Oecologia (2015) 178:61–74
DOI 10.1007/s00442-014-3213-2

SPECIAL TOPIC: INDIVIDUAL-LEVEL NICHE SPECIALIZATION

Timescales alter the inferred strength and temporal consistency of intraspecific diet specialization

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Received: 24 April 2014 / Accepted: 19 December 2014 / Published online: 6 February 2015
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Abstract Many populations consist of individuals that differ substantially in their diets. Quantification of the magnitude and temporal consistency of such intraspecific diet variation is needed to understand its importance, but the extent to which different approaches for doing so reflect instantaneous vs. time-aggregated measures of individual diets may bias inferences. We used direct observations of sea otter individuals (*Enhydra lutris nereis*) to assess how: (1) the timescale of sampling, (2) under-sampling, and (3) the incidence- vs. frequency-based consideration of prey species affect the inferred strength and consistency of intraspecific diet variation. Analyses of feeding observations aggregated over hourly to annual intervals revealed a substantial bias associated with time aggregation that decreases the inferred magnitude of specialization and increases the inferred consistency of individuals' diets. Time aggregation also made estimates of specialization more sensitive to the consideration of prey frequency, which decreased estimates relative to the use of prey incidence; time aggregation did not affect the extent to which under-sampling contributed to its overestimation. Our analyses demonstrate the importance of studying intraspecific diet variation with an explicit consideration of time and thereby suggest guidelines for future empirical efforts. Failure to consider time will likely produce inconsistent predictions regarding the effects of intraspecific variation on predator–prey interactions.

Keywords Individual variation · Predation · Prey switching · Seasonal prey selection · Time-averaging

Introduction

The presence of intraspecific variation in the morphology, behavior, and resource-use patterns of individuals is a cornerstone of evolutionary theory. Qualitative descriptions of its patterns and discussion of the underlying mechanisms on ecological timescales are now also burgeoning (Bell et al. 2009; Bolnick et al. 2003, 2007), as are efforts to determine its consequences for the functioning of ecological communities (Bolnick et al. 2011; Hughes et al. 2008; Pettorelli et al. 2011). The presence of intraspecific variation can have marked effects on communities, both in theory (Bolnick et al. 2011; Okuyama 2008; Schreiber et al. 2011) and in experiments (Harmon et al. 2009; Rudolf and Rasmussen 2013), particularly when manifested as individual diet specialization (but see Ingram et al. 2011). For example, theory on predator–prey interactions suggests that individual variation in prey preferences and switching rates can qualitatively alter community structure and dynamics (Abrams and Matsuda 2004; Chesson 1978; Murdoch and Oaten 1975). Quantification of both the strength (incidence and magnitude) and the temporal consistency of individual diet specialization in natural populations is needed to further our understanding of its empirical importance (Araújo et al. 2011; Bolnick et al. 2011).

Communicated by Craig A. Layman.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-3213-2) contains supplementary material, which is available to authorized users.

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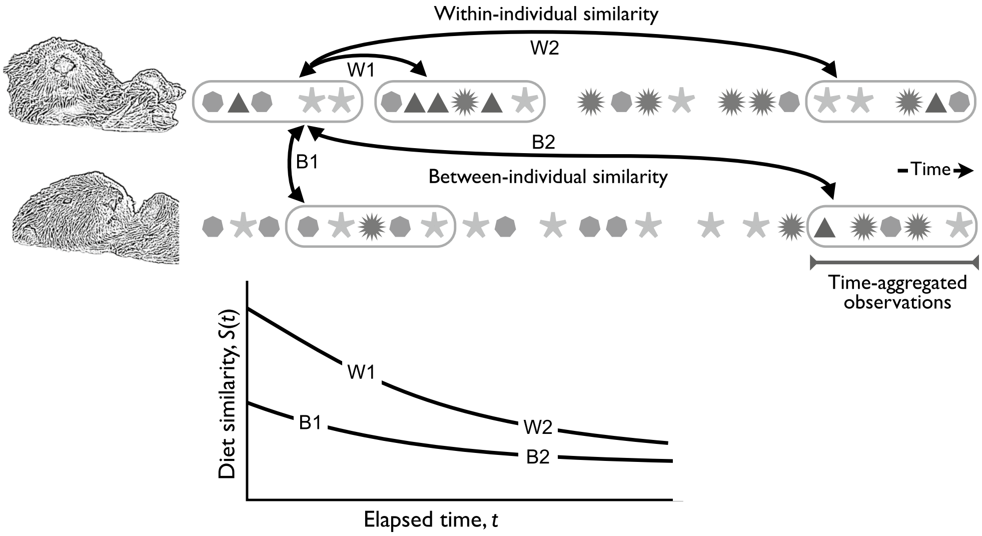

Fig. 1 The concept of intraspecific diet specialization is implicitly temporal. Distinguishing between the strength of specialization (the converse of the between-individual similarity of two different individuals, as estimated by comparisons such as B1 and B2) and the temporal consistency of each individual (the within-individual similarity, as estimated by comparisons such as W1 and W2) is key to understanding its importance. Both between- and within-individual diet similarities are likely to decline as the amount of elapsed time (*t*) between observations of the individuals' diets increases. This temporal nature of diet specialization also suggests that empirical measurements of its strength and consistency will be altered by the timescale over which diet observations are aggregated

The distinction between the strength and the temporal consistency of individual specialization is key to understanding its importance (Fig. 1) (Bolnick et al. 2003). High or low levels of between-individual variation are expected to have qualitatively different effects if specialization is temporally consistent, by virtue of being a fixed behavior or a cross-generationally heritable trait, versus when it is labile or environmentally driven (Schreiber et al. 2011; Yoshida et al. 2007). Both forms of temporal consistency are observed in nature. For example, individual cabbage butterflies, *Pieris rapae*, exhibit substantial specialization in their selection of flowers on hourly timescales, but are temporally inconsistent generalists on longer timescales because their flower preferences are learned anew each day (Lewis 1986). In contrast, the diet specializations of Darwin's medium ground finches, *Geospiza fortis*, exhibit a longer-term heritable component, with individual differences in seed choice being correlated with differences in morphology (Grant et al. 1976; Price 1987).

These considerations indicate that an understanding is needed of how the timescale over which observations of individual prey selection are made affect empirical inferences regarding the strength and consistency of specialization (Fig. 1). Clearly, knowledge of an individual's diet will increase as sampling time and the number of feeding observations increases. Increasing the sampling frame for too long, however, may come at the expense of the ability to detect meaningful temporal patterns of prey selection. For example, the pooling of observations over too large a time window may conceal variation associated with diel, seasonal, or annual changes in prey availability or prey preferences (i.e., switching) (Araújo et al. 2010; Newsome et al. 2010) and may alter perceived levels of specialization. Then again, inferences may be little affected by such pooling if prey selection is considered on a qualitative presence-absence basis, as may be appropriate if only gross variation in prey selection is of interest.

