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Individual variation in prey selection by sea otters: patterns, causes and implications

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Summary

1. Longitudinal records of prey selection by 10 adult female sea otters on the Monterey Peninsula, California, from 1983 to 1990 demonstrate extreme inter-individual variation in diet. Variation in prey availability cannot explain these differences as the data were obtained from a common spatial-temporal area.
2. Individual dietary patterns persisted throughout our study, thus indicating that they are life-long characteristics.
3. Individual dietary patterns in sea otters appear to be transmitted along matrilines, probably by way of learning during the period of mother–young association.
4. Efficient utilization of different prey types probably requires radically different sensory/motor skills, each of which is difficult to acquire and all of which may exceed the learning and performance capacities of any single individual. This would explain the absence of generalists and inertia against switching, but not the existence of alternative specialists.
5. Such individual variation might arise in a constant environment from frequency-dependent effects, whereby the relative benefit of a given prey specialization depends on the number of other individuals utilizing that prey. Additionally, many of the sea otter's prey fluctuate substantially in abundance through time. This temporal variation, in conjunction with matrilineal transmission of foraging skills, may act to mediate the temporal dynamics of prey specializations.
6. Regardless of the exact cause, such extreme individual variation in diet has broad ramifications for population and community ecology.
7. The published literature indicates that similar patterns occur in many other species.

Key-words: California, diet, foraging models, matrilineal transmission.

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Introduction

The reproductive success of all consumers is influenced by what they choose to eat because each prey type has particular costs and benefits to the consumer. Variation in net benefit among prey types has been used in a number of ways to define dietary optima (Krebs & Davies 1987). One such approach attempts to predict optimal diet based on the maximization of some 'currency' (e.g. net rate of energy gain, foraging efficiency and offspring provisioning), given various assumptions about which decisions are important to fitness, the range of possible choices, and appropriate behavioural and physiological constraints (Stephens & Krebs 1986). This quest for general decision rules in foraging behaviour seems to have led to the still widely held view that optimal diet is dictated largely by characteristics of a consumer species on one hand and its environment on the other, thus being a population-level phenomenon.

Recent elaborations of foraging theory adopt a more comprehensive, dynamic and multifactorial approach to predicting diet and foraging strategies, in which variation among individuals is no longer irrelevant noise, but a focus of interest (e.g. Mangel & Clark 2000).

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It has been shown, for example, that risk-sensitive foraging behaviour may result in context-dependant optimal strategies (Caraco, Martindale, & Whitman 1980; Gillespie & Caraco 1987; McNamara & Houston 1992). Similarly, state-dependent models, in which the current condition of the forager affects its decisions, also predict intrapopulation variation (Houston & McNamara 1985; McNamara & Houston 1986). Ecologists outside of this increasingly specialized branch of decision theory, however, have largely failed to incorporate such individual variation into models of population or community-level dynamics. Part of this failure may reflect the difficulties of documenting individual foraging variation in most wild populations. Notably, empirical support for foraging theory, where the focus is on individuals, mainly derives from laboratory studies or carefully controlled field experiments. An important challenge for field ecologists is therefore to design studies that measure diet and foraging behaviour at the level of the individual, rather than the population.

Data from a growing number field studies suggest that long-term individual differences in behaviour and diet are quite common (e.g. Partridge 1976; Ehlinger 1990; Schindler, Hodgson, & Kitchell 1997; Annett & Pierotti 1999; Bolnick *et al.* 2003), some of which cannot be explained by environmental or phenotypic variation (e.g. Bridcut & Giller 1995; Werner & Sherry 1987; West 1988). The few theoretical reviews of the subject that exist (Partridge & Green 1985; Magurran 1986; Smith & Skúlason 1996) deal primarily with avian and fish taxa and provide a starting point for interpreting these patterns. Even so, there is still no generally recognized theoretical framework for understanding the mechanisms by which such alternative foraging specializations arise or their implications for population and community-level processes.

Here we investigate long-term individual variation in diet in the sea otter (*Enhydra lutris*, Linnaeus). Sea otters are ideal for such a study, for several reasons. They are abundant in many areas, easy to observe from shore and have the fortunate habit of returning to the water's surface to consume their prey after each foraging dive, at which point the prey can be identified. Individual sea otters (especially adult females) spend most of their lives in restricted areas (Ralls, Eagle, & Siniff 1996), making possible the collection of longitudinal data. Finally, like many carnivorous mammals, their success or failure depends on complex hunting skills, they have a high capacity for learning, and food is often the important limiting resource. Thus, variation in foraging behaviour is expected to be ecologically relevant and have important fitness consequences.

The sea otter's diet has been described in a number of prior studies from a range of locations and ecological conditions (Riedman & Estes 1990; Watt, Siniff & Estes 2000). These studies indicate that sea otters select a broad range of prey in any given location; dietary diversity is highest where populations exist at high levels and food resources have become limiting; and much of the variation in diet and foraging behaviour within a population is accountable at the level of individual feeding bouts (Estes, Jameson, & Johnson 1981). This latter result prompted us to wonder if diet varies among individuals and whether any such variation persists as they move through space and time. We were able to address these questions by observing tagged sea otters over relatively long time periods. In this paper we present information obtained during an 8-year period on the diet of tagged animals and some of their offspring. While diet at the level of the population was expectedly diverse, most individuals specialized on a very limited subset of the overall prey base, and these individualized dietary patterns persisted over time and space. As this view emerged we began to wonder why sea otters specialize and how individual dietary patterns arise and are maintained. Female sea otters and their dependent young spend about 6 months together from birth to weaning and it is during this time that the young apparently learn to forage. Thus, a second goal of our study was to determine if individual patterns of diet and foraging behaviour are matrilineally transmitted. This goal was achievable because mothers and pups can be viewed while they are still together, and we were able to mark several pups as dependents and later document their diets as adults.

