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SPECIAL TOPIC: INDIVIDUAL-LEVEL NICHE SPECIALIZATION

The cost of reproduction: differential resource specialization in female and male California sea otters

Emma A. Elliott Smith · Seth D. Newsome · James A. Estes · M. Tim Tinker

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Abstract Intraspecific variation in behavior and diet can have important consequences for population and ecosystem dynamics. Here, we examine how differences in reproductive investment and spatial ecology influence individual diet specialization in male and female southern sea otters (*Enhydra lutris nereis*). We hypothesize that greater reproductive constraints and smaller home ranges of females lead to more pronounced intraspecific competition and increased specialization. We integrate stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of sea otter vibrissae with long-term observational studies of five subpopulations in California. We define individual diet specialization as low ratios of within-individual variation (WIC) to total population niche width (TNW). We compare isotopic and observational based metrics of WIC/TNW for males and females to data on population densities, and movement patterns using both general linear and linear mixed-effects models. Consistent with our hypothesis, increasing population density is associated with increased individual diet specialization by females but not by males. Additionally, we find the amount of coastline in a sea otter's home range positively related with individual dietary variability, with increased range span resulting in weaker specialization for both males and females. We attribute our results to sex-based differences in movement, with females needing to specialize in their small ranges to maximize energy gain, and posit that the paradigm of individual prey specialization in sea otters with increased intraspecific competition may be a pattern driven largely by females. Our work highlights a potentially broader role of sex in the mechanistic pressures promoting and maintaining diet specialization.

Keywords Individual diet specialization · Stable isotopes · Reproductive investment · Spatial ecology · *Enhydra lutris*

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E. A. Elliott Smith (✉) · S. D. Newsome
Biology Department, University of New Mexico, Albuquerque, NM 87131, USA
e-mail: eaelliot@unm.edu

J. A. Estes
Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95060, USA

M. T. Tinker
US Geological Survey, Western Ecological Research Center, Santa Cruz, CA 95060, USA

Introduction

A recent surge of studies has demonstrated that individual-level variation in dietary niche is both widespread and ecologically significant (Bolnick et al. 2003; Kondoh 2003; Araújo et al. 2011). Such specialization results from a complex interplay between ecological and morphological characteristics of consumers and resources, and requires several conditions. First, potential prey species must be both diverse and abundant enough to provide the "ecological opportunity" for a consumer to diversify its diet (Darimont et al. 2009; Araújo et al. 2011). Second, a strong ecological or physiological pressure is needed to induce individuals to stray away from preferred prey and focus on alternative resources (Bolnick et al. 2003; Araújo et al. 2011). Studies consistently find intraspecific competition increases the degree of individual specialization (Tinker et al. 2008a; Svanbäck and Bolnick 2007; Svanbäck and Persson 2009), while both interspecific competition and predation appear

to dampen it (Peacor and Pfister 2006; Eklov and Svanbäck 2006; Bolnick et al. 2010). Lastly, behavioral, physiological, and/or morphological variation that create inter-individual differences in the ability to capture, process, or assimilate prey must be maintained over time (Bolnick et al. 2003; Araújo et al. 2011).

Sex can be an important potential source of intraspecific niche variation (Clutton-Brock 2007; Ruckstuhl 2007). In mammals, males and females tend to differ in size, shape, behavior, and most notably, reproductive investment. For example, most mammals are sexually dimorphic, with males typically larger than females (Ralls 1977; Lindenfors et al. 2007). Additionally, females necessarily must invest more resources in offspring, owing to the fundamental limitations of anisogamous reproduction (Bateman 1948; Trivers 1972; Clutton-Brock 2007). Mammalian lactation, for example, has been shown to double or triple postpartum energy demands (Millar 1977; Williams et al. 2007; Thometz et al. 2014). Consequently females are typically the "choosy" sex, as they risk losing substantial time and resources by mating with a "low quality" male (Trivers 1972; Lima and Dill 1990; Charnov 1993; Clutton-Brock 1991, 2007). Conversely, males are limited in reproductive success only by the number of individuals they successfully mate with, and, consequently, often compete strongly for access to females and provide little or no parental care (Bateman 1948; Clutton-Brock 1991, 2007).

With males and females experiencing fundamentally different evolutionary and energetic pressures, there is reason to expect different responses to the ecological conditions that contribute to the development of individual diet specialization. Because females are tied to their young—either physically during gestation, or by postpartum parental care—they often experience restrictions in movement and range of behavior (Trivers 1972; Kleiman 1977; Ralls 1977; Trillmich 1990; Grigione et al. 2002; Loveridge et al. 2009). Lower investment in offspring by males means they can afford to engage in such behaviors as movement between habitats/populations, and immigration into novel territories (Clutton-Brock 1991; Clutton-Brock et al. 2002). This sex-specific life history limitation is relatively common among mammals: in marine carnivores such as California sea lions (*Zalophus californianus*) income breeding females are restricted to foraging near rookeries while males wander (Trillmich 1990). Similar patterns hold for terrestrial carnivores such as African lions (*Panthera leo*), where non-dominant males roam great distances while females remain in smaller territories with their cubs (Stander 1991; Loveridge et al. 2009), and pumas (*Puma concolor*), where female home range shrinks during periods of cub care (Grigione et al. 2002). Thus, females may be unable to escape ecological pressures such as high degrees of intraspecific competition, whereas males may be free to move to areas where resources are more abundant (Clutton-Brock et al. 2002). Given the importance of intraspecific competition in driving patterns of individual diet specialization, it is reasonable to expect that females may be under stronger selection for specialization than males.