These issues are of particular relevance because the two approaches that predominate the empirical quantification of diet specialization and its temporal consistency—the use of stomach contents and stable isotope ratios—are both susceptible to sampling effort and timescale effects. That is, both approaches are influenced by potential biases that increase or decrease the inferred magnitude and temporal consistency of specialization. Stomach contents provide only a snapshot of an individual's most recent prey choices and are vulnerable to the vagaries of stochastic sampling. Even generalists may appear strongly specialized if insufficient prey items are recovered, or if individuals encounter high densities of particular prey just prior to capture (Bolnick et al. 2002). Similarly, the apparent consistency of specialization will be reduced if individuals encounter different prey prior to consecutive captures, even when prey preferences remain unchanged. Stomach contents may also be biased by prey-specific differences in digestion rates (Legler et al. 2010).

Stable isotope ratios can overcome such limitations to inferring the strength of individual specialization by integrating the source signatures of all consumed prey over time (O'Reilly et al. 2002). However, by being time-aggregated indicators of an individual's diet, stable isotope ratios may inflate the apparent consistency of an individual's diet even when sampled longitudinally. The use of stable isotope ratios is therefore complicated by unresolved variation in tissue-specific turnover rates [ranging from weeks to years of temporal averaging (e.g., Boecklen et al. 2011; McIntyre and Flecker 2006)]. Their use also remains limited by assumptions of spatially and temporally constant prey isotope signatures (Araújo et al. 2007; Jennings et al. 2008), the inability to distinguish prey having similar isotopic signatures (Phillips et al. 2005; Yeakel et al. 2011), and the inability to detect temporal switches between, for example, two prey species whose average contributed signature is equivalent to that of a third prey species (Ward et al. 2011). Direct observations of prey choice through time can avoid these limitations and offer a means to assess the importance of these potential biases (Bolnick et al. 2002; Tinker et al. 2008).

We used direct observations of prey selection by southern sea otters (*Enhydra lutris nereis*) to quantify how the timescale of sampling, under-sampling, and the qualitative vs. quantitative consideration of prey choices affect the inferred strength and temporal consistency of individual diet specialization. In central California, sea otters exhibit high levels of intraspecific diet variation, with some individuals specializing on snails, others on crabs and abalone, and others feeding as relative generalists (Estes et al. 2003; Tinker et al. 2008). Population-level patterns of between-individual differences exhibit both a modular and a nested network structure, with groups of individuals sharing different sets of core prey species nested within a suite of less commonly but more generally consumed peripheral prey (Tinker et al. 2012). Specialization appears to be, at least in part, a learned behavior that is passed from mother to pup, and has been shown to occur independently of variation in prey availability or an individual's age, sex, or morphology (Estes et al. 2003; Tinker et al. 2008). As in other species (Svanbäck and Bolnick 2007), the prevalence of specialization in sea otters is positively correlated with intraspecific competition for limited resources (Tinker et al. 2008, 2012). For sea otters, specialization improves energy acquisition by increasing foraging efficiency for preferred prey (Tinker et al. 2008, 2012), despite the fact that specialization on certain types of prey is associated with increased risk of disease (Johnson et al. 2009). Insight into the strength and temporal consistency of diet specialization therefore contribute to our understanding of the population dynamics and community impacts of this federally threatened keystone species.

Materials and methods

Sea otters feed by diving to the sea floor and retrieving benthic invertebrate prey, and bringing these prey to the surface to consume. This foraging behavior occurs in discrete bouts, typically consisting of ~18–250 dives for prey (not all are successful) and lasting 0.5 to 7 h, and is followed by several hours of non-foraging activity, primarily resting (Bodkin et al. 2007; Tinker et al. 2007). We studied 82 uniquely tagged sea otters between 1998 and 2008 at two focal study areas [Monterey Peninsula (MON), and the coast between Point Piedras Blancas and Point Estero (PBL)] and used daytime shore-based surveys to identify the prey of their successful foraging dives. Individuals within each study area exhibit largely overlapping home ranges, foraging in both rocky and sand-bottom habitats (see Estes et al. 2003; Tinker et al. 2007, 2008, 2012 for details and methods of data collection).

Time-independent estimates of individual specialization

We first estimated the magnitude of specialization at each study site by calculating individual-to-individual diet similarity scores between all pairs of otters using the cumulative set of prey observed in each individual's diet over the entire 10-year study period. This fully aggregated use of all available observations for each individual is the standard fashion by which specialization is assessed. We note that diet similarity reflects the converse of diet dissimilarity on which indices of between-individual specialization are typically based, but provides a simpler means to interpret and contrast levels of variation observed between individuals (between-individual similarity) to levels of variation observed in the temporal consistency of each individual's diet (within-individual similarity) (Fig. 1). Indeed, although the consideration of individual specialization by means of similarity can introduce non-intuitive phrasing (e.g., greater individual specialization is indicated by smaller values of pairwise similarity), the consistent use of similarity for both between- and within-individual comparisons can suggest alternative definitions of individual specialization that combine measures of both between-individual differences and temporal consistency into a single metric (see Supplementary Electronic Materials S3).

We implemented four indices to quantify diet similarity: the classic incidence-based Jaccard index (S_J) (Jaccard 1901), the frequency-based Jaccard index (S_{Ja}) (Chao et al. 2005), the frequency-based Jaccard index estimator (S_{Je}) (Chao et al. 2005), and, for reference, the more typically used index of proportional similarity (S_{PS}) (Renkonen 1938; Schoener 1968; Zaccarelli et al. 2013) (see Supplementary Electronic Materials S1 for details). All indices of similarity vary from a value of 0 (no similarity between two diets) to 1 (two diets are identical). Differences between the values of S_J and S_{Ja} reflect the degree to which individuals differ in their quantitative selection of the prey they share in common. Differences between the values of S_{Ja} and S_{Je} reflect the degree to which the diets of individuals may be undersampled with respect to their true diets (Chao et al. 2005).

The overall mean magnitude of diet similarity ($\bar{S}$) was estimated for each index and site by averaging across all unique pairwise individual-to-individual comparisons (Araújo et al. 2008, 2009). The probability of obtaining mean magnitudes of diet similarity less than or equal to those observed (under the null hypothesis of random selection by all individuals from a common prey pool) was estimated using a nonparametric Monte Carlo procedure (Bolnick et al. 2002).

Time-dependent estimates of individual specialization

The above consideration of the cumulative set of prey observed in each individual's diet represents the maximum extent of time-aggregated sampling. For our study, with observations made on a given individual being aggregated over 140–2,068 days (see "Results"), this is akin to the isotopic sampling of tissues with slow turnover rates. At the other extreme are observations made for an individual within a single foraging bout, akin to the sampling of an individual's gut contents. Thus, to assess the effects of sampling timescale on the inferred magnitude of specialization, we repeated our analysis of each site's between-individual comparisons at the finest temporal scale possible by calculating the pairwise diet similarity of all possible combinations of every otter pair's foraging bouts. The effects of intermediate timescales were assessed by calculating the pairwise similarity of each otter pair's foraging observations after aggregating these by the day (i.e., multiple foraging bouts), week, month, or year in which they were made.