Materials and methods

Our study had two parts. The first part, done between 1983 and1990, provided information on the diet of 10 adult female sea otters (hereafter referred to as focal animals) during periods when they were not accompanied by dependent pups. The data obtained between April 1983 and December 1985 are all taken from the unpublished PhD dissertation of K. J. Lyons (1991). The data obtained from 1986 to 1990 are from our own field studies. Early on, we realized that dietary composition varied greatly among individuals; thus, the second part of the study, done between 1985 and 1990, was undertaken to determine if dietary variation among individuals is transmitted matrilineally.

Field research was conducted on the Monterey Peninsula of central California, mostly between Point Pinos and Del Monte Beach and between the Great Tide Pool and Spanish Bay (Fig. 1). Sea otters recolonized the Monterey Peninsula in the 1960s after having been nearly exterminated in the Pacific maritime fur trade. They were well established on the Monterey Peninsula during our study (Riedman & Estes 1990). The shoreline and shallow seafloor within the study area is mostly rock substrate interspersed with sandy areas, together supporting a diverse assemblage of benthic invertebrates, many of which are consumed by sea otters.

We obtained longitudinal records of diet from individual sea otters that were tagged in the Monterey area beginning in the late 1970s by the California Department of Fish and Game, US Fish and Wildlife Service,

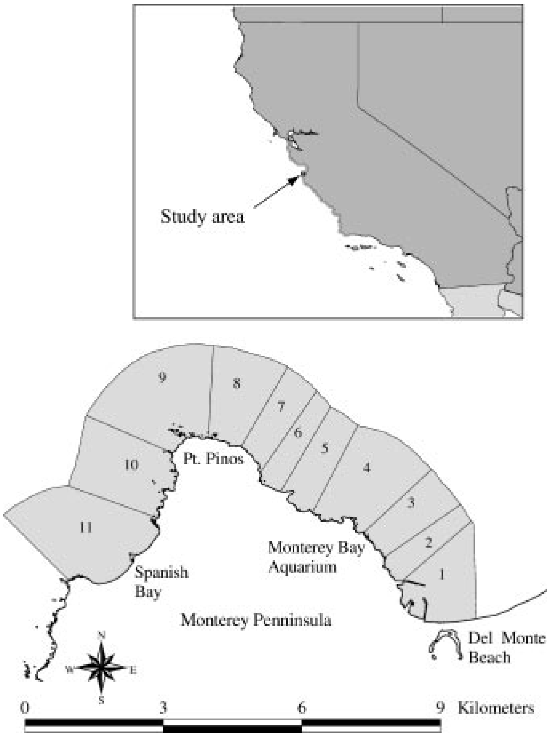

Fig. 1. Map of study area on the Monterey Peninsula, California, showing coastal segments used in the spatial analysis of foraging and resting depicted in Fig. 3.

and our own research group (Ames, Hardy, & Wendell 1983). Age and gender were determined at the time of capture. Part 1 of our study was based on records subsequently obtained from 10 adult females, all but one of which were 6–9 years old at the onset of fieldwork (otter no. 1 was 3–4 years old).

The study area was surveyed periodically, during which the location and activity of each tagged individual was recorded. Frequency distributions of habitat use (by coastal segments; Fig. 1) were constructed from these records. Foraging animals were observed from shore at distances of about 10–500 m using a 50–80X Questar telescope (Questar Corp., New Hope, PA, USA). Location, prey type and number of prey captured were recorded after each foraging dive.

An episode of continuous feeding is hereafter termed a feeding bout. Repeated feeding bouts were measured from each individual over periods ranging from 9 to 19 months. These animals were followed less systematically for up to 5 years.

Dietary composition was measured as the percentage occurrence of each prey type in successful foraging dives. Occasionally, prey type could not be determined because of poor viewing conditions and these records were not included in the analyses. Although 31 prey species were identified during this study, most of our analyses are restricted to 8 of these, each comprising > 10% of the diet for at least one individual. The diets of individuals were determined by averaging frequencies of occurrence, by prey type, across feeding bouts. This approach was used because feeding bouts vary considerably in duration. To obtain a population-level measure of diet, these frequencies were further averaged across all 10 individuals. Data from females with dependent pups were not used in these analyses.

Chi-square contingency analyses were used to determine if diet varied (i) among individuals, and (ii) within individuals over time (seasonally and between years) and space (among coastal segments). Seasons were defined by periods of roughly similar water temperature, as follows: winter (December through February), spring (March through May), summer (June and July), and autumn (August through November). The frequency distribution of feeding and resting locations was compiled for each individual to determine variation in spatial use of the study area among individuals and through time.

To determine if individual foraging patterns are transmitted matrilineally, we captured and tagged 11 dependent pups (5 females; 6 males) that were near weaning age. Their mothers were tagged or retagged at the same time. Information on post-weaning diets was obtained from three female offspring whose mothers' diets were also known (subsequently referred to as pairs 1, 2 and 3). We studied offspring 3 from age 4–7·8 years, offspring 1 from birth to age 4·4 years, and offspring 2 from birth to age 2·4 years. Additionally, the diet of 9 adult females and their dependent pups (5 males, 2 females and 2 of undetermined sex) were recorded during the pup dependency period.

Results

DIETARY COMPOSITION OF INDIVIDUALS

The foraging data, when averaged across the 10 focal sea otters over the > 2 years of field observation, portrays a highly generalized consumer with a diet consisting of 32 common prey types. However, most individuals specialized on 1–4 prey types, and diets differed remarkably among individuals (Fig. 2). Each of the eight most commonly consumed prey types was absent (or nearly so) from the diet of at least one individual while being common (> 20% of the foraging dives) in the diet of at least one other individual, and for some prey types the difference among individuals was even more extreme. For example, otter 8 consumed turban snails (*Tegula* spp.) on almost 70% of its successful foraging dives whereas otters 1, 2, 4, 5, 7, 9 and 10 never ate turban snails on a combined total of 11 800 observed dives. There was little overlap in diet among certain individuals (e.g. otters 7 and 8) while others were qualitatively similar (e.g. otters 4, 9 and 10). However, each individual was distinctive in some way. Abalone (*Haliotis* spp.) were the most commonly eaten prey by five individuals but among these 'abalone specialists' four different prey types ranked second in frequency of occurrence and 5 different prey types ranked third. Similarly, the second and third

