

Measuring the realized niches of animals using stable isotopes: from rats to bears

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Summary

1. Stable isotope analysis is a powerful method for estimating the impacts animals have on their environment (resource use), revealing their ecological niches.
2. We demonstrated the use of a stable isotope mixing model for measuring the ecological niches of consumers. In particular, we used the model IsotopeR to estimate the resource use of two species with complex, omnivorous diets: invasive Norway rats from the Aleutian Islands, AK, and American black bears from Yosemite National Park, CA. Marginal posterior distributions for major food sources (for populations, groups and individuals) described the resource axes that partly define the realized niches of these omnivores. We used measures of these resource axes to inform resource management in the Aleutians and Yosemite.
3. Results from our analyses confirm that coastal rats did not rely on marine birds on rat-infested islands in the Aleutians. Instead, rats foraged primarily on terrestrial plants and preferred amphipods when they were available. We also use stable isotopes to confirm that plants and acorns are the largest contributors to black bear nutrition in Yosemite and learned that female bears foraged for acorns and pine nuts more heavily than males.
4. Although it is unclear if Norway rats can maintain viable populations in the Aleutians without access to marine-derived animal protein, results from our analyses suggest their dependence on such nutrients. In addition, sex-specific differences in foraging for high-fat acorns and pine nuts in Yosemite suggest black bear populations in the Sierra Nevada may be limited by the productivity and health of hard mast species. As demonstrated here, stable isotope analysis has wide applicability for investigating the resource use and ecological niches of animals. We anticipate and encourage its rapid development in this fundamental field of ecology.

Key-words: carbon, diet, food habits, invasive species, mixing model, nitrogen, nutrition, *Rattus norvegicus*, resource use, *Ursus americanus*

Introduction

Although the niche is central to ecology (Hutchinson 1957; Peterson, Soberón & Sánchez-Cordero 1999; Soberón 2007), it is conceptually elusive and difficult to measure (Chase & Leibold 2003; Newsome *et al.* 2007). Methods for quantifying niches have resurged recently in the scientific literature partly due to the urgency of predicting the ecological effects that result from rapid environmental change (Holt 2009). Measuring the ecological niche of a species and predicting niche responses are challenging because the niche includes both the impacts a species has on its environment and the environmental conditions a species requires (Chase & Leibold 2003).

In 1957, G. E. Hutchinson proposed the modern concept of the ecological niche by defining the difference between an organism's fundamental versus realized niche (Hutchinson 1957). The fundamental niche is the multi-dimensional hyper-volume of limiting environmental conditions and resources that allows a species to maintain a viable population in the

absence of competitors and predators, whereas the realized niche incorporates competition and predation, thereby reducing the number of niche dimensions (Hutchinson 1957; Begon, Townsend & Harper 2006).

Nearly a decade after Hutchinson introduced his modern concept, 'niche width' was used to empirically describe the realized niche (Van Valen 1965). Early studies measured a realized niche dimension (prey size) of a lizard (*Anolis roquet*) population (Schoener & Gorman 1968) and described it in terms of its niche width (the variance of the resource the population utilized) (Roughgarden 1972). Recently, some studies have attempted to quantify realized niches (Chase & Leibold 2003), leading to new concepts such as Hubbell's unified neutral theory (Hubbell 2001), which has also resulted in a resurgent interest in the Hutchinsonian niche (Holt 2009). This revival has led to new niche-related terms and concepts, along with methods for measuring their dimensions (Pulliam 2000; Bolnick 2001; Chase & Leibold 2003; Odling-Smee, Laland & Feldman 2003; Elith, Graham & Group 2006; Holt 2009), including resource use.

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Stable isotope analysis has emerged during this resurgence as a powerful technique for quantifying the resource use of consumers (Phillips *et al.* 2014). In the past, it was a common practice for researchers to measure the food habits of animals by observing their feeding activities, examining their feeding sites, or calculating the relative frequency of occurrence or volume of indigestible foods in their faecal material. Stable isotope analysis now complements such traditional methods by measuring the natural abundances of stable isotopes in known digestible foods and relating them to those assimilated in consumer tissues (Dalerum & Angerbjörn 2005). This complementary approach to measuring resource use allows researchers to gain new insights into the importance of food sources to animals, especially those with complex, omnivorous diets. Because animal tissues have different turnover rates (defined as the time required for stable isotopes in consumer tissues to equilibrate to isotopes derived from the diet), each tissue provides dietary information related to a different time period in their life history. For example, stable isotopes from metabolic tissues such as liver represent the diet of a consumer over the past several days, whereas inert tissues, such as hair keratin, generally indicate the diet of a consumer when the tissue was grown (Kurle 2009).

Newsome *et al.* (2007) described the 'isotopic niche' of a species as the area (or volume) contained within the lines connecting their dietary sources in a multivariate plot of isotope ratios (hereafter, isotopic mixing space). Stable isotope data derived from the tissues of resources that consumers use can partly describe the habitat in which they occur and their trophic position. Isotopic mixing spaces, if estimated accurately, can illustrate the mechanistic relationship between consumers and their habitat. While interactions between consumers and their resources elucidate their environments, strong interactions (those that affect fitness) between consumers and their resources partly define their realized niches (Kearney 2006). Researchers use stable isotope mixing models (hereafter, SIMMs; Hopkins & Ferguson 2012) to estimate the proportional contributions of important resources to the diets of consumers (Phillips 2001; Hopkins & Ferguson 2012; Parnell *et al.* 2013; Phillips *et al.* 2014). Unlike measures of stable isotope data in the isotopic niche (Bearhop *et al.* 2004; Layman *et al.* 2007; Newsome *et al.* 2012; Swanson *et al.* 2015), dietary contributions derived from SIMMs are direct measures of resource use (Newsome *et al.* 2007), which in turn can define some of the resource axes of realized niches.

Here, we demonstrate the use of stable isotope analysis as a tool to investigate the realized niches of consumers by measuring the resource use of omnivorous Norway rats (*Rattus norvegicus*), an invasive species from the Aleutian Islands, Alaska, and American black bears (*Ursus americanus*) from Yosemite National Park, California. First, we used stable isotope data from the tissues of Norway rats and American black bears and their foods and a SIMM model to estimate the omnivorous diets of rats and bears. Then, we examined variation in resource use among populations, within populations (groups and individuals) and for an individual through time. Estimating (and illustrating) the resource axes for populations allows

researchers to quantify the direct impacts animals have on their environment, revealing an important component (diet) of their realized niches.

We measured the resource use of Norway rats from the Aleutians and black bears from Yosemite for three main reasons. First, both rats and black bears are omnivores with complex diets consisting of both plants and animals. To our knowledge, no study has accurately estimated the relative importance of plants and animals to the diets of these populations. Secondly, rats and bears both forage for foods (plants and animals) which have different carbon and nitrogen isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$), thereby improving our ability to estimate their diets using simple, two-isotope SIMMs. Thirdly, the foraging behaviours of rats and bears have negative impacts on native species (Atkinson 1985; Kurle, Croll & Tershy 2008) and on visitor experience (Hopkins 2013), respectively. Invasive rats are known to devastate native bird and plant populations directly and restructure intertidal marine communities in the Aleutian Islands indirectly via a trophic cascade (Major & Jones 2005; Major *et al.* 2006; Kurle, Croll & Tershy 2008), whereas black bears that forage for anthropogenically derived foods (hereafter, human foods) in Yosemite are often in conflict with people and their property (Hopkins *et al.* 2012, 2014). Although the main purpose of our study is to demonstrate the use of stable isotopes in measuring the realized niches of consumers, we also aim to inform wildlife management in the Aleutian Islands and Yosemite National Park by estimating the resource use of omnivorous Norway rats and American black bears.

