



Original Article

Ecological drivers of variation in tool-use frequency across sea otter populations

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Sea otters are well-known tool users, employing objects such as rocks or shells to break open hard-shelled invertebrate prey. However, little is known about how the frequency of tool use varies among sea otter populations and the factors that drive these differences. We examined 17 years of observational data on prey capture and tool use from 8 sea otter populations ranging from southern California to the Aleutian Islands in Alaska. There were significant differences in the diets of these populations as well as variation in the frequency of tool use. Sea otters at Amchitka Island, Alaska, used tools on less than 1% of dives that resulted in the capture of prey compared with approximately 16% in Monterey, California. The percentage of individuals in the population that used tools ranged from 10% to 93%. In all populations, marine snails and thick-shelled bivalves were most likely to be associated with tool use, whereas soft-bodied prey items such as worms and sea stars were the least likely. The probability that a tool would be used on a given prey type varied across populations. The morphology of the prey item being handled and the prevalence of various types of prey in local diets were major ecological drivers of tool use: together they accounted for about 64% of the variation in tool-use frequency among populations. The remaining variation may be related to changes in the relative costs and benefits to an individual otter of learning to use tools effectively under differing ecological circumstances.

Key words: foraging specialization, learned behavior, sea otter, tool use.

INTRODUCTION

Tool use has been identified in a wide range of animals including primate (Nishida and Hiraiwa 1982) and nonprimate mammals (Smolker et al. 1997), birds (Orenstein 1972), fishes (Brown 2012), and insects (Pierce 1986) although the vast majority of species do not use tools (Bentley-Condit and Smith 2010). In some tool-using species, tool use occurs in only a subset of populations or individuals, or the rate of tool use drastically differs across populations or individuals (Humble and Matsuzawa 2002; Mann et al. 2008). These differences are presumed to be due to variation in genetics, ecological conditions, and/or cultural knowledge. The influence of genetics and learning is difficult to demonstrate conclusively because of numerous confounding effects (Whiten et al. 1999; Lycett et al. 2010; Langergraber et al. 2011), whereas the influence of ecological factors can often be identified through comparative studies (Collins and McGrew 1987; McGrew et al. 1997; Fox et al. 2004; Rutz and St Clair 2012).

Previous studies suggest that animals use tools to acquire difficult-to-access resources that have high gains (i.e., a high cost/high reward situation), but only do so when under external pressures such as high inter- or intraspecific competition (Patterson and Mann 2011; Sanz and Morgan 2013) or limited resources during times of drought or other adverse environmental conditions (Tebbich et al. 2002). Others suggest that high encounter rates with difficult-to-access resources may lead to invention or maintenance of tool use (Sanz et al. 2012; Spagnoletti et al. 2012; Koops et al. 2013).

Sea otters (*Enhydra lutris*) provide an excellent model system for examining tool-use behaviors, their variation across populations, and the ecological drivers that maintain these behaviors. Tool use in sea otters is unusually conspicuous and well developed (Fisher 1939; Riedman and Estes 1990; Shumaker et al. 2011). This behavior occurs when foraging animals acquire a rock, empty shell, or other hard object and use it as either a hammer or an anvil to crack open invertebrate prey (Riedman and Estes 1990). Individuals will often keep the same tool for multiple dives by tucking it under their armpit (even if they do not use the tool each time they surface) and then drop it when it is no longer

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needed (Hall and Schaller 1964). Tool use is readily observed because sea otters return to the surface and float on their backs while processing and handling prey items.

Sea otters are distributed over a wide range of latitudes in the northeast Pacific Ocean, from southern California to northern Japan (Figure 1). Alaskan and Californian populations are considered morphologically and genetically distinct subspecies (Wilson et al. 1991; Scribner et al. 1997). Hall and Schaller (1964) and Riedman and Estes (1990) suggest that the Alaskan populations may use tools less frequently than the Californian ones. Both subspecies encompass similar habitats ranging from forests of giant kelp to sandy bays. Therefore, it is possible that any ecological differences seen at a population level would not be seen at the subspecies level. Sea otters consume a wide array of marine benthic invertebrates, some of which have soft bodies and others whose bodies are surrounded by shells, spines, or chitinous exoskeletons.