We expected the similarity of each otter pair's prey choices to decline as the time that had elapsed between the diet observations of the two individuals increased. That is, we expected diet similarity to vary with the timescale to which observations were aggregated and with the degree to which aggregations were temporally separated. We therefore fit four models to the similarity scores of each site, index, and level of temporal aggregation. These models described diet similarity (S) by different functions of the time (t; in days) having elapsed between observations:

$$S(t) = \begin{cases} S_0 e^{\lambda t} & M1 \\ S_0 e^{\lambda t} + \mu & M2 \\ S_0 e^{\lambda t + a\ \sin(ft+p)} & M3 \\ S_0 e^{\lambda t + a\ \sin(ft+p)} + \mu & M4 \end{cases}$$

The simplest base model (M1) was an exponential model describing the temporal decline in diet similarity from an initial value of S_0 with a constant proportional rate, λ (i.e., a log-linear decline). The plateauing model (M2) described this decline as asymptotically reaching a constant value $\mu > 0$, reflecting an average minimum similarity to which the diets of individuals declined with elapsed time. The seasonal (M3) and a plateauing seasonal (M4) models corresponded to models M1 and M2 respectively, but allowed for sinusoidal fluctuations in the rate at which diet similarity declined. These models were included because we hypothesized that seasonal variation in individual prey choices, driven either by changes in prey preference or availability, could result in pairs of observations that were made a half year apart being less similar than pairs of observations that were made within the same season of different years. Parameters a, f, and p respectively reflect the amplitude, frequency, and phase of these potential seasonal fluctuations, with the elapsed time t having been transformed to radians ($t = \pi$ days/182.5). Model-fit estimates of S_0 for the two non-plateauing M1 and M3 models, and of $S_0 + \mu$ for the two plateauing M2 and M4 models, reflect the diet similarity of a hypothetical pair of bouts observed at exactly the same time [i.e., $S(t = 0)$, henceforth referred to as "concurrent observations;" see Fig. 1]. These estimates would be equivalent to the time-independent estimates of diet similarity calculated using the cumulative sets of each individual's observations if the similarity of individual prey choices, and thus the inferred magnitude of specialization, did not change as a function of elapsed time (i.e., if $\lambda = 0$).

Model-fitting was performed by constrained nonlinear least squares with each pairwise similarity score weighted by the number of feeding observations of the bout (or aggregated set of observations) having the fewer feeding observations. We constrained S_0, μ, and a to values between 0 and 1, f and p to values greater than or equal to 0, and left λ unconstrained. For temporal aggregations above the day scale, the span of time having elapsed between two aggregated time periods was calculated as the number of days between the starting days of the two time periods (Fig. S2.1). The relative performance of the models in describing time-dependent changes in diet similarity between individuals was compared for each index and aggregation level using the small-sample Akaike information criterion (AICc) with log likelihoods summed across sites (Burnham and Anderson 2002; Hurvich and Tsai 1989). The seasonal models M3 and M4 were not fit to observations aggregated at the annual scale. Although not all model fits reached convergence for all indices and aggregation levels, convergence failures were always manifested as singular convergences. Because the four models are nested, and because singular convergence indicates an over-parameterized model, convergence failure provided complementary evidence for the superior performance of a simpler model.

Time-dependent estimates of temporal consistency

We estimated the temporal consistency of individual diets by quantifying the time-dependent similarity of foraging

Table 1 The overall magnitude of intraspecific diet specialization observed at each study site as quantified by each of four indices of diet similarity using the cumulative set of prey observed in each individual's diet over the entire study period

Index	Monterey Peninsula (MON)			Point Piedras Blancas (PBL)		
	Observed	Expected	p	Observed	Expected	p
S_J	0.41	0.74–0.78	<0.001	0.55	0.72–0.77	<0.001
S_{Ja}	0.48	0.97–0.97	<0.001	0.70	0.98–0.98	<0.001
S_{Je}	0.51	0.98–0.99	<0.001	0.73	0.99–0.99	<0.001
S_{PS}	0.28	0.86–0.88	<0.001	0.38	0.89–0.90	<0.001

Higher similarity indicates a lower magnitude of specialization. Corresponding p-values and 95 % confidence range of expected magnitudes were obtained using a Monte Carlo procedure under the null hypothesis of no individual specialization

S_J Incidence-based Jaccard index (Jaccard 1901), S_{Ja} frequency-based Jaccard index (Chao et al. 2005), S_{Je} frequency-based Jaccard index estimator (Chao et al. 2005), S_{PS} index of proportional similarity (Renkonen 1938; Schoener 1968; Zaccarelli et al. 2013)

observations made for each individual (Fig. 1; Fig. S2.1). These self-similarity scores were calculated for each individual using all pairs of its own sets of foraging observations aggregated by the bout, day, week, month, or year in which they had been made. The four models were fit to each individual's similarity scores as had been done for the between-individual comparisons. Analogous to the between-individual comparisons, each individual's model-fit estimates of within-individual S_0 for non-plateauing M1 and M3 models, and of $S_0 + \mu$ for the plateauing M2 and M4 models, reflect the diet similarity of hypothetically concurrent observations (Fig. 1). Similarly, estimates of λ describe the rate at which an individual's level of diet consistency changed to a potential μ plateau, and estimates of a, f, and p describe temporal fluctuations in this rate of change associated with seasonal variation in prey availability or the individual's preferences for them. The combination of a high S_0 value with either a small value of λ or a high value of μ reflects an individual with a high level of temporal diet consistency.

The relative performance of the models in describing within-individual changes in diet similarity as a function of elapsed time was assessed for each index at each aggregation level using the AICc with log-likelihoods summed across the individuals for which the fitting of the models reached convergence. The seasonal M3 and M4 models were not fit when observations were aggregated at the annual scale. Only individuals having a number of pairwise comparisons exceeding the number of model parameters by more than one were included in model comparisons of each aggregation level. When AICc scores indicated the superior performance of a simpler model, or when the fitting of the more complicated models achieved convergence for only a subset of individuals, we repeated model fitting and comparisons after excluding the more complex models and refit all individuals with only the resultant best-performing converging model. This allowed us to increase the number of individuals for which parameter estimates could be obtained.

Results

A total of 29,128 feeding observations of identifiable prey were made on 42 individuals at MON and 32 at PBL ($n = 146$–861 observations per individual, mean ($\bar{x}$) ±1 SD: $\bar{x} = 393 \pm 166$ SD); eight additional individuals were excluded from analyses due to insufficient sampling as assessed by the visual inspection of individual-specific prey-accumulation curves. Individuals were observed for a total of 7 to 45 bouts ($\bar{x} = 20.4 \pm 8.9$ SD) over a total of 140–2,068 days ($\bar{x} = 640 \pm 364$ SD; MON, 178–2,068, $\bar{x} = 708 \pm 447$ SD; PBL, 140–857, $\bar{x} = 549 \pm 180$ SD) and fed on a total of 42 differentiable taxa (from 6 to 19 per individual, $\bar{x} = 12.1 \pm 3.7$ SD, see Table S4.1 for taxonomic resolution).