Methods

STUDY AREAS

The Aleutian Islands

The Aleutian Archipelago is a remote series of islands extending 1900 km west of the Alaska Peninsula (Fig. 1). The Aleutian Islands have similar geologic features and climate, and homogenous floral and faunal assemblages. Most islands in the Aleutians currently lack human settlements or other anthropogenic influences, the main exception being non-native rats. As early as the late eighteenth century, exotic rats began settling in the Aleutian Islands via shipwrecks, military operations and other human activities (Bailey & Kaiser 1993). The presence of Norway rats on a subset of islands within the Aleutians makes the archipelago an ideal location to study the effects of an invasive species on the structure and function of ecological communities.

For this study, we sampled Norway rats on Hawadax (formerly Rat Island), Adak and Great Sitkin Islands in the Aleutians (Fig. 1). Norway rats forage for three main food sources along the coast on the Aleutian Islands: marine birds, marine amphipods and terrestrial vegetation (Major *et al.* 2006; Kurle 2008). Unlike seasonal foods (marine birds and amphipods), the underground structures of plants are likely available year-round to coastal rats (S. Talbot, US Fish and Wildlife Service, pers. comm.; Major *et al.* 2006). Consequently, plants are likely the most consistent food source for rats throughout the year. Rats also prey on marine birds and their eggs in late spring and early summer when they are available along the coast (Irons,

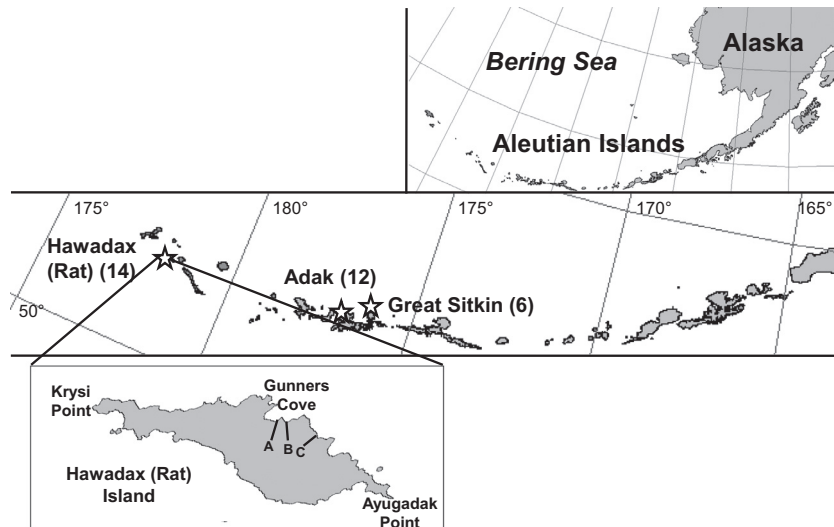


Fig. 1. Hawadax (formerly Rat Island), Adak and Great Sitkin Islands, Aleutian Islands (inset), AK. Stars indicated sites where rats were sampled on each island. Sites A (51.48586° E, 178.18819° N), B (51.48531° E, 178.18910° N) and C (51.48441° E, 178.19447° N) correspond to the three unnamed coves where rats were sampled on Hawadax Island.

Anthony & Estes 1986; Verbeek, Braithwaite & Boasson 1993; Major & Jones 2002, 2005; Major *et al.* 2006). Point counts (U.S. Fish and Wildlife Service 2004) and personal observations suggest that very few birds nest along the coast on the islands in our study, likely because rats have historically kept bird numbers very low. By late summer, *Alaria fistulosa*, the major biomass and only canopy forming kelp in the Aleutian Islands, undergoes a significant die-off with large amounts washing onto the beaches (B. Konar, pers. comm.). Amphipods feed on this beach wrack and their populations increase significantly in late summer and early fall (Pennings, Carefoot & Zimmer 2000; Lewis *et al.* 2007), providing an abundant, high-protein and heavily utilized food source for coastal-dwelling rats (Kurle, Croll & Tershy 2008).

Yosemite National Park

Yosemite National Park encompasses approximately 3080 km² on the western slope of the Sierra Nevada mountain range in east-central California. Approximately 95% of the park is designated as wilderness. Yosemite attracts nearly 4 million visitors each year in April–October when black bears are active. Since the early 1900s, Yosemite Valley (~18 km², <0.01% of the park) has been recognized as an area to view black bears foraging on both human foods and ‘natural foods’ consisting of both plants and animals. Some bears seek out human foods on a daily basis, often resulting in conflicts with people. Bears that do not search for human foods generally feed on herbage in the spring at lower elevations, and follow snowmelt and sprouting vegetation upslope in the summer. By late summer, bears commonly return to lower elevations to forage for hard and soft masts (Graber & White 1983). Based on results from scat analysis, black bears also forage for insects (*Campanotus* spp., *Vespa* spp., Apidae, Isotera) regularly and mule deer (*Odocoileus hemionus*) when available (Graber & White 1983).

SAMPLING

We trapped rats by baiting approximately 20 snap traps with peanut butter and oatmeal, positioning them at 5- to 10-m intervals where the terrestrial vegetation meets the beach on each island. We trapped rats for one trap night (August 16, 2002) on Great Sitkin Island ($n = 6$), for two trap nights (August 7 and 8, 2003) on Hawadax Island ($n = 15$) and for four trap nights (July 15, 17 and 21 and August 25, 2004) on Adak Island ($n = 12$). We sampled liver and muscle from dead rats

following each night of trapping. As determined by a controlled study of Norway rats, stable isotopes from liver and muscle reflect diets of rats from several days to ~2 months prior to sampling, respectively (Kurle 2009). Because we collected rat tissues in mid- to late summer, stable isotope values from muscle represent the diets of rats from late spring/early summer through the summer, whereas stable isotopes from liver represents rat diets in either mid- or late summer.

For a previous investigation, we sampled black bears throughout Yosemite National Park via hair snare (2006 and 2007) and predicted the foraging behaviour of each bear in 2005–2007 (Hopkins *et al.* 2012). In this study, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values derived from the hair of bears that were predicted to forage for plants and animals exclusively (hereafter, NFC bears or bears not conditioned to forage for human foods) in 2005 and 2006 (Hopkins *et al.* 2012). We did not include bears in this study if they were sampled in the late summer and fall of 2006 and 2007 because isotopes in their hair do not represent bear diets for a full year. Instead, we used isotope values derived from the full-length guard hair of bears (22 Males, 29 Females) sampled in the spring and early summer of 2006 ($n = 27$) and 2007 ($n = 24$); stable isotopes from the hair of these bears represent their diets in 2005 and 2006 ($n = 51$). We also measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in two full-length guard hairs from two female black bears sampled in Yosemite National Park in 2007; one of these bears was conditioned to forage for human foods (hereafter, FC bear) and one was NFC (Hopkins *et al.* 2012). We cut the guard hairs (FC: $n = 14$, NFC: $n = 11$) for these bears into consecutive 5-mm segments for analysis.

