

Food limitation leads to behavioral diversification and dietary specialization in sea otters

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Dietary diversity often varies inversely with prey resource abundance. This pattern, although typically measured at the population level, is usually assumed to also characterize the behavior of individual animals within the population. However, the pattern might also be produced by changes in the degree of variation among individuals. Here we report on dietary and associated behavioral changes that occurred with the experimental translocation of sea otters from a food-poor to a food-rich environment. Although the diets of all individuals were broadly similar in the food-rich environment, a behaviorally based dietary polymorphism existed in the food-poor environment. Higher dietary diversity under low resource abundance was largely driven by greater variation among individuals. We further show that the dietary polymorphism in the food-poor environment included a broad suite of correlated behavioral variables and that the individuals that comprised specific behavioral clusters benefited from improved foraging efficiency on their individually preferred prey. Our findings add to the growing list of examples of extreme individuality in behavior and prey choice within populations and suggest that this phenomenon can emerge as a behavioral manifestation of increased population density. Individuality in foraging behavior adds complexity to both the fitness consequences of prey selection and food web dynamics, and it may figure prominently as a diversifying process over evolutionary timescales.

foraging efficiency | niche width | polymorphism | prey handling

A large and long-standing body of theoretical and empirical research has led to the well established view that the dietary diversity of consumers increases as food becomes limiting (1–4). The implicit assumption underlying both the theory and observation is that individuals within populations are responding to changing prey availability in broadly similar ways. However, the commonly observed population-level pattern of increased dietary diversity with reduced prey abundance could also occur via individual diversification (5, 6), in which case the dietary breadth of any given individual in response to prey limitation might change very little. We subsequently refer to the former process as the within-individual diversity hypothesis (WIDH) and the latter as the among-individual diversity hypothesis (AIDH), recognizing that the two processes are not mutually exclusive. The WIDH and AIDH involve fundamentally different mechanisms that have very different implications for population, community, and evolutionary ecology (7), yet the relative importance of these two processes remains largely unevaluated for most free-living consumers, particularly large vertebrates. This lack of attention likely reflects the fact that long-term dietary records from specific individuals are difficult to obtain, and comparable samples of individual behavior and diet under conditions of high and low resource abundance are seldom available.

California sea otters (*Enhydra lutris nereis*) provide a unique opportunity to explore the WIDH–AIDH dichotomy. Diet in this species is easily determined from shore-based observations because sea otters invariably return to the surface to consume

their prey, and we have obtained longitudinal records of sea otter diet and foraging behavior from tagged individuals that span multiple years (8). Moreover, the experimental translocation of sea otters from central California (henceforth CC) to San Nicolas Island (henceforth SN) in the southern California Bight in 1987–1990 established a second population in a comparatively food-rich environment where the diversity of potential invertebrate prey is similar or slightly greater than that at CC (9). After an initial posttranslocation decline (resulting largely from dispersal back to CC), the SN population stabilized in the early 1990s and then began growing at $\approx 9\%$ per year. This growth trend is expected to continue because the current population size (≈ 40 individuals) is well below the estimated equilibrium density (Fig. 1A). The abundance of commonly consumed sea otter prey at SN exceeds that at CC by as much as three orders of magnitude (Fig. 1B), a difference that results from the sea otter's well known ability to limit its invertebrate prey populations (10) and the comparative low density and long period of absence of sea otters from the SN system.

Between 2003 and 2005, we collected detailed information on diet and foraging behavior from 11 radio-tagged animals at SN, and we collected similar data from 34 animals at CC between 2001 and 2004. At each site, the samples consisted of adult animals (≥ 3 years of age) of both sexes with largely overlapping home ranges, and individuals at both sites foraged in generally similar mixed rocky and sand-bottom habitats. The average food intake rate was more than twice as great at SN than at CC (Fig. 1C); animals at SN thus spent only half as much time foraging (Fig. 1D) and were in better body condition (Fig. 1E) compared with animals at CC. The difference in prey abundance between CC and SN is typical of other areas with and without sea otters (11), and the associated interpopulation differences in body condition, rate of food intake, and daily activity budget occur at the extremes of the recorded values for each metric in this species (12–15). Taken together, these data suggest that food resources are effectively unlimited for sea otters at SN but are strongly limiting to the CC population. The SN–CC comparison thus provides an experimental means of evaluating the behavioral responses of individuals in a wild predator population to release from food limitation.