California sea otters (*Enhydra lutris nereis*) provide a useful system for exploring these concepts. Populations of sea otters differ significantly in density of individuals and degree of intraspecific resource competition, with corresponding variation in the degree of individual diet specialization (Estes et al. 2003; Tinker et al. 2008a). When sea otter population densities are low and food is abundant, individual adult females tend to target the most energy-rich prey and have similar, overlapping diets (Tinker et al. 2008a). As competitive pressure and thus resource limitation increases, these individuals tend to specialize on a few unique prey, so that dietary diversity of the population increases while dietary niche width of individuals remains small and may even decline (Tinker et al. 2008a, 2012). Additionally, male and female sea otters exhibit different patterns of movement and reproductive investment (Jameson 1989; Ralls et al. 1996; Tinker et al. 2008b). Females are solely responsible for parental care and are either in a continuous state of pregnancy or provisioning a dependent pup, which can increase daily energetic requirements by up to 96 % over the lactation period (Thometz et al. 2014). Adult female sea otters are thus energetically constrained by reproduction and show high site fidelity, rarely moving more than 20 km from the center of their home range [Loughlin 1980; Tinker et al. 2008b; US Geological Survey (USGS), unpublished data]. Males are not constrained by parental care, and often travel distances of 50–200 km throughout the subspecies range (Jameson 1989; Ralls et al. 1996; Tinker et al. 2008b). These differences in reproductive investments and movement patterns among the sexes may well contribute to differences in the degree of specialization.

Here, we explore the hypothesis that individual diet specialization in sea otters differs between the sexes. More specifically, we hypothesize that due to their inability to move away from conspecific competitors, female sea otters should be more sensitive to intraspecific pressures and thus display greater degrees of prey specialization in resource-limited areas. In contrast, males are less constrained energetically by reproduction and may have a reduced response to intraspecific pressures and exhibit a wider range of foraging strategies. We use a combination of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of sub-sampled vibrissae and long-term observational studies of five sea otter subpopulations in central and southern California to characterize individual diet specialization in males and females. Our work provides further insight into the topic of individual

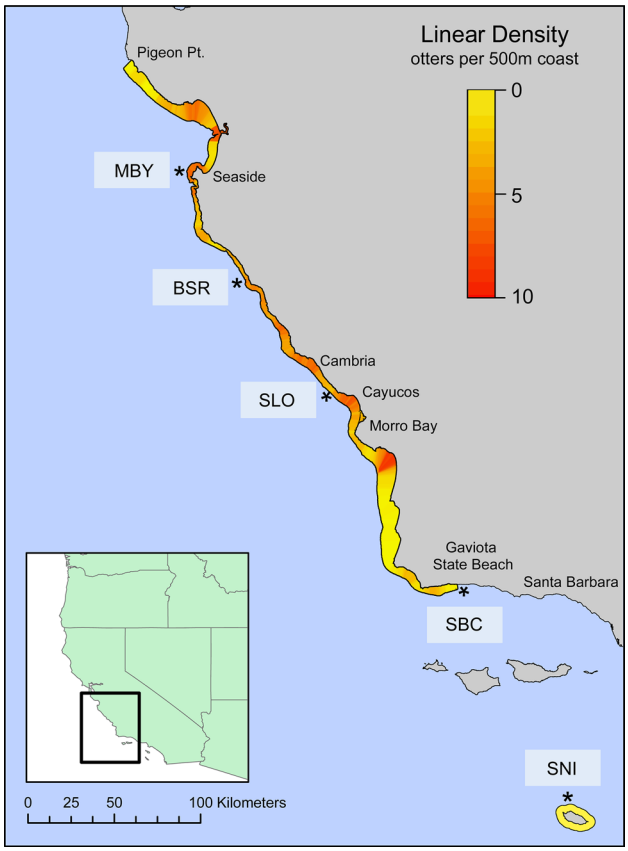

Fig. 1 Geographic location of study sites. The five sites are located along the Pacific coast of North America and represent localities that have been occupied by sea otters for different periods of time. Range limits are based on 2013 survey data. Site codes are in *blue boxes* and approximate central location of sites are marked by *stars*. Note the substantial differences in density among the different locations. The most recently occupied site is Santa Barbara Channel (*SBC*), occupied by females only since 2013. *MBY* Monterey Bay, *BSR* Big Sur, *SLO* San Luis Obispo County, *SNI* San Nicolas Island (color figure online)

diet specialization by highlighting the importance of sexual selection in indirectly shaping these ecological patterns.

Materials and methods

We characterized the degree of individual diet specialization by males and females for five subpopulations of southern sea otters (*Enhydra lutris nereis*) along the coast of central and southern California. To maximize our statistical power in evaluating broad ecological patterns between the sexes we employed two independent metrics of specialization: field observations and stable isotope analysis. Our five subpopulations encompass most of the sea otter's distribution in California, from Monterey Bay (MBY) in the north, through Big Sur (BSR) and San Luis Obispo County (SLO) in the center, and Santa Barbara Channel (SBC) and San Nicolas Island (SNI) in the south (Fig. 1). Physical habitats were generally similar at all sites, including rocky reefs, patchy areas of soft sediment, and dominated by canopy-forming kelps (Tinker et al. 2012, see SOM). Long-term records from each site included data on population densities, foraging behavior, diets and movements/home range size (USGS, unpublished data; Kage 2004; Tinker et al. 2006, 2008a, b; Newsome et al. 2009, 2010; Caswell et al. 2011; Staedler 2011; Tinker et al. 2012). We integrated these data sets with isotopic analysis of sea otter vibrissae sampled from animals at all five sites (Table 1). Details of the procedures for the capture, handling, radio-tagging, and telemetric/observational monitoring of study animals are provided in Tinker et al. (2006, 2008a); all collection activities were authorized by federal, state, and institutional permits issued to M. T. Tinker.

Collection of density, movement and observational dietary data

Where possible we obtained data on population densities, movement patterns and prey selection of males and females for each study location (Table 1). Population censuses are conducted each year by the US Geological Survey, California Department of Fish and Wildlife, Monterey Bay Aquarium, University of California-Santa Cruz and the US Fish and Wildlife Service using both aerial and shore-based survey techniques as developed by Estes and Jameson (1988). Here we used 2013 spring census (early May) data for all sites (Estes and Jameson 1988; Tinker et al. 2006). We obtained movement data from long-term observations of individuals for all sites except SNI, where appropriate data were not available (Table 1). We described spatial use patterns in terms of "linear range span," defined as the distance of coastline (kilometers) encompassed by an individual's movements within its annual home range. Individual home ranges were estimated by fitting a one-dimensional kernel density function to coastal resight locations (see Laidre et al. 2009 for details) and we calculated range span as the distance of coastline within the 90 % utilization probability contour. At four sites (MBY, BSR, SLO and SNI) we made shore-based observations of sea otter foraging bouts (as described in Tinker et al. 2012) in order to estimate diet composition, collecting longitudinal data from individual sea otters over 2- to 5-year periods (Table 1). At the time of this study, observational dietary data were not available from the SBC site as data collection was still in progress.

