ECOLOGY LETTERS

Ecology Letters, (2012) doi: 10.1111/j.1461-0248.2012.01760.x

LETTER

Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters

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Abstract

Studies of consumer-resource interactions suggest that individual diet specialisation is empirically widespread and theoretically important to the organisation and dynamics of populations and communities. We used weighted networks to analyze the resource use by sea otters, testing three alternative models for how individual diet specialisation may arise. As expected, individual specialisation was absent when otter density was low, but increased at high-otter density. A high-density emergence of nested resource-use networks was consistent with the model assuming individuals share preference ranks. However, a density-dependent emergence of a non-nested modular network for 'core' resources was more consistent with the 'competitive refuge' model. Individuals from different diet modules showed predictable variation in rank-order prey preferences and handling times of core resources, further supporting the competitive refuge model. Our findings support a hierarchical organisation of diet specialisation and suggest individual use of core and marginal resources may be driven by different selective pressures.

Keywords

Bipartite networks, diet specialisation, modularity, nestedness, prey preference, sea otter.

Ecology Letters (2012)

INTRODUCTION

Recent literature on consumer-resource utilisation reveals the ubiquity of differences in the diets of individuals, even within animal populations that are otherwise considered to be generalists (e.g. Werner & Sherry 1987; Bridcut & Giller 1995; Baird *et al.* 2000; Bolnick *et al.* 2003; Swanson *et al.* 2003; Dupont *et al.* 2011). Traditional ecological theory has implicitly assumed that such intraspecific variation, often expressed as individual diet specialisations, can be safely ignored for the purposes of studying processes such as niche partitioning (Chase & Leibold 2003) or food web dynamics (Dunne 2006). This assumption has increasingly been challenged, as theoretical explorations have highlighted the potential importance of intraspecific diet variation in affecting the structure and dynamics of populations and their communities (Okuyama 2008; Tinker *et al.* 2009; Araujo *et al.* 2011; Bolnick *et al.* 2011; Schreiber *et al.* 2011). More broadly, there is a growing recognition of the importance of individual ecological differences for the evolution of species, species interactions, and the generation of biodiversity in nature (Pelletier *et al.* 2009). A better understanding of the processes that lead to intraspecific diet variation is needed to determine when, how and to what degree its presence in populations is to be expected.

Conceptual models of the processes leading to individual diet specialisation have been proposed by extending classical optimal diet theory (Schoener 1971; Pulliam 1974) to include phenotypic variation in predator foraging efficiency and thus diet assembly rules (Robinson & Wilson 1998; Svanbäck & Bolnick 2005). As with the earlier models, individuals are assumed to prefer one prey type over another if it is more profitable, as measured by the ratio of energy gain to handling time. However, because individuals can vary with respect to traits that affect handling efficiency or capture success of a particular prey, and because there are often associated trade-offs between traits (e.g. a trait that improves handling efficiency of small prey may reduce capture success for large prey), the rank order of prey preferences can vary among individuals (Svanbäck & Bolnick 2005; Tinker *et al.* 2008). Three distinct hypotheses about how intraspecific specialisation may arise correspond to alternative models of how individual's vary in their prey preferences, and their likelihood of adding low-ranked resources to their diets (Svanbäck & Bolnick 2005). In the shared preference model, all individuals exhibit identical rank-order preferences for their suite of resources, but differ in their likelihood of including low-ranked resources in their diets when competition for high-ranked resources is high. In the competitive refuge model, individuals share the same high preference for optimal resources, but differ in their preference ranking of sub-optimal resources. Finally, in the distinct preferences model, individuals vary in the ranking of their preferences for optimal resources as well. Although these models do not encompass all possible patterns of individual variation in rank-order

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preferences, they represent a useful starting point for exploring how individual foraging decisions can scale up to intraspecific diet variation. An appealing feature of these models is that each is associated with predictions about how variation in diet among individuals is affected by resource availability (Svanbäck & Bolnick 2005, 2007; Pires *et al.* 2011).

Network analysis has proven to be an effective tool for linking theoretical models with empirical data on individual resource-use patterns (Araújo *et al.* 2010; Dupont *et al.* 2011; Ramos-Jiliberto *et al.* 2011), much in the same way that it has been used for linking food web models with data on species-level resource-consumer interactions (reviewed by Pascual & Dunne 2006). The network approach interprets individual-resource interactions as a bipartite network in which two set of nodes, one representing individual consumers and the other representing their prey resources (Pires *et al.* 2011), are connected by links to reflect the utilisation of each resource by each individual (Fig. 1). Network analysis includes three descriptive measures of a network's structure of direct interest for models of individual diet choice: nestedness, modularity and the average density of connections (Araújo *et al.* 2008, 2010). Nestedness occurs when the prey species utilised by the individuals with the least diverse diets are a nested subset of the prey utilised by individuals with more diverse diets. A network exhibits modularity if it is possible to segregate individuals and their resources into different groups (modules), such that there are resources shared by individuals within the same module, but few (or no) resources shared by individuals from different modules. The average density of connections refers to the degree of diet similarity between individual consumers.

Competition-dependent changes in nestedness and modularity can be used to distinguish between alternative predictions of the three models described elsewhere (Pires *et al.* 2011). For instance, the shared-preferences model predicts that a nested network structure should emerge under high competition (Fig. 1a–b, Bascompte *et al.* 2003; Araújo *et al.* 2010). In contrast, the competitive refuge model predicts that increases in competition should lead to the emergence of a modular network structure (Fig. 1c–d, Araújo *et al.* 2008). Modularity is also predicted by the distinct preferences model, but only when resources are abundant and intra-specific competition is low (Fig. 1e–f). The structure of empirical individual-resource networks therefore provides insight into the processes that generate observed levels of intraspecific diet specialisation.

