropogenic sources (trout + human food contributions) for time periods 1 and 2 to human food in time periods 3 and 4 to determine if these source estimates were different over time. Lastly, we compared human food contribution among time periods. For these analyses, we calculated the probability of bear diets being similar for each set of time periods. This test was equivalent to a two sample, two-tailed t-test, but allowed us to use the entire posterior distribution without resorting to transformations (because distributions are non-normal). We interpreted a relatively small *P*-value (e.g., <0.05) as a shift in anthropogenic food consumption between time periods and a high *P*-value suggested proportional dietary contributions were similar.

RESULTS

We derived estimated measurement error ($\delta^{13}C = 0.35$, $\delta^{15}N = 0.12$), and the isotopic distributions (Fig. 1, Table 2) and elemental concentrations of dietary sources (Table 2) to define the isotopic mixing space for each time period (Fig. 1). The isotopic distribution of FC bears expanded during period 2 (Fig. 1A and 1B) due to the abundance of human food at the feeding areas and bear pits. The YV fish hatchery was no longer operating in YNP during period 3 and 4 and trout were in low numbers in the Park. As a result, the isotopic distribution of bears during period 3 responded by collapsing along the isotopic mixing line connecting human food and their natural diet (Fig. 1C). During period 4, Yosemite implemented a rigorous proactive human-bear management strategy, which resulted in FC bears having a distribution of $\delta^{13}C$ values similar to their natural diet (i.e., the isotopic distribution of NFC bears) and lower than $\delta^{15}N$ values for historic FC bears (Fig. 1D, Table S1).

IsotopeR also estimated proportional source contributions to bear diets at the population- (Table 3) and individual-level (Table S1) for each time period. The contribution of human food increased, natural food decreased, and trout proportions were similar in bear diets during period 2 (Fig. 2, 3, Table 3). Although the proportions of human food in bear diets likely increased in response to the YV hatchery closing in YNP during period 3 (Fig. 2, 3, Table 3), the total anthropogenic source contribution may have been similar (period 2: trout [4%] + human food [27%] = ~31% compared to period 3: human food = ~35%, SD = 5%; Table 3). The contribution of human food decreased drastically from period 3 to 4 (Fig. 2, 3, Table 3), suggesting human-bear management was successful at reducing the amount of human food available to bears since 1999; however, some current FC bears continue to consume large quantities of human food (Table 3, S1; Hopkins et al. 2011). Finally, we note that the contribution of human food in current (period 4) bear diets may be similar to period 1 (Fig. 2, 3, Table 3).

DISCUSSION

The isotopic niche (Newsome at al. 2007) of black bears in YNP has changed over time (Fig. 1). Specifically, it appears the isotopic niche expanded when bears freely consumed human food at feeding areas and bear pits (Fig. 1A and 1B) and collapsed when trout were removed from the ecosystem (Fig. 1C). These isotopic responses resulted in an increase of human food in bear diets from period 1 to period 3 (Fig. 2, 3, Table 3, S1); however, we note that results may be an artifact of a relatively small sample of bears killed during period 1.

Although it is likely that human food increased (Fig. 2, 3; Table 3, S1) in suspected FC bear diets from period 2 ($\bar{x}$ = 27%, SD = 7%) to period 3 ($\bar{x}$ = 35%, SD = 5%), our analysis suggests the proportion of total anthropogenic food estimated for period 2 (trout and human food) may be similar to the contribution of human food in period 3 (Table 3).

During period 3 the YV hatchery and bear pits and feeding areas were closed. As a result, FC bears were forced to seek out high calorie anthropogenic foods from others locations. Similar to FC bears in Yellowstone National Park, WY, USA during this era, bears ransacked campgrounds, hotels, and other human-use areas in search for human food. This increase of human food in bear diets during period 3 may have been a response by the bear population seeking out new sources of anthropogenic food and over-compensating for the loss of high nitrogen sources (trout and human food) of food that were easily accessible (Table 2).