Stable isotope analysis

Previous work has demonstrated that stable isotope analysis of sea otter vibrissae is a robust proxy for long-term observational dietary data and an effective tool for studying individual- and population-level diet variation in this

Table 1 Summary of sample sizes and collection dates for observational and isotopic data

Site	Vibrissae (isotopic analysis)			Dietary data			Range span		
	Year(s)	Females	Males	Year(s)	Females	Males	Year(s)	Females	Males
Monterey Bay (MBY)	2003–2005	16	15	2000–2012	77	16	2000–2012	83	23
Big Sur (BSR)	2008–2012	22	6	2008–2012	31	5	2008–2012	29	7
San Luis Obispo County (SLO)	2010–2013	41	8	2001–2013	27	8	2011–2013	30	3
Santa Barbara Channel (SBC)	2010–2013	17	20	–	–	–	2011–2012	12	13
San Nicolas Island (SNI)	2004	6	7	2003-2005	7	4	–	–	–

Population density estimates obtained from all sites in 2013. *N* represents the number of individuals, not within-individual sampling. For example, with vibrissae, *n* represents the number of vibrissae from different individuals, *not* the total number of sub-sampled vibrissae segments

system (Newsome et al. 2009, 2010, 2012, 2015). Sea otters are particularly well suited to an isotopic approach as they consume a wide variety of functionally distinct macroinvertebrate prey in a system fueled by two sources of primary production (phytoplankton and macroalgae) that vary by 5–10 ‰ in $\delta^{13}C$ (Fogel and Cifuentes 1993; Kelly 2000; Vanderklift and Ponsard 2003; Page et al. 2008; Newsome et al. 2009, 2010). For example, mussels and clams filter feed particulate organic matter that is a mixture of phytoplankton (low $\delta^{13}C$) and macroalgae (high $\delta^{13}C$), leading to lower $\delta^{13}C$ values than macroalgae browsers and grazers such as sea urchins (*Strongylocentrotus* spp.) (Page et al. 2008; Newsome et al. 2009). Isotope values of consumers reflect these baseline differences, but change in predictable amounts with each increase in trophic level. The offsets between consumer's tissues and that of its prey are commonly called trophic discrimination factors and, on average, are ~3.5 ‰ per trophic level for $\delta^{15}N$ (Kelly 2000; Vanderklift and Ponsard 2003). Thus, red sea urchins (*Strongylocentrotus franciscanus*), which are primary consumers and eat macroalgae, have lower $\delta^{15}N$ values by about 3–4 ‰ than carnivorous Dungeness crabs (*Metacarcinus magister*; Page et al. 2008; Newsome et al. 2009). This large degree of variation in prey functional group and thus isotope values enhances our ability to examine sea otter dietary ecology and individuality. In sea otters, trophic discrimination factors have been measured as $+2.2 \pm 0.7$ and $+3.5 \pm 0.6$ ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (Newsome et al. 2010). However, for our analyses it was not necessary to correct for trophic discrimination as we examined population vs. individual dietary variation rather than diet composition.

Sea otter vibrissae were cleaned to remove surface contaminants before isotopic analysis by rinsing with a 2:1 chloroform:methanol solvent mixture. Each whisker was sub-sampled from base to tip in 0.5- to 0.6-mg segments using nail clippers, and $\delta^{13}C$ and $\delta^{15}N$ values of each segment were measured separately using a Costech 4010 (Costech, Valencia, CA) elemental analyzer interfaced with a Thermo-Finnigan Delta Plus XL mass spectrometer (Thermo Scientific, Bremen) at the University of Wyoming Stable Isotope Facility (Laramie, WY). Isotopic results are expressed as δ values, where $\delta^{13}C$ or $\delta^{15}N = 1{,}000\,[(R_{sam}/R_{std})-1]$, and R_{sam} and R_{std} are the ^{13}C:^{12}C or ^{15}N:^{14}N ratios of the sample and standard, respectively. The internationally accepted standards are Vienna-Pee Dee belemnite limestone for C and atmospheric N_2 for N. The units are expressed as parts per thousand, or per mil (‰). The standard deviation of organic references within a run was ≤0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. To control for the quality of vibrissae protein (keratin) we also measured the ratio of [C]/[N] for each subsample—these values were within the range of unaltered protein (Ambrose 1990).

Characterization of individual diet specialization

We applied the same theoretical (Roughgarden 1972; Bolnick et al. 2003) framework to both isotopic and observational data sets to characterize individual diet specialization of male and female sea otters. As per convention, we define a specialist as an individual whose niche is substantially smaller than that of the population as a whole (Bolnick et al. 2003). The total population niche width (TNW) is the sum of within- and between-individual components of variation (Roughgarden 1972; Newsome et al. 2009, 2012). The individual component of variation (WIC), reflects the average variance of resources within an individuals' niche, whereas the between-individual component of variation (BIC), is indicative of differences among individuals (Roughgarden 1972). A common metric for evaluating the degree of individual diet specialization is the WIC/TNW ratio that ranges from 0 to 1 with low values indicating strong specialization within a population, and high values representing a more generalist population (Bolnick et al. 2003).

We first used the field observations of prey use to calculate metrics of individual diet specialization (WIC_O, BIC_O, TNW_O) for males and females at MBY, BSR, SLO and SNI. Following methods described in detail by Tinker et al. (2012), we used a Monte Carlo simulation algorithm to estimate the proportional contribution of each prey to the diet, and then

calculated niche statistics from the resulting matrix of individual prey frequencies using standard methods (Bolnick et al. 2002; Tinker et al. 2012). In order to correct for differing sample sizes between study sites and to estimate variances and 95 % confidence limits we used 1,000 bootstrap resamples of ten individuals from each study site (11 was the actual sample size for SNI, the smallest study site) (Tinker et al. 2012).