Time-independent estimates of individual specialization

The overall mean magnitude of specialization was higher than expected by chance for all indices at both sites when pairwise diet similarity was quantified using the cumulative set of prey observed in each individual's diet over the entire study period (Table 1). While the distributions of between-individual similarities exhibited considerable variation in both populations (Fig. S2.2), estimates of mean similarity (the converse of specialization) were higher at PBL than at MON regardless of the index used. Estimates were more sensitive at PBL than at MON to between-individual differences in the quantitative uses of prey species ($\bar{S}_{Ja} - \bar{S}_J$), but were no different in the degree to which individual diets were under-sampled with respect to their true diets ($\bar{S}_{Je} - \bar{S}_{Ja}$). The overall magnitude of specialization as inferred by the index of proportional similarity ($\bar{S}_{PS}$)

was always higher than was indicated by the three Jaccard indices.

Time-dependent estimates of individual specialization

The similarity of between-individual diet comparisons was dependent on the length of time that had elapsed between two sets of feeding observations. Model M4, which assumed a seasonally varying and plateauing decay in similarity over time, performed best at describing the temporal dependency of between-individual diet comparisons across most indices and non-annual levels of aggregation (12 out of 16 cases; Tables S2.2–2.3). In one of the four exceptions (S_{Ja} with observations aggregated by day) the non-plateauing seasonal model M3 outperformed all others, while in the other three exceptions the non-seasonal plateauing model M2 performed better than the two seasonal models (though only marginally so in two cases, dAICc $\leq$ 5). At the annual scale of aggregation, the plateauing M2 model outperformed the non-plateauing M1 model for all indices.

Parameter estimates of the best-performing models indicate that the average between-individual similarity of concurrent foraging observations, $S(t = 0)$, was always higher at PBL than at MON for all indices (Figs. 2, 3a). The rate at which similarity declined as time between observations elapsed was very small: the model-fit diet similarity of two individuals observed 600 days apart was virtually equivalent to their estimated concurrently observed diet similarity (lower two curves in Fig. 2), and would typically be expected to drop by only 10–25 % if observations were to be separated by half the ~20-year maximum lifespan of sea otter individuals (Fig. 3a, b); only for two levels of temporal aggregation at PBL would diet similarity decline to zero (Fig. 3b). Despite the generally superior performance of plateauing seasonal model M4 at the non-annual scales of aggregation, the amplitude of the seasonal dependence was very small (Fig. 2).

Despite the slow rate at which between-individual similarity decayed over time, time aggregation had a strong effect on the inferred strength of individual diet specialization. Estimates of the between-individual similarity of concurrent observations increased dramatically as aggregation increased (Fig. 3a). Model-estimated concurrent observations aggregated over hours (i.e., bouts) were almost half as similar as when aggregated over a year. This decline in apparent specialization with increased aggregation was particularly apparent in the three Jaccard indices.

Aggregation also affected the extent to which a qualitative vs. a quantitative consideration of prey selection altered the inferred strength of specialization, with increasing aggregation leading to greater estimates of between-individual diet similarity when prey frequency rather than incidence was used ($\bar{S}_{\mathrm{Ja}} - \bar{S}_{\mathrm{J}}$; Fig. 4a). This effect was stronger at PBL than at MON. However, aggregation did not affect the influence of under-sampling with respect to the comparison of each individual's true diet ($\bar{S}_{\mathrm{Je}} - \bar{S}_{\mathrm{Ja}}$; Fig. 4b).

Time-dependent estimates of temporal consistency

Estimates of within-individual diet similarity were also dependent on the length of time having elapsed between two sets of feeding observations. The ability of the four models to describe these temporal changes varied among individuals (Table S.2.4–2.5). The convergence of all four models across all four indices was achieved for only a small subset of individuals at each level of non-annual aggregation (9–14 %). However, AICc model comparisons indicated that for these individuals the non-plateauing seasonal model M3 typically outperformed all other models; only at the week level of aggregation for the proportional similarity index, and at the month level of aggregation for all but the classic Jaccard index, did the plateauing seasonal model M4 marginally outperform M3. Model comparisons performed after removing the most complicated model from the list of candidate models in order to increase the number of individuals for which remaining candidate models reached convergence for all indices always resulted in the next-most complicated model outperforming the others. That is, when model M4 was excluded to increase the combined convergence of models M1–M3 for a larger fraction of individuals (45–60 %), the non-plateauing seasonal M3 model outperformed both non-seasonal models. Similarly, the combined convergence of the non-seasonal M1–M2 models was achieved for many more individuals (68–85 %) when the seasonal M3–M4 models were excluded. In this case the plateauing M2 model always outperformed the non-plateauing M1 model. Model M2 also outperformed M1 when observations were aggregated by year, though the convergence of both models was achieved for only eight individuals since all other individuals had not been observed for a sufficient number of years.

Despite their differing ability to reach convergence for all individuals across all indices and aggregation levels, all four models produced very similar estimates for the self-similarity of the average individual's concurrent observations and the overall rate at which similarity declined with elapsed time (Fig. 2). Even so, the average self-similarity of individuals for whom the non-plateauing seasonal model M3 reached convergence exhibited substantial season-dependent variation (Fig. 2). Diet similarity was highest for observations that were made concurrently or a year apart, and lowest for observations made a half year or more than a year apart. The amplitude of this seasonal dependence was

