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Individual Prey Choices of Octopuses: Are they Generalist or Specialist?

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Individual prey choices of octopuses: Are they generalist or specialist?

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Abstract Prey choice is often evaluated at the species or population level. Here, we analyzed the diet of octopuses of different populations with the aim to assess the importance of individual feeding habits as a factor affecting prey choice. Two methods were used, an assessment of the extent to which an individual octopus made choices of species representative of those population (PSi and IS) and 25% cutoff values for number of choices and percentage intake of individual on their prey. In one population of *Octopus cf vulgaris* in Bermuda individuals were generalist by IS=0.77, but most chose many prey of the same species, and were specialists on it by >75% intake. Another population had a wider prey selection, still generalist with PSi=0.66, but two individuals specialized by choices. In Bonaire, there was a wide range of prey species chosen, and the population was specialists by IS= 0.42. Individual choices revealed seven specialists and four generalists. A population of *Octopus cyanea* in Hawaii all had similar choices of crustaceans, so the population was generalist by IS with 0.74. But by individual choices, three were considered a specialist. A population of *Enteroctopus dofleini* from Puget Sound had a wide range of preferences, in which seven were also specialists, IS=0.53. By individual choices, thirteen were also specialists. Given the octopus specialty of learning during foraging, we hypothesize that both localized prey availability and individual personality differences could influence the exploration for prey and this translates into different prey choices across individuals and populations showed in this study [*Current Zoology* 58 (4): 597–603, 2012].

Keywords Octopuses, Prey choice, Specialist, Generalist

The ecological niche of animals is often calculated at the species level, while the variation amongst individual is overlooked (Bolnick et al., 2003). Calculation of the niche in terms of prey choice by populations of generalist predators may be particularly unrealistic. Studies on foxes (Angerbjorn et al., 1994), frogs (Araujo et al., 2009), kestrels (Costantini et al., 2005) and sunfish (Ehlinger and Wilson, 1988; Wilson, 1998) have all uncovered prey choice variability within single individuals. There are definite cross-population variations in these generalists, but even when the authors look within a single population, individual differences appear in prey species taken. This paper will evaluate the prey choice differences in a generalist invertebrate predator, the octopus, and discuss possible cause of these variations.

Octopuses are well known as generalist foragers in the shallow-water marine environment, taking a variety of mollusks and crustacean prey, as revealed by the shell remnants that they discard outside their sheltering dens (Ambrose, 1984; Mather, 1991a; Vincent et al., 1998;

Anderson et al., 2008; Leite et al, 2009). They actively select prey species, although some species are preferred in the laboratory, they may not be common in the natural environment and therefore be poorly represented in prey remains samples. (Ambrose, 1984; Mather, 1991a; Vincent et al, 1998). Prey taken are not just a reflection of prey availability, as habitat quality would reflect prey diversity in the habitat in the midden piles of *Enteroctopus dofleini* (Scheel, Lauster and Vincent, 2007). A test of Cardona's niche breadth index (Anderson et al, 2008) showed that individual octopuses within a restricted area in Bonaire were specializing on a few of the many prey species taken by the population area. As in many other studies of individual specialization, the authors uncovered the phenomenon but did not address its scope (though see West, 1986; 1988), or source.

Individual differences in prey choice are often rightfully seen as due to age, sex, size or morphology and thus traced to sub-populations (Svanbäck and Bolnick, 2008). Yet there is variation within these categories as

well, and octopuses are good animals to study for within-group specialization. With a semelparous reproductive strategy (see Hanlon and Messenger, 1996), cephalopods such as the octopus spend most of their life as non-reproductive adults, and during this large proportion of their lifespan (Mather, 2006), few sex and maturity differences in prey choice appear (Leite et al., 2009). While octopus size has some effect on prey choice (Steer and Semmens, 2003), it is not a major influence on prey selection.

Within a social group, prey choice may be influenced by territoriality, as in bears (Mattson & Reinhart, 1995) or the social status and parental influence seen in oystercatchers (Sutherland, 1987). Octopuses do not hold territories and are somewhat asocial during the non-reproductive phase of the life cycle, more influenced in their distribution by the presence of shelter (Mather, 1982; though see Huffard et al., 2010).