A number of empirical tests of theoretical models of individual specialisation have been conducted to date, using a variety of taxa and study systems (Araújo *et al.* 2010; Pires *et al.* 2011). These previous tests have demonstrated the power of network analysis to describe individual resource-use patterns, but they have mostly been qualitative in nature, examining only the presence or absence of each prey type in an individual's diet. Yet the foraging decisions of individual predators are rarely absolute, and in most populations it is the relative utilisation of resource types that differs among individuals. Herein, we apply quantitative extensions of network analysis that take into account not only the qualitative structure of the network but also the quantitative strengths of the links. We present a new approach for examining how patterns of nestedness and modularity vary among individuals when diets are filtered by prey importance (defined as the relative contribution to total consumed biomass). We also evaluate correlations in the rank order of prey utilisation by individuals, to test whether observed patterns of nestedness or modularity are driven by shared (or divergent) prey preferences, as predicted by theory (Svanbäck & Bolnick 2005; Pires *et al.* 2011). We apply this approach to an extensive dataset on diets of southern sea otters (*Enhydra lutris nereis*). Sea otters are keystone predators in near-shore marine ecosystems of the north Pacific (Estes & Palmisano 1974), and have been shown to exhibit pronounced individual diet specialisation in the high-density populations of central California, but not in a low-density population of southern California (Estes *et al.* 2003; Tinker *et al.* 2008).

Our objectives were to use quantitative analyses of individual-resource networks to determine (1) the support for the three alternative models of diet specialisation, (2) the role of density-mediated trade-offs in shaping patterns of resource partitioning in sea otters and (3) whether observed individual differences in prey preference rankings correspond to differences in prey handling efficiency.

METHODS

Field sites and data collection

Data on prey utilisation by southern sea otter individuals were collected from three study sites in California between 2001 and 2007: Monterey peninsula (MON), the coast between Pt. Piedras Blancas and Pt. Estero (PBL), and San Nicolas Island (SNI; see Fig. S1 in Supporting Information). All three study sites are characterised by similar, predominantly rocky-bottom kelp-forest habitats, but whereas the MON and PBL populations exhibit high-sea otter densities (5.7 otters·km^{-1} ± 1.24 and 3.7 otters·km^{-1} ± 1.06, respectively), the more recently established and still growing population at SNI has a lower density (0.8 otters·km^{-1} ± 0.13) and greater abundance of prey resources (Tinker *et al.* 2008). We captured 58, 47 and 25 individuals from these populations respectively, tagging and subsequently monitoring each by radio telemetry for 1–5 year periods. Individuals were located 3–7 times per week by shore-based observers and, as possible, observed for contiguous sequences of ≥ 20 feeding dives (henceforth referred to as feeding bouts) to record the identity and size of captured prey using 50–80× power spotting scopes (Questar Corporation, New Hope, PA, USA). The dive duration and prey handling time (the at-surface time required to process and consume a captured prey item) was also recorded. Individuals at each site had largely overlapping annual home ranges (Tinker *et al.* 2008), and thus similar access to foraging micro-habitats and prey types over the period of data collection.

To obtain quantitative measures of each prey's contribution to an individual's diet, counts of prey frequency and size were converted to estimates of biomass as follows. First, we collected, measured, and weighed the edible and in-edible components of each potential prey taxon observed in the sea otter diet (10–50 items per taxon) to generate power functions for converting prey diameter to wet edible biomass (Oftedal *et al.* 2007). These were incorporated into a Monte Carlo procedure used to estimate each individual's diet composition in terms of the proportion of consumed biomass contributed by each prey taxa (Tinker *et al.* 2008). This procedure served to quantify sampling uncertainty and adjust for a number of recognised biases associated with shore-based observations of sea otter diets (Appendix S1). To account for inconsistencies in the taxonomic resolution of prey capture records, all prey items were subsequently classified into 14 distinct functional groups of taxonomically and/or morphologically similar species (Table S1).