We opportunistically collected the main food sources for coastal rats (Kurle, Croll & Tershy 2008) and black bears (Graber & White 1983; Greenleaf *et al.* 2009; Hopkins *et al.* 2012). For rats, we collected terrestrial vegetation and amphipods on Hawadax and Adak Islands and Glaucous-winged gull (*Larus glaucescens*) feathers and egg membranes on Hawadax Island in 2002 (Table S1). For bears, we opportunistically collected grasses, forbs, berries, acorns, pine nuts and animals in 2006 and 2007 (Table S1; Hopkins *et al.* 2012).

SAMPLE PREPARATION AND ANALYSIS

We cleaned rat tissues and rat foods with water, freeze-dried all samples and removed lipids using petroleum ether (Dobush & Ankney 1985) in a Dionex ASE-200 Accelerated Solvent Extractor. We ground all samples into a powder by hand and sealed them (0.9–4.1 mg) into 5×9 mm tin capsules (Costech Analytical Technologies, Inc., Valencia, CA, USA).

We rinsed bear hair with a 2:1 chloroform–methanol solution to remove surface oils and then air-dried the samples for 24 h. We oven-dried plant samples and freeze-dried animal tissues collected from Yosemite, removed lipids from animal tissues using petroleum ether, powdered all tissues for subsampling and weighed samples into tin capsules. We measured the isotope ratios from all samples at the Stable Isotope Laboratory at the University of California, Santa Cruz, using a Carlo Erba CE1108 elemental analyser interfaced via a CONFLO III device to an isotope ratio-monitoring mass spectrometer (Delta-XP IR-MS; Thermo-Scientific, Waltham, MA, USA).

We used conventional delta (δ) notation to report the relative difference of isotope ratios (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in parts per thousand, ‰) for samples and the international measurement standards: Vienna Pee Dee belemnite (VPDB) for carbon and atmospheric N_2 (Air) for nitrogen. The laboratory estimated analytical error for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at ± 0.2 ‰ and ± 0.3 ‰, respectively.

ISOTOPIC MIXING SPACES

To accurately estimate the diets of animals using SIMMs, we first estimated each isotopic mixing space (Hopkins *et al.* 2014). Not estimating an isotopic mixing space carefully can severely bias dietary estimates computed by SIMMs. We added stable isotope discrimination factors (small offsets of stable isotope values between dietary sources and animal tissues due to metabolic and digestive processes; expressed as $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) to the isotope values of each food source (Figs 2 and 3; Table 1). We used discrimination factors for muscle, liver and hair derived from a captive experiment using Norway rats (Kurle *et al.* 2014). We also calculated the digestible elemental concentrations of C and N for each food (Table S1). Not accounting for differences in stoichiometry and digestibility of elements among food sources can severely bias dietary estimates calculated by SIMMs (Koch & Phillips 2002; Phillips & Koch 2002). In particular, the relative differences in the concentrations between plant and animal matter ingested by omnivores can cause the mixing lines to bend between sources, creating a concave, nonlinear mixing space (Koch & Phillips 2002; Phillips & Koch 2002; Hopkins & Ferguson 2012). We used the discrimination-corrected stable isotope values for foods (Figs 2 and 3) and the relative differences in stoichiometry and differential digestibility of C and N to estimate each isotopic mixing space (Koch & Phillips 2002; Hopkins & Ferguson 2012).

We added discrimination factors ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) for captive Norway rats held on known diets composed of either plants (wheat gluten) or animals (fish meal) (Kurle *et al.* 2014) to the isotope values for plants and animals sampled in this study, respectively (Table 1, Fig. 2a,b). Before adding the discrimination factors determined for muscle collected from rats held on all-fish diets to the isotope values from feathers of Glaucous-winged gulls (*Larus glaucescens*), we adjusted feather isotope values to muscle isotope values (Table S1) using the difference in mean discrimination factors for feathers and muscle of ring-billed gulls (*Larus delawarensis*) ($\Delta^{13}\text{C}_{\text{feather-muscle}} = -0.1$ ‰; $\Delta^{15}\text{N}_{\text{feather-muscle}} = 1.6$ ‰) fed an all-perch (*Perca flavescens*) diet ($\delta^{13}\text{C} = -24.3 \pm 0.2$ ‰, $\delta^{15}\text{N} = 14.2 \pm 0.2$ ‰) (Hobson & Clark 1992).

No study has accurately estimated the discrimination factors of bear hair. Because black bears and Norway rats are monogastric mammalian omnivores, we assumed these species discriminate against ^{14}N and ^{12}C by a similar magnitude (Hopkins *et al.* 2012). We added discrimination factors obtained from the hair of captive Norway rats held on the same all-plant or all-fish diets described above (Kurle *et al.* 2014; Table 1) to the stable isotope values for the plants and animals

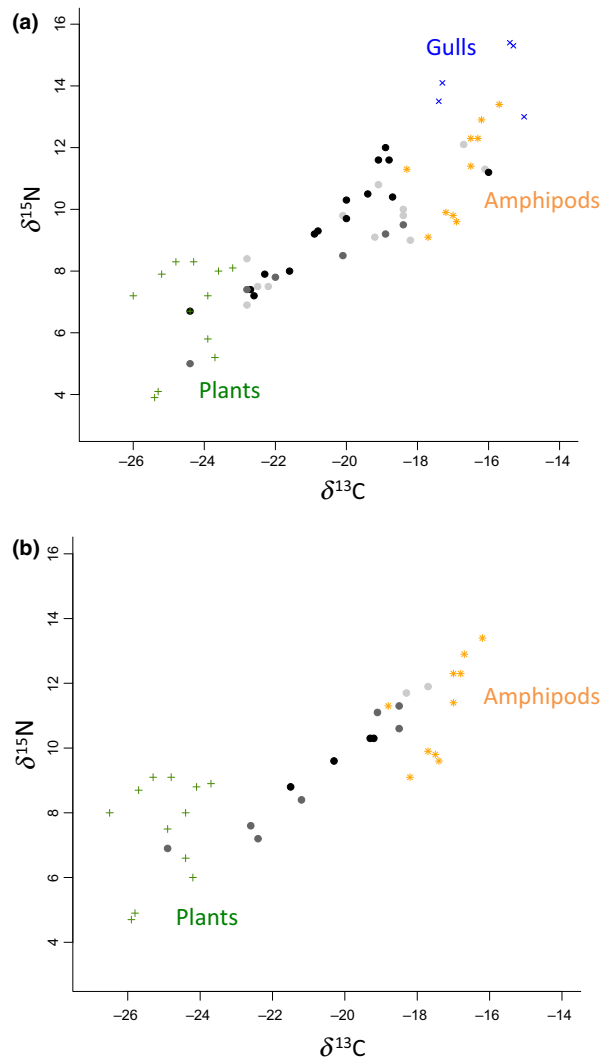


Fig. 2. Stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) derived from Norway rat (a) muscle and (b) liver and their major foods (corrected for isotopic discrimination: $\Delta^{13}\text{C}$, $\Delta^{15}\text{N}$) (‰) in (a) summer on Hawadax (formerly Rat Island) (•), Adak (◦) and Great Sitkin (◊) Islands and (b) late summer in A (◊), B (•) and C (◊) Coves on Hawadax Island, Aleutian Islands, AK, 2003.

bears are known to forage for in Yosemite, respectively (Fig. 3). We used these discrimination-corrected isotope values for foods to estimate the four resource aggregates (hereafter, endmembers) of the isotopic mixing space for NFC bears. We used the same strategy in Hopkins *et al.* (2014) to estimate the isotopic mixing space for the FC bear. We used isotope values for the hair of NFC bears ($n = 51$; Fig. 3) as a plant and animal endmember and isotope values for the hair of humans ($n = 72$; Hopkins *et al.* 2014) as a human food endmember.