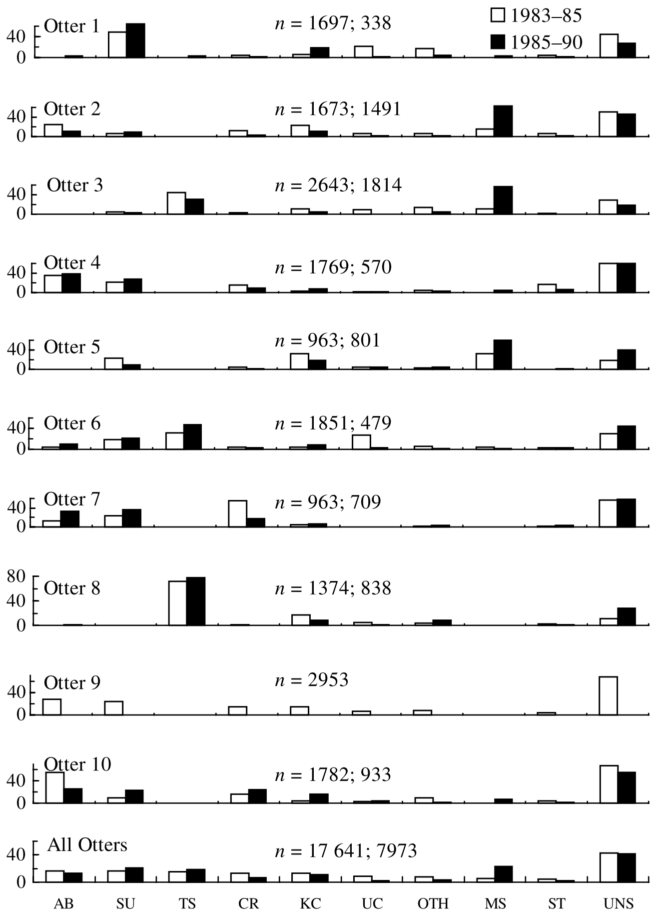

Fig. 2. Dietary composition of the 10 focal adult female sea otters. Prey type is shown on the horizontal axis (AB, abalone; SU, sea urchins; TS, turban snails; CR, *Cancer* crabs; KC, kelp crabs; UC, unidentified crabs; OTH, other prey types; MS, mussels; ST, sea stars; UN, unknown; UNS, unsuccessful). Dietary composition is shown separately for the 1983–85 (open bars) and 1985–90 (closed bars) periods. Sample sizes (*n*) refer to the number of foraging dives observed. Numbers to the left of semicolons are for 1983–85; those to the right are for 1985–90.

ranked prey items were different for each of three otters that selected turban snails as their most common prey.

Forty-four percent of the observed foraging dives were unsuccessful although this ranged from 10% to 68% among the 10 focal animals. Unsuccessful dive rates were highest for individuals that specialized on abalones or cancer crabs (*Cancer* spp.) and lowest for those that specialized on kelp crabs (*Pugettia* spp.), turban snails, purple urchins or mussels (*Mytilus californianus*, Conrad).

TEMPORAL PATTERNS IN THE DIET OF INDIVIDUALS

The diets of most individuals remained largely unchanged throughout the study. Temporal variation in diet was evaluated with chi-square contingency analyses on season and year across the frequency distributions of prey types for each individual otter. Most of these contrasts failed to detect significant differences, despite generally powerful tests (Table 1). Only one of nine inter-seasonal contrasts (otter 5), and one of eight inter-annual contrasts (otter 9) were significant.

Although brief departures from the typical diets occasionally were noted (see below), none of the focal animals displayed obvious dietary shifts during the period of intensive study and there also was no evidence for such shifts in the years following. Occasional feeding observations were made after December 1985 (the formal end to part 1 of our study). Otter 3 was observed feeding mainly on kelp crabs and sea urchins until she died in 1988; otter 5, a specialist on abalones, sea urchins and mussels, was frequently observed eating mussels until her death in 1988; and otter 6, a specialist on urchins and turban snails, was observed feeding on turban snails from 1986 to 1990. These observations and analyses demonstrate that individualized dietary patterns in adult sea otters persist for years.

Feeding on pelagic red crabs (*Pleuroncodes planipes*, Stimpson) constituted the single exception to the recurrent selection of specific prey types by individual sea otters. This species, not typically found in Monterey Bay, occurred in large ephemeral patches on and near the sea surface during the 1983–85 El Niño event. All but one of the focal animals were seen feeding on pelagic red crabs at various times from August 1984 to

Table 1. Dietary variation through time for individual sea otters. Analyses were done by sorting the dietary data by (i) season (Win, December–February; Spring, March–May; Summer, June–July; Autumn, August–November) and (ii) for similar seasons among years, and testing for differences among the resulting frequency distributions using chi-square contingency analyses. Exact P-values are given for each test (NS refers to $P > 0{\cdot}05$). The statistical power of the test to detect a medium effect size (*sensu* Cohen 1988) is reported for all nonsignificant results

Otter number	Season/year	Number of feeding bouts	Number of successful dives	P		Power
1	Season: Sp × Au × Win	22	603	0·169	NS	0·9995
	Year: Sp84 × Sp85	9	378	0·347	NS	0·9944
2	Season: Win × Au	19	217	0·535	NS	0·8946
	Year: Win84 × Win85	6	67	0·138	NS	0·3404
3	Season: Win × Sp	23	605	0·711	NS	0·9999
	Year: Win84 × Win85	10	304	0·074	NS	0·9764
4	Season: Su × Win × Au	23	241	0·378	NS	0·8368
	Year: Win84 × Win85	14	107	0·786	NS	0·5444
5	Season: Au × Win	6	180	0·0001		
6	Season: Sp × Su	10	239	0·503	NS	0·9261
	Year: Sp84 × Sp85	4	103	0·124	NS	0·5251
8	Season: Win × Sp × Su	22	785	0·072	NS	0·9999
	Year: Win84 × Win85	10	391	0·183	NS	0·9957
9	Season: Win × Sp × Au	14	105	0·062	NS	0·3975
	Year: Au84 × Au85	14	141	0·008		
10	Season: Au × Win × Sp	19	184	0·564	NS	0·6923
	Year: Win84 × Win85	4	34	1·000	NS	0·1760

June 1985. These foraging episodes were typically sporadic and asynchronous among individuals, short-lived (even when dense concentrations of pelagic red crabs persisted around the foraging otters), and normal dietary patterns resumed immediately thereafter.