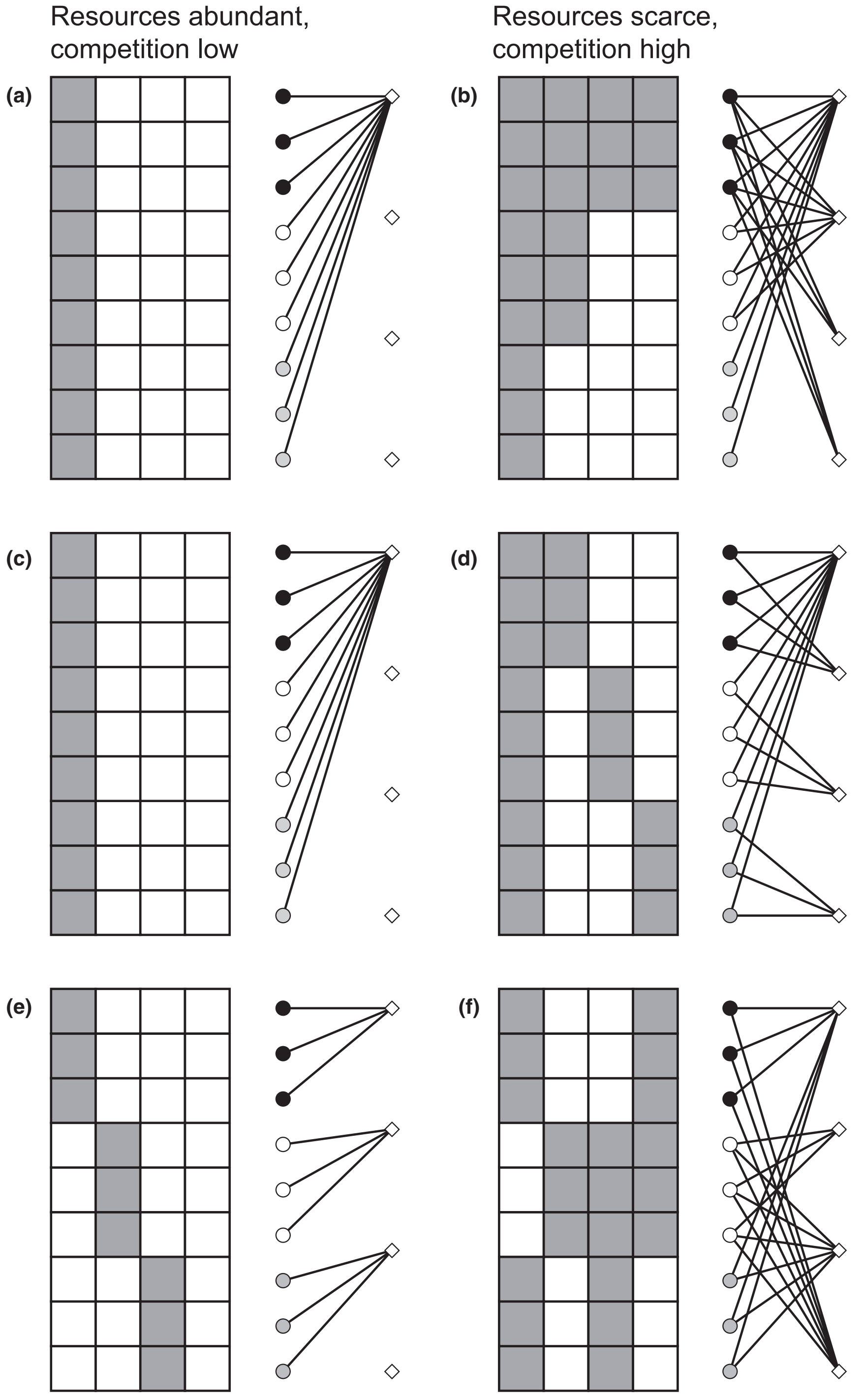

Figure 1 Individual-resource networks predicted by three distinct models of the processes leading to intraspecific diet variation, when resources are abundant (a, c, e) and when resources are scarce (b, d, f). Predictions are shown for (1) the shared-preferences model (a, b), (2) the competitive refuge model (c, d) and (3) the distinct preferences model (e, f). For each combination of model and resource abundance, predicted network structure is shown in matrix form (with individuals as rows, prey types as columns and filled cells indicating feeding links) and as node diagrams (with individuals as circles, prey types as diamonds and connecting lines indicating feeding links). Symbol-matched individuals in node diagrams share resources, rank preferences, and degree of specialisation.

Patterns of individual resource-use variation

To ensure that within-site dietary differences represent differences in prey preference rather than differences in the array of habitats or the abundance of various prey available to different individuals, we restricted our analyses to 28, 35 and 11 adult study animals at each site having largely overlapping home ranges and a minimum of 300 recorded feeding dives spanning > 1 years (Tinker *et al.* 2008; Johnson *et al.* 2009). Using previously described methods (Roughgarden 1972; Bolnick *et al.* 2002; see Appendix S2 for equations, computer program links and/or source code for all reported statistics), we quantified: (1) each population's total diet variation (its total niche width, TNW_S), (2) each individual's diet variation (the within-individual component, WIC_S) and (3) the proportion of each population's TNW_S contributed by within-individual variation (WIC_S/TNW_S). The ratio WIC_S/TNW_S approaches one when all individuals utilize the full population niche width, whereas values significantly less than one indicate niche partitioning (diet specialisation) by individuals. To account for differences in sample size between study sites, we used a bootstrap re-sampling routine to calculate niche statistics: specifically, for each site we drew (with replacement) 10 000 random samples of 11 individuals (the number of individuals studied at SNI, the smallest sample size), and used the bootstrapped sample distributions to calculate the mean, standard error and 95% confidence intervals (CI_{95}) for WIC_S/TNW_S.

Weighted measures of individual-resource network structure

For each population we compiled the records of individuals feeding on resources into an individual-resource matrix ($\mathbf{R}$), with individual otters as rows and resources as columns. The $\mathbf{R}$ matrix defines a network in which individual otters and prey types are depicted as different sets of nodes, and links connect individual otters to each of their recorded prey types (Pires *et al.* 2011). A quantitative version of the network is represented by the matrix $^{\#}\mathbf{R}$, where each cell represents the proportional biomass contribution of resource *j* to the diet of individual *i*, such that $0 \leq {^{\#}r_{ij}} \leq 1$.

We used weighted indices to describe population-wide patterns of the density of connections, nestedness and modularity in the $^{\#}\mathbf{R}$ networks from MON, PBL and SNI. The average density of connections was quantified for each site using the E index of Araújo *et al.* (2008), where E is 1 minus the average pairwise similarity of individual diets and varies from 0 (all individuals exhibit identical diets) to 1 (all individuals differ completely in their diets). Degrees of nestedness were quantified using the *WNODF* metric (Almeida-Neto & Ulrich 2011), a recent extension to the qualitative *NODF* metric of nestedness (Almeida-Neto *et al.* 2008) that takes into account the quantitative information for each interaction (Appendix S2). Both nestedness indices vary from zero (no nestedness) to 100 (perfect nestedness). Degrees of modularity were quantified using the weighted clustering coefficient (*WCC*) developed for bipartite networks (Opsahl & Panzarasa 2009). This index varies from 0 (no modularity) to 1 (high modularity).

Although patterns of nestedness and modularity may be used to distinguish between the hypothesised processes generating individual variation (Fig. 1), some level of diet variation is expected even if individuals are sampling the entire population niche randomly. Therefore, we determined the probability of observing the degrees of nestedness, modularity and density of connections seen in the empirical $^{\#}\mathbf{R}$ networks by comparing them to distributions of these scores generated for each population by random sampling (Araújo *et al.* 2008). We did so using a bootstrapping procedure that randomly distributed the number of dives recorded for each individual among the different resources, assuming that the probability of individual *i* obtaining a given resource on a given dive was proportional to the average contribution that this resource's biomass made to the population's diet ($n = 100$ iterations). Empirical degrees of E, *WNODF* and *WCC* were deemed statistically significant if their value occurred with < 5% frequency in the randomly generated distributions.