Thus, the edible portions of some species are well protected and difficult for sea otters to access. Sea otter populations in different locations often consume different diets because the assemblage of invertebrate species that are suitable prey varies with latitude and between rocky and sandy substrates (Riedman and Estes 1990).

Extensive observations on foraging and tool use have been conducted on populations throughout the sea otter range over the past 17 years, providing the opportunity for comparing the frequency of tool use in sea otter populations with similar and different genetics and ecological conditions. Our goal was to describe how the frequency of tool use varied across sea otter populations and identify the factors explaining variation in the frequency of tool use. We tested the hypothesis that different sea otter populations would exhibit different frequencies of tool use and that the proportion of hard-shelled prey in the diet would explain a large amount of any variation.

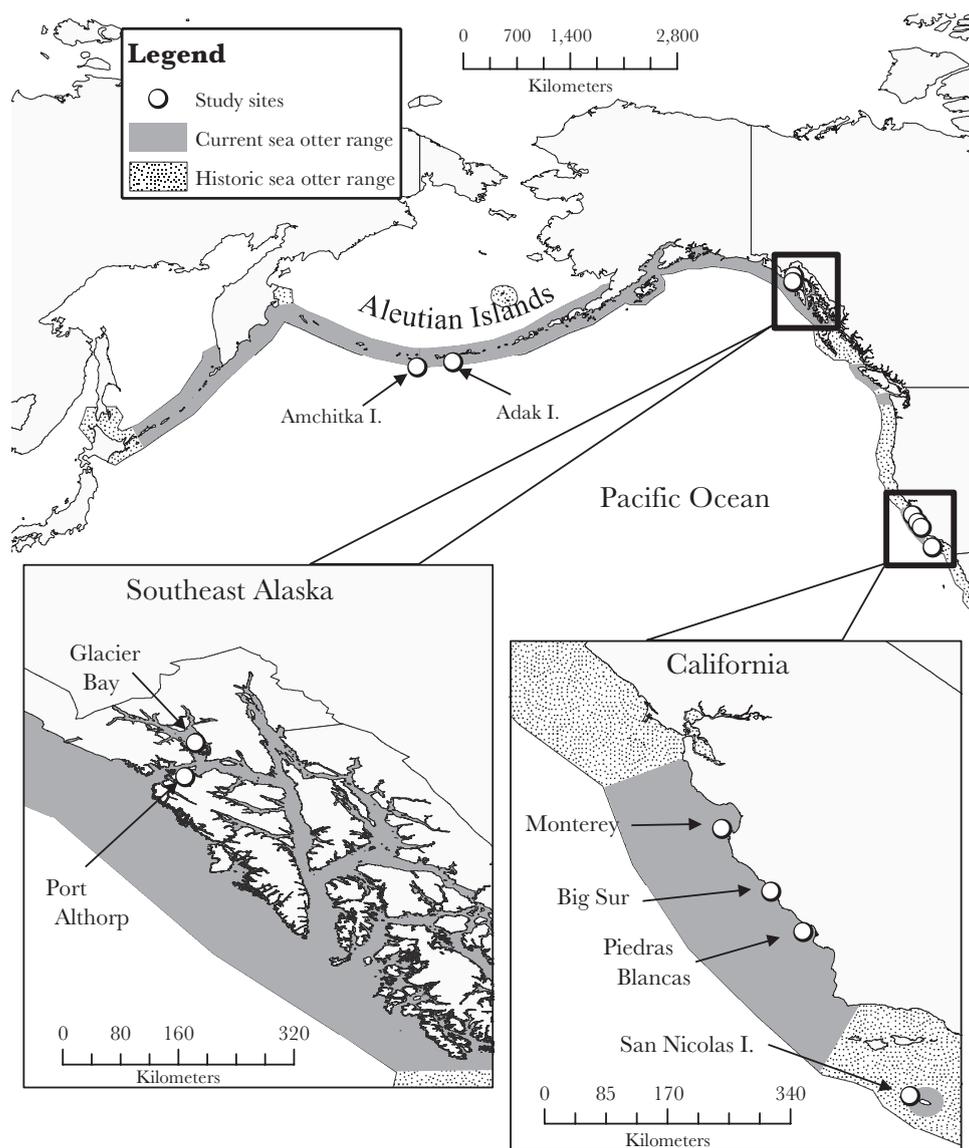


Figure 1

Map of historic and current sea otter range, showing the general locations of the study populations (white circles) and the 3 regions (Aleutian Islands, southeast Alaska, and California) into which the populations were grouped. Close-up views of the southeast Alaska and California regions shown in insets.

METHODS

Study sites

We used foraging data collected between 1994 and 2011 at 8 locations across the sea otter range in the northeast Pacific Ocean (Figure 1). The populations at these locations are geographically distinct with only occasional movement of individuals across some relatively nearby sites (Tinker et al. 2006). Each study site was characterized by a dominant substrate but encompassed a variety of habitats including rocky intertidal and subtidal substrates, kelp forests, sandy bottom areas, and mixed substrates of mud and silt. These diverse habitats provided a rich prey base for sea otters, with over 100 species of consumable benthic invertebrates (Riedman and Estes 1990).