The isotopic data (Fig. 1C and 1D) and dietary estimates (Table 3, S1) suggest the contribution of human food has substantially decreased in suspected FC bear diets from period 3 to period 4 (Fig. 2, 3). This result suggests YNP was successful at reducing the proportion of human food in bear diets since the Park began to carry out the proactive measures outlined in the Human-bear Management Plan. This result may indicate that there has been a considerable reduction in the amount of human food available to bears in YNP. In fact, the estimated contribution of human food in current FC bear diets and bears from the early 1900s may be equivalent (Fig. 3). This result suggests the Park may currently provide FC bears similar access to human food as it did in the early 1900s when only thousands of visitors (versus ~4 million currently) traveled to the Park each year (Yosemite National Park, http://www.nature.nps.gov/stats/viewReport.cfm).

MANAGEMENT IMPLICATIONS

Despite recent successes in human-bear management in YNP, many FC bears continue to cause hundreds of bear incidents and thousands of dollars in property damage each year.

To reduce the number of incidents and property damage and further reduce the amount of human food available to bears in the Park, we suggest the human-bear management program continue implementing proactive management as well as remove problem bears. As suggested by Hopkins et al. (2011), this strategy would reduce a majority of bear incidents and simultaneously prevent new bears from becoming FC throughout the Park. Such management activities and methods for evaluating human-bear management as described in this study may be applicable to other bear population management programs.

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Table 1. Terms and definitions used in human–bear management. Important human-bear management terms are cited in the text the first time they are used. All definitions (except for “suspected FC bear”) were extracted verbatim from the lexicon in [a]Hopkins et al. (2010) or from [b]Hopkins et al. (2011).

Definitions for terms and concepts

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anthropogenic food[a]: foods or attractants having a human origin

bear incident[a]: an occurrence that involved a human–bear conflict or episodes where bears caused property damage, obtained anthropogenic food, killed or attempted to kill livestock or pets, or were involved in vehicle collisions (Gunther 1994, Schirokauer and Boyd 1998, Gunther et al. 2004, Wilder et al. 2007)

food-conditioned (FC) bear[a]: a bear that has learned to associate people (or the smell of people), human activities, human-use areas, or food storage receptacles as sources of anthropogenic food (Herrero et al. 2005)

known FC bear[b]: a bear classified food-conditioned based on location data and a qualitative assessment of the bear’s behavior as suggested by human-bear management staff

predicted FC bear[b]: a bear predicted to have a food-conditioned management status based on results from logistic regression (predictor: δ^{15}N value for bear’s hair)

suspected FC bear: a bear assumed to be FC based on historical records

human food[a]: anthropogenic foods that only include human foodstuff and food waste

non-food-conditioned (NFC) bear[b]: a bear that does not seek out people (or the smell of people), human activities, human-use areas, or food storage receptacles as sources of anthropogenic food

predicted NFC bear[b]: a bear predicted to have a non-food-conditioned management status based on results from logistic regression (predictor: δ15N value for bear's hair)

proactive human–bear management[a]: a population-level management strategy that aims to deter or prevent individual bears not previously or currently involved in bear incidents from being involved in incidents

proactive human–bear management success[a]: when the proportion of predicted FC bears park-wide is relatively small or the estimated proportions of human food in known FC bear diets decrease through time

Table 2. Parameter estimates for bear dietary sources sampled in Yosemite National Park, CA, USA, 2007. IsotopeR (Hopkins and Ferguson 2011) estimated the isotopic distribution (mean and SD in ‰ units for $\delta^{13}C$ and $\delta^{15}N$), C and N concentrations (corrected for digestibility; Table S3, S4), and isotopic correlation (*r*) of each source.