SPATIAL VARIATION IN HABITAT USE AND FORAGING BEHAVIOUR

While all of the 10 focal animals moved extensively among adjacent coastal segments, each showed particular patterns of habitat use (Fig. 3). Otters 2, 3, 5 and 8 were most often seen in coastal segments 1–5 in the eastern half of the study area; otters 1, 6, 9 and 10 occurred mainly in segments 6–10, in the western half of the study area; and otters 4 and 7 ranged more broadly throughout the study area. For each individual the distribution of foraging and resting areas were roughly coincident, although foraging ranges were more dispersed than resting ranges.

Table 2. Spatial distributions of resting and foraging observations by coastal segment (see Fig. 1) for each of the 10 focal sea otters. The otters are segregated into three groups depending on whether the majority of their activities occurred (i) in the eastern half, (ii) the western half, or (iii) throughout the study area. Prey types are as follows: AB, abalone; SU, sea urchin; CR, *Cancer* crab; KC, kelp crab; UC, unidentified crab; TS, turban snail; MS, mussel

Area	Otter number	Most common prey (descending order)
East half	2	AB, KC, MS
	3	TS, MS, KC
	4	KC, MS, SU
	8	TS, KC, SU
West half	1	SU, UC, KC
	6	TS, UC, SU
	9	AB, SU, KC
	10	AB, CR, SU
Throughout	4	AB, SU, CR
	7	CR, SU, AB

We examined the data for spatial associations between diet and habitat use by listing the three most frequently eaten prey types for each individual and then sorting these data into the three spatial groupings noted above (Table 2). No clear patterns of spatial association with diet were evident. Abalones and turban snails were the most frequently eaten prey type by seven of the 10 otters, yet at least one abalone specialist occurred in each of the three habitat groups and turban snail specialists occurred in two of the three habitat groups. Six of the eight prey types were among the three most highly preferred species by two or more of the focal otters, yet with a single exception (the three animals that preferred mussels – otters 2, 3 and 5 – were all members of group 1 that used the eastern half of the study area), the otters that consumed these prey occurred in spatial groupings that spanned the study area. We also looked for spatially explicit dietary patterns among the several individuals that foraged widely throughout the study area, but found none.

FORAGING PATTERNS OF MOTHERS AND THEIR DEPENDENT OFFSPRING

Prey was identified for both individuals in nine mother-dependent pup pairs. Dietary similarities between

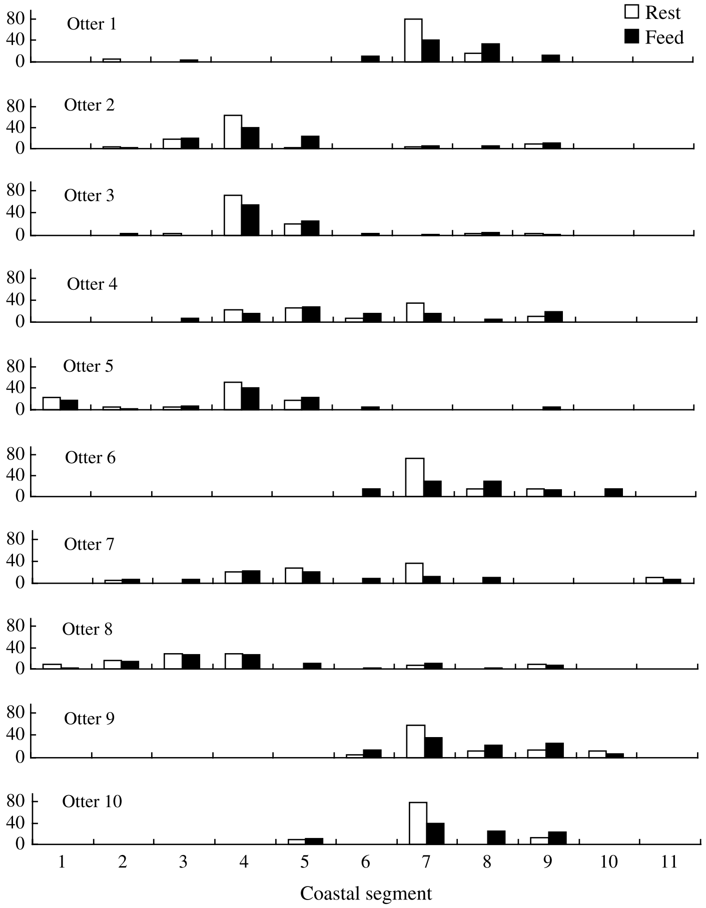

Fig. 3. Habitat use for foraging and resting by each of the 10 focal adult female sea otters. Frequency distributions are computed from resightings of focal animals during daily surveys. Boundaries of coastal segments are shown in Fig. 1. Sample sizes (numbers of daily resightings) range among individuals from 70 to 101 (resting) and 95–107 (feeding).

mothers and their dependent pups were evaluated using two methods. First, a prey type matrix containing 279 elements was created (9 mother-pup pairs × 31 identified prey types). Each element was defined according to whether a particular prey was consumed by the mother and her pup (+/+), the mother but not her pup (+/–), the pup but not its mother (–/+), or neither the mother nor her pup (–/–). Two hundred and eighteen (77%) of the elements were either +/+ or –/–, indicating that most mother-pup pairs engaged in similar foraging behaviours; 193 of these were –/–, further demonstrating that individual otters did not eat most prey types. Of the remaining 63 elements, 83% were +/– while 17% were –/+, thus indicating that mothers sometimes consumed prey not eaten by their pups but pups rarely consumed prey not eaten by their mothers.