Four studies took place along the California coast and 4 in Alaska (Table 1). For most analyses, we combine the California populations into a single group and the Alaskan populations into 2 regions, southeast Alaska (Glacier Bay and Port Althorp) and the Aleutian Islands (Adak and Amchitka Island). Although the Alaskan populations are considered one subspecies, the 2 regions in Alaska are separated by approximately 2600 km with no known movement between the two and are characterized by distinctly different habitats and prey assemblages.

With the exception of the 2 southeast Alaska populations, individual sea otters were captured and tagged with colored plastic cattle tags on the hind flippers (Kvitek et al. 1993) and very high frequency (VHF) radio transmitters (Ralls et al. 1989). Thus, observations at most sites were on known individuals that could be identified by their tags and followed over time. All field work was conducted with authorization by the US Fish and Wildlife Service under permits issued to M.T. Tinker (California), J.A. Estes (southwest Alaska), and J.L. Bodkin (southeast Alaska) and with oversight by the Institutional Animal Care and Use Committee at University of California Santa Cruz. Standardized methods of data collection were used across the sites with only minor differences, as described below.

Foraging and tool use

Foraging data were collected opportunistically over the duration of each study. We used focal animal sampling (Altmann 1974) to record foraging data on individual otters. A focal sea otter was considered to be foraging when it was observed repeatedly diving underwater and returning to the surface to either consume prey or breathe before diving again. A series of continuous feeding dives by a given individual was considered one forage bout, with

a bout ending if the animal was not observed to dive again within 30 min (Ralls et al. 1995). Observational data on diet and foraging behavior were obtained with the aid of 10×50 binoculars and Questar 50×80 power spotting scopes (Questar Corporation, New Hope, PA), following methods previously described by Kvitek et al. (1993), Estes et al. (2003), and Tinker et al. (2008). Data collection on each forage bout continued as long as observers could clearly see the otter ($n = 1\text{--}212$ dives per forage bout). Foraging data on untagged otters in southeast Alaska were collected for a maximum of 25 dives before moving on to a new foraging individual. Physical appearance and relative location were used to minimize possible resampling of individuals.