The ideal method for estimating endmembers in an isotopic mixing space is to use stable isotope values for the tissues of free-ranging animals on a known diet (e.g. isotope values from NFC bear hair represents the diets of bears that forage for plants and animals exclusively). This method circumvents the need of adding discrimination factors (which are estimated by feeding captive animals foods that are usually different than those sampled in the field) to food isotope values before estimating dietary contributions using SIMMs. Unfortunately, this technique is challenging to apply to the study of free-ranging animals because it is often difficult to identify animals with different diets *a*

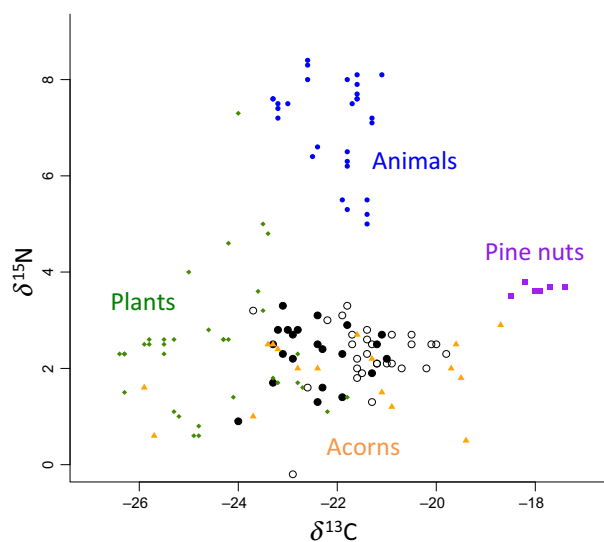


Fig. 3. Stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) derived from the hair and major foods (corrected for isotopic discrimination: $\Delta^{13}\text{C}$, $\Delta^{15}\text{N}$) (‰) of American black bears that do not forage for human foods in Yosemite National Park, CA, 2006–2007. Male and female black bears denoted by closed and open circles, respectively.

Table 1. Discrimination factors derived from a controlled study that fed Norway rats diets where the protein was provided by either wheat or fish (Kurle *et al.* 2014). We added the discrimination factors from either the wheat- or fish-based diets to the isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) for plant and animal sources, respectively.

Tissue	Diet	$\Delta^{13}\text{C}$		$\Delta^{15}\text{N}$	
		Mean	1 SD	Mean	1 SD
Liver	Wheat	1.2	0.5	3.1	0.2
	Fish	0.7	0.3	3.1	0.4
Muscle	Wheat	1.7	0.1	2.3	0.3
	Fish	1.2	0	3.1	0.4
Hair	Wheat	3.4	0.5	2.4	0.2
	Fish	2.1	0.1	3.9	0.3

priori (e.g. bears that forage for human-derived foods vs. bears that forage for plants and animals only). If such prior information is not available, and it is often not, we recommend adding reliable discrimination factors derived from controlled diet studies of the same species (e.g. Norway rats for Norway rats; 2nd best option) or animals of a similar taxa and foraging behaviour (e.g. omnivorous rats and black bears; 3rd best).

We used digestible [C] and [N] for sampled foods to estimate each isotopic mixing space for rats and bears (Table S1). We calculated concentrations and digestibility using data from past studies (Hopkins *et al.* 2012) or comparable food items from the USDA Nutrient Database (www.nal.usda.gov/fnic/foodcomp/search; Table S1).

STATISTICAL ANALYSES

We conducted three sets of statistical analyses. First, depending on whether isotope values were normally distributed or not (using a Shapiro–Wilk test, $\alpha = 0.05$), we used either an ANOVA or Kruskal–Wallis one-way analysis of variance test to compare isotope values among discrimination-corrected foods for both rats and bears, and

among rat tissues sampled on islands (muscle) and in coves (livers). We also used either a *t*-test or a Mann–Whitney *U*-test to compare isotope values of bears (hair) sampled during different years, and by sex, and by foraging behaviour (i.e. hair segments for FC and NFC bears). Secondly, we used IsotopeR to estimate the proportional dietary contributions of major foods to the diets of rats and bears at the population-, group- and individual-level (Hopkins & Ferguson 2012). We used the SIMM, IsotopeR, instead of other Bayesian mixing models (Moore & Semmens 2008; Semmens *et al.* 2009; Parnell *et al.* 2010; Ward, Semmens & Schindler 2010), because of its ability to simultaneously estimate all parameters (utilizing a fully Bayesian approach), including those that define the isotopic mixing space and proportional dietary contributions at multiple levels; its hierarchical design (i.e. population estimates influence group estimates and, in turn, individual estimates); its inclusion of stoichiometric effects and differential digestibility (i.e. concentration dependence; Koch & Phillips 2002; Phillips & Koch 2002) as well as various sources of uncertainty when estimating dietary parameters using stable isotopes; and its ease of use and informative graphical displays (Hopkins & Ferguson 2012). We ran a burn-in of 10^3 draws for all IsotopeR models, followed by 10^4 iterations of Markov chain Monte Carlo (MCMC). For each analysis, we considered the marginal posterior distributions for each food source for all individuals as a resource axis. We described both the position and width of each resource axis using two metrics. We considered the mean and median of each group- or population-level posterior as the position of the resource axis and its width as the 95% credible interval (CI) or range of all median posteriors for individuals. Generally, steep and narrow posteriors for populations or groups denote low variability of resource use, whereas short and wide posteriors suggest higher dietary plasticity. A large range of median posteriors for individuals, with little overlap, suggests consumers have heterogeneous diets. The width of posteriors is also related to the variability of isotope values for each endmember and their positions relative to one another in the isotopic mixing space. An increase in the isotopic variation of an endmember or the overlap of isotope values for endmembers may decrease the precision of dietary estimates, increasing credible intervals. Such overlap can lead to the multimodality observed in posterior distributions. Relatively flat, overlapping posteriors for individuals suggest poor precision overall.