Dietary Source	**Time Period**	**$\delta^{13}C$**	**$\delta^{15}N$**	**[C]**	**[N]**	***r***
Plants and animals	1	-22.0 (0.9)	2.4 (0.8)	47.7 (4.2)	4.0 (4.4)	0.02
	2	-22.0 (0.9)	2.4 (0.8)	47.7 (4.2)	3.9 (4.4)	0.03
	3	-22.0 (0.9)	2.3 (0.8)	47.7 (4.2)	4.2 (4.4)	0.03
	4	-22.0 (0.9)	2.4 (0.8)	47.4 (3.5)	2.6 (3.0)	0.12
Trout	1	-22.3 (0.3)	13.0 (0.3)	53.9 (1.3)	12.2 (0.7)	0
	2	-22.3 (0.3)	13.0 (0.3)	53.8 (1.4)	12.2 (0.7)	0
Human food	1	-17.5 (0.5)	11.0 (0.6)	52.8 (2.5)	6.9 (1.1)	0
	2	-17.5 (0.5)	11.0 (0.6)	52.8 (2.5)	6.9 (1.1)	0
	3	-17.2 (0.6)	9.5 (0.8)	52.8 (2.5)	6.9 (1.1)	-0.03
	4	-17.0 (0.8)	8.8 (0.7)	52.8 (2.5)	6.9 (1.1)	0.64

Table 3. Estimated proportional dietary contributions to FC bear diets during each human-bear management time period in Yosemite National Park, CA, USA, 1915–2007. IsotopeR (Hopkins and Ferguson 2011) estimated proportional source contributions (mean, SD, 95% credible interval) to bear diets at the population-level for each human-bear management time period. Last column lists the ranges of individual mean proportional dietary estimates for each time period (period 1: <1923; period 2: 1923–1970; period 3: 1971–1998; period 4: >1998). Contributions for time period 4 were extracted from Hopkins et al. (2011).

				Population CI (95%)			
Dietary Source	**Time Period**	**Mean**	**SD**	**0.025**	**0.5**	**0.975**	**Range for individuals**
Plant 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 food	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