After locating a feeding animal, we recorded information on age, sex, and female reproductive status (presence or absence of a pup). Age was categorized as subadult (<3 years) or adult (>3 years) based on body size, grizzle (lightening of fur color and degree of body coverage, which generally increases with age), and dentition. For each feeding dive, we recorded a standardized series of data: dive and surface interval durations, dive outcome (whether or not prey were captured), prey identification, number and size of the prey items, and the presence or absence of tool use. Prey items were identified to the lowest possible taxon during data collection (Supplementary Material). However, prey items were collapsed into 5 prey classes for data analysis (bivalves, crabs, snails, urchins, and soft-bodied prey). Type of feeding habitat (rocky, sandy, or mixed substrate) was not recorded in all studies and so could not be included as a factor. However, we observed that sea otters feeding in sandy or muddy habitats will use any hard object, including shells, other prey, and anthropogenic litter as a tool. This suggests that the presence of tool use is not limited by the prevalence of rocks in an area.

An otter was considered to be using a tool if it was observed at the surface using an external object (such as a rock or empty shell) to aid in prey consumption. Tools are also sometimes used underwater by sea otters to dislodge prey from the substrate (Hall and Schaller 1964; Houk and Geibel 1974). This behavior was particularly common when an otter was attempting to capture abalone (*Haliotis* spp.), but we excluded abalone captures from prey-specific analyses because we could not consistently determine the frequency of underwater tool use (Ebert 1968).

Analyses

We used a prey capture event, defined as one or more individuals of a given prey species brought to the surface for handling and

Table 1
Summary of sample sizes for each sea otter population

Region	Population	Years	Known individuals	Forage dives	Male	Female	Subadult	Adult
California	San Nicolas	2003–2006	Yes	2702	5	8	2	11
California	Piedras Blancas	2001–2004	Yes	25873	16	34	8	42
California	Big Sur	2008–2011	Yes	8079	6	31	6	30
California	Monterey	2000–2011	Yes	34717	28	80	15	93
Southeast Alaska	Port Althorp	2011	No	1205	17	65	13	67
Southeast Alaska	Glacier Bay	2011	No	1886	19	103	39	96
Aleutian Islands	Adak Is	1995–2008	Yes	11188	58	369	21	406
Aleutian Islands	Amchitka Is	1992–1994	Yes	10389	46	175	33	165
			Total	96612	195	865	137	910

In southeast Alaska populations, the number of individuals was based on number of forage bouts, which were presumed to represent a single individual.

consumption after a feeding dive, as the basic statistical unit for our analyses. If multiple prey species were retrieved during the same dive, each species was analyzed independently. Although successive prey captures by one animal may not be completely independent events in terms of tool use, we observed that individuals did not use a tool after every successful dive in a continuous series, suggesting that a decision is made as to whether or not to use a tool on each prey item.

In order to explore the prevalence of tool-using individuals among populations, we compared the proportion of tagged individuals observed using tools at least once in each population. We used bootstrap resampling to estimate proportion of individuals in southeast Alaskan populations to account for the lack of repeated samples per individual.

To determine how tool use varied across populations, we developed a series of generalized linear mixed models (GLMMs) fitted by Laplace approximation to examine the relative contributions of potential explanatory factors to the probability of tool use occurring across populations. The occurrence of tool use on each dive was treated as a binomial response variable (1 = presence of tool use and 0 = absence of tool use). The fixed effects we considered for inclusion in the GLMMs were region, sex, age class, and prey type (Table 2). We also explored potential interactions between region and prey type; however, not all prey types could be included due to small sample size in some regions. We used a nested model structure to account for potential autocorrelation among dives, with forage bouts nested within population and population nested within region (the nesting terms were treated as random effects). To examine the role of interindividual variation, we also included models with and without an otter ID as a random effect nested in population and region. For models with otter ID, southeast Alaska data were excluded because they lacked repeated samples for known individuals.

We used variance components analysis (calculated using reduced maximum likelihood) to determine which factors played the largest role in predicting tool use (Noh and Lee 2007). Each predictor variable was tested for significance using Wald's test. Akaike information criteria (AIC) corrected for finite sample size (AICc) were compared to determine the best-supported model (Burnham and Anderson 1998). All data manipulations and statistical analyses were completed using R.3.1.1 (R Core Team 2014).