We next used sub-sampled sea otter vibrissae to calculate equivalent isotopic metrics of individual diet specialization; observation and isotopic statistics are distinguished with respective O or I subscripts –e.g., TNW_I. These metabolically inert tissues provide a longitudinal ~1-year record of dietary variation when sub-sampled (Tyrrell et al. 2013). This serves as a robust proxy for WIC_I, whereas variation between individual vibrissae serves as a measure of BIC_I (Newsome et al. 2009). This isotopic approach has been previously shown in southern sea otters to be an accurate proxy for observed population level dietary niche, and degree of individuality (Newsome et al. 2009, 2010). We computed variance components (WIC_I, BIC_I, TNW_I) using restricted maximum likelihood methods using the statistical program JMP (SAS Institute; version 10.0.2). Following Newsome et al. (2009), we estimated the variance components separately for $\delta^{13}C$ and $\delta^{15}N$, but combined the results and report average values of proportions of variance explained. As with the observational dietary data, we computed mean niche statistic values and associated variance (SD) from 1,000 bootstrap resamples of ten individuals from each study site (Tinker et al. 2012).

For individual otters we characterized diet variability using the standard ellipse area (SEA), which represents the amount of space occupied by an individual in bivariate $\delta^{13}C$ versus $\delta^{15}N$ space. We calculated SEA for each individual sea otter using the Bayesian-based statistics library "Stable Isotope Bayesian Ellipses in R" (SIBER; Jackson et al. 2011), with sequential segments from each vibrissae as inputs into the model (16 ± 4 segments per individual). Results are in units of per mil squared (‰^{2}). We calculated mean SEA and SD for each individual from 10,000 iterations of the model. We then computed average SEA for males and females at each site.

Statistical methods

We examined the effect of sample size on our isotopic specialization metric (WIC_I/TNW_I ratio) by computing a sampling saturation curve (Fig. 2). Using data from female sea otters at SLO, which was our largest isotopic sample size of 41 individuals (Table 1), we estimated WIC_I/TNW_I using three to 25 individuals randomly sampled from the population without replacement, and repeated this process 1,000 times. We plotted the mean and variation in this estimate as a function of sample size, to evaluate the relative effect of sampling error as one reduces sample size.

We used general linear models, assuming a normal error distribution and estimated using least squares, to evaluate the relationship between WIC_I and TNW_I, and to determine whether this relationship differed between the sexes. We compared alternative models within an information theoretic framework, evaluating relative support for models with one or both of two main effects: sex (a categorical variable) and TNW_I (a continuous variable) as well as a model with an interaction between main effects. We also used general linear models to evaluate potential predictors of WIC_I/TNW_I, including population density (a continuous variable, the number of sea otters per square kilometer of sub-tidal habitat from 0- to 40-m depth) and sex, as well as the interaction between sex and density. Note that density was used as a proxy for per capita food abundance, a relationship that has been well documented in previous analyses of these same populations (Tinker et al. 2008a, 2012; Newsome et al. 2009, 2012, 2015). In both of the above analyses we also evaluated support for a constant model (i.e., no significant effects or interactions), and the model having the lowest Akaike information criterion (AIC) score was considered to be the best-supported model. We then combined isotopic and observational data and repeated the comparison of general linear models to evaluate potential predictors of WIC/TNW, this time including a categorical variable for sampling method (isotopic vs. observational). We note that the observational data sets generally spanned 2–3 years of observations, approximately twice as long as the sample periods for isotopic data from vibrissae (Tyrrell et al. 2013).

To evaluate the relationships between range span, sex and diet diversity, we used linear mixed-effects models to test for effects of sex and range span on individual diet variability, that we measured as the SEA of individuals (Jackson et al. 2011), while accounting for the random effect of study site. We evaluated models with one or both main effects and with an interaction between sex and range span, as well as a constant model, and AIC scores were used to select the best-fit model. For this analysis we used data from adult sea otters only, to avoid confounding effects of age. General linear models, linear mixed models, and all resampling analyses were conducted using the statistics toolbox in MATLAB (Release 2014a, MathWorks, Inc.).

Results

Individual diet specialization

Stable isotopes

Our saturation curve (Fig. 2) suggests that sample sizes below ten individuals reduce confidence in isotopic characterizations of individual diet specialization. For a sample

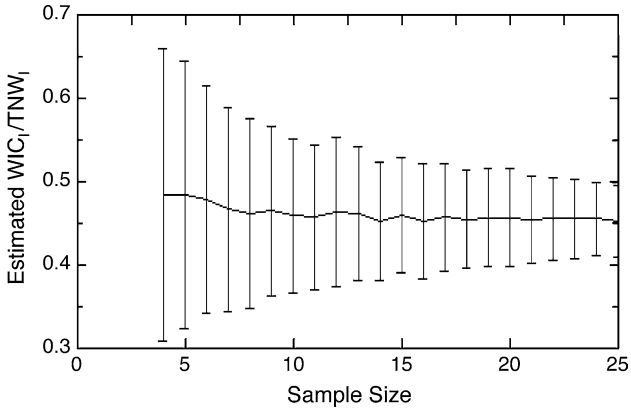

Fig. 2 Influence of sample size on isotopic diet specialization results. The degree of diet specialization was characterized using the ratio of the within-individual component of variation (WIC_I) to total population niche width (TNW_I); where subscript I indicates isotopic metrics. WIC_I/TNW_I was estimated using data from female sea otters at SLO, which had the largest sample size of 41 individuals (Table 1), using from 3 to 25 individuals randomly sampled from the population without replacement, repeating this process 1,000 times. We plotted the mean estimate and variation in this estimate as a function of sample size, to evaluate the relative effect of sampling error as one reduces sample size. Our saturation curve suggests that as sample size decreases below ten individuals we have reduced confidence in our isotopic characterizations of dietary specialization. For sample sizes of five, for example, the variance in our estimate of WIC_I/TNW_I increases by almost 50 %

size of six, the variance in our estimate of WIC_I/TNW_I increases by almost 50 % (Fig. 2), and so the WIC_I/TNW_I from SNI (which is based on seven males and six females) must be interpreted cautiously. However, we note that because of the extremely low population densities at SNI, our data actually represented 30 % of the population at the time of collection (2004; Table 1). Additionally, WIC_I/TNW_I estimates for males at BSR ($n = 6$) should be interpreted with caution, and to a lesser extent the estimates for males at SLO ($n = 8$) (Tables 1, 2).