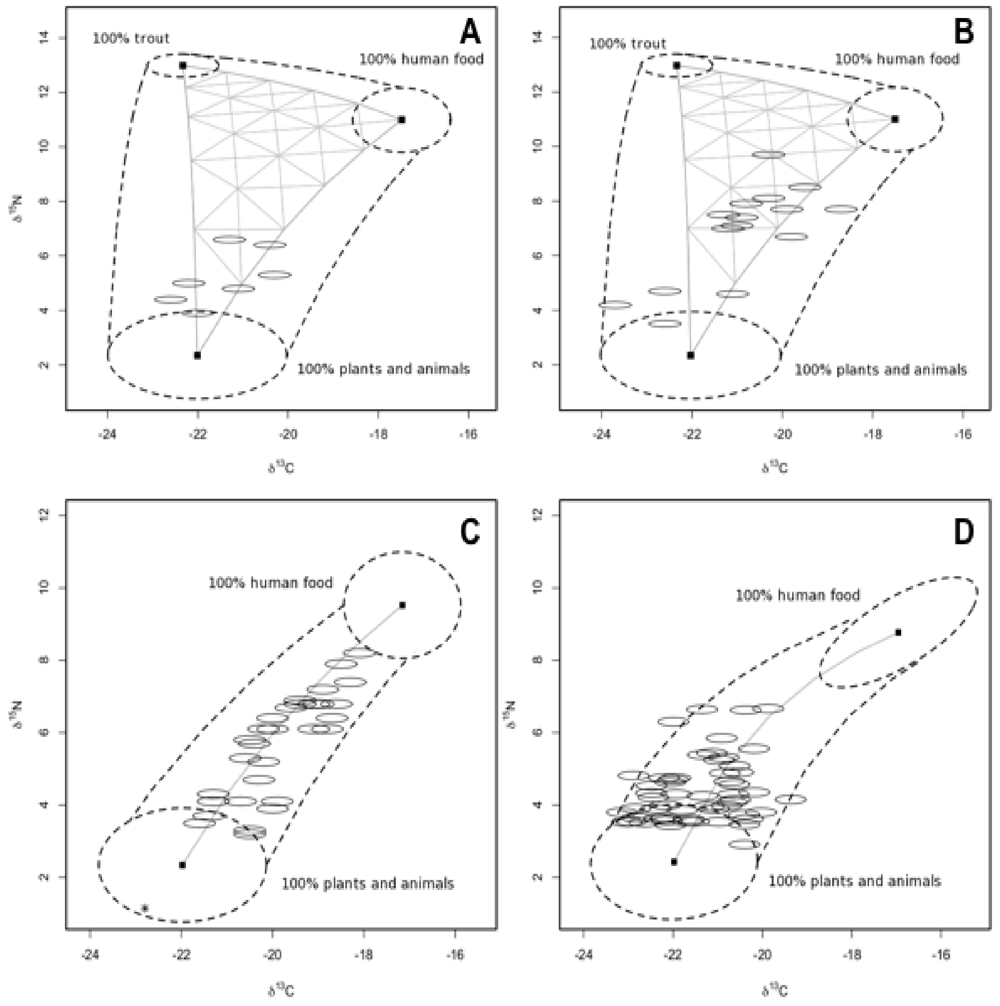

Figure 1. Suspected and known FC bears were killed or captured from 1915–2007 in Yosemite National Park, CA, USA. Bears are grouped by human-bear management time period. Bears were killed or captured during the following years during each time period: (A) period 1 (<1923): 1915–1919, (B) period 2 (1923–1970): 1928–1939, (C) period 3 (1971–1998): 1975–1985, and (D) period 4 (>1998): 2001–2007. Isotope values for bears (ovals illustrate measurement error, and asterisk in panel C represents a bear illegally hunted in the park [i.e., assumed *a priori* to be NFC]) are corrected to bear hair (period 1–3: $\delta^{13}C = -0.7‰$; $\delta^{15}N = -$

0.3‰); differences are due to differences in bone and hair discrimination. In addition, we corrected sources (dashed ovals defined by mean (square), and source variation: 2 SDs, measurement error, and discrimination error) and bears $\delta^{13}C$ values for the Suess effect: -0.005‰ per year from 1915–1960 and -0.022 per year from 1960–2009 (Chamberlain et al. 2005). The shape of each source illustrates the degree of estimated isotopic correlation of observations used to define each aggregate. The mixing triangle (solid gray line) connects estimated source means, and the gray dashed iso-diet lines (within the triangle) illustrate how dietary proportions are estimated; we note that during the estimation process this triangle contorts (due to various sources of error) and moves within the entire isotopic mixing space (outside black dashed lines connecting sources). IsotopeR (Hopkins and Ferguson 2011) also estimated measurement error ($\delta^{13}C = 0.35$, $\delta^{15}N = 0.12$), but error bars for bears are not included in the figure. IsotopeR used sources and bear isotope values (with associated error) to simultaneously estimate dietary proportions.