Results

On the basis of extensive foraging observations ($n = 37,255$ observed feeding dives and 23,339 prey captures for CC; $n = 5,341$ observed feeding dives and 2,361 prey captures for SN)

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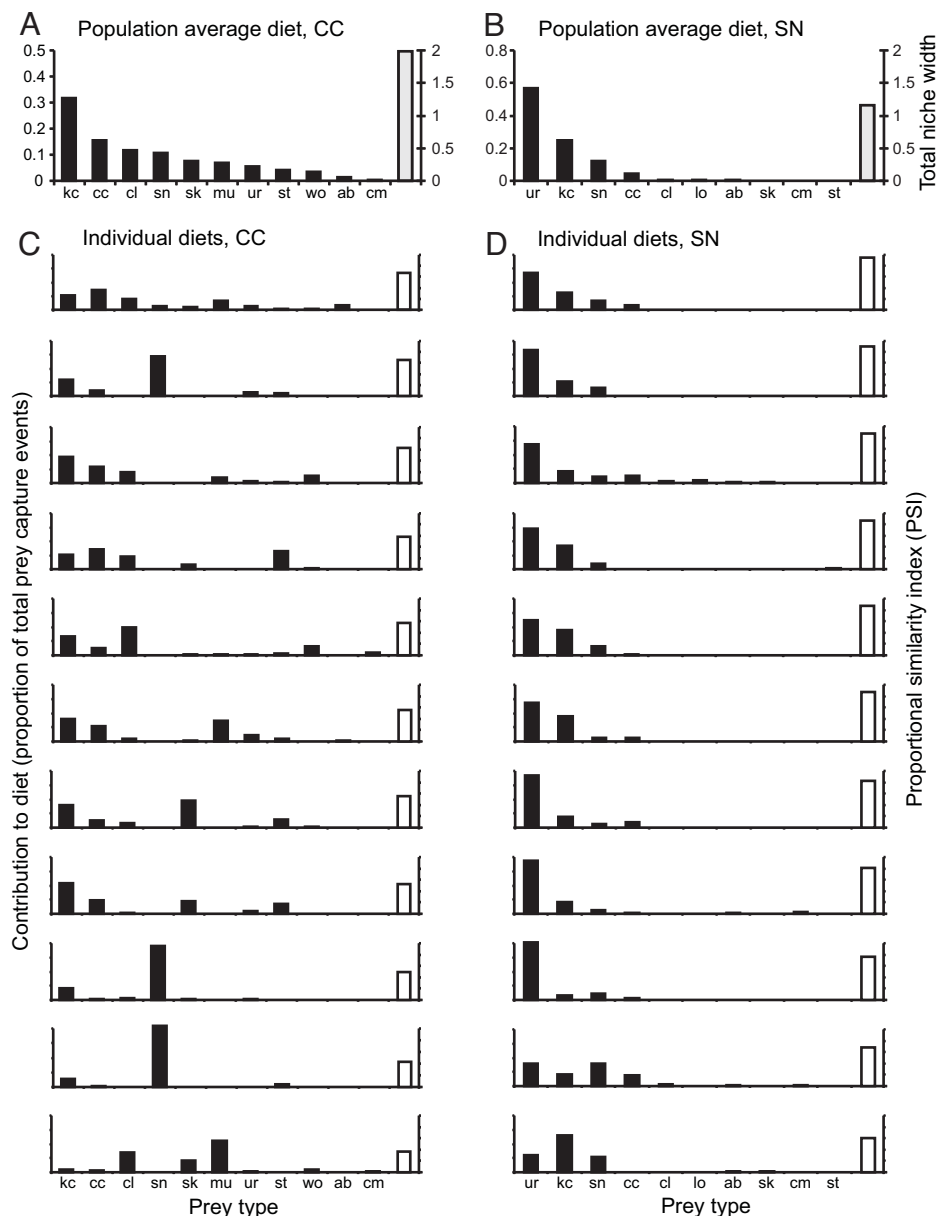


Fig. 2. Population-level and individual diet histograms for sea otters at CC (Left) and SN (Right), illustrating differences in total niche width and individual diet specialization between the two populations. The left vertical axis of each graph indicates the dietary prevalence of various prey types (measured as the proportion of total prey capture events). A and B show the mean diet composition for otters at CC and SN, respectively, with the rightmost bar in each graph indicating the total niche width for each population as measured by the Shannon–Weiner index (right vertical axes). Prey types consumed at each site are indicated by two letter codes on the horizontal axis: ur, urchins; kc, kelp crabs; sn, marine snails; cc, *Cancer* crabs; cl, clams, scallops, and other infaunal bivalve mollusks; lo, lobster; ab, abalone; sk, small unidentified kelp-dwelling invertebrates; cm, cephalopod mollusks; st, sea stars; mu, mussels; wo, worms; sd, sand dollars. C and D depict the corresponding diet histograms for 11 individuals at each site, with the rightmost bar in each graph indicating the proportional similarity index (PSI, right vertical axes), or the degree to which each individual's diet matches the population-level diet. Tick marks on both the left and right vertical axes in C and D are at intervals of 0.2.

favoring improved foraging efficiency by specialists over non-specialists (Table 1). Despite the low statistical power associated with the small number of contrasts, the probability of this pattern resulting from chance alone is 0.031. Overall, individuals that specialized on a particular prey type were able to process 25% more prey items per unit of time than were nonspecialists.