We used isotopic mixing spaces, posteriors (proxies for resource axes) and proportional dietary contributions to examine resource use (i) among rats from different islands, (ii) among rats sampled from different locations on an island with availability to a recent pulse of amphipods, (iii) between male and female black bears that forage for natural foods and (iv) for an individual bear that foraged for human foods. For our fourth analysis, we first compared the isotope values of hair (5-mm segments) between two female bears with different foraging behaviour (FC vs. NFC). We used isotope values from 5-mm hair segments to estimate the plant and animal versus human food diet for the FC bear (3821) through time. We did not estimate the seasonal diet of the NFC bear because, unlike FC bear 3821, we are not certain which food sources should be included in our model. We know that FC bear 3821 foraged for plants, animals and human foods consistently throughout the year (Hopkins & Kalinowski 2013); therefore, including plants and animals as the first endmember, and human foods as the second, is appropriate for an analysis of all hair segments. On the other hand, it is not appropriate to include all plant and animal food sources (such as those used in our third analysis) in the mixing space for the NFC bear because some of these foods are only available seasonally. We note that if we knew the rate at which hair grew, we could use a series of mixing spaces to estimate the diet of the NFC

bear during each season using certain segments of hair. Lastly, we compared proportional dietary contributions for male and female black bears by estimating the probability that the posterior distributions were similar (as formulated in Hopkins *et al.* 2014).

Results

We found that the stable isotope values among major food sources for rats and bears, corrected for isotopic discrimination of rat muscle ($\delta^{13}\text{C}$: $H = 19.7$, $P < 0.001$; $\delta^{15}\text{N}$: $H = 22.0$, $P < 0.001$; Fig. 2a), liver ($\delta^{13}\text{C}$: $t = -22.0$, $P < 0.001$; $\delta^{15}\text{N}$: $W = 1$, $P < 0.001$; Fig. 2b) and hair ($H = 49.0$, $P < 0.001$; $\delta^{15}\text{N}$: $H = 63.8$, $P < 0.001$; Fig. 3), were all significantly different, the exception being the $\delta^{13}\text{C}$ values for acorns and animals ($W = 283$, $P = 0.895$; Fig. 3). Differences in isotope values among known dietary sources (Figs 2 and 3) allowed us to accurately estimate proportional dietary contributions using IsotopeR.

We investigated the diets of coastal-dwelling rats on three islands in the Aleutian Archipelago using stable isotope values from rat muscle. Rat isotope values were not different among islands ($\delta^{13}\text{C}$: $F = 0.817$, $P = 0.452$; $\delta^{15}\text{N}$: $F = 2.14$, $P = 0.135$; Fig. 2a), suggesting that the resource use of rats was similar on these three islands. As mentioned above, rats preyed on birds that have historically nested along the coast in the Aleutians, resulting in low numbers of birds observed on rat-infested islands. We expected that rats would not rely on birds and their eggs during summer, and results from our SIMM analysis confirmed this ($\bar{x} = 14\%$, median = 0%, CI = 0–61%; Fig. 4, Table 2); instead, we found that rats foraged primarily for plants ($\bar{x} = 50\%$, median = 51%, CI = 21–80%, range = 9, 92%) and amphipods ($\bar{x} = 36\%$,

median = 42%, CI = 0–78%, range = 4, 89%) during these months (Fig. 4, Table 2).

We examined the diets of rats sampled in three adjacent coves on Hawadax Island using isotope values derived from their livers (Fig. 2b). We did not include gulls and their eggs as a dietary source in this analysis because these resources were not available to rats in late summer, as the few birds on the island would have laid their eggs in spring. We also note that we identified marine amphipods and terrestrial vegetation in the stomachs of rats on Adak Island (Kurle 2008) and observed rats feeding on marine amphipods at night on Hawadax Island (C. Kurle, pers. obs.). The stable isotope values for rats were not different among the coves ($\delta^{13}\text{C}$: $F = 0.608$, $P = 0.562$; $\delta^{15}\text{N}$: $F = 1.85$, $P = 0.203$), suggesting that rats at all three coastal locations on Hawadax Island foraged similarly (Fig. 2b). Using IsotopeR, we found that rats responded to the pulse in amphipod availability by foraging for this food source extensively ($\bar{x} = 73\%$, median = 77%, CI = 8–98%, range = 9, 98%; Fig. 5, Table 3). Although most rats fed primarily on amphipods for several days before they were euthanized for this study, some rats continued to forage for plants almost exclusively ($\bar{x} = 27\%$, median = 23%, CI = 2–92, range = 2, 91%) (Fig. 5, Table 3).

We compared isotope values and proportional dietary contributions for male and female black bears sampled in Yosemite National Park in 2006–2007. We found that $\delta^{13}\text{C}$ (2005: $\bar{x} = -21.9 \pm 1.0$ ‰, 2006: $\bar{x} = -21.7 \pm 1.1$ ‰) and $\delta^{15}\text{N}$ (2005: $\bar{x} = 2.3 \pm 0.6$ ‰; 2006: $\bar{x} = 2.2 \pm 0.7$ ‰) values for black bear hair was similar between years ($\delta^{13}\text{C}$: $t = -0.8311$, $P = 0.4102$; $\delta^{15}\text{N}$: $W = 341$, $P = 0.7547$). We discovered that $\delta^{13}\text{C}$ values for males ($\delta^{13}\text{C}$: $\bar{x} = -22.4 \pm 0.8$ ‰) and females ($\delta^{13}\text{C}$: $\bar{x} = -21.3 \pm 0.9$ ‰) were different ($t = -4.6809$, $P <$

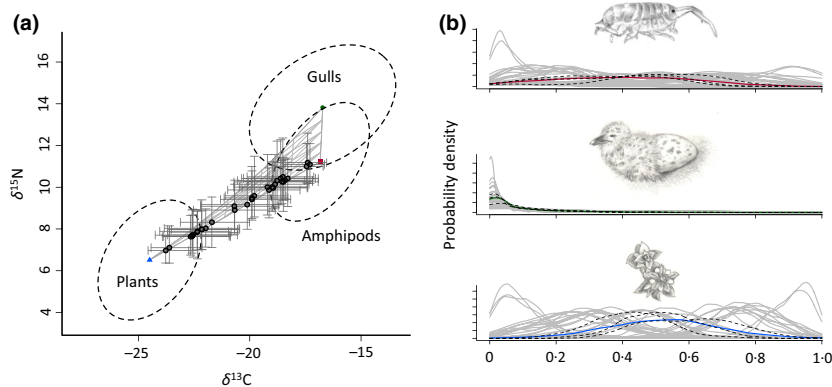


Fig. 4. The estimated stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) for Norway rats and their major food sources in summer (a), and the proportional dietary contributions (expressed as marginal posterior distributions) (b) for rats sampled on Hawadax (formerly Rat Island), Adak and Great Sitkin Islands, Aleutian Islands, AK, 2002–2003. IsotopeR estimated proportional dietary contributions at the interisland- (solid coloured lines), island- (dashed lines) and individual-level (grey lines) (b).

Table 2. Dietary contributions for Norway rats on Hawadax (formerly Rat Island), Adak and Great Sitkin Islands, Aleutian Islands, AK, 2002–2003. Rat muscle was sampled in July and August, reflecting the diets of rats approximately 2 months prior to collection (Kurle 2009). Range denotes the minimum and maximum estimate for individual dietary contributions (median of posterior distributions) on each island.