Table 2
Best fit binomial GLMM showing the relationship between the odds of a tool being used during a dive and the geographical region and prey type captured

Factor	Level	β	β SE	OR	<i>P</i>
Intercept		-10.68	0.45	0.00002	0.0001
Region	Aleutian Is. ^a				
	Southeast Alaska	3.01	0.54	20.31	0.0001
	California	3.85	0.43	47.16	0.0001
Prey type	Soft-bodied prey ^a				
	Crab	0.87	0.15	2.38	0.0001
	Urchin	1.48	0.17	4.43	0.0001
	Bivalve	3.27	0.15	26.38	0.0001
	Snail	8.65	0.19	5735.40	0.0001

Forage bouts were nested within study populations, and populations were nested within geographical region. All nested terms were treated as random effects. OR, odds ratio.

^aReference term.

RESULTS

A total of 6638 forage bouts and 96612 dives were recorded for 1060 individuals over 17 years. The mean \pm SE frequency of tool use varied across the 8 sea otter populations, ranging from $16.6 \pm 0.2\%$ of successful forage dives in Monterey to $0.28 \pm 0.06\%$ of forage dives in Amchitka (Figure 2a). The Aleutian Island populations had the lowest frequency of tool use (0.28–1.45%) compared with southeast Alaska and California (9.8–16.5%). Within each region, the frequency of tool use did not vary significantly across populations. In each region, tool use was not universal among all individuals. In California, 65.8–92.8% of individuals used tools at least once compared with 10–20.5% in the Aleutian Islands and an estimated 26.3–29.9% in southeast Alaska (Figure 2b). These estimates of the proportion of individuals that used tools are underestimates because we were unable to quantify underwater tool use.

The variance component analysis indicated that prey type and geographical region accounted for 45.39% and 18.04% of the total explained variation in tool use, respectively. In contrast, sex (0.73%) and age class (0.48%) explained little additional variation, leaving 35.37% of the total explained variation in tool use attributable to inter- and intraindividual variation. Age and sex parameters were subsequently dropped, and a model including population and prey type was determined to be the best fitting model for the complete data set (Δ AICc = 5.9, Table 3). Including individual ID (for the subset of data where this was possible) significantly improved the model fit (Δ AICc = 512.2, Table 3). Variation among individuals accounted for 23.85% of the explained variation, whereas intraindividual variation contributed about 15% of total variation.

Marine snails and bivalves were most likely to be accessed with the aid of a tool across all populations. However, the probability of using a tool on a given prey type varied across regions (Figure 3b). In California, the probability of using a tool while consuming snails was $93.7 \pm 0.32\%$. Although snails were still the prey type with the highest probability of tool use in the Aleutian Islands, the probability of tool use with snails was only $20 \pm 9.1\%$ (Figure 3b). Crabs and urchins were only occasionally associated with tool use in California and very rarely in both regions in Alaska. Adding an interaction between prey type and region improved our model fit (Table 3), with significant interactions found between all 3 regions when consuming bivalves (snails were excluded from our interaction models due to small sample size). In southeast Alaska, bivalves were the prey most likely to be consumed with tools ($16.8 \pm 0.9\%$ of dives).

Overall diet composition varied substantially among Aleutian Islands, southeast Alaska, and California (Figure 3a). By frequency of occurrence, Californian populations had the highest percentage of marine snails in the diet ($12.2 \pm 2.6\%$ of feeding dives), whereas the Aleutian Islands had the lowest ($0.1 \pm 0.07\%$). Sea urchins were most prevalent in the Aleutian diet ($58.1 \pm 21.9\%$), whereas southeast Alaskan populations had core diets composed mostly of bivalves ($70.8 \pm 9.4\%$).

DISCUSSION

Our results indicate that the probability of tool use in sea otters varies from dive to dive for a given individual, among individuals within a population, and between different populations. Patterns of variation in tool use can provide clues as to the proximate and ultimate mechanisms that underlie the observed behavior. As in some other tool-using species (Tebbich et al. 2002; van Schaik et al.