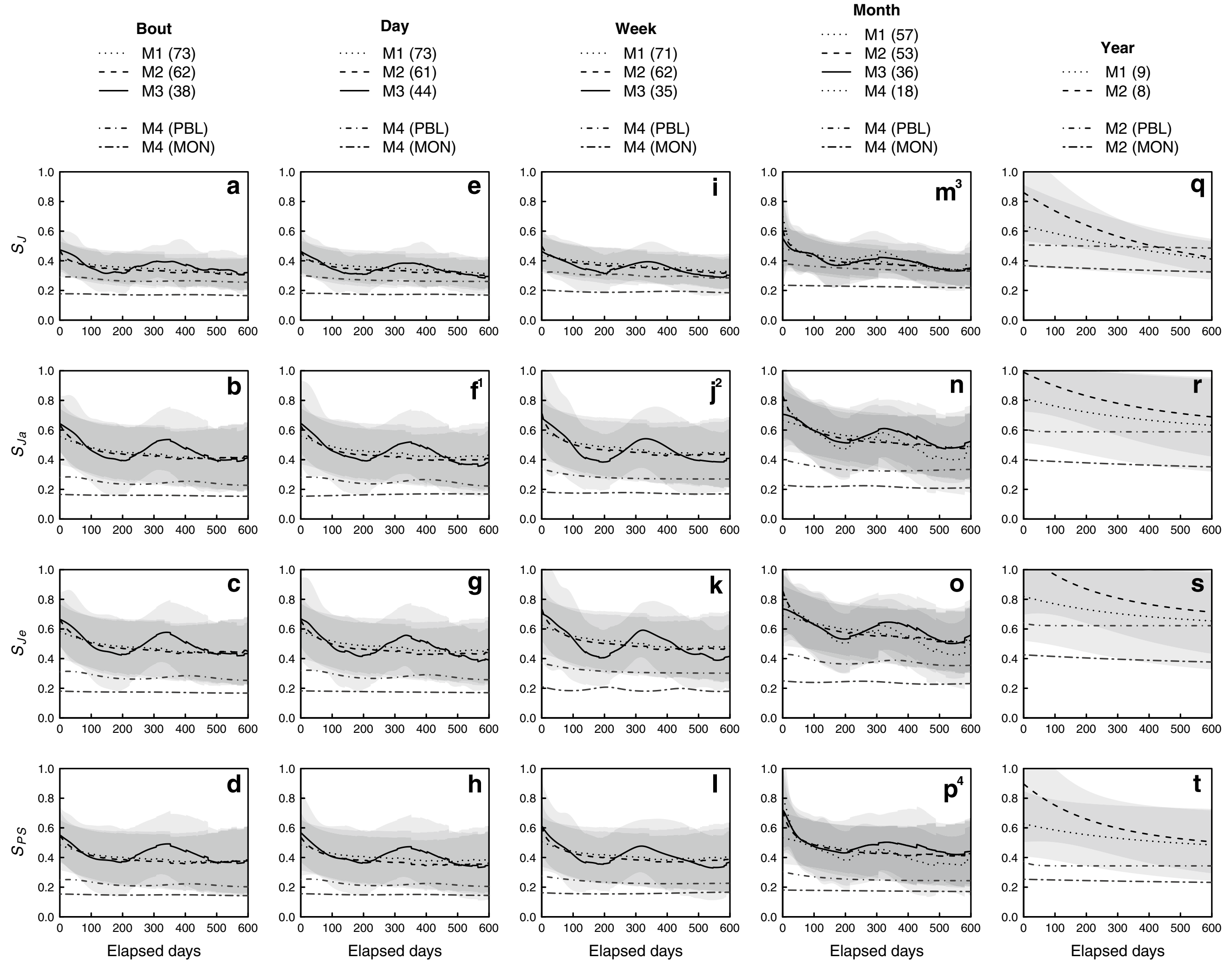

Fig. 2 The time-dependent strength of intraspecific diet specialization and individual diet consistency evidenced by the change in between- and within-individual diet similarity as a function of the time having elapsed between foraging observations. *Cross-column comparisons* reflect the effects of aggregating observations at time-scales of a bout (**a**–**d**), a day (**e**–**h**), a week (**i**–**l**), a month (**m**–**p**), and a year (**q**–**t**). *Cross-row comparisons* reflect the effects of considering diet composition on a presence-absence basis [*row 1* classic Jaccard index (S_J)] vs. a quantitative basis [*row 2* frequency-based Jaccard index (S_{Ja})] vs. accounting for under-sampling [*row 3* frequency-based Jaccard estimator (S_{Je})], or on the basis of proportional diet similarity [*row 4* index of proportional similarity (S_{PS})]. **a**–**t** The *lower two curves* reflect the site-specific magnitude of between-individual similarity as estimated by the best-performing model (the plateauing seasonal M4 model for bout, day, week and month; and the plateauing M2 model for year; see exceptions below). The *higher two to four curves* (corresponding to models M1–M4) reflect the magnitude of within-individual similarity after being averaged across all individuals at each point in elapsed time. The *gray* regions surrounding each of the within-individual curves reflect ±1 SD of the distribution of within-individual similarities at each point in elapsed time. Only the best-performing within-individual model and all simpler models applied to the subset of individuals for which each model reached convergence for all indices are shown (see Table S2.4). *Numbers in parentheses* indicate the number of individuals for which convergence was reached for the within-individual comparisons. Between-individual comparisons are for 42 individuals at the Monterey Peninsula (*MON*) and 32 individuals at the coast between Point Piedras Blancas and Point Estero (*PBL*). Exceptions: in **f** the best-performing between-individual model was the non-plateauing seasonal model (*M3*), while in **j**, **m**, and **p** it was a non-seasonal plateauing model (*M2*) (see Table S2.3 and main text for details)

higher when prey selection was considered quantitatively than when prey incidence alone was considered (Fig. 2).

The within-individual diet similarity of the average individual was always higher than either population's between-individual similarity (Fig. 3a, c), although this was not true for all individuals (see also Fig. S3.2). Indeed, individuals exhibited substantial variation in diet similarity for observations made concurrently or 10 years apart (Fig. 3c, d). Nevertheless, time aggregation had a strong influence on the inferred temporal consistency of individual diets with estimates of the within-individual similarity for concurrent observations increasing as aggregation increased (Fig. 3c).

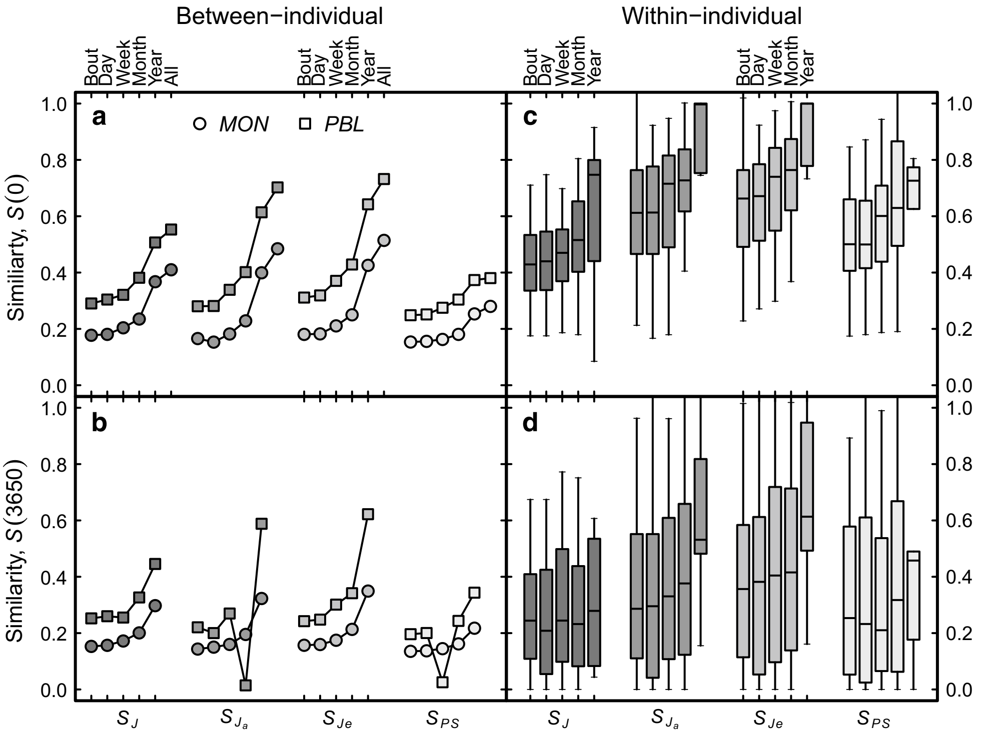

Fig. 3 Time-aggregated sampling increased the inferred strength and temporal consistency of intraspecific diet variation as evidenced by the best-performing model-fit estimates of the **a**, **b** between- and **c**, **d** within-individual diet similarity of **a**, **c** concurrent foraging observations, $S(t = 0)$, or **b**, **d** when observations were to be separated by 10 years, $S(t = 3{,}650)$ (half the maximum lifespan of a sea otter individual). *Boxplots* in **c**, **d** indicate the values of each distribution's median, first, and third quartiles, with *whiskers* extending to the most extreme similarity score that is no more than the interquartile range of the distribution. See Fig. 2 for sample sizes and abbreviations

Aggregation had little influence on the extent to which the frequency vs. incidence of prey ($\bar{S}_{\mathrm{Ja}} - \bar{S}_{\mathrm{J}}$; Fig. 4c), or under-sampling ($\bar{S}_{\mathrm{Je}} - \bar{S}_{\mathrm{Ja}}$; Fig. 4d), altered the inferred magnitude of temporal consistency.