We determined whether these patterns differed significantly from that expected if the mother/pup pairs foraged independently of one another. The expected distribution was computed by letting X_{ij} and Y_{ij} represent the element at the ith row (prey) and jth column (pair) of the matrix for mothers and pups, respectively, and setting X_{ij} and Y_{ij} equal to 1 when the prey type was + and 0 when it was –. Thus, the probability that a particular prey type (selected at random) was eaten by a particular mother (also selected at random) during our study (p_{m}) is $\Sigma\Sigma X_{ij}/279$, and the comparable probability for a dependent pup (p_{d}) is $\Sigma\Sigma Y_{ij}/279$. The respective probabilities that a prey type was not observed being eaten by a mother (q_{m}) and dependent pup (q_{d}) are $1 - p_{\mathrm{m}}$ and $1 - p_{\mathrm{d}}$. These probabilities are estimated as $p_{\mathrm{m}} = 0{\cdot}27$, $q_{\mathrm{m}} = 0{\cdot}73$, $p_{\mathrm{d}} = 0{\cdot}12$ and $q_{\mathrm{d}} = 0{\cdot}88$. Because $p_{\mathrm{m}} + q_{\mathrm{m}} = p_{\mathrm{d}} + q_{\mathrm{d}} = 1$, and $(p_{\mathrm{m}} + q_{\mathrm{m}})(p_{\mathrm{d}} + q_{\mathrm{d}}) = 1$, the expected probabilities for each of the four possible outcomes are: $p_{\mathrm{m}}p_{\mathrm{d}} = P(+/+)$, $p_{\mathrm{m}}q_{\mathrm{d}} = P(+/-)$, $q_{\mathrm{m}}p_{\mathrm{d}} = P(-/+)$ and $q_{\mathrm{m}}q_{\mathrm{d}} = P(-/-)$, if mothers and their pups selected prey independently of one another. This expected distribution differed significantly (and in the proper direction if mothers and their young were selecting similar prey) from that observed ($\chi^2 = 13{\cdot}14$, d.f. = 3, $P = 0{\cdot}0043$).

The degree of dietary similarity between mothers and their dependent pups was also evaluated by scoring which prey types consumed by a given pup were present or absent in (i) the diet of its mother, and (ii) in the diets of the remaining 8 non-mothers. The percentages of prey types consumed by a pup that were also consumed by its mother or by all the non-mothers were computed from this record (Table 3). The hypothesis that percentage dietary similarity was not significantly different

Table 3. Percentage of prey consumed by pups that were eaten by mothers vs. non-mothers

Pup Number	Mothers	All non-mothers
1	71·4	48·2
2	100·0	41·6
3	100·0	87·5
4	100·0	8·2
5	87·0	77·2
6	87·5	75·0
7	77·9	72·9
8	92·9	83·0
9	28·6	14·3
Total	94·3	48·6

between mother/pup and non-mother/pup pairs was rejected (Wilcoxon's Signed Ranks Test, $T = 0$, $P << 0{\cdot}01$).

Dependent pups had significantly more unsuccessful dives (87%; 4708 of 5413 dives) than their mothers (30%; 2672 of 8844 dives; normal approximation to the binomial, $z = 57{\cdot}00$, $P < 0{\cdot}0001$). While foraging, sea otters often obtained inedible items (e.g. rocks, empty shells and carapaces, metal cans, driftwood, urchin tests, plastic bags, golf balls and occasionally other items), which they sometimes attempted to eat. Pups brought such objects to the surface on 9% of their dives (467 of 5413 dives), whereas mothers rarely captured non-prey objects (on 0·1% of their dives; 9 of 8844 dives).

FORAGING PATTERNS OF MOTHERS AND THEIR WEANED OFFSPRING

Sufficient information on dietary composition was available for three pairs of mothers and their weaned daughters to begin evaluating whether otters follow their mothers' foraging patterns as juveniles and adults. After weaning, all three daughters captured and consumed the same types of prey as their mothers (Fig. 4). Pair 2 fed mainly on rock oysters (*Pododesmus cepio*, Gray), as well as smaller amounts of crabs, fat innkeepers (*Urechis caupo*), and occasionally squid (*Loligo opalescens*, Berry), while pairs 1 and 3 both fed mainly on kelp crabs, purple sea urchins,and mussels.

Dietary similarity between these mothers and their weaned offspring was evaluated by comparing the post-weaning diet of each offspring with (i) that of its mother and (ii) those of the two non-mothers. For each of the nine possible adult/offspring combinations, we tallied the number of foraging dives made by the offspring for which the prey type comprised part of the diet of the adult. These figures were then summed for all mother/pup and non-mother/pup pairs, and the overall proportion of offspring dives in which the prey type comprised part of the diet of the adult was calculated for both groups. Eight hundred and forty-three post-weaning foraging dives were observed, of which 94·7% (798) resulted in the capture of prey species that were also eaten by their respective mothers. In contrast, using a pair-wise analysis to avoid biases from increased sample sizes, only 46·6% of these dives resulted in the