Fractional analysis of individual resource-use networks

Weighted indices offer single measures of nestedness and modularity in the individual-resource networks, that take into account the entire quantified diets of sampled individuals. However, these indices cannot reveal the degree to which the detected patterns reflect individual differences in utilisation of 'core' prey types ($^{\#}r_{ij} \rightarrow 1$) or of 'marginal' prey ($^{\#}r_{ij} \rightarrow 0$). To disentangle the contributions of core and marginal prey types to the patterns of nestedness and modularity, we performed a fractional diet composition analysis (FDCA). FDCA reveals how qualitative resource-use patterns vary as one shifts focus from the entire diet to just the core resources used by each individual, and is accomplished through sequential examination of a series of qualitative networks (similar approaches have been used for analysing other weighted networks; Perez *et al.* 2009; Novak *et al.* 2011). Specifically, for each individual we sorted resources in decreasing order of their dietary contribution and considered just those resources whose cumulative contribution represented a specified fraction, *f*, of the diet (Fig. 2). The resulting network of remaining resources was then expressed in binary form ($^{\circ}\mathrm{R}$, with elements $^{\circ}\mathrm{r}_{ij} = 1$ if resource *j* is a core resource and $^{\circ}\mathrm{r}_{ij} = 0$ otherwise) to characterize qualitative patterns of nestedness and modularity. Varying *f* from a value of 1 (i.e. all resources) to 0.1 (i.e. the core 10% of resources), we calculated indices of nestedness and modularity for each fractional sub-set of the diet.

Patterns of nestedness in the qualitative $^{\circ}\mathrm{R}$ networks were measured using the *NODF* index implemented in the programme ANINHADO (Guimarães & Guimarães 2006). We measured patterns of modularity in the $^{\circ}\mathrm{R}$ qualitative networks using the M statistic (as described by Guimerà & Amaral 2005), where putative modules are identified by a simulated annealing algorithm, $M \rightarrow 0$ if there is no modularity (the probability that two nodes interact is just as high for nodes within a module as it is for nodes in different modules) and $M \rightarrow 1$ if there are multiple modules with many links connecting nodes within a module and few links connecting nodes in different modules (Appendix S2). To test if the patterns of nestedness and modularity present in the qualitative networks were larger than expected by simple random variation of individual diets, we compared the measured values of M and *NODF* to the distribution of randomised theoretical networks, using the same algorithm described elsewhere for weighted indexes ($n = 100$ iterations for each combination of site and *f*). Because both M and *NODF* might be affected by small sample sizes and changes in the proportion of observed interactions, we repeated all calculations and randomisation tests using a boot-strap resampling routine to control for differing sample sizes, as described above for analysis of niche statistics ($n = 100$ bootstrap samples for each site), and computed the 95% bootstrap confidence intervals at each site assuming an equal sample size of $n = 11$ individuals.

To examine the mechanistic basis for patterns of modularity and nestedness, we measured the degree to which individuals within each population shared similar prey preferences and prey foraging skills. Note that feeding observations provide information on prey utilisation, not prey preference, but because individuals at each site experienced similar prey availability at the temporal scale of our study (years) we can assume that rank-order differences in prey utilisation reflect underlying differences in relative prey preferences. To assess patterns of shared-prey preferences, we calculated Spearman's rank order correlation ($-1 < \rho < 1$) of resource contributions for all pairs of otters within each site. We contrasted the distribution of