If these influences do not dictate what prey species an individual animal will choose, what will? Every animal individually faces trade-offs based on encounter rate with prey, resource value, prey escape rates, handling times and risk of predation on itself (Bolnick et al., 2003; see Vincent et al., 1996). Octopus are well known for their intelligence and learning capacity (Wells, 1978). Yet, not all individuals will calculate the trade-offs in the same way, likely influenced by experience, which can lead to learning and memory of prey types and handling (Sutherland, 1987), search efficiency (Ehlinger and Wilson, 1988) and adaptation to and selection for particular micro-habitats (Wilson, 1998). Such cognitive abilities and differences are important to foraging strategies of octopuses (Mather, Leite, Anderson & Wood, in sub) and may be attributed to differences in personality (see definition in Mather and Anderson, 1993).

While the study of personality is extensive in humans, the area is now beginning to be explored in non-human animals, particularly the intersection of such variation with cognition (Carere and Locurto, 2011) and the extent to which it might be selected for (Dingemanse and Réale, in press). Octopuses have clear personality variation on three dimensions: activity, reactivity and avoidance (Mather and Anderson, 1993). How could this personality variation affect individual trade-offs in octopus foraging? One way it could affect prey choice is through exploration, as octopuses are highly exploratory animals (Mather and Anderson, 1999). Personality variation such as risk aversion could affect the amount

of exploration done, information received and thus range of prey available to an individual (Carere and Locurto, 2011). In rats (Matzel et al., 2006), more exploration in a laboratory environment led to better learning. Personality could also affect learning directly, when individual sooty grunter fish learn to avoid noxious cane toads at quite different speeds (Crossland, 2001).

Mather reported results from an octopus that went through test for spatial memory of landmarks (Mather, 1991b); it swam around the periphery of the circular tank time after time throughout lab tests and never learned the tasks it was given. Thus we can expect that active choices will influence prey selection, resulting in some octopus populations including individual animals making a variety of choices, between strict specialists and wide generalists (see Bolnick et al., 2003). This paper begins the study of octopus individual variation with an evaluation of their prey choice, in order to find patterns of prey selection in individual within three species and five populations.

1　Materials and Methods

Prey assessment was made easy because octopuses only consume the soft parts of their prey, removing the flesh by external digestion, scraping with the radula and digging with the chitinous beak, and subsequently discard skeletal and shell remains (Nixon, 1987). Crabs were tallied by carapace and gastropods by shell, both of which are unique. Bivalves valves were matched where possible but unmatched valves indicated an animal as well. This method had been used by several studies (Mather, 1991a; Vincent et al., 1998) and it is able to sample the range and number of prey species taken, especially with daily sampling (see Smith, 2003).

Data for the focus on individual specialization of octopus prey choice was taken from five field studies (Mather, 1991a; Anderson et al., 2008: Mather, in press; Scheel and Anderson, in press). In all cases, prey remains were retrieved from outside the sheltering dens of octopuses, and collection only continued as long as the octopus stayed in that den (only occasionally could individual octopuses be identified). Remains of prey were collected during snorkeling or scuba visits and subsequently identified, usually to genus (in Bonaire and Puget Sound they were identified to species but summed to genus for this investigation). In Bermuda, prey of *O. cf vulgaris* were collected daily from the area of the Coney Island Bridge in 1984 and subsequently from

Whalebone Bay, 0.5 km away, in 1985 (Mather, 1991a). Water depth ranged from intertidal to 3 m, the habitat was mixed rock, rubble and sand/mud. In Bonaire, prey remains were collected from the lee side of the island in 2002–2003, along 1 km of shoreline (Anderson et al., 2008). Water depth ranged from 0.5 to 5 m, collection was every 1–2 days and the bottom was coral reef, reef rubble and pockets of sand/mud. In Hawaii, individuals of *Octopus cyanea* were located on the reef of Coconut Island, Kaneohe Bay, Oahu, in 1993, in water of 1–2 m depth, and prey remains were collected daily over four weeks to evaluate intake (Mather, 2011). The substrate was coral reef and reef rubble, with occasional mud patches. In Puget Sound, dens of *E. dofleini* were evaluated during 2009, depth ranging from 9 to 25 m and habitat varying between rock, rubble and sand/mud. Summer water temperature was 25–28 degrees C in all sites except Puget Sound, where it was 8–12 ℃.