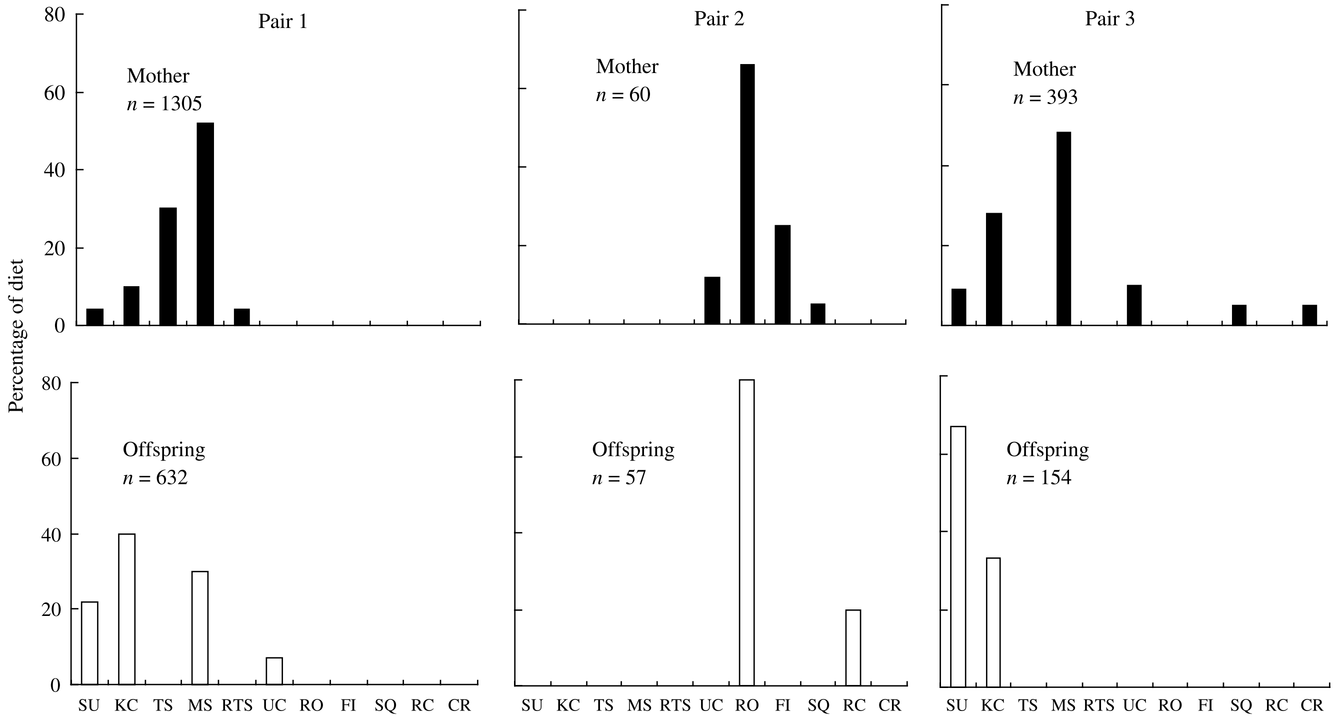

Fig. 4. Dietary composition of three adult female sea otters (above, solid bars) and their grown female offspring (below, open bars). Sample sizes (n) = number of successful foraging dives observed for each. Prey items are SU, sea urchin; KC, kelp crab; TS, turban snail; MS, mussel; RTS, red top shell (*Astrea gibberosa*); UC, unidentified crab; RO, rock oyster ( ); FI, fat innkeeper (*Urechis caupo*); SQ, squid; RC, razor clam (*Siliqua patula*); CR, *Cancer* crab.

capture of species that were eaten by each of the non-mothers (Table 3). The difference between these proportions is highly significant (normal approximation to the binomial, $z = 27{\cdot}95$, $P < 0{\cdot}0001$), thus supporting the hypothesis that the diets of weaned offspring are more similar to those of their mothers than to those of other adults.

Discussion

ECOLOGY AND EVOLUTION OF FORAGING SPECIALIZATIONS

Intra-specific variation in diet is known or suspected in a wide variety of species including various mollusks (Grantham, Moorhead, & Willig 1995), insects (Howard 1993; Cronin *et al.* 1999), fishes (Bridcut & Giller 1995; Schindler *et al.* 1997), reptiles (Daltry, Wusler & Thorpe 1998), birds (Giraldeau & Lefebvre 1985; Annett & Pierotti 1999), ungulates (Clutton-Brock, Guiness, & Albon 1982), bats (Fleming & Heithaus 1986), and mammalian carnivores (Kruuk & Moorhouse 1990; Ragg 1998). In many instances, differences in diet composition between conspecifics can be explained by environmental factors, such as variation in the availability or quality of food. For example, marine- and freshwater-living populations of European otters (*Lutra lutra*, Brünnich) in Scotland have vastly different diets (Kruuk 1995); the diet (and consequent social behaviour) of coyotes (*Canis latrans*, Say) varies seasonally with food availability (Bekoff & Wells 1986); and many species of herbivores alter their diets in response to changing plant quality in environments where plant species composition remains unaltered (Rosenthal & Janzen 1979; Thomas 1987). Dietary variation in sexually dimorphic species is also well known (e.g. Clutton-Brock *et al.* 1982), as are ontogenetic dietary shifts because of morphological change and learning (McLaughlin & Grant 1994; Barbosa, Barluenga, & Moreno 2000). Most of the above cited examples are consistent with the predictions from simple optimal foraging theory because individuals of a particular sex and phenotypic status are selected to adopt a single 'optimal diet', given the current set of environmental conditions.

Examples of individual dietary variation that cannot be explained by environmental, phenotypic or class-specific effects are harder to chronicle and more perplexing. To demonstrate such variation one must document persistent differences among individuals, while controlling for both phenotypic and environmental variation. The findings reported here for sea otters meet these criteria, as do those for two species of carnivorous marine snails, *Thais* spp. (West 1986, 1988); the Cocos Island finch, *Pinaroloxias inornata*, Gould (Werner & Sherry 1987); largemouth bass, *Micropterus salmoides*, Lacepede (Schindler *et al.* 1997); the spice finch, *Lonchura punctulata*, Linnaeus (Beauchamp, Giraldeau, & Ennis 1997); bumblebees, *Bombus pennsylvanicus*, De Geer (Heinrich 1976); European oystercatchers, *Haematopus ostralegus*, Linnaeus (Norton-Griffith 1967); and killer whales, *Orcinus orca*, Linnaeus (Baird, Abrams & Dill 1992). But how does such intraspecific diversity arise, and why do all individuals not converge on the same optimal diet? To answer these questions, we first consider the factors that favour the evolution of specialization, and then discuss the particular case of diversification without environmental or phenotypic variation.