Discussion

Our results indicate that, for southern sea otters, higher dietary diversity under low resource abundance is largely driven by variation among individuals. Within-individual diet diversity was

also slightly higher in the food-limiting environment, demonstrating that both within- and among-individual variation can contribute to population-level patterns; however, the qualitative differences between the two sites with respect to individual specialization are most consistent with the AIDH. Conceivably, these differences are related to some factor other than food abundance [the most plausible alternative hypotheses, and the reasons we have discounted them, are summarized in the [supporting information \(SI\) Text](#)], but this is the simplest and most parsimonious explanation.

Individuality in animal behavior is now well established and widely reported (7). Alternate foraging modes associated with

creased variation in the fitness of individuals (21), may serve as an important diversifying mechanism on evolutionary timescales (5, 7), and adds complexity to consumer–prey interactions (32). Food webs, defined by the suite of all trophic linkages, are invariably described at the level of species, or even groups of species, but intraspecific diet specialization could introduce substantial variability to food web topology, thereby affecting community dynamics and stability (33).

The interindividual differences in diet and foraging behavior we report for sea otters in central California are far greater than those that have been used to characterize many competing species based on population-level averages (8). It is possible that behavioral polymorphisms such as those we describe here, especially those that are maintained along matrilineal lines (8, 31), represent an important substrate for the tempo and mode of evolutionary diversification. At very least, it would appear that macroevolutionary drivers of diversity among species (i.e., within-guild competition and niche diversification) are also evident in extreme form at the level of individuals within populations (6).

We suspect that the patterns reported in this paper are not unique to sea otters but occur in many other species, including other large, wide-ranging vertebrates for which longitudinal data on individual diets and feeding behavior have been logistically difficult to acquire. Recent advances such as molecular techniques for diet characterization and bio-logging technology provide new opportunities for the detection and measurement of individual specialization in diet and foraging behavior (34). We hope that these results and our interpretations of them will encourage others to look for similar patterns in other species and ecosystems, and to begin a more systematic and rigorous search for their causes and consequences.

Methods

Community Metrics. The CC study site consisted of nearshore waters between Pt. Piedras Blancas and Pt. Estero along the central coast of California; the SN study site consisted of nearshore waters surrounding San Nicolas Island in the southern California Bight (SI Fig. 4). Sea otter densities at each site (km^{-2}) were measured as the number of animals counted during annual spring censuses (2001–2003 average counts for CC, 2003–2005 average counts for SN) divided by the area of suitable habitat (subtidal benthos between the mean low tide line and the 40-m isobath) (35). Relative prey availability at each study site was evaluated by using standardized scuba-based sampling protocols (36), as described in SI Text.

Study Animal Sampling. Captures and radio-tagging of study animals were conducted in 2001–2003 at CC ($n = 48$) and in 2003–2005 at SN ($n = 13$). Sea otters were captured by using scuba-based methods (37), and then anesthetized, flipper-tagged, and surgically implanted with VHF radio transmitters by using standardized procedures (38). Body condition was measured as the weight/length ratio ($\text{kg}\cdot\text{m}^{-1}$), with total length (snout to tail) measured on a flat surface. Details of the capture, anesthetics, tagging, and subsequent monitoring by radio telemetry of sea otters included in this study are provided elsewhere (39). All activities were covered by an institutional permit issued by University of California, Santa Cruz, to J.A.E. and M.T.T. and a Federal Permit (MA672624) issued by the U.S. Fish and Wildlife Service to J.A.E. To ensure representative dietary composition data for each individual, we restricted further analyses to those animals from which we were able to record ≥ 10 independent feeding bouts spanning at least 1 year, and comprising ≥ 300 known-outcome feeding dives ($n = 34$ at CC and $n = 11$ at SN). The male/female ratios of the two samples, 0.21 at CC and 0.36 at SN, were not significantly different (Fisher's exact test, $P = 0.421$).