Remains of prey were gathered over several weeks in two different summers for the two Bermuda populations of *O.* cf *vulgaris,* and over two summers for the Bonaire population, and identified to genus (distinctions by species were very small and difficult to evaluate). A cut-off of 4 days sampling duration was applied to the Hawaiian *O. cyanea* population and the mean collection duration was 9 days. For four octopuses the sampling period was 16 days or more, which gave us the opportunity to divide the sampling time into first and second halves to look for stability of prey choice. In Puget Sound, dens were sampled once during 2009 by a variety of recreational divers. In every case the minimum number of prey individuals necessary for an octopus' choice data to be included was 15.

For calculating the degree of individual diet specialization we first used a distribution-overlap approach, proportion similarity index (PS), for the diet overlap between an individual *i* and the population (Svanbäck and Bolnick, 2008).

$$\mathrm{PS}_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j)$$

where: the variable *pi* is the proportion of all resources used by the population that are used by individual *i*, *qi* is the proportion of the *j*th resource category in the population's niche (This calculation is easily done by the program IndSpec 1.0 (Bolnick et al., 2002), available in Bolnick et al. (2002). By their definition individuals that consume resources in direct proportion to the population as a whole, PS*i* = 1 (generalist). The population-wide prevalence of IS (Individual Specialization) is then measured by the average of individuals' PS*i* values. In this, animals and populations were considered Specialists when indices were less than 0.5 and Generalist when they were greater (Bolnick et al., 2002; Svanbäck and Bolnick, 2008). For this analysis, Generalist means that the individual eats most of the same preys species that the population does, while Specialist means that the individual eats different prey species compared with the population.

Another method for an individual to be considered a Specialist by further diet assessment is an arbitrary cut-off if it only sampled less than a quarter of the genera that the population to which it belonged had sampled (number), and/or that it consumed over 75% of its intake of one species (percentage). A Generalist would have consumed 75% of the range of prey taken by the group (number), and/or less than 25% of its most common one (percentage). While these are arbitrary cut-offs, they capture some of the variation in prey choices.

2 Results

2.1 Bermuda population One

For the first Bermuda population of *O. cf vulgaris*, 13 individuals were included in the analysis, with a mean sample size of prey animals from remains of 48. Within the population only one animal was a specialist by the PS*i* index (0.42). This one consumed more of the crab *Mithrax*, different from the others who all consumed more of the bivalve *Lima/Ctenoides*, and were therefore considered generalists. The population consumed resources in a similar way, especially the single resource, resulting in low variation between individuals, and a specialization index IS of 0.77 (generalist population) (Table 1). The number of genera taken by all the animals was 13, and the mean taken by individuals was 4.7 (range 3–7, *SD* 1.2). Twelve of the 13 octopuses consumed the most prey of the fragile-shelled bivalve *Lima* (*Ctenoides*), and one of the crab *Mithrax*. Specialization on the leading prey was very high, ranging from 26% (for the *Mithrax*) to 93% on *Lima*, with a mean of 70%. While the population could be considered a specialist, only seven of the individuals within it were specialists by percentage of preferred prey and three by number (Table 2). None of the octopuses was a generalist by either measure.