Two conditions must exist if individual foraging specializations are to occur in nature. First, specialists must be favoured over generalists. Second, selection must also favour diversification into multiple foraging specialists that can coexist in the same population. Without selection for diversification, selection for specialization will merely lead to a population with a single type of specialist. The evolution of ecological specialization is fairly well understood (Futuma & Moreno 1988), and several studies have demonstrated enhanced foraging intake rates for specialist foragers due to more efficient searching or handling times (Heinrich 1976). In contrast, the factors that promote diversification of a generalist population into alternative foraging specialists are less well understood, but three potential mechanisms have been proposed: environmental variation in food supply (spatial or temporal), phenotypic differences among individuals that influence foraging success, and frequency-dependent fitness benefits (Partridge & Green 1985; Magurran 1986; Beauchamp *et al.* 1997).

Partridge & Green (1985) noted the close parallel between multiple individual foraging specializations in a population and the alternative reproductive and developmental strategies that have now been documented in a wide variety of taxa (e.g. Dawkins 1980; Dominey 1984; Pfennig 1992). Accordingly, they suggested that the same conceptual framework that has proven so useful in understanding the evolution of these other forms of intraspecific variation – evolutionary stability rather than optimality – can provide insights into the conditions that lead to some alternative foraging specializations. Specifically, diversification of specialist types may be favoured when the benefit an individual gains from consuming specific prey types depends, in part, on what other individuals in the population are doing. Several authors have echoed the potential role of frequency-dependent prey choices in diversification (Magurran 1986; Beauchamp *et al.* 1997), but it is important to stress that density-dependent effects are also crucial. Without density-dependent prey depletion driving intraspecific competition, frequency-dependence will not lead to diversification.

The frequency-dependent scenario outlined by Partridge & Green (1985) is essentially Fretwell & Lucas's (1970) theory of ideal free distributions applied to foraging specialists. Consider a consumer species that is a generalist at the population level (i.e. it has several prey items available to it), but where individual specialization is favoured due to enhanced efficiency at finding or handling prey. The value of different types of prey to a forager depends not only on the prey's intrinsic value (e.g. their energetic and nutritive values), but also on prey abundance, which itself is affected by foraging choices of the predators. If all individuals were to specialize on the best intrinsic prey item, prey depletion would depress the realized benefit of the prey item below that of other intrinsically inferior prey items. Accordingly, it would pay some individuals to specialize on these other prey items. In theory, an equilibrium frequency of different foraging types can be reached where all prey items yield an equal benefit (Partridge & Green 1985).

This theory of ideal free foraging specialization makes two important predictions. First, if a population is at equilibrium, all foragers should obtain the same intake rate, a prediction supported in a laboratory study of finches (Beauchamp *et al.* 1997). This prediction, however, provides a weak test because it is supported only by failure to reject the statistical null hypothesis of no difference (Partridge & Green 1985; Beauchamp *et al.* 1997). Second, diet breadth at the population level should be affected by changes in population size. For example, if the density of consumers is reduced sufficiently, individuals should cease specializing on the lowest quality prey items, with a corresponding reduction in the diversity of prey consumed by the entire population. The temporal scale of the predicted response depends on how quickly individuals can switch specializations: in the most extreme case, the responses to changes in the density of predators and/or prey may occur on an inter-generational time scale. The predicted change in diet breadth was not found in a study of largemouth bass; instead, individuals became less specialized as population density decreased (Schindler *et al.* 1997). Heinrich (1979) found similar density-dependent changes in specialization in bumblebees; increases in the number of bees specializing on the most profitable flower, jewelweed (*Impatiens biflora*, Walt) decreased the nectar reward in this flower, after which individual bees became less specialized.

Behavioural foraging specializations potentially share much in common with a morphologically based foraging specialization, trophic polymorphisms. Trophic polymorphisms are morphological polymorphisms that are associated with discrete differences in feeding behaviour or habitat use (Robinson & Wilson 1994; Smith & Skúlason 1996). In contrast to many foraging specializations that result from phenotypic variation, such as those based on gender or size outlined above, the phenotypic differences in trophic polymorphism are thought to be a consequence of the diversification process, not a cause. Thus, the main difference between trophic polymorphisms and behavioural specializations is the means by which specialization is achieved: in the former, efficiency is enhanced through specialized trophic apparatus (e.g. the beak polymorphism in fire finches, *Pyrenestes ostrinus* (Vieillot), Smith 1987), while in the latter, foraging success is enhanced through increased experience. Despite this important difference, trophic polymorphism and behavioural specializations are both discrete patterns of intraspecific variation, and likely stem from similar diversifying mechanisms, frequency– and density–dependent fitness interactions (Smith & Skúlason 1996).

The broader ecological circumstances that promote the evolution of foraging specializations are also likely to be similar for behavioural and trophic polymorphisms. Two ecological prerequisites, in particular, are important: weak interspecific competition coupled with strong intraspecific competition. Intraspecific foraging polymorphisms, equivalent in a sense to a single species filling the ecological niche of two or more species, require reduced interspecific competition. This could explain why many of the documented foraging specializations occur in ecological situations involving empty niches and reduced interspecific competition (Smith & Skúlason 1996), such as isolated islands (e.g. behavioural polymorphism in Cocos Island finches) or low diversity postglacial lakes (e.g. trophic polymorphisms in various fish taxa). In addition, strong intraspecific competition for limiting resources is required to drive the diversification into multiple foraging specialists. Strong intraspecific competition is most likely in species whose populations are regulated from the trophic level below, rather than by physical disturbance or the one above. For this reason, individualized foraging specializations might be expected to occur more frequently in apex predators as opposed to species of lower trophic status, among species in systems under bottom-up as opposed to top-down control, and in systems regulated by resource competition as opposed to physical disturbance.

FORAGING SPECIALIZATIONS IN SEA OTTERS

The fact that sea otters are specialist predators is not especially surprising. After all, they live in a diverse environment with a large number of potential prey species, many of which probably require different hunting tactics and handling skills to process efficiently. Specialization on limited suites of prey and specific foraging tactics may be a more efficient way to forage after weaning (Caldow *et al.* 1999; Stillman *et al.* 2000). Sea otters, with their high metabolism and substantial energetic requirements (Costa & Kooyman 1982) and their limited capacity for energy storage, live in a marine environment in which food can be difficult to obtain, especially in areas where otter populations have existed for some time. Individuals must be efficient foragers to survive under these conditions. These circumstances also would be expected to promote dietary specialization in the sea otter, just as they apparently have in many other consumer–prey systems.