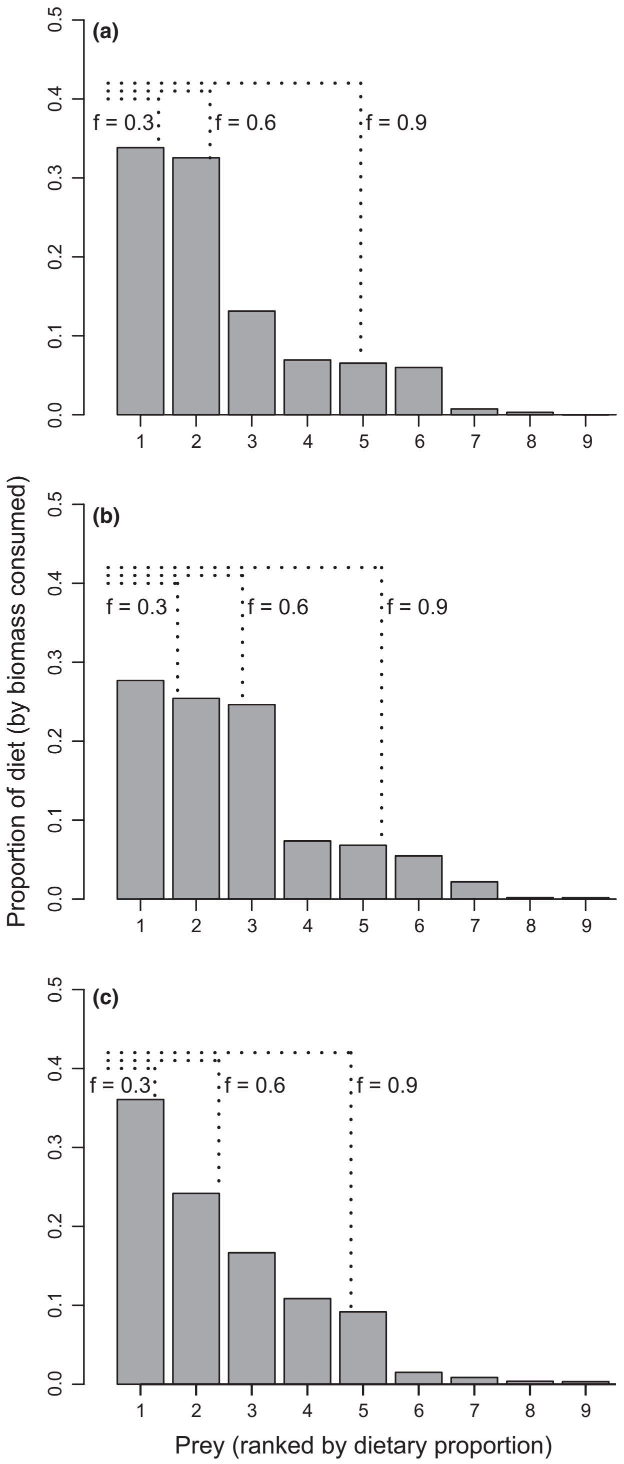

Figure 2 Diet histograms for 'average' individual sea otters at SNI (a), PBL (b) and MON (c) study sites. Contributions of prey types to individual diets were estimated and ranked in decreasing order of importance for each individual. Dashed lines delineate fractional sub-sets of each diet, excluding marginal prey types and retaining the top 90% ($f = 0.9$), 60% ($f = 0.6$) and 30% ($f = 0.3$) of consumed prey biomass. For example, 60% of the diet of an average individual at SNI (A) is made up of just two prey types.

pairwise correlations for members of the same module with the pairwise correlations of individuals belonging to different modules, repeating this comparison for each f-dependent qualitative matrix generated by the FDCA. We calculated correlation coefficients in two ways: (1) by including all resources on which the population was observed feeding (ρ_{all}) and (2) by including only resources shared between pairs of individuals (ρ_{sh}), discarding resources fed upon by only one or neither individual of each focal otter pair. This allowed us to disentangle similarities of rank preferences for core resources from similarities in preference for core vs. marginal resources.

Finally, to test whether differences in prey preference rankings reflected differences in individual foraging skills for alternative prey types, we compared prey-specific handling efficiency (handling time^{-1}) among individuals from different modules. Specifically, we tested the prediction that individuals assigned to modules whose core diet includes a particular prey ('specialists') exhibit greater handling efficiency than individuals assigned to modules whose core diet does not include that prey ('occasional users'). We focused only on those prey types that occurred in the core diets ($f = 0.3$) of the individuals at PBL and MON (as SNI individuals exhibited no modularity for core prey), and used a general linear model (GLM) to compare recorded handling times between specialists and occasional users. The GLM controlled for prey size effects and included individual otters as random effects (individuals were nested within core diet type).

RESULTS

We recorded a total of 63 701 feeding dives from 74 tagged otters, although sample sizes varied between populations as a result of logistical constraints and population sizes (25 269 dives from 28 otters at MON, 33 050 dives from 35 otters at PBL, and 5382 dives from 11 otters at SNI). Even after accounting for differences in the number of individuals and dives, population-level niche width (TNW_S) was significantly greater at MON (2.04, CI_{95} = 1.83–2.21) and PBL (1.80, CI_{95} = 1.53–2.07) than at SNI (1.04, CI_{95} = 0.76–1.30). Nevertheless, in contrast to SNI, most individual otters at MON and PBL were diet specialists that typically relied on just 2–3 prey types for the bulk of their diet (Fig. 2), so that the proportion of total niche width comprised of within-individual diet variation (WIC_S/TNW_S) was relatively low at MON (0.62, CI_{95} = 0.52–0.71), slightly higher at PBL (0.69, CI_{95} = 0.58–0.81), and much higher at SNI (0.85, CI_{95} = 0.80–0.92).

The average network density of connections varied significantly between sites: sea otters at the MON site showed a high degree of pairwise diet dissimilarity ($E = 0.679$, $E_{null} = 0.061 \pm 0.003$, $P < 0.01$), three times higher than at SNI ($E = 0.247$, $E_{null} = 0.045 \pm 0.005$, $P < 0.01$). Individuals at PBL showed an intermediate degree of diet dissimilarity ($E = 0.521$, $E_{null} = 0.058 \pm 0.003$, $P < 0.01$). The MON and PBL populations exhibited degrees of weighted nestedness that were higher than expected if individuals were randomly sampling the population niche, but the degree of weighted nestedness observed at SNI was not significant (Table 1). In contrast, all populations exhibited evidence for higher weighted modularity than expected by chance (Table 1).

The FDCA revealed differences in how individuals selected core and marginal resources, and how these patterns varied with population density (Fig. 3). When all resources were considered ($f = 1$), individuals at all three sites exhibited a nested pattern of diet selection ($NODF > 40$ at all sites) and relatively low levels of modularity ($M < 0.2$, Fig. 3a–c). Increasing focus on just the core resources used by each individual ($f < 1$) caused patterns of nestedness and modularity to change in similar ways at PBL and MON, with nestedness decreasing and modularity increasing to high levels ($M > 0.6$) as f was reduced (Fig. 3b–c). When $f = 0.3$, individuals were partitioned into seven (PBL) or eight (MON) modules, with all members of a module feeding on the same one or two core resources. The six largest modules at both PBL and MON were defined by the same six prey types: purple urchins, abalone, Cancer crabs, kelp crabs, marine snails and clams (Table S1). At the low-density site (SNI), both nestedness and modularity declined to 0 as f was reduced, with all individuals utilising the same core resource (red urchins), and assigned to a single module, when $f < 0.4$ (Fig. 3a). These site-specific patterns were consistent even after controlling for sample-size differences among sites (Fig. S2). The correspondence of empirical resource networks (Fig. 4) to alternative theoretical networks (Fig. 1) thus depended on what fraction of the diet was being considered.