2.2 Bermuda population Two

In the second Bermuda population of the same species (*n*=13), the number of genera taken was similar, at 12), but the mean number was somewhat higher at 6.4

Table 1   Values of IS (population-wide prevalence of Individual Specialization) and PS*i* (Proportion Similarity), of three octopus species (*E. dofleini, O. cyanea* and *Octopus* cf *vulgaris*) from five different populations

	Octopus cf *vulgaris*	*Octopus* cf *vulgaris*	*Octopus* cf *vulgaris*	*Octopus cyanea*	*Enteroctopus dofleini*
	Bermuda Pop1	Bermuda Pop2	Bonaire	Hawaii	Puget Sound
IS	0.77	0.61	0.42	0.74	0.49
Individual PS*i*	0.88	0.73	0.60	0.61	0.55
	0.85	0.65	0.20	0.74	0.51
	0.65	0.55	0.58	0.92	0.50
	0.79	0.68	0.67	0.94	0.83
	0.83	0.74	0.28	0.80	0.42
	0.90	0.70	0.29	0.72	0.78
	0.42	0.51	0.50	0.59	0.47
	0.82	0.60	0.37	0.89	0.68
	0.83	0.37	0.55	0.65	0.58
	0.56	0.65	0.24	0.66	0.66
	0.85	0.47	0.34	0.75	0.31
	0.87	0.60	0.44	0.72	0.62
	0.81	0.67		0.90	0.38
				0.50	0.85
				0.63	0.19
					0.22
					0.44

Table 2   Selection of prey genera by octopuses from three species (*E. dofleini, O. cyanea* and *O.* cf *vulgaris*) from five different population

Octopus species	Place	Octopus *n*	N of prey species *n* (average)	Leading prey	Generalist		Specialist	
					n	%	*n*	%
Octopus cf *vulgaris*	Bermuda, pop 1	13	13 (4.7)	2 genera (crab, bivalve)	0	0	3	7
Octopus cf *vulgaris*	Bermuda, pop 2	13	12 (6.4)	4 genera (crab, bivalve, gastropod)	2	1	1	0
Octopus cf *vulgaris*	Bonaire	12	52 (11.3)	4 genera (crab, bivalve, gastropod)	0	4	7	1
Octopus cyanea	Hawaii	15	18 (5.5)	2 genera (crab)	0	0	3	3
Enteroctopus dofleini	Puget Sound	23	12 (3.3)	5 genera (crab, bivalve)	1	0	13	13

Specialists had remains of fewer than 25% of the prey selected by the population as a whole, and/or consumed 75% or more of their prey from one genus. Generalists had remains of more than 75% of the prey selected by the population as a whole and/or less than 25% of their prey from one prey species.

(range 3–11, *SD* 2.3). The mean sample size of prey remains was 36. In this population two animals were considered specialists by the PS*i* index. One consumed only two prey, the crab *Mithrax* and bivalve *Semele* (PS*i* = 0.37), and another consumed mainly the gastropod *Columbella* (PS*i* = 0.47). The population in general had indices above 0.5, and so individuals were considered to be generalist (IS = 0.61). Three individual consumed mostly *Mithrax* crabs, one *Semele* bivalves, three *Columbella* gastropods and four *Ctenoides* bivalves, a far greater diversity than the first population. In addition, the proportion of remains from the leading prey was lesser, a mean of 44%. Only one of the animals could be considered a specialist by the criterion of number of prey genera (3), and none was a specialist by the criterion of over 75% of prey composed of one species. De-

spite the diversity of prey intake, only two animals were generalist by number and one by percentage.

2.3   Bonaire population

In the Bonaire population (*n*=12), also of *O. cf vulgaris*, sampling took place over a longer period and the sample was larger, with a range of 52 genera (mean of 11.3) and a mean sample size of prey remains of 69. The range of individual choices was wider (3 to 16, s.d. 4.4). The majority of individuals of this population (*n*=7) were individuals specialists, according to PS*i* indices of < 0.5 (see Table 1). So this population can be considered specialist (IS = 0.42). Four octopuses consumed most of the crab *Mithrax* and four the scallop *Chlamys*, one the gastropod *Nerita*, one the gastropod *Bursa*, and two had equal numbers for two species. The mean percentage of the leading prey taken was also lower, at 35%. By the

criterion of less than 1/4 of prey genera taken, seven animals were specialists (sample sizes of 3 (48), 10 (102), 10 (51), 7 (47), and 10 (26)) but only one by percentage, 85% (48). Four octopuses were generalists by a percentage <25%, but none by number, given the large number of prey genera taken (see Table 2).