Activity Budgets and Home Ranges. Activity was measured by sampling instantaneous behavior at 10-min intervals throughout continuous 12- to 24-hour focal animal monitoring sessions (15). These data were available for 28 of the 34 animals at CC and 7 of the 11 animals at SN, and they were used to estimate the average proportion of a 24-h period allotted to feeding behavior at each site. To quantify individual home ranges, each study animal was located three to seven times per week, and its precise geographic position, recorded by using GPS, was entered into a Geographic Information System (GIS) database.

We collected a minimum of 200 daily locations per animal and used fixed kernel density estimation techniques (40) to delineate annual home-range polygons for each animal (see SI Text).

Diet Composition, Diversity, and Rate of Food Intake. Observational data on foraging behavior and diet composition were recorded by using standardized methods (41, 42). The relative frequency of capture of each prey type was used to calculate diet composition for each study animal (SI Table 2) and to estimate diet diversity (measured as the Shannon–Weiner index) at both the individual and population levels. Using estimation procedures described elsewhere (43), we calculated the ratio of within-individual diet diversity to total population niche width, and the PSI, where PSI values $\ll 1$ indicate nonoverlapping diets, or individual specialization. These metrics were estimated for the 11 animals at SN and for the 11 animals at CC whose degree of home-range overlap most closely matched the SN sample. We then repeated the analyses using 5,000 bootstrap samples drawn from each study group (11 animals were selected randomly with replacement for each iteration), thereby allowing us to estimate the mean, standard deviation and CL_{95} limits for each parameter based on comparable sample sizes. Prey biomass intake ($\text{g}\cdot\text{min}^{-1}$) was estimated as the product of the number of prey items captured (and consumed) and the estimated edible biomass of each item, summed across all dives in a foraging bout and then divided by the total duration of the bout. Intake rates were averaged across bouts for each individual and then across individuals at each study site.

Analysis of Foraging Behavior. In addition to quantifying diet composition, observational data were used to characterize individual foraging behavior. We used principal components analysis to collapse 14 behavioral variables (SI Table 3) into a smaller number of orthogonal factors before contrasting behavioral variation at SN and CC. Examination of eigenvalues indicated that five principal components captured the majority (90%) of the variance among animals. We calculated the among-individual variance in PCA scores at each study site, averaging variance estimates for the five principal components (weighted by their associated eigenvalues) to obtain a single representative index of individual behavioral variability at CC (var_{CC}) and at SN (var_{SN}). To account for the differing sample sizes, we repeated this entire analysis for 5,000 bootstrap samples of 11 animals from each study site and, for each sample pair, calculated the ratio of variance indices ($\text{var}_{\text{CC}}/\text{var}_{\text{SN}}$), reasoning that if individual behavioral variation did not differ between sites, the average ratio for all 5,000 samples should be approximately equal to one.

We next analyzed the 14 behavioral parameters, using hierarchical cluster analysis, to determine whether individuals exhibited consistent and distinct patterns of foraging behavior. Ward's minimum variance method was used to link similar individuals based on standardized Euclidean distances (44), and examination of the resulting dendrogram and scree-plot of internode distances (SI Fig. 5) indicated four clusters. We used linear discriminant analysis to assess (i) the efficacy of the behavioral classification scheme, (ii) which behavioral parameters were most useful for distinguishing between clusters, and (iii) how individuals from each study site were distributed among clusters. Wilks' λ was used to test for multivariate differences among clusters (45), and we also measured the proportion of individuals consistently assigned to the same cluster using jackknife resampling of the classification matrix (44). We then plotted all individual otters on an ordination of the first two discriminant factors, interpreting each axis on the basis of the standardized canonical discriminant functions and the mean parameter values for animals in each cluster (SI Table 4). To examine the relationship between behavioral mode and diet composition for CC study animals, we calculated the mean proportional contribution of each prey type to the diets of animals in each cluster, and graphically contrasted the resulting diet histograms. We used a numerical approximation to Fisher's exact test (46) to evaluate the null hypothesis that specialists for each prey type (as defined below) were distributed randomly among clusters.

Handling Efficiency. We measured prey-specific handling efficiency as the number of items handled at the surface per unit time (subsurface prey handling was excluded from this analysis as it was impossible to measure), and for each study animal at CC, we calculated mean handling efficiency for every prey type used. To avoid the confounding effects of prey size (larger items take longer to handle and consume than small items), we limited analysis to the most frequently captured size class of each prey type. We identified specialists for each prey type as those animals for which the proportional contribution to the diet of the prey exceeded the 80th percentile value measured across all individuals. We compared handling efficiency between specialists and non-specialists for the nine predominant prey types by using two-tailed t tests and adjusting for separate variances. The sample unit for this contrast was a single