Island	Amphipods				Gulls				Plants			
	Mean	Median	95% CI	Range	Mean	Median	95% CI	Range	Mean	Median	95% CI	Range
Hawadax	34	43	0–69	4, 88	15	0	0–61	0	51	52	30–71	10, 90
Adak	41	51	0–78	15, 89	15	0	0–62	0	44	45	22–65	9, 80
Great Sitkin	31	36	0–68	5, 71	11	0	0–52	0	57	58	32–82	28, 92

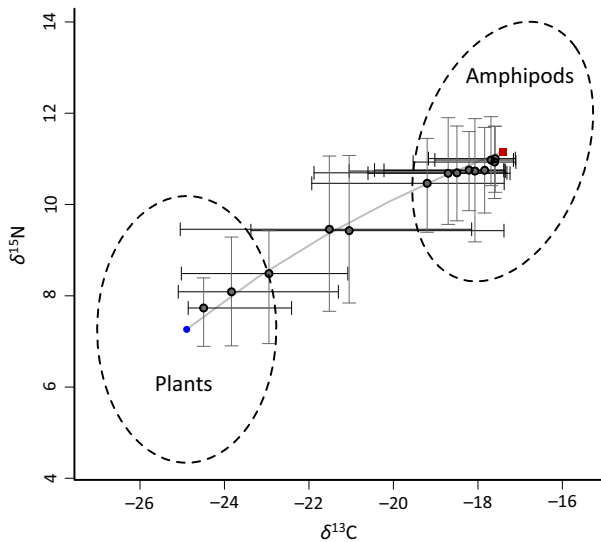


Fig. 5. The estimated stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) that define the isotopic mixing space for Norway rats and their major food sources on Hawadax (formerly Rat) Island, Aleutian Islands, AK, 2002.

Table 3. Island- and individual-level dietary contributions for Norway rats sampled from three coves (see Fig. 1) on the north side of Hawadax (formerly Rat) Island, Aleutian Islands, AK, 2002. Rat livers were collected on 7–8 of August, reflecting the diets of rats several days prior and up to sampling (Kurlle 2009).

	Amphipods			Plants		
	Mean	Median	95% CI	Mean	Median	95% CI
Cove A	61	63	13–95	39	37	5–87
1	80	80	50–100	20	20	0–50
2	88	92	58–100	12	8	0–42
3	95	97	80–100	5	3	0–20
4	82	78	62–100	18	22	0–38
5	22	23	0–49	78	77	51–100
6	28	28	0–46	72	72	54–100
7	9	9	0–23	91	91	77–100
8	42	42	24–64	58	58	36–76
Cove B	72	78	27–97	28	22	3–73
9	79	79	52–100	21	21	0–48
10	65	63	33–95	35	37	5–67
11	82	81	53–100	18	19	0–47
12	41	38	15–80	59	62	20–85
Cove C	87	92	36–100	13	8	0–64
13	93	98	70–100	7	2	0–30
14	93	96	72–100	7	4	0–28

0.001), and $\delta^{15}\text{N}$ values for males ($\bar{x} = 2.3 \pm 0.6$ ‰) and females ($\bar{x} = 2.3 \pm 0.7$ ‰) were similar ($W = 333.5$, $P = 0.7894$) (Fig. 3). Using IsotopeR, we determined that plants ($\bar{x} = 46\%$, median = 38%, CI = 18–95%, range = 19, 59%) and acorns ($\bar{x} = 38\%$, median = 40%, CI = 3–63%, range = 31, 64%) were the largest contributors to bear diets in 2005–2006, followed by pine nuts ($\bar{x} = 15\%$, median = 13%, CI = 1–40%, range = 7, 29%) and animals ($\bar{x} = 1\%$, median = 1%, CI = 0–4%, range = 0, 2%) (Fig. 6). We also found that female bears foraged for more acorns ($\bar{x} = 49\%$,

median = 50%, CI = 35–64%, range = 42, 64%) and pine nuts ($\bar{x} = 22\%$, median = 22%, CI = 13–31%, range = 13, 29%) than males (acorns: $\bar{x} = 40\%$, median = 41%, CI = 19–59%, range = 31, 47%; pine nuts: $\bar{x} = 10\%$, median = 10%, CI = 1–17%, range = 7, 13%) during the 2 years they were sampled (probability of similarity = 26% for acorns and 2.3% for pine nuts), whereas males consumed more plants ($\bar{x} = 49\%$, median = 48%, CI = 36–65%, range = 40, 59%) than females ($\bar{x} = 27\%$, median = 27%, CI = 15–46%, range = 19, 36%) during these years (probability of similarity = 3.8%) (Fig. 6).

The isotope values for hair segments were higher ($\delta^{13}\text{C}$: $t = 7.8$, $P < 0.001$; $\delta^{15}\text{N}$: $t = 9.5$, $P < 0.001$) for the FC bear ($n = 14$; $\delta^{13}\text{C}$: $\bar{x} = -18.6 \pm 0.6$ ‰, $\delta^{15}\text{N}$: $\bar{x} = 5.3 \pm 0.5$ ‰) than the NFC bear ($n = 11$; $\delta^{13}\text{C}$: $\bar{x} = -20.4 \pm 0.5$ ‰, $\delta^{15}\text{N}$: $\bar{x} = 2.3 \pm 0.9$ ‰) (Fig. 7a,b). We used IsotopeR to estimate the isotopic mixing space and dietary contributions for the FC bear through time (Fig. 7c,d). We found that this FC bear ate a substantial amount of human food ($\bar{x} = 39\%$, median = 37%) consistently throughout the year (CI = 30–57%; Fig. 7d).

Discussion

We demonstrated the use of stable isotope analysis to measure the resource use of rats from the Aleutian Islands and American black bears from Yosemite National Park. We used IsotopeR to estimate the isotopic mixing spaces for rats and bears, revealing their environments (defined as the interactions

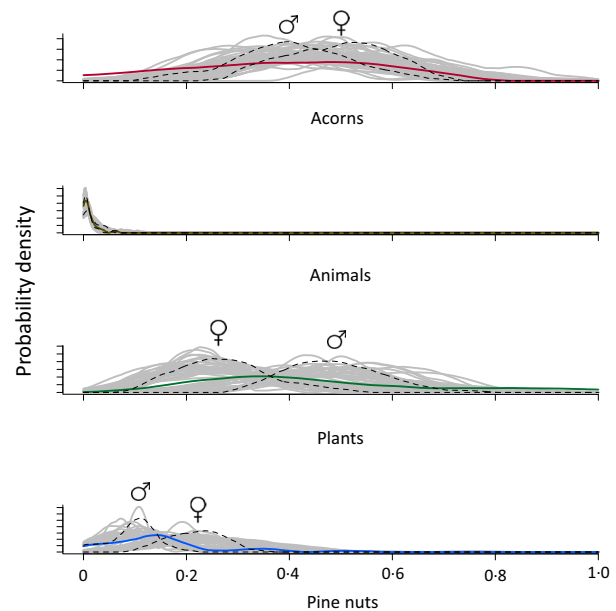


Fig. 6. The proportional dietary contributions (expressed as marginal posterior distributions) for bears sampled in Yosemite National Park, CA, 2006–2007. Because bears were sampled in spring and early summer, the isotopes derived from their hair represent their diets in 2005–2006. IsotopeR estimated proportional dietary contributions at the population- (solid coloured lines), group- (by sex, dashed lines) and individual-level (grey lines). The median of each marginal posterior distribution for each sex is indicated by the appropriate symbol.