2.4 Hawaiian *O. cyanea* population

For the 15 Hawaiian *O. cyanea*, the range of prey taken was smaller, 18 species, mean number of prey remains per animal, *n*=47, with most remains from five genera of crabs. The mean number of prey species taken per individual was 4.7 (range 3−6, *SD* 0.94). In this population no animal was considered specialist by the PS*i* index, while some animals were generalist (Ps*i* > 0.9). As a result, the population was generalist (IS = 0.74). Eleven octopuses consumed most of the crab *Thalamita,* and four of *Leptodius.* The proportion of the most common prey was variable, a mean of 57%, ranging from 39% to 86%. With 19 possible prey sources, three individuals were specialists by the 25% criterion for prey type, (*n*=4 (19), 3 (29), 4(15)) and three by percentage (81% *n*=32, 84% *n*=67 and 87%, *n*=38). None was a generalist. Prey choices of the four octopuses were stable over two halves of the sampling period (Table 3).

Table 3   Number of prey choices in the first and second half of the sampling period (16 days or more) of four *Octopus cyanea* from Hawaii

Octopus	Period	Prey species			
		1	2	3	other
2	1 half	24	8	25	5
2	2 half	37	16	56	2
4	1 half	49	4	16	7
4	2 half	20	5	4	2
5	1 half	31	1	5	12
5	2 half	29	1	3	10
11	1 half	30	0	0	5
11	2 half	28	2	1	4

2.5 Puget sound *E. dofleini* population

23 dens had as much as or more than the cutoff n of 15; with 12 prey genera identified and a mean of 3.3 (range 1−9, *SD* 2.2). The mean number of prey remains was 28. In this population five animals consumed only one prey item (three consumed only *Cancer* sp. and two consumed only the bivalve *Clinocardium nuttallii*), and were considered very specialist. Seven other animals were considered specialists (PS*i* < 0.5). Although most were specialists some animals were generalists, so the population had a median IS of 0.49. Eleven individual

consumed the most of *Cancer* crabs, two of *Pododesmus* clams, one of *Clinocardium* cockles, one of *Saxidomus* clams and one of *Chlamys* scallops. The proportion of the most common prey ranged from 100% (*n*=6) to 22%, mean 73%. By the criterion of 75% or more, there were 13 specialists and for under 25% there was one generalist. By the number criterion, 13 were specialists, including those who had only consumed one prey item, and none made the generalist cut-off.

3   Discussion

One notable fact about this assessment is that the answer to "Is the animal a specialist or generalist?" depends on how you ask the question. At the level of the population, selection of only a few prey types or selection of prey across a limited phylogenetic range, as the octopuses did in Hawaii, suggests specialization, though oystercatchers specialize narrowly across one species of prey but take a different sample of them depending on bivalve opening technique (Sutherland, 1987). At the level of the fit of the individual into the population (Bolnick et al., 2002), generalists are considered to take the same array of prey, regardless of whether that range is large or small. At the individual level, specialists do not take a wide array, or narrow their repeated choices to a large percentage of one or a very few genera. And by these measures, sometimes the answer is different.

No pattern of octopus prey intake appears across these data. Prey remains collected unselectively across octopus middens suggest wide generalization (Ambrose and Nelson 1983, and Mather 1991a for *O. vulgaris*; Hartwick et al., 1978; Vincent et al., 1998; Scheel and Anderson, in press, for *E. dofleini*; Leite et al., 2008, for *O. insularis*), although there are major differences in the prey collection even of *O. vulgaris.*