We find male and female sea otters exhibit different degrees and patterns of isotopic individual diet specialization among and within sites (Table 3). Females show greater overall isotopic niche space (TNW_I) compared to males at all sites but SBC (Table 3). Females also show less variance in average individual niche width (WIC_I) across sites than males by approximately a factor of 2, with males ranging (± SD) from 0.185 ± 0.035 at SNI to 0.513 ± 0.116 at SLO, and females from 0.274 ± 0.057 at MBY to 0.417 ± 0.083 at SBC (Table 3). A comparison of general linear models shows strongest support for a model including an interaction between sex and TNW_I in terms of their effects on WIC_I (Table 4): males exhibit a positive relationship between WIC_I and TNW_I, while females show a slightly negative relationship (Fig. 3).

Table 2 Summary of observational data results

Site	Density[a] (otters km^{-2})	Range span[b] (km)	
		Male ± SD	Female ± SD
Monterey Bay (MBY)	5.9	30.6 ± 39.7	19.1 ± 27.7
Big Sur (BSR)	3.1	49.4 ± 65.7	18.1 ± 10.4
San Luis Obispo County (SLO)	2.6	30.3 ± 26.7	22.5 ± 15.3
Santa Barbara Channel (SBC)	0.9	87.5 ± 95.2	24.2 ± 5.8
San Nicolas Island (SNI)	0.9	–	–

[a] Density represents the average number of sea otters per square kilometer of benthic sub-tidal habitat (measured from the low tide line to the 40-m isobath) at each study site

[b] Range span represents the average number of kilometers of coastline between the northernmost and southernmost points of the 90 % home-range polygons (fit using fixed kernel density methods)

Observational

Our observational foraging data are generally in agreement with isotopic data in terms of patterns of variation in diet specialization, with a few key differences. As with isotopic data, females display greater TNW_O than males at most sites. However, the exception in this case is SLO, where male and female TNW_O is nearly equivalent (Table 3). Additionally, females vary (±SD) by only 0.19 in WIC_O/TNW_O values, from 0.646 ± 0.052 at BSR to 0.837 ± 0.031 at SNI, whereas males vary by 0.515 from 0.413 ± 0.056 at BSR to 0.928 ± 0.012 at SNI (Table 3).

Diet and population density

Males and females appear to differ in terms of the relationship between diet specialization and population density, although our results for isotopic and observational data are not entirely consistent. When considering just the isotope data, there is weak but significant support for an interaction between sex and density (Table 4) such that diet specialization increases with density for females (i.e., WIC_I/TNW_I decreases) but not for males (Fig. 4a). When isotopic and observational data are combined the sex-density interaction is no longer supported (Table 4), although there is support for an increase in diet specialization with density for both sexes (i.e., a decrease in WIC_I/TNW_I; Fig. 4b). Based on isotopic data, females show a greater degree of individual specialization (lower WIC_I/TNW_I values) than males at the sites with highest population densities (MBY, BSR and SLO; Table 3); in contrast, observational data suggested that females are less specialized (higher WIC_O/TNW_O) than their male counterparts at every site except SNI (Table 3).

Table 3 Summary of observational and isotopic individual specialization metrics

Site	Female			Male		
	$WIC_O \pm SD$	$TNW_O \pm SD$	$WIC_O/TNW_O \pm SD$	$WIC_O \pm SD$	$TNW_O \pm SD$	$WIC_O/TNW_O \pm SD$
Observational specialization						
Monterey Bay (MBY)	1.504 ± 0.119	2.230 ± 0.105	0.675 ± 0.047	1.185 ± 0.159	1.918 ± 0.108	0.617 ± 0.065
Big Sur (BSR)	1.330 ± 0.113	2.063 ± 0.127	0.646 ± 0.052	0.840 ± 0.143	2.026 ± 0.165	0.413 ± 0.056
San Luis Obispo County (SLO)	1.594 ± 0.097	2.047 ± 0.107	0.779 ± 0.043	1.261 ± 0.125	2.048 ± 0.185	0.618 ± 0.061
Santa Barbara Channel (SBC)						
San Nicolas Island (SNI)	0.946 ± 0.066	1.131 ± 0.083	0.837 ± 0.031	0.761 ± 0.062	0.819 ± 0.062	0.928 ± 0.012
	$WIC_I \pm SD$	$TNW_I \pm SD$	$WIC_I/TNW_I \pm SD$	$WIC_I \pm SD$	$TNW_I \pm SD$	$WIC_I/TNW_I \pm SD$
Isotopic specialization						
Monterey Bay (MBY)	0.274 ± 0.057	1.127 ± 0.205	0.249 ± 0.059	0.408 ± 0.178	0.848 ± 0.315	0.492 ± 0.134
Big Sur (BSR)	0.346 ± 0.088	1.180 ± 0.251	0.301 ± 0.078	0.238 ± 0.051	0.610 ± 0.124	0.394 ± 0.064
San Luis Obispo County (SLO)	0.399 ± 0.073	0.898 ± 0.147	0.455 ± 0.106	0.513 ± 0.116	0.841 ± 0.101	0.610 ± 0.115
Santa Barbara Channel (SBC)	0.417 ± 0.083	0.600 ± 0.094	0.696 ± 0.090	0.454 ± 0.104	1.101 ± 0.265	0.436 ± 0.139
San Nicolas Island (SNI)	0.340 ± 0.086	0.855 ± 0.123	0.402 ± 0.100	0.185 ± 0.035	0.527 ± 0.054	0.350 ± 0.053

Isotopic variance components use an average of stable C isotope ratio (δ^{13} C) and stable N isotope ratio (δ^{15}N) values. For both data sets, mean niche statistic values (and associated SDs) were calculated from 1,000 bootstrap resamples of ten individuals from each study site

WIC Within-individual component of variation, *TNW* total population niche width, *subscript O* Observational specialization metric, *subscript I* isotopic specialization metric

Isotopic specialization and range span

We find males and females exhibit substantially different patterns of movement within and among sites. Males have, on average, larger range spans than females at all four sites where data were available (Table 2), although there is also greater variation among individual males. The amount of coastline encompassed by an individual's home range has a significant effect on diet variability: the best-supported model explaining variation in SEA includes a fixed effect for range span (log transformed) as well as a random effect for site (Table 4). The increase in diet variability as a function of range span is consistent across sites and applies to both males and females (Fig. 5).