Discussion

The concept of individual specialization is implicitly temporal, yet only few studies have considered the axis of time explicitly. Central to our study is the distinction between the magnitude of individual differences (the converse of between-individual similarity) and the temporal consistency of the individuals' diets (the within-individual self-similarity); genuine specialists are both temporally consistent and different from the rest of their syntopic and contemporaneous population (Fig. 1; Bolnick et al. 2003). Indices of similarity (or dissimilarity) are a natural way to quantify and describe these two aspects of diet specialization, but it is likely that such indices are sensitive to the different methods of quantifying diets (stomach contents, direct diet observations or stable isotope ratios), which reflect differing points on a spectrum of temporal scales. Our analyses of the dive-to-dive foraging decisions of individual sea otters at scales ranging from hours to years show how inferences regarding both the magnitude of individuals' differences and their temporal consistency can be altered by the timing and duration of sampling, and the analytical treatment of observations. These insights suggest a way forward for empirical efforts aimed at disentangling the mechanisms that generate intraspecific variation to understand its consequences for the functioning of ecological communities. We therefore suggest the following guidelines for future empirical efforts:

1. Quantify and report the amount of time that is represented by each diet sample (i.e., the magnitudes of temporal aggregation). For isotope ratios, sample multiple tissues and do not assume that the tissue with the slowest turnover rate is necessarily the most appropriate for describing diet specialization or temporal consistency just because it integrates over the greatest amount of time.
2. Sample concurrently or correct for non-concurrent sampling (i.e., how much time elapses between samples). Estimates of between- and within-individual similarities will provide the most meaningful insights

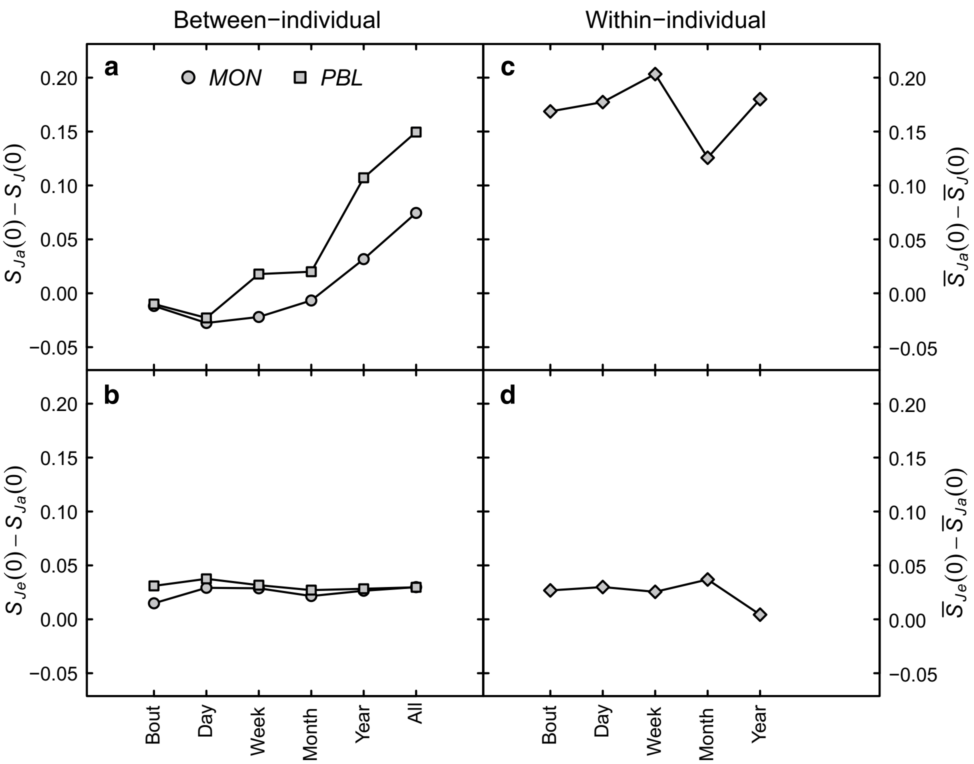

Fig. 4 Differences in the values of the three Jaccard indices for the best-performing models reveal that time-aggregated sampling can alter the importance of considering between- and within-individual diet similarities on **a**, **c** a qualitative vs. quantitative basis ($S_{\mathrm{Ja}}-S_{\mathrm{J}}$), but, in this study, did not affect **b**, **d** the influence of under-sampling with respect to the comparison of each individual's true diet ($S_{\mathrm{Je}}-S_{\mathrm{Ja}}$). Within-individual comparisons in **c** and **d** are averaged across the individuals of both sites. See Fig. 2 for sample sizes and abbreviations

when the observations from which they are calculated are made contemporaneously.

3. Consider potential sources and patterns of temporal variation in individual diets, and sample or account for these accordingly; organisms can experience cyclic patterns at multiple temporal scales which can mask or strengthen estimates of individual variation.
4. Consider both prey incidence and frequency; they provide complementary and synergistic insight into the relative importance of dominant and rare prey to patterns of diet specialization (Tinker et al. 2012). The varied indices that have been developed for quantifying the similarity of two samples each have strengths and weaknesses.
5. Quantify sampling completeness and assess its potential effects not only on statistical power but also on the inferred strengths of diet specialization and temporal consistency.

These five suggestions are explored in more detail in the following sections and are applicable whether measures of individual variation are made on an absolute basis or on a relative basis (e.g., in the contrast of two experimental treatments). Note that, although we used indices of diet similarity in the presentation of our analyses to more easily contrast between- and within-individual diet comparisons, we will henceforth often refer to the effects of temporal scale on the perceived magnitude of specialization using diet dissimilarity to facilitate understanding.

Quantify the magnitude of temporal aggregation

Our analyses indicate that the perceived magnitude of diet specialization of sea otter individuals generally decreased (between-individual similarity increased) as we increased the temporal scale over which foraging observations were pooled. Estimates of concurrent diet similarity were roughly 1.25–two times larger at monthly and annual scales of temporal aggregation than at bout to daily scales (Fig. 3). Thus, as intuition would suggest, estimates of diet specialization derived from stable isotope ratios will tend to indicate less specialization than those derived from snapshot diet surveys or short-term observational data. Indeed, apparent diet similarity differed so much between timescales that the interpretation of magnitudes alone could lead one to infer only weak specialization at the monthly and annual scales but strong specialization at bout or daily scales (e.g., PBL $S_{\mathrm{Je}} = 0.73$ at the annual scale vs. 0.31 at the bout scale; Fig. 3a).