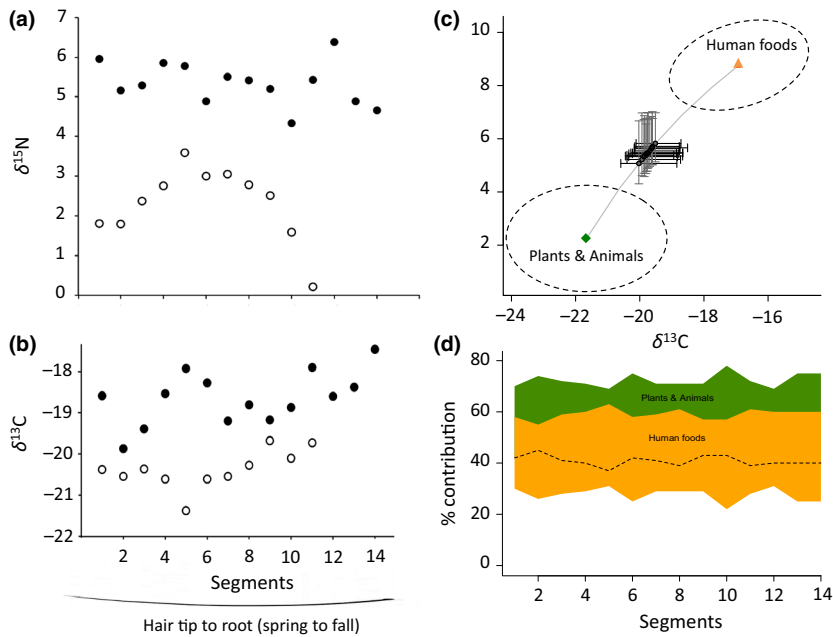


Fig. 7. Stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (‰) derived from the hair (5-mm segments) of two American black bears from Yosemite National Park, CA (a, b). Hair segments were cut from the tip to the root, reflecting the diet of bears from spring through the fall of 2006, respectively (a, b). One bear foraged for human foods (black circles) and one foraged for plants and animals exclusively (open circles) (a, b). Whole hair isotope values for bears in this study that did not forage for human foods and isotope values for human hair were used as endmembers in an isotopic mixing space (c) used to estimate proportional dietary contributions for a bear that foraged for human foods through time (d).

between consumers and their food sources). We also used IsotopeR to estimate the resource axes (expressed as marginal posterior distributions) that describe the resource use of populations, groups, and individual rats and black bears. These measures of resource use provide insight into the realized niches of consumers. Below, we discuss what we learned about the resource use of rats and black bears and conclude with final remarks related to our tool for investigating the ecological niches of animals.

NORWAY RATS

The stable isotope values derived from rat muscle indicate that rats did not rely on gulls in the late spring and summer on sampled islands (Fig. 4, Table 2). Birds that nest on the coast, along with bird eggs, would provide rats with a high-protein food source in the late spring and early summer when birds are present, nesting and thus available as prey (Irons, Anthony & Estes 1986; Verbeek, Braithwaite & Boasson 1993). Previous studies have ascribed significant reductions in birds on islands to predation by invasive rats (Towns, Atkinson & Daugherty 2006; Jones *et al.* 2008), including in the Aleutian Islands (Kurle, Croll & Tershy 2008). It is likely that rats exploited this food source during colonization; however, this food source is now scarce because marine birds no longer breed in large numbers on rat-infested islands in the Aleutian archipelago. Our results support our personal observations, expert opinion (J. Williams, US Fish and Wildlife Service, pers. comm.) and surveys that reported relatively low numbers of coastal birds on rat-infested Aleutian Islands (U.S. Fish and Wildlife Service 2004). Rock ptarmigans (*Lagopus muta*) and other ground nesting land birds could also be vulnerable to rat predation, leading to population-level effects that mirror those of seabirds. In this study, however, we focused sampling efforts

along the coast, biasing our inferences to the coastal diets of rats. Future investigations should assess the diets of rats both coastally and inland to determine if land birds sustain inland rat populations in the Aleutians as a high-protein food source.

We found that rats sampled on the coast primarily foraged for plants in the late spring and summer (Fig. 4; Table 2) and amphipods in the late summer (Fig. 5; Table 3). Although credible intervals for amphipods are wide (Table 2) and posteriors that define the resource axis are relatively flat (Fig. 4b), due to small samples and overlapping isotope values from two of the resources (gulls and amphipods; Fig. 4a), a large range of median posteriors for plants suggest individual rats have heterogeneous diets in the summer. Although evidence from our study reinforces the claim that Norway rats rely on vegetation as a primary food source (Whishaw & Whishaw 1996; Fig. 2, Table 2), rats seem to prefer amphipods when they are available (Fig. 5, Table 3). Stable isotope values from rat livers suggest that most rats foraged exclusively for amphipods following an episode when amphipod-infested algal wrack washed up on the beaches we sampled. Amphipods provide rats high-quality marine protein at a low cost, as this food source is plentiful, and, as we observed, easy and safe to forage for at night (C. Kurle, pers. obs.). It is unknown, however, if coastal rats can sustain their populations without the influx of amphipods, as a past study, our personal observations and other opinions suggest these rats do not feed extensively on other invertebrates (Kurle, Croll & Tershy 2008). Because amphipods are likely not available in the winter, we assume that rats forage for underground plant parts such as rhizomes, bulbs, corms and tubers to sustain their populations during these harsh months. As a result, the impacts rats have on vegetation are likely year-round, pointing to potential ecosystem-level impacts. To better understand the effects of rats on terrestrial ecosystem structure and function, we recommend studies

that investigate the population dynamics of inland and coastal rats and their major foods, especially plants (Nogales, Rodriguez-Luengo & Marrero 2006; Towns, Atkinson & Daugherty 2006) on either islands that have had rats removed (e.g. Hawadax) or among islands with and without rats throughout the Aleutian Archipelago. We also advocate a comprehensive diet study using direct observation, scat and gut contents, and stable isotope analysis. Stable isotope analysis of fur sampled from rats in the early spring would be particularly informative as these hairs provide insight into the foraging behaviour of rats in the winter (i.e. the last ~3–4 months of diet; Kurlle 2009), a difficult time to access the Aleutian Islands. In addition to informing management and policy in the Aleutians, such studies conducted on a number of rat-infested islands could contribute to the development of testable ecological niche models for rats and other omnivores.

BLACK BEARS

Results from our analysis (Fig. 6) support the general notion that plants and acorns are major contributors to black bear nutrition in the Sierra Nevada of California (Graber & White 1983; Greenleaf *et al.* 2009; Mazur, Klimley & Folger 2013). In spring, plants are higher in protein content and lower in fibre than later in the year (Mealey 1980) and herbage is virtually unlimited to black bears, providing the protein necessary for their growth in spring (Noyce & Garshelis 1998). In fall, acorns provide the carbohydrates and fat necessary for weight gain before denning in winter (Beeman & Pelton 1980; Eagle & Pelton 1983; Graber & White 1983; Mazur, Klimley & Folger 2013). Because black bears are only 5% less efficient at extracting protein from plants than ruminants and have similar passage rates and digestive efficiencies as giant pandas (*Ailuropoda melanoleuca*) (Pritchard & Robbins 1990), these monogastric omnivores are able to use fibrous plants for nutrition when high-calorie hard masts are unavailable in spring and summer. By late summer, many bears leave the high country in the Sierra Nevada where they forage for herbage, berries and insects and return to lower elevations to feed on berries, acorns and sugar pine (*Pinus lambertiana*) nuts (Graber & White 1983; Mazur, Klimley & Folger 2013). Acorns and pine nuts are relatively high in carbohydrates and fat and low in fibre compared to other foods available to bears, making them highly digestible and preferred (Beeman & Pelton 1980; Eagle & Pelton 1983). In addition, these hard masts provide bears the energy needed to forage for long hours (e.g. into the night) during hyperphagia in the fall and to fuel metabolism in their dens as they hibernate over winter (Elowe & Dodge 1989).