Discussion

Our findings highlight the importance of sex-based differences in reproductive investment and behavior, particularly movement, in driving dietary individuality in sea otters. Consistent with our hypothesis, we find differences for both isotopic and observational metrics in the extent and variability of individual diet specialization between males and females both within and among sites along the California coast. Isotopic data suggest females are more specialized than males at sites with high sea otter densities (MBY, SLO, BSR), and less specialized at the two low-density sites: SBC and SNI (Tables 2, 3; Fig. 5a). Our observational data exhibit a different pattern; male otters appear to be more specialized than females at MBY, BSR, and SLO (Tables 2, 3; Fig. 5b). One possible explanation for this difference is that prey-stealing (kleptoparasitism) by male sea otters (Riedman and Estes 1990) leads to greater diet diversity, and this is reflected in the isotopic data more than the observational data. This explanation seems unlikely however, since male kleptoparasitism was consistently recorded and accounted for in the analysis of observational data (Tinker et al. 2012), and was not found to have a significant effect on diet-diversity estimates for males. Moreover, if such a bias occurred it should affect high-density and low-density sites equally. Instead, we suspect this finding is associated with a spatial bias in observational data for highly mobile males. Specifically, many males have home ranges that are divided into several distinct "centers-of-use" distributed widely throughout the range (Ralls et al. 1996; Jameson 1989; Tinker et al. 2008b). Observational dietary data were typically collected from just one or two of these centers where observers had the best access for shore-based observation. In contrast, the isotopic data are integrated across the males' full ranges, or at least everywhere they have foraged within the previous year (Tyrrell et al. 2013). For such mobile males, the isotopic data thus provide a less-biased sampling method and result in more reliable estimates of dietary diversity. In contrast, the much smaller range of females minimizes the potential for observational bias. Hence, we consider the isotopic data to correctly reflect a greater degree of specialization in females

Table 4 Summary of results from general linear models (*GLM*) and linear mixed effects models (*LMM*)

Model	AIC	Parameter	Estimate	SE
Isotope data, GLM, $n = 10$				
WIC ~ 1	−16.425			
WIC ~ 1 + TNW	−15.508			
WIC ~ 1 + sex	−14.431			
WIC ~ 1 + TNW × sex	−22.125[a]	(Intercept)	0.523	0.142
		Sex (M)	−0.578	0.189
		TNW	−0.180	0.149
		TNW × Sex (M)	0.708	0.214
Isotope data, GLM, $n = 10$				
WIC/TNW ~ 1	−10.676			
WIC/TNW ~ 1 + density	−9.703			
WIC/TNW ~ 1 + sex	−8.872			
WIC/TNW ~ 1 + sex × density	−10.784[a]	(Intercept)	0.586	0.097
		Sex (M)	−0.178	0.138
		Density	−0.062	0.030
		Sex(M) × density	0.080	0.043
Isotope + observational data, GLM, $n = 18$				
WIC/TNW ~ 1 + method	−16.343			
WIC/TNW ~ 1 + method + density	−17.623[a]	(Intercept)	0.520	0.064
WIC/TNW ~ 1 + method + sex	−14.441	Method (obs)	0.264	0.066
WIC/TNW ~ 1 + method + sex × density	−14.725	Density	−0.031	0.018
Isotope and movement data, LMM, $n = 74$				
SEA ~ 1 + (1|site)	127.150			
SEA ~ 1 + sex + (1|site)	128.520			
SEA ~ 1 + log(range) + (1|site)	119.720[a]	(Intercept)	0.677	0.197
SEA ~ 1 + sex + log(range) + (1|site)	121.570	log(range)	0.202	0.064
SEA ~ 1 + sex + log(range) + sex × log(range) + (1|site)	122.310			

Alternate models and their associated Akaike information criterion (*AIC*) values are shown, as well as parameter estimates (and SEs) for the best-supported models. For categorical effects, comparison effect level is identified *in parentheses*

SEA Standard ellipse area; for other abbreviations, see Table 3

[a] Lowest AIC

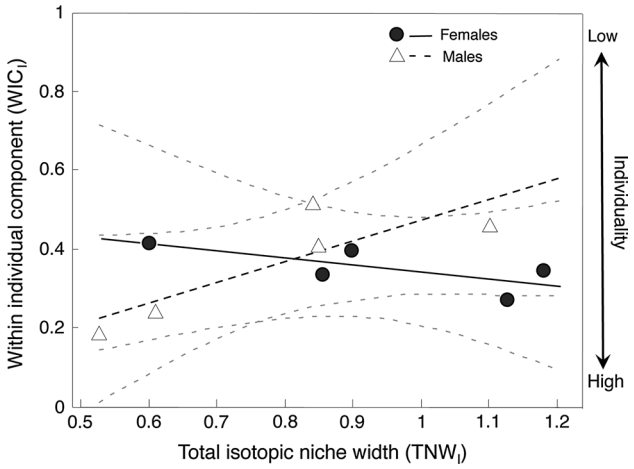

Fig. 3 The average variation within individuals in isotopic space compared to that of the overall sea otter population for five California sites. Males represented by *open triangles*, females by *filled circles*. *Trend lines* represent predictions of a general linear model describing the relationship between WIC_I and TNW_I, and detailed statistics, including parameter estimates, model-selection criteria and alternate models, are provided in Table 4. TNW_I represents total isotopic niche width utilized by the population and is the sum of within (WIC_I) and between individual components (BIC_I) of variance. Areas of relative low and high degrees of individuality are shown by the *right-hand scale*; the *bottom right corner* of the *graph* is the region of highest degree of individual diet specialization where the total niche width is large, but variation within individual diets is low. Note that trends for males and females have opposite slopes; the *shallow slope* exhibited by females reflects that their total dietary niche space increases due to increased variance between individuals rather then by an increase in the variation within individuals. For abbreviations, see Fig. 2