In Bermuda across two different years and at two places 0.5 km apart, one population nearly all mostly chose the same prey and the other less so, despite a wider prey choice range. Populations differed in the number of prey species chosen. The Bermuda animals collected 12 and 13 prey species, compared to the 52 in Bonaire, perhaps reflecting the difference in faunal richness of prey species, as the Bermuda fauna is depauperate (Sterrer, 1986). The Puget Sound *E. dofleini* also collected the same small number of species, which could be expected as benthic diversity decreases from the tropical to the polar region (Nybakken and Bertness, 2004). In contrast, across decades the *O. cyanea* from Hawaii have basically consumed crabs (Mather, 2011), despite the fact that the reefs crawled with *Tegula* snails,

which *O. bimaculoides* selected in California (Ambrose, 1984). Yet because they all selected the same crab species, they were generalists by the IS measure (Bolnick et al., 2002). While octopuses are often selective of prey (Ambrose, 1984; Vincent et al., 1998), the basis of their selectivity is not clear.

At the individual level, the variety was even more striking, as PS*i* values for *E. dofleini*, for instance, ranged from 0.19 to 0.85. Only two of the five populations contained no generalists, and there was always at least one specialist. This is true even in the Bonaire population, as with a huge range of 52 different genera taken, seven animals were specialists by both the PS*i* measure and proportions taken (and see Anderson et al., 2008). As for many vertebrates (Ehlinger and Wilson, 1988; Angerbjorn et al., 1994; Costantini et al., 2005; Araujo et al., 2009), different individuals in the same population took different prey. The concentration of individual *E. dofleini* on five different prey species suggests localized prey concentrations such that individuals learned different things about prey acquisition (Cortez et al., 1998; Leite et al., 2009; Anderson and Mather, 2010).

Natural selection might maintain such variation amongst individuals by a variety of processes, including heterogeneous selection and such life-history tradeoffs. Hartwick et al. (1978) saw several middens with multiple remains of *Clinocardium* that were a long distance from the cockles' mud/sand habitat and speculated that the octopus had learned the location of a concentration of prey, even though it was far from the den. Yet five of the 23 *E. dofleini* individuals consumed only *Cancer* crabs, following the octopod preference, and see Vincent et al (1998) for a parallel selection. Similarly, one of the *O. vulgaris* in Bonaire ate a series of *Strombus* gastropods, which must have been taken from sand/mud habitat not near the den, and which also had been penetrated with the hole drilling method necessary for extracting this prey (Anderson et al., 2008). Such learning of prey handling techniques (Sutherland, 1987, for oystercatchers, and see Anderson and Mather, 2007 for octopuses) reminds us that learning is a specialty of the octopus (see Wells, 1978) and this learning might have been applied differently by different individuals.

In the face of population specialization, why might some few individuals be generalists, or vice versa? Perhaps some individual were more active and less avoidant (Mather and Anderson, 1993), and spent much of their time in exploration, encountering a wider variety of prey species (see Mather and O'Dor, 1991, for

trade-offs of foraging effectiveness with predation risk). While octopuses may search for prey in likely habitat (Mather, 1991a), they also opportunistically take the occasional prey animal which has placed itself at risk (Leite et al., 2009). Individuals with different personalities might minimize predation risk and specialize, as Leite et al., 2009 speculated for *O. insularis,* or might maximize intake as Scheel et al. (2007) observed for *E. dofleini*. The process of foraging in the predator-rich diverse shallow water ocean habitat is a difficult one, with spatial memory, saltatory search (O'Brien et al., 1990), selection of predator avoidance strategies and memory of suitable prey and extraction techniques all part of the process (Mather et al., in sub). It is not surprising that individuals of the octopus might use the considerable cognitive ability (Carere and Locurto, 2011) to make different life history trade-offs (Bolnick et al., 2003).

This varied data set should remind the reader that foraging by generalist predators is not the simplistic process it was often painted to be. Obviously prey selection is influenced by habitat, prey density, resource value of particular prey and predation risk, but this is not a passive process where all animals simply and similarly respond to these variables (Bolnick et al., 2003). Instead we would do better to evaluate the individual animal as an active agent in its environment, using cognitive abilities (Carere and Locurto, 2011) and individual personality tendencies (Mather and Anderson, 1993) to maximize its own patterns of survival and growth (Dingemanse and Réale, in press).

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