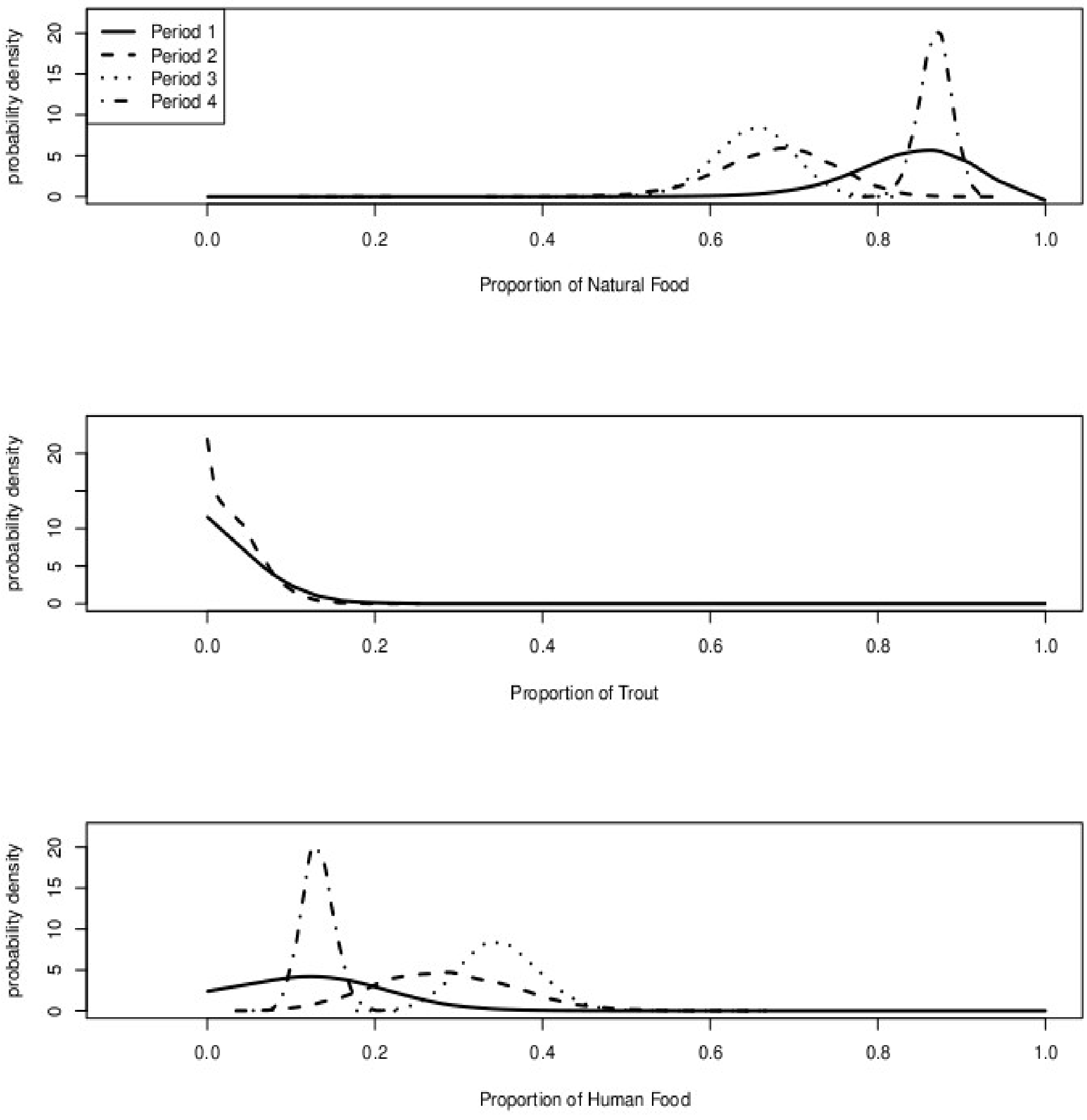

Figure 2. Marginal posterior distributions of estimated population-level proportional dietary contributions to bear diets from 1915–2007 in Yosemite National Park, CA, USA. All marginal posterior distributions were calculated by IsotopeR (Hopkins and Ferguson 2011). Population- and individual-level proportional dietary estimates are listed in Table 3 and Table S1, respectively.