All populations exhibited positive (negatively skewed) distributions in the pairwise correlations of their individuals' rank preferences when all resources were considered (mean $\rho_{\text{all}} > 0$ at $f = 1$, Fig. 3, Table S2). Individuals within the same module had more similar rank preferences than did individuals of different modules, although at PBL this was only marginally significant (Table S3). At MON and PBL the difference between within-module and between-module correlations increased as marginal resources were removed ($f < 1$); individuals within the same module exhibited increasingly similar rank preferences for their core resources, whereas individuals from different modules exhibited increasingly weaker correlations in rank preferences (Fig. 3e, f). The pattern at SNI differed in that the between-module correlations did not decrease with f (Fig. 3d), and in fact no between-module comparisons remained when $f < 0.4$ because all individuals belonged to the same module and exhibited precisely the same rank preferences ($\rho_{\text{all}} = 1$). The distributions of shared-prey correlations (ρ_{sh}) exhibited significantly larger ranges than did those of the all prey correlations, with a large number of individuals exhibiting only weak (SNI) or even strongly negative (MON and PBL) correlations in their rank order preferences for shared prey even when they were part of the same module (Table S3).

Table 1 Summary statistics for the weighted indices of nestedness (*WNODF*) and modularity (*WCC*) calculated for sea otter individual-resource networks at three study sites

	Nestedness			Modularity		
Study site	$WNODF_{obs}$	$WNODF_{null}$	*P*-value	WCC_{obs}	WCC_{null}	*P*-value
MON	38.60	4.66 ± 3.22	< 0.01	0.227	0.072 ± 0.001	< 0.01
PBL	40.34	28.67 ± 1.96	< 0.01	0.177	0.071 ± 0.001	< 0.01
SNI	27.27	27.41 ± 6.53	0.55	0.547	0.144 ± 0.012	< 0.01

Null model values presented for comparison represent the mean ± one SD of randomisation simulations, as described in the text, with the *P*-values representing the probability that the observed values come from the null model distributions.

Differences in prey handling efficiency among individuals belonging to different core diet modules at PBL and MON were consistent with theoretical expectations in the case of four of the six most frequently utilised prey types (Table S4). Specifically, specialists had significantly faster handling times than did occasional users in the case of kelp crabs ($F = 23.21$, $P < 0.0001$), urchins ($F = 6.78$, $P = 0.0097$), marine snails ($F = 4.66$, $P = 0.0325$) and clams ($F = 12.18$, $P = 0.0005$). On average, specialists for a given prey type could handle and consume 43% more prey per unit time than occasional users. Differences in handling efficiency were not significant in the case of Cancer crabs ($F = 0.44$, $P = 0.5053$) and abalone ($F = 0.23$, $P = 0.6307$).

DISCUSSION

For sea otter populations in California, niche width varies negatively with resource abundance (Tinker *et al.* 2008), in agreement with basic

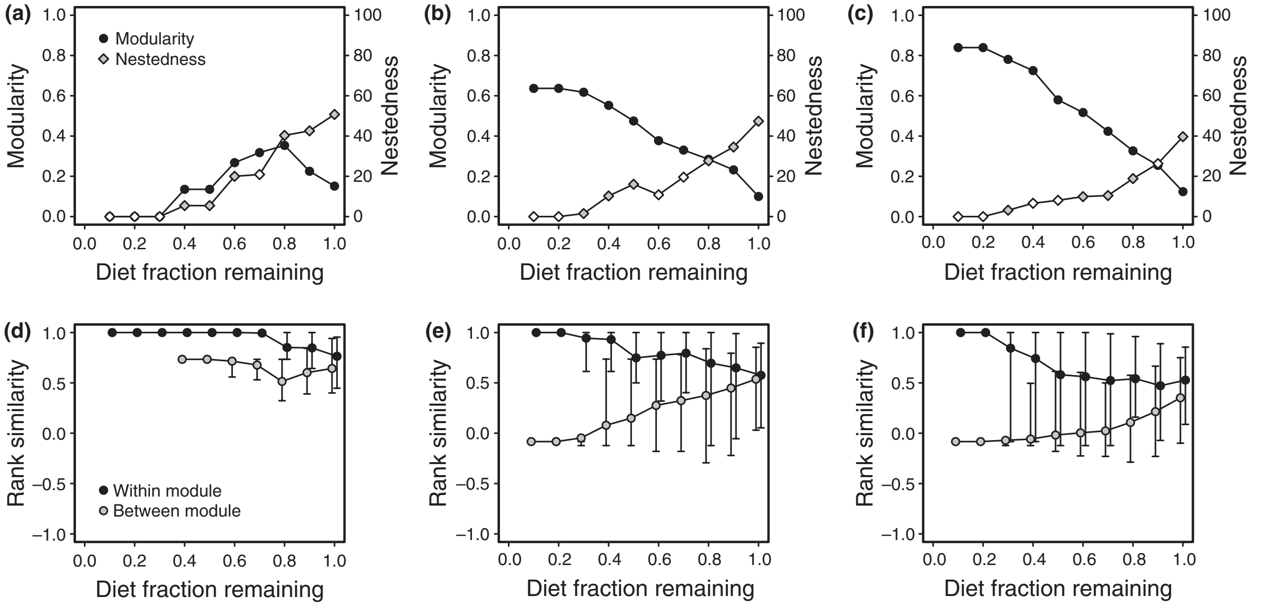

Figure 3 Results of fractional diet composition analysis (FDCA) for sea otters at SNI (a, d), PBL (b, e) and MON (c, f). Top panels (a–c) show variation in two indices of network structure as a function of the fraction (f) of the diet considered, with marginal prey types excluded when $f < 1$. Filled symbols indicate significant structural patterns (based on comparison to randomised null matrices), whereas open symbols indicate non-significant values. Bottom panels (d–f) show variation in pairwise similarities in the rank ordering of prey preferences as a function of f, with Spearman correlation coefficients calculated for pairs of individuals belonging to the same dietary module (solid circles) and pairs of individuals from different modules (grey circles).