At our focal study sites, where otter population densities and resource competition are high (Tinker et al. 2008, 2012), the magnitude of specialization was statistically significant at even the most coarse level of temporal aggregation when all observations were pooled (Table 1). However, this will likely not be the case in all study systems and highlights the importance of considering time explicitly when comparing across populations and studies. In reviews and meta-analyses (e.g., Araújo et al. 2011; Bell et al. 2009), for example, the inverse relationships that are to be expected between timescales and both the mean and variance of specialization estimates suggest that counts of the incidence of individual specialization across different study systems will hinge on the temporal scales of the included studies. Similarly, studies involving the comparison of two or more experimental treatments should ensure that each treatment's samples span the same time frame.

Sample concurrently

Our results highlight the importance of contemporaneous sampling effort. As was the case for our study, diet surveys are often conducted opportunistically with different individuals being observed or recaptured at different times. This lack of contemporaneous sampling will cause the apparent magnitude of specialization to increase, as diet samples become less similar over time. If logistical constraints prevent contemporaneous sampling, then researchers must quantify the relationship between elapsed time and diet (dis)similarity, and use this relationship to adjust for the potential effects of non-contemporaneous observation periods. We assumed that diet similarity declined in an overall exponential fashion (i.e., at a constant proportional rate). As in models of population growth (Edelstein-Keshet 2005), exponential change may be considered the simplest of first-order approximations to reality; other more complicated relationships between similarity and elapsed time are also conceivable (e.g., Weibull or Gompertz-Makeham forms). Indeed, the most appropriate functional form to describe the temporal dynamics of diet similarity will likely differ between the mechanisms that generate consistency in an individual's diet choices (e.g., memory vs. genetics).

Conversely, the perceived magnitude of an individual's temporal consistency increased with sampling timescales but decreased with the time elapsed between samples. There are a number of mechanisms that could produce such a pattern. For example, individual prey preferences may vary over time, reflecting new learned skills or ontogenetic changes. Conversely, the relative availability of prey may change, reflecting temporal dynamics or spatial variation (β-diversity) through which an individual passes. The effects of these two potential mechanisms will likely saturate across increasing temporal and spatial (γ-diversity) scales in different ways.

In our study, individual otters showed considerable variation in the temporal consistency of their prey selection (Fig. 3c), but the average level of self-similarity remained almost unchanged over ~2 years (Fig. 2) and is extrapolated to have only dropped to no less than 20 % for the average individual after 10 years (i.e., 3,650 days) regardless of index or aggregation level (Fig. 3c, d). Thus, while our data do illustrate a slow decay in temporal consistency over time, most individual sea otters in our study remained considerably more self-similar than the average between-individual similarity of their population, even after multiple years had elapsed (see also Fig. S3.2). The slow rate of temporal decline in consistency is not surprising given the high consistency of the individuals' home ranges and the strong community-structuring effects that sea otters have had at our study sites (Tinker et al. 2008, 2012). This may not be the case for other species, such as species with weak community effects or colonizing species still effecting a change in community structure. This insight highlights another important reason for quantifying the relationship between elapsed time and temporal consistency: it provides a baseline for comparing and interpreting the magnitude of between-individual diet specialization. That is, if there is a period of elapsed time after which the similarity of an individual's within-individual diet comparisons converges on the average similarity of between-individual diet comparisons, then it can be inferred that the individual is a diet specialist only at timescales that are shorter than this amount of elapsed time (see Supplementary Online Material S3).

The overall superior performance of the non-plateauing seasonal M3 model over the plateauing seasonal M4 model may seem to suggest that, for many otters, individual diets no longer exhibit any self-similarity after enough time has elapsed. Although possible, we believe this is unlikely. Instead, we believe this occurred because the rate of decline in similarity is so small over the timescales of our data that there is insufficient power to support the additional plateau parameter. This may also not be the case in other species [e.g., cabbage butterflies (Lewis 1986)] where individuals exhibit diet changes within much shorter periods of time.

Consider temporal variation

All organisms experience daily, lunar, or seasonal cycles that can affect their foraging behavior and diet. The existence of such cycles can be masked by insufficient sample sizes, low sampling frequency, or sampling that reflects too coarse a window of time aggregation. The presence of a cycle could also increase the inferred magnitude of between-individual variation if individuals are observed in different phases of the cycle. In our study, we found strong support for the existence of seasonal cycles in the diet consistency of 19–30 % of the individuals depending on the timescale being considered. The diets of these individuals were more self-similar when sampled 1 year apart than when sampled 6 months apart. These individuals were not studied for longer periods of time than other otters, nor were they observed more frequently (Fig. S2.3–S2.4).

Seasonal cycles likely reflect the increased consumption of one or more preferred prey types at a particular time of year, and may occur in response to prey reproductive cycles that increase prey availability (e.g., Dungeness crabs are more frequently found at shallow depths when they are reproducing) or result in greater energy content and thus profitability when prey are gravid (Oftedal et al. 2007). In sea otters, seasonality expressed itself more weakly in the incidence-based Jaccard index than in the other indices. Thus, although some seasonality can be attributed to a seasonal loss or addition of prey species from the individuals' diets, much more of it is attributable to variation in the relative frequency of prey species.

Whether seasonality in sea otter diets is driven by changes in prey availability or preference cannot be disentangled on the basis of individual diet consistencies alone. However, although seasonality was also evident in the between-individual comparisons with the plateauing seasonal M4 model outperforming all others for most indices and levels of aggregation (Tables S2.2–S2.3), the magnitude of this seasonality was quite small (Fig. 2). This indicates that all individuals did not respond to seasonal variation in prey availability or energy content in the same way. Instead, different individuals' diets fluctuated in different ways, suggesting that the seasonality of within-individuals diets was driven more by temporal variation in prey preferences than prey availability.

That individuals differ in their response to seasonal variation in prey availability or energy content is not surprising given the modular structure of diet specialization that has been reported for these same sea otter populations (Tinker et al. 2012): individuals can be classified into groups (modules) whose members share the same rank-order preferences for the one to three prey types that comprise the core of their diet. Individuals from different modules having different rank preferences are therefore not expected to respond similarly to seasonal changes in the availability or profitability of the prey. This insight has implications for other species as well: temporal variation in diet specialization will be most evident when it reflects variation in universally shared prey, or when strong modularity in individual-resource network structure is recognized and accounted for.