Masting trees are particularly important for female bears, as past studies have shown that good mast years are correlated with successful bear reproduction and cub survival (Rogers 1987; Elowe & Dodge 1989; Schwartz *et al.* 2006). Unfortunately for black bears, however, both oaks (acorns) and sugar pines (pine nuts) are hard mast species with unpredictable availability in the Sierra Nevada and are threatened by white pine blister rust (*Cronartium ribicola*) and both mule deer foraging and fire exclusion, respectively (Mazur,

Klimley & Folger 2013); in addition, sudden oak death (*Phytophthora ramorum*) could threaten oaks if this disease moves in from coastal California. Female bears move great distances (Koike *et al.* 2012) and have high activity levels (Garshelis & Pelton 1980), especially during low mast years (Mazur, Klimley & Folger 2013). High levels of activity by lactating black bears suggest that increased foraging efforts are required to meet the additional energy and protein requirements for lactation and cub growth (Eagle & Pelton 1983). We found that the hair collected from females had higher $\delta^{13}\text{C}$ values compared to males (~1.0 ‰ shift in $\delta^{13}\text{C}$), suggesting females had different plant-based diets than males in 2005–2006 (Fig. 3). The posteriors that define the resource axes for acorns and pine nuts suggest female bears foraged more heavily on hard mast than males, especially pine nuts, which both have higher $\delta^{13}\text{C}$ values than the other C_3 plants bears eat in the Sierra Nevada (Fig. 3).

We propose 3 hypotheses that potentially explain the sex-specific differences in diet for adult black bears. (i) Adult females generally seek out foods high in fat to trigger implantation of blastocysts in November or December (Wimsatt 1963), build or replace body fat reserves, or increase the probability of cub survival (Rogers 1976, 1987; Graber 1982; Elowe & Dodge 1989). As a result, adult females may often forgo seeking out foods higher in protein in favour of those high in fat. Such foraging decisions can stunt the growth of females (Jonkel 1960), but increase their reproductive success by improving body condition (Rogers 1987) and by allowing them to avoid males foraging on the higher protein foods, thereby circumventing infanticide (Ben-David, Titus & Beier 2004). Females with cubs typically lose weight when lactating (Noyce & Garshelis 1998), necessitating extended foraging periods. Therefore, female bears lactating in spring and summer may have foraged to a larger degree on more high-energy acorns and pine nuts than males in the fall (e.g. during the night when bears are typically not active; Garshelis & Pelton 1980) to replace their body fat reserves (Eagle & Pelton 1983). (ii) Female bears may have foraged heavily on overwintered masts (Graber & White 1983). Because hair growth in bears is rapid in spring following their moult (Graber 1982; Noyce & Garshelis 1998), a disproportionately large section of the hair shaft may contain stable isotopes from the spring diet. It is also plausible, depending on mast production the previous year, that females could have consumed acorns with relatively high $\delta^{13}\text{C}$ values (canyon oak) compared to preferred acorns (black oak) that had lower $\delta^{13}\text{C}$ values (Table S1). (iii) To reduce competition during years of poor acorn production, females remained in their mid-elevation summer ranges to forage for disproportionately more pine nuts (Mazur, Klimley & Folger 2013).

Females had similar and relatively low $\delta^{15}\text{N}$ values compared to male black bears and grizzly bears (*Ursus arctos*), respectively, indicating that black bear diets in Yosemite are low in animal protein (Mowat & Heard 2006). Moreover, $\delta^{13}\text{C}$ (-24.9 ± 0.6 ‰) and $\delta^{15}\text{N}$ values (3.0 ± 1.0 ‰) for mule deer indicate that bears may have lower protein diets (consisting of acorns and pine nuts) than this herbivore. Despite results from

past studies that found that bear scats frequently contained ants (Graber & White 1983; Greenleaf *et al.* 2009), we found that ants and other animal matter were not major contributors to the diets of black bears in Yosemite. Although animal matter composes a small overall proportion of bear diets in Yosemite, it is plausible that ants and other sources of animal protein are very important for gaining the essential amino acids required for nutrient balance (Eagle & Pelton 1983; Noyce, Kannowski & Riggs 1997).

Black bears in Yosemite can experience two vastly different environments: one in which animals strictly interact with non-human-related components of the habitat in which they occur (as previously discussed; Fig. 6), and one in which individuals also interact with people or their property, namely human foods (Fig. 7c). We found that bear 3821 foraged for protein- and corn-rich human foods from spring through fall (Fig. 7d). Bears conditioned to forage for human foods often seek out these sources consistently because they are high in protein, carbohydrates and fat (Schoeller *et al.* 1986; Chesson *et al.* 2008). Human food causes bear tissues to become more enriched in ¹⁵N because it is high in animal protein (Hopkins *et al.* 2012, 2014), and, like acorns, human foods provide bears enough energy and fat to survive the winter and reproduce. In fact, bears that forage for human foods in Yosemite have higher annual reproductive rates and litter sizes (Graber 1982) and a lower breeding age compared to conspecifics that forage for natural plants and animals exclusively (Keay 1995). Because the diets of most bears are proportionally low in animal protein, bears that forage for human foods in Yosemite gain additional protein for growth (i.e. they are larger than their conspecifics; Graber 1982) and function. In summary, human foods are bear superfoods. These high-calorie food sources are generally easy to find in Yosemite and digest. Unfortunately though, the acquisition of human foods can come at a high cost for bears. Bears that are in conflict with people or their property are eventually killed in Yosemite (Hopkins & Kalinowski 2013).

Conclusion

The use of stable isotopes to estimate the diets of animals is one of the greatest breakthroughs in nutritional ecology in the last 20 years (Schwartz *et al.* 2014). We recommend researchers expand their efforts beyond simply comparing stable isotope data from consumers and their foods (or their overlap) in multivariate space and also use those data to make accurate dietary inferences using SIMMs. For example, SIMMs provide researchers the ability to estimate individual diets, measure realized niches for populations and incorporate the mechanistic relationships between known consumers (with complex, omnivorous diets) and their habitat into ecological niche or community models. We urge ecologists to link spatial and demographic information for consumers and their foods through time to their diets (using SIMMs) and other environmental conditions as these data sets are notoriously difficult and expensive to collect using traditional methods. These data would be widely useful for management and conservation (e.g.

for predicting the bottom-up effects of a rapidly changing environment on focal species such as Aleutian rats and American black bears) and to develop models that help unravel the fundamental mysteries of the ecological niche.

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Data accessibility

Stable isotope values for consumers are provided in Figs 2 and 3, and all isotope values and digestible elemental concentrations for foods are provided in Table S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, reported in ‰) and digestible elemental concentrations ([C], [N]) for Norway rats from the Aleutian Islands, AK, and American black bears from Yosemite National Park, CA.