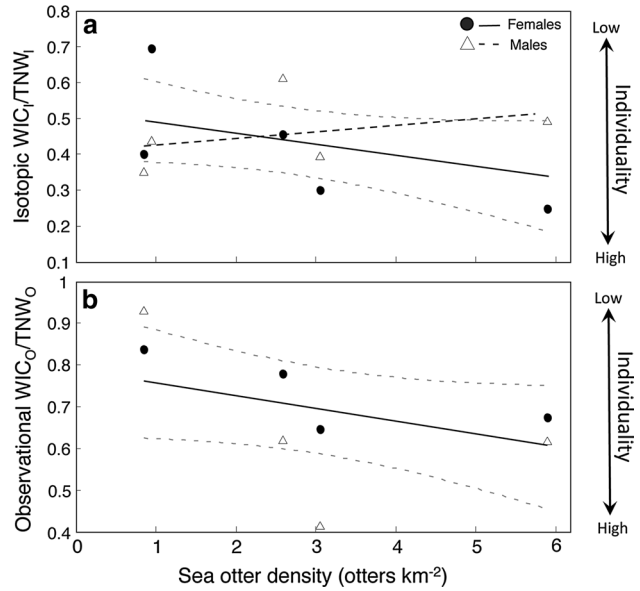

Fig. 4 The influence of density on sea otter dietary individuality. Shown are data derived from isotopic analysis (**a**) and observational studies (**b**) for females (*filled circles*) and males (*open triangles*). *Trend lines* represent predictions of general linear models describing the relationship between WIC/TNW and density, and detailed statistics, including parameter estimates, model-selection criteria and alternate models, are provided in Table 4. Density was determined by annual aerial census counts performed by the US Geological Survey. The degree of dietary specialization was characterized using the WIC/TNW ratio where TNW is the sum of WIC and BIC. The relationship between isotopic (WIC_I/TNW_I) and observational (WIC_O/TNW_O) specialization and density was evaluated using general linear models, and Akaike information criterion (AIC) statistics, combining isotopic and observational data and including a categorical variable for sampling method. The *solid line* represents the best-fit function (see Table 4), with surrounding confidence intervals (*dotted lines*) estimated for females when isotopic and observational metrics were combined. The *dashed line* represents the best-fit function for males only from isotopic data, as there is some support for a sex/density interaction in this data set. For abbreviations, see Figs. 2 and 3

as compared to males at high-density sites where there is strong intraspecific competition.

Our results also suggest that male and female sea otters respond differently to increased intraspecific competition (Fig. 4), although we note that the model including a sex-density interaction received only marginally more support than a constant model (Table 4). Females tend to become more specialized with increasing population densities, a pattern supported by both isotopic and observational analyses (Fig. 4a, b). At the population level, TNW increases at higher density sites; however, the variability of individual female diets (WIC) remains unchanged or even decreases (Fig. 3). These opposing trends result in a positive relationship between density and female diet specialization indicated by lower WIC_O/TNW_O and WIC_I/TNW_I ratios (Table 4; Fig. 4a, b). This relationship does not exist for males, and based on the analysis of isotope data, which we believe provides the most reliable estimate of male diet diversity, TNW_I and WIC_I are positively correlated (Fig. 3). This suggests that individual diet diversity of males tracks population-level diversity. While the statistical significance of this sex-based difference (Fig. 4) is marginal at best, we note that this is not surprising given a sample size of five sites and the complexities of our study system. It was for this reason that we employed two independent lines of evidence (isotopic and observational), which produced largely similar results in consideration of their respective strengths and biases. We therefore suggest that the previously reported pattern of density-dependent emergence of diet specialization in sea otters (Estes 2003; Tinker et al. 2008a, 2012) may be largely driven by the behavioral responses of females. Our results also suggest a potential explanation for this sex dependency: specifically, the contrasting spatial ecologies of male and female sea otters.

The suggested link between spatial, reproductive, and foraging ecology is a novel aspect of our work on intrapopulation diet variation. We provide the first empirical evidence that diet diversity in sea otters is explained in large

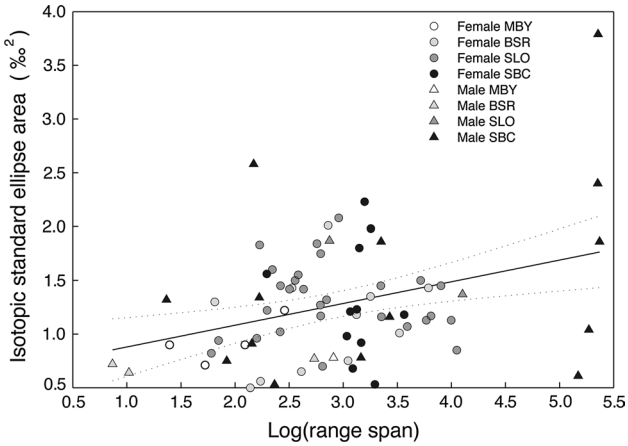

Fig. 5 The influence of range span on sea otter dietary individuality. Individual diet variability was characterized using standard ellipse areas (SEA) run using Stable Isotope Bayesian Ellipses in R (SIBER), which represents the amount of space occupied by an individual in bivariate $\delta^{13}C$ and $\delta^{15}N$ space; SEA units are $‰^2$. Mean SEA for each individual was calculated from 10,000 iterations of the model. *Range span* is defined as the linear distance of coastline encompassed by an individuals movements within its annual home range; movement data were log transformed. The relationship between range span and diet diversity was evaluated using linear mixed-effects models, using AIC scores and study site as a random effect. *Solid line* represents the best-fit function with surrounding confidence intervals (*dotted lines*); detailed statistics, including parameter estimates, model-selection criteria and alternate models, are provided in Table 4. The amount of coastline within an individual's home range has a significant effect on diet variability consistent across sites and sexes. For other abbreviations, see Fig. 1