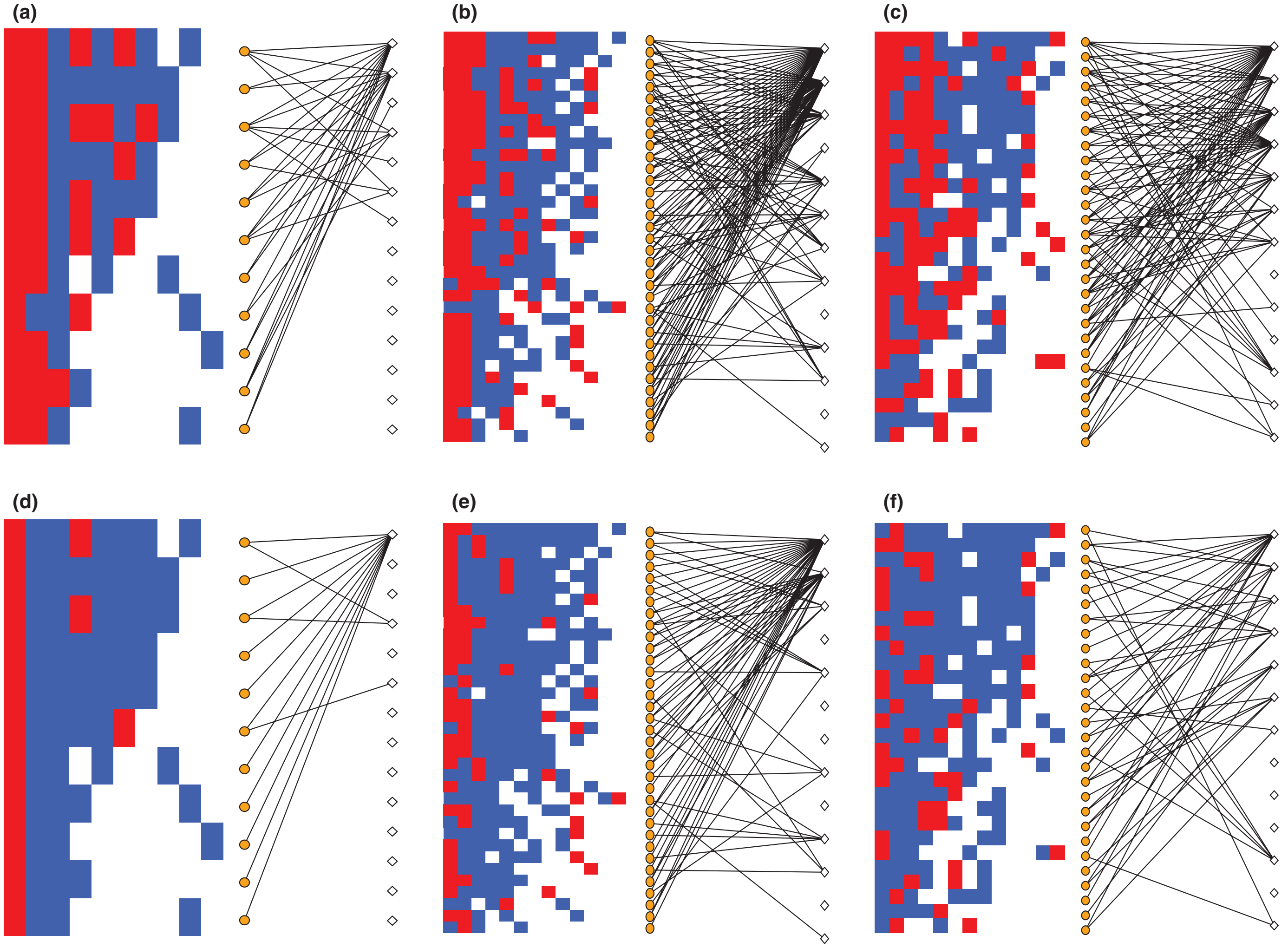

Figure 4 Graphical representation of individual-resource networks for sea otters at SNI (a, d), PBL (b, e) and MON (c, f). Network structure is shown for fractional sub-sets of individual diets at each site, excluding marginal prey types and retaining the top 90% (a–c) and 60% (d–f) of consumed prey biomass. Each panel depicts a unique combination of study site and diet fraction (*f*), for which network structure is shown in matrix form (on left of each panel) and as node diagrams (on right of each panel; see Fig. 1). In matrix representations, red cells indicate individual-resource links occurring at the specified value of *f*, whereas blue cells indicate individual-resource links occurring when $f = 1$.

predictions of optimal diet theory (Schoener 1971; Pulliam 1974). At the SNI site most individuals tend to utilize the full population niche (represented by high values of WIC_S/TNW_S) and have similar diets (represented by a low value of E). At high-density sites (MON and PBL) there is greater population-level niche width and a lower WIC_S/TNW_S ratio, reflecting greater diet dissimilarity among individuals (higher values of E). While alternative explanations for the differing patterns of diet variation at SNI as compared with MON and PBL cannot be definitively ruled out because our data includes only one low-density site, several lines of evidence – including the similarity between sea otter diets at SNI and sea otter diets at several central California sites surveyed shortly after their re-colonisation in the 1970s (Estes *et al.* 1981; Ostfeld 1982; Fig. S3) – suggest that a process of density-mediated competition for preferred prey is the most plausible explanation (Appendix S3).