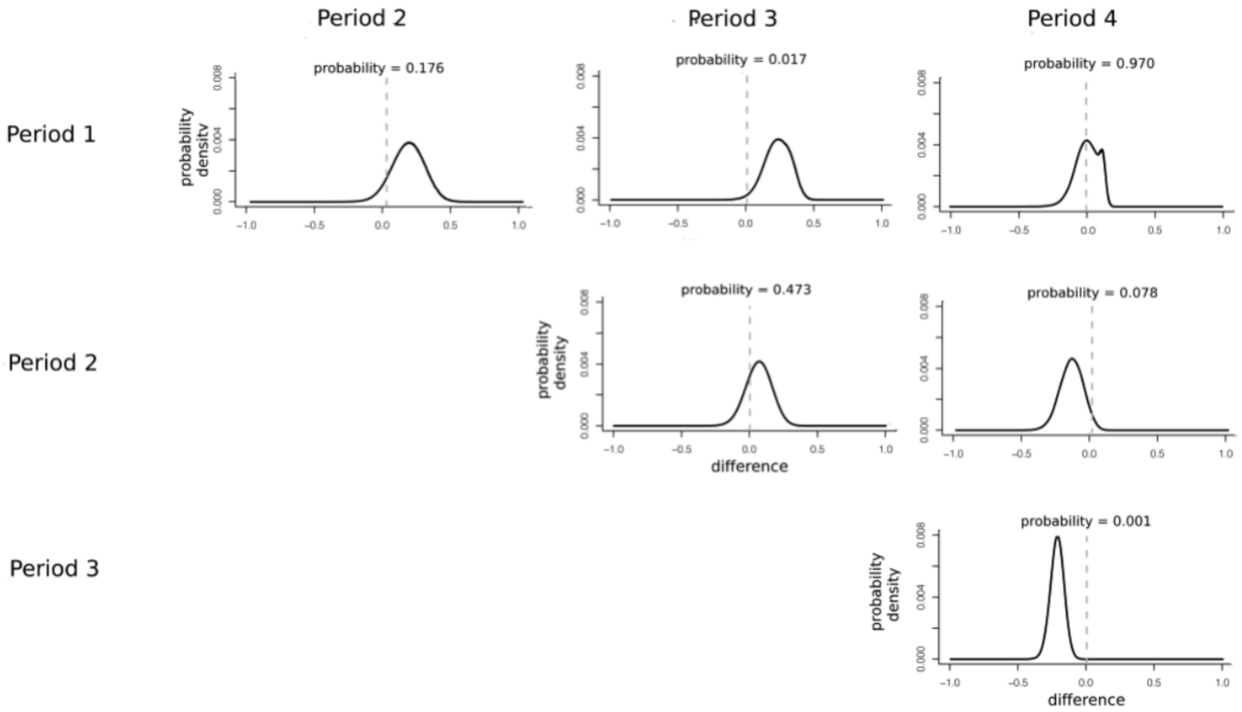

Figure 3. A comparison of human food contributions between human-bear management time periods in Yosemite National Park, CA, USA, 1915–2007. Analogous to a t-test, a probability density (y-axis) different than zero on the x-axis (Difference in Human Food) results in a relatively low probability of similarity, suggesting a shift in human food consumption between time periods. Specifically, distributions to the left of zero (i.e., negative difference values) suggest a decrease in population-level human food consumption between time periods and distributions to the right of zero suggest an increase in human food consumption.

CONCLUSION

Results from this study provide quantitative evidence that the amount of human food in FC bear diets has decreased since the government began appropriating funding to implement proactive management in YNP. This suggests human-bear management has been effective at reducing the amount of human food available to bears for the past decade. However, reported incidents continue to occur at relatively high levels and are likely a function of the number of FC bears in the park. To reduce the number of FC bears and the number of total incidents over the long-run, we suggest YNP use the following management practices:

- Focus proactive management efforts in areas where a relatively high number of bears were identified, and increase such efforts in neighborhoods and backcountry locations throughout YNP.

- Collect more recapture data to evaluate reactive human-bear management. Based on the results from this study, Wildlife Management has not been effective in changing the management status of individuals (i.e., from FC to NFC) or reducing the amount of human food in bear diets since 2001. As a result, we suggest the Park remove problem bears from the population to reduce incidents, while implementing the current proactive strategy to prevent new bears from becoming FC.

- Develop research projects with the purpose of evaluating the effectiveness of each proactive and reactive management method. Only three studies have evaluated such management practices: Lackey and Ham (2003) assessed the effectiveness of the Park communicating issues related to human-bear conflict; Wildlife Management evaluated the effectiveness of aversive conditioning to modify FC bear behavior (Yosemite National Park, unpublished data); and McCurdy and Martin (2007) evaluated food storage (i.e., bear canister use) in the YNP wilderness.

- Collect more isotopic data for NFC bears. These data could be used to redesign the logistic regression model and increase its ability to correctly classifying the management status of unknown bears. In addition, collecting NFC bear (and FC bear) population data could be used to estimate other black bear population parameters (e.g., survival, reproductive rates, etc.). We suggest Park staff collect such data by collaring bears throughout the park (i.e., outside Yosemite Valley) and monitoring them over time.

- Record the genetic signature, isotopic data, and management status (determined via observation or predicted using isotopic analysis) of each bear sampled in YNP over time; specifically, this information could be included in the Park's Human-Bear Management Database. These data could be used for future research, to evaluate the program, to link individual bears to bear incidents, and to monitor individuals over time.

- Repeat this study in the future. A replicate study would elucidate the effectiveness of our management recommendations and their ability to reduce incidents and the amount of human food available to bears.