degree by individual mobility (Table 4; Fig. 5), and thus the greater mobility of males may be the proximate cause of sex-based differences in diet specialization. In grey wolves (*Canis lupis*), landscape and subsequent resource heterogeneity have been shown to influence the competitive environment and potential resources available to individuals, leading to greater population-level dietary variation (Darimont et al. 2009). Similarly with sea otters, it is reasonable to expect that a wide-ranging male is more likely to encounter greater environmental heterogeneity and thus prey diversity than a less mobile female (Table 2). The smaller home ranges used by females (Table 2: Loughlin 1980, Tinker et al. 2008b) may reflect their greater reproductive constraints, as adult female sea otters are constantly in a state of pregnancy or lactating and provisioning a dependent pup after reaching sexual maturity at 2–4 years of age (Estes 1980; Jameson and Johnson 1993; Riedman et al.1994; Thometz et al. 2014). The cost of this parental care is tremendous, elevating a female's daily energetic requirements by 17–96 % over the ~6-month lactation period (Thometz et al. 2014). In stark contrast, reproductive investment in male sea otters is limited to territory defense, which does not appear to incur high energetic costs (Loughlin 1980; Pearson et al. 2006). As measured by one study, there was no significant difference in body condition between adult males holding high- or low-quality territories (Pearson et al. 2006). Thus, adult females have a smaller energetic margin of error and must rely more on extensive knowledge of local prey patches with less latitude for exploratory movements to unfamiliar habitats. The result of high site fidelity for females is a consistent pattern of local resource competition, and in such a scenario there is likely strong selection to specialize to maximize energy gain (Tinker et al. 2012).

Consistent with this prediction, we find the amount of coastline encompassed by an individual sea otter's home range has a significant effect on diet variability (Table 4; Fig. 5). We find females from the highest density sites (MBY and BSR) are the most specialized and have the smallest range spans (Tables 2, 3). At low-density sites (SBC), females are less constrained by intraspecific competition (Tinker et al. 2008a, 2012; Newsome et al. 2012), have larger range spans, and exhibit weaker individual specialization (Tables 2, 3). Males are not constrained by the same reproductive demands as females, and can thus escape local resource competition by moving elsewhere, thereby gaining access to episodically abundant prey in diverse habitats spread throughout the range. The vagabond nature of males could actually select against diet specialization, as generalists may be better equipped to take advantage of a broader array of habitats and prey types (Bolnick et al. 2003; Darimont et al. 2009).

Recent reviews have called for more studies focused on elucidating the relative importance of four identified ecological mechanisms in maintaining individual specialization in natural populations (Araújo et al. 2011). Ecological opportunity and intraspecific competition have been proposed and demonstrated to promote intrapopulation variation (Svanbäck and Bolnick 2007; Tinker et al. 2008a, b; Darimont et al. 2009; Svanbäck and Persson 2009; Araújo et al. 2011), whereas interspecific competition and predation are thought to dampen it (Eklov and Svanbäck 2006; Peacor and Pfister 2006; Bolnick et al. 2010). Here, we argue that females are more sensitive than males to intraspecific competition (Fig. 4), reflecting differing spatial scales of habitat use that are in turn driven by differing life history constraints. Intense reproductive investment (Thometz et al. 2014) likely prevents female sea otters from moving away from conspecifics as food resources become limiting, and thus there is strong selection to avoid competition by partitioning resources and becoming more specialized. This sex-based difference in specialization driven by intraspecific competition might well be a general pattern in nature, as females of many taxa are constrained energetically and behaviorally to varying degrees by reproductive investments (Trivers 1972; Trillmich 1990; Charnov 1993;

Ruckstuhl 2007; Grigione et al. 2002). In particular, female mammals may be especially susceptible to intraspecific pressure as they are typically the sole providers of parental care and the physiological costs of producing young are quite high (Kleiman 1977; Ralls 1977; Charnov 1993; Lindenfors et al. 2007).

Sex-based differences in intrapopulation niche partitioning might also be expected to occur in response to predation, interspecific competition and ecological opportunity. For example, in laboratory experiments, female rats (*Rattus norvegicus*), guppies (*Poecilia reticulate*) and lizards (*Anolis carolinensis*) demonstrated more defensive behavioral patterns than males with exposure to predatory stimuli (Magurran and Nowak 1991; Klein et al. 1994; Irschick et al. 2005). This could lead to: (1) decreased individual diet specialization if other females behave similarly and converge on "predator-safe" resources or habitats, or (2) a feedback loop where similar predator-avoidance behavior by all females leads to an increase in intraspecific competition and thus stronger specialization (Eklov and Svanbäck 2006; Araújo et al. 2011). In the case of interspecific competition, males may be more able to escape areas of high competition and thus utilize a greater range of resources, resulting in decreased individual diet specialization (Bolnick et al. 2010; Araújo et al. 2011). Finally, differences between males and females in size, behavior and energetic demands may lead to different rank preferences of prey. In sea otters, females have been observed to switch diets depending on reproductive stage, consuming less common but calorie-rich prey such as urchins during pregnancy and switching to nutritionally poor but abundant prey items such as snails during lactation (Staedler 2011). These different preferences could potentially lead to the sexes responding divergently to the same set of variable resources, thereby promoting or limiting ecological opportunity between females and males (Bolnick et al. 2003).

Individual-level niche variation can have substantial impacts on population, community and ecosystem dynamics (Bolnick et al. 2003; Kondoh 2003; Araújo et al. 2011). For example, individual diet specialization can lead to: (1) decreased strength in trophic interactions, (2) individuals within the same population being subject to different selective pressures, and (3) populations that are buffered against ecological perturbations (Bolnick et al. 2003; Kondoh 2003). Intra- and interspecific competition, predation and ecological opportunity all play roles in determining the incidence and magnitude of such specialization (Eklov and Svanbäck 2006; Peacor and Pfister 2006; Svanbäck and Bolnick 2007; Tinker et al. 2008a; Darimont et al. 2009; Svanbäck and Persson 2009; Bolnick et al. 2010). Our work suggests that the sexes experience these mechanistic pressures differently, and that females may be under stronger selection to specialize under some scenarios. We expect this pattern will be especially evident in taxa with high reproductive costs and differences between males and females in terms of offspring investment/care that ultimately impact mobility. Future research into sex-based specialization will be necessary to fully understand the mechanisms governing intrapopulation niche variation, and its implications for individual populations and food web dynamics.

Author contribution statement EES formulated the research questions with input from MTT, JAE and SDN. SDN and MTT provided data; EES, SDN and MTT conducted statistical analyses. EES wrote the manuscript with editorial advice from all co-authors.

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