The pairwise diet dissimilarity at MON and PBL was accounted for in part by individual variation in propensities to consume low-value prey types, and was reflected in significant nestedness of quantitative resource-use networks (less-diverse diets were sub-sets of more diverse diets). The density-dependent emergence of nestedness is consistent with predictions of optimal diet theory under a shared-preferences model. In contrast, the weighted indices of network modularity were also highly significant at the high-density sites, a pattern more consistent with the competitive refuge model (Araújo *et al.* 2010). Using FDCA allowed us to resolve the apparently contradictory results of weighted network analyses. When all prey types are considered, qualitative individual-resource networks at all sites exhibit nestedness consistent with the shared-preferences model. Excluding marginal prey types caused a reduction in nestedness in all three populations, and modularity to decline in the low-density population (because all individuals shared the same highest-ranked prey type as their core diet component), but increase in the medium and high-density populations, consistent with the competitive refuge model. The strong modularity that emerged in the high-density populations at low values of *f* reflects clusters of individuals specialising on alternative suites of resources for their core diets. Thus, diet specialisation in sea otters can be viewed as supportive of either the shared-preferences model or the competitive refuge model, depending upon whether one considers all prey or just those prey species that comprise the majority of the biomass/energy consumed.

The shared-preferences model is appropriate for describing individual variation in utilisation of low-ranked prey, and is consistent with the fact that correlations between individual prey preference rankings were highest at SNI when marginal prey were excluded. However, as competition for resources increases and individuals become more skilled at handling secondary prey types (through experience and/or social learning), they may lose (or fail to develop) foraging skills for other prey types (Svanbäck & Bolnick 2007; Tinker *et al.* 2008). The inevitable outcome of these trade-offs is the diversification of individual core diets into modules (Araújo *et al.* 2008), each corresponding to an alternative set of prey preference rankings. This scenario, predicted by the competitive refuge model, is supported by the fact that that prey preference rankings were positively correlated within, but not between modules at the high-density sites.

Differences in prey preference rankings by individual sea otters presumably correspond to differences in the realised profitability of 'less-optimal' prey types. Indeed, individuals belonging to four of the modules at both PLB and MON exhibited substantially greater foraging efficiency for their preferred prey as compared with individuals from other modules. While similar differences in foraging efficiency were not evident for Cancer crabs or abalone, it is noteworthy that foraging success for these larger and more cryptic prey is less dependent upon at-surface handling efficiency than on the ability to locate and extract items from sub-tidal crevices (i.e. cryptic habitats), parameters that were not directly measurable by our observational techniques (Tinker *et al.* 2008).

Interestingly, at low values of f we found that the rank correlations of shared prey were often negative for within-module pairwise contrasts. This result was unexpected, and indicates that differences in prey ranking can occur even among individuals that specialize on the same core diets. That is, if two individuals in the same module both rely on prey types A and B for the majority of their consumed biomass, there is a high likelihood that one will show a preference for A over B, whereas the other will prefer B over A. This finding points towards a hierarchical interpretation of resource use by sea otters, whereby individuals that cluster together based on correlated prey preferences at one level (preferring prey types A and B vs. prey types C and D), may be further sub-divided based on secondary prey preference rankings (preferring prey type A over B). We suggest that future studies should investigate how general this pattern is across animal populations.

The more nuanced views of network structure revealed by FDCA highlight the complexity of resource partitioning at the individual level, and suggest that multiple trade-offs, driven by different selective forces, may be operating at the same time. For example, core prey and marginal prey may serve different functions, and thus utilisation of these two classes of resource could follow independent or even conflicting sets of behavioural decision rules. Temporal or seasonal variation in prey quality or abundance could contribute to the use of marginal resources: for example, individuals may utilize marginal resources only in certain seasons of the year when prey are gravid and thus have higher energy content (Newsome *et al.* 2009). Such seasonal variation begs the question of what time scales are appropriate for measuring diet composition. Our sea otter dataset spans periods of 1–3 years for each individual, long enough to ensure that real individual differences are distinguishable from sampling artifact, but perhaps too long in that temporal variation due to seasonal effects could confound otherwise clear patterns.

Discrepancies in the here-inferred rules of prey selection for core and marginal resources, and complexities introduced by temporal variation in prey choice, both illustrate the importance of quantitative examinations of individual resource-use patterns. When examining individual diets at temporal scales longer than hours or days, the relevant question is not whether a given resource is utilised by a given individual, but rather how much does that resource contribute to the individual's diet. Empirical tests of theoretical models of individual diet specialisation will benefit from the approaches for analysing quantitative individual-resource networks that we have demonstrated here, including weighted analyses of nestedness and modularity and FDCA.

ACKNOWLEDGEMENTS

This work was supported by the US Geological Survey Western Ecological Research Center and Alaska Science Center, the Monterey Bay Aquarium, California Department of Fish and Game, University of California Santa Cruz, the NRS Kenneth S Norris Rancho Marina Reserve, the US Fish and Wildlife Service, the US Navy, and a grant from the Minerals Management Service. PRG and FMDM were supported by FAPESP. We are grateful to the many colleagues and volunteers that assisted with data collection, especially C. Alfano, J. Ames, D. Canestro, B. Cummings, G. Esslinger, M. Harris, B. Hatfield, D. Jessup, A. Kage, M. Kenner, N. Laroche, C. Lin, M. Miller, D. Monson, M. Murray, T. Nicholson, O. Oftedal, J. Perry, K. Ralls, M. Ramirez, J. Stewart, J. Tomoleoni, S. Wolrab and L. Yeates, and numerous volunteers from the Monterey Bay Aquarium. 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.

AUTHORSHIP

MTT, PRG, and MN designed the study, MTT co-led the PBL field study, collected and analysed dietary data and wrote the first draft of the manuscript, PRG conducted network analyses and co-wrote the first draft, MN analysed data for rank preference correlations and co-wrote the first draft, FMDM assisted with network analyses and assembled figures, JB co-led the MON field study and collected data, MS co-led the MON field study and collected data, GB co-led the SNI field study and collected data, JAE co-led the PBL and SNI field studies and advised on analyses, and all authors contributed substantially to revisions.

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Editor, John Fryxell
Manuscript received 8 December 2011
First decision made 17 January 2012
Manuscript accepted 8 February 2012