The observed individual-level differences in sea otters, while somewhat more surprising, are also consistent with both expectations from theory and many features of sea otters and their associated ecosystems. As discussed above, a diversity of specialized behaviours is most likely to arise in systems with weak interspecific competition and strong intraspecific competition. Sea otters and kelp forests appear to meet these conditions. While several other consumers (e.g. diving sea ducks, benthic feeding fishes, lobsters and predatory sea stars) feed on many of the same prey species as sea otters, none appear to effectively compete with sea otters for food. This conclusion is based in part on the fact that documented prey population increases and declines in response to the removal or addition of sea otters are far greater than those that accompany the addition or removal of any of the potential competitors (see Riedman & Estes 1990 for a summary of the evidence). This is probably due in large measure to the comparatively high population density, large body size, and high field metabolic rate of sea otters. In contrast, competition among individual sea otters must be intense when food resources are limiting, judging from the high level of starvation-induced mortality in equilibrium populations (Bodkin, Burdin & Ryazanov 2000; Monson *et al.* 2000). If individual differences in dietary diversity are promoted by strong intraspecific competition, then this diversity should decline or even disappear when intraspecific competition is relaxed. The available information for sea otters is consistent with this expectation. In a comparative study of adjacent high and low density sea otter populations in three widely separate regions of the North Pacific Ocean, dietary diversity was consistently greater for the high-density populations (Estes *et al.* 1981). Furthermore, Watt *et al.* (2000) reported little individual variation in diet of sea otters at Amchitka Island in the early 1990s, a time at which sea otter numbers had been depressed by killer whale predation (Estes *et al.* 1998) and sea urchin (the otter's preferred prey) abundance had responded by increasing about two-fold.

The above discussion focused on the selective mechanisms that could result in individual variation arising within a population. Once alternative specializations have arisen in a population, however, other factors may become important in maintaining them, or in mediating their relative frequencies over time. One such factor, of particular significance in sea otters, is the matrilineal transmission of foraging preferences and/or foraging skills. Although no direct evidence of this exists, it is conceivable and even likely that sea otter females actively teach foraging skills to their offspring. Teaching is most likely to occur among kin (parent and offspring), and to have evolved when parental instruction is critical for the young to learn difficult or specialized foraging skills (Caro & Hauser 1992), as appears to be the case for sea otters. Even if direct teaching does not occur, the offspring dependency period can still be viewed as a period of subsidized learning, when pups are able to practice and improve their capture and handling skills while having their energy reserves boosted by maternal input. After they have been weaned, individuals may face significant 'performance penalties' associated with learning or acquiring new skills. With virtually no body fat, sea otters have very limited energy reserves, and even minor, short-lived decreases in their rate of energy intake can be fatal (Kenyon 1969). If the energetic penalties of switching to a new prey type are prohibitive, transmitted specializations may act as a local optimum, even though some other prey type might offer a higher net rate of energy intake (Dukas & Clark 1995; Schindler *et al.* 1997). The principal effect of cultural transmission may therefore be one of inertia, introducing a time-lag into the frequency-dependent switches in foraging specializations, or even perpetuating particular specializations generations after they would otherwise have disappeared (Partridge & Green 1985).

Another factor that may play a part in maintaining individual variability is temporal or spatial variability in prey populations. The overabundance or near extinction of a particular prey could shift the economics of prey choice to the point of causing some individuals to include or exclude that item, despite a high cost of switching. Similarly, once an individual has become proficient at exploiting a familiar prey, it might continue to do so even when the prey was rare, and a prey species excluded from the diet during periods of rarity might not be added again during periods of abundance. In conjunction with the cultural inertia discussed above, temporal variation of prey resources may result in the maintenance of apparently 'suboptimal' specializations over multiple generations. Many of the sea otter's prey populations are in fact characterized by considerable temporal variation in abundance. For instance, purple sea urchins in Monterey Bay recruit episodically, are superabundant following strong recruitment events, and are generally rare during the intervening periods (Pearse & Hines 1987). Environmental shifts resulting from El Niño events and other less well-known oceanic processes cause similar variation in the distribution and abundance of other prey species.

Regardless of the ultimate cause, individual dietary variation has broad ramifications to population and community ecology. The reproductive success of many consumers critically depends upon their ability to compete for food, especially when food is a limiting resource. Ecological forces of this nature are widely held to be responsible for divergence among closely related or ecologically similar species (MacArthur 1972; Roughgarden 1972; Schoener 1986). Our findings suggest dietary differences can just as easily act to reduce intraspecific competition among individuals. Individual dietary variation would necessarily cause food-limitation to act differentially on different individuals, perhaps thereby explaining the often-observed variation in body condition among individuals in populations that are purportedly food-limited. Individual variation has equally important implications to food web dynamics. Just as Polis *et al.* (2000) pointed out the distinction between community-level and population-level trophic cascades, per capita interaction strengths (Berlow *et al.* 1999) for particular consumer–prey combinations may vary more among individuals than they do among many species. Because so much of nature's fabric is defined by food web interactions, individual differences in foraging specialization are probably relevant to every important dimension of population and community ecology.

Although individual variation in diet remains largely unexplored from the standpoints of both theory and empirical detail, there would seem to be many parallels with human survival systems in the sense that humans succeed or fail through their work just as individual animals in food-limited populations succeed or fail through their ability to obtain enough to eat. Few humans in modern societies are capable of immediate career changes because of the extensive learning needed to compete successfully in almost any line of work and the limited capacity to compete successfully in more than several of these. Such qualities may help explain why there is a diversity of observed patterns as opposed to a single optimum, and for humans as well as sea otters, why a jack-of-all-trades is the master of none.

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