Consider both prey incidence and frequency

A primary advantage of the suite of three Jaccard-based indices is that they may be used to tease apart variation in diet similarities related to differences in prey incidence, frequency, and sampling completeness. For example, magnitudes of diet specialization estimated by considering prey frequency (S_{Je}) were lower at shorter timescales and higher at longer timescales than when estimated by prey incidence (S_{J}) (Fig. 4a). This likely reflects the hierarchical network nature of diet specialization in sea otters, which is not only modular but also nested (Tinker et al. 2012). Specifically, individuals within each module share the same core high-frequency prey, but differ in their selection of peripheral low-frequency prey. The diets of individuals from different modules will therefore be less similar, increasing overall population-level estimates of diet specialization, when similarities are assessed on a frequency rather than an incidence basis at low levels of temporal aggregation. With such modularity, aggregating samples over time will increase frequency-based diet similarities more so than incidence-based similarities because the frequency of commonly selected core prey species increased faster with time than the addition of more rarely selected peripheral prey species. The lack of an effect of aggregation on the relative magnitudes of frequency- and incidence-based similarities for the within-individual comparisons indicates that the relative importance of core vs. peripheral prey in each individual's diet remained constant over time (Fig. 4c).

Of course, a number of other indices have been used to quantify individual diet specialization (e.g., Araújo et al. 2008; Bolnick et al. 2002; Newsome et al. 2012; Zaccarelli et al. 2013). The most commonly used of these include niche-based metrics [e.g., the ratio of the within-individual component of diet composition (WIC) to total dietary niche width of the population (TNW)], the individual specialization index [the mean proportional similarity (PS) of the individuals' diets with their whole population's diet], and the *E*-index (equivalent to $1-S_{\mathrm{PS}}$), though many other measures of overlap and similarity are possible (Jost 2006; Poisot et al. 2012; Wolda 1981). Each of these indices will reflect different aspects of diet similarity which can affect inferences made about its incidence and magnitude (Schatzmann et al. 1986; Wolda 1981). For example, the WIC/TNW and individual specialization indices compare individual diets to the whole population's diet, and will therefore tend to overestimate specialization due to differences in the number of items observed for each individual (Novak, unpublished simulations). Similarly, we found that the between-individual implementation of the proportional similarity index (S_{PS}) resulted in higher estimates of specialization than the Jaccard indices, but was also less sensitive to temporal aggregation (Fig. 3). It thereby behaved most like the incidence-based Jaccard index, being less influenced by the presence of rare, peripheral prey species than the two frequency-based Jaccard indices.

Consider sampling completeness

A final and surprisingly overlooked consideration in studies of diet specialization is the degree to which individual diets have been adequately sampled. While the effect of under-sampling on statistical power is generally recognized, under-sampling will also lead to underestimated magnitudes of similarity (Chao et al. 2005). The difference between S_{Je} vs. S_{Ja} provides a measure of the degree to which under-sampling alters ones inferences. In our study, the difference between these indices was very small (<5 %) and invariant with respect to timescales (Fig. 4b, d), suggesting that under-sampling had little effect on the inferred magnitude and consistency of individual variation (see also Supplementary Online Material S5). However, our data consisted of individuals whose diets had been measured extensively and more or less continuously over multiple years; for many studies such sampling will not be feasible. At a minimum, prey species accumulation curves (or their isotopic equivalents) should be used to evaluate the degree to which sample sizes are sufficient for characterizing each individual's diet. If there are indications of under-sampling or large differences in pairwise sample sizes exist, then indices such as S_{Je} that consider sample-size effects ought to be the preferred measure of within- and between-individual diet similarities.

The issue of sampling completeness also relates to the often-used approach of combining rare, taxonomically difficult, or isotopically indistinguishable prey species into categories. For example, previous analyses of the same data presented here have combined prey species into functional categories of taxonomically and/or morphologically similar species (e.g., Tinker et al. 2008, 2012). As expected, repeating our analyses with such categorization increased the magnitude of concurrent diet similarity, both for between- and within-individual comparisons, but for our data this effect was very small (cf. Fig. 2a–b and Fig. S4.3a–b). The rate at which similarity declined as the time between observations increased was also little affected (cf. Fig. 2c–d and Fig. S4.3c–d). However, prey categorization did have an effect on inferences made using the incidence-based Jaccard index (cf. Fig. S2.2 and Fig. S4.1). As a result, there was a reduced influence of temporal aggregation on the extent to which a qualitative vs. a quantitative consideration of prey selection ($S_{\mathrm{Ja}}-S_{\mathrm{J}}$) altered the inferred magnitude of intraspecific diet specialization (cf. Fig. 3a and Fig. S4.4a). Prey categorization had no discernible effect on the degree to which under-sampling with respect to each individual's true diet altered inferred magnitudes of diet similarity (cf. Fig. 3b, d and Fig. S4.4b, d), or on the inferred length of time that individuals were more self-similar than was the average individual to another (cf. Fig. S3.2 and Fig. S4.5). Studies with fewer diet observations are likely to be more sensitive to the resolution of prey categories.

Conclusion

The foraging observations on sea otters are atypical for their quantity and temporal duration, and may remain so for all but a relatively small number of well-studied populations or species (Araújo et al. 2011). We therefore consider the insights afforded by these data as being informative for the study of intraspecific diet specialization in general. Any meaningful description of the phenomenon of intraspecific variation requires an understanding of how the methods with which it is measured influence our inferences. The results we present here demonstrate that empirical patterns of diet specialization and consistency can, and likely often do, vary across timescales. Just as importantly, our perception of these patterns will also vary as a function of time scale and the degree to which dietary data are time aggregated. Accordingly, we suggest that the explicit consideration of time is not only important for how we compare across studies, but also how we use empirical estimates to parameterize future theoretical models. We anticipate, for example, that index-based measures of individual diet specialization and consistency will form a basis for parameterizing dynamic models of intraspecific variation and its effects on populations and communities, akin to the manner in which such indices have been used to inform models of interspecific competitive interactions (MacArthur and Levins 1967; May 1975). Thus, more than simply understanding the biases of alternative indices and approaches, we need to recognize that any empirical measure will be based on data that are implicitly temporal. Put simply, the timescale of empirical estimates must match the timescale of the model's other parameters. This is not to say that any specific estimate or timescale is inherently more correct or appropriate than another in describing intraspecific variation per se. All may be equally informative given the appropriate consideration of the time frame and degree of time aggregation that the estimates represent.

Author contribution statement MTT and MN contributed to study design and the writing of the manuscript; MTT led the fieldwork, and MN conducted the analyses.

Acknowledgments We are grateful to the many people who contributed to field research and data collection, especially C. Alfano, J. Ames, G. Bentall, J. Bodkin, B. Cummings, G. Esslinger, J. Estes, M. Harris, B. Hatfield, D. Jessup, A. Kage, M. Kenner, C. Lin, D. Monson, M. Murray, T. Nicholson, J. Perry, M. Staedler, J. Stewart,

S. Wolrab and L. Yeates. We also thank D. Bolnick, P. Guimarães, Jr., K. Laidre, J. Yee and two anonymous reviewers for suggestions made on the manuscript. Support for field work was provided by the US Geological Survey, the California Department of Fish and Game, the Monterey Bay Aquarium, the Kenneth S. Norris Rancho Marina Reserve, and a grant from the Minerals Management Service. M. N. received partial support from National Science Foundation OCE-1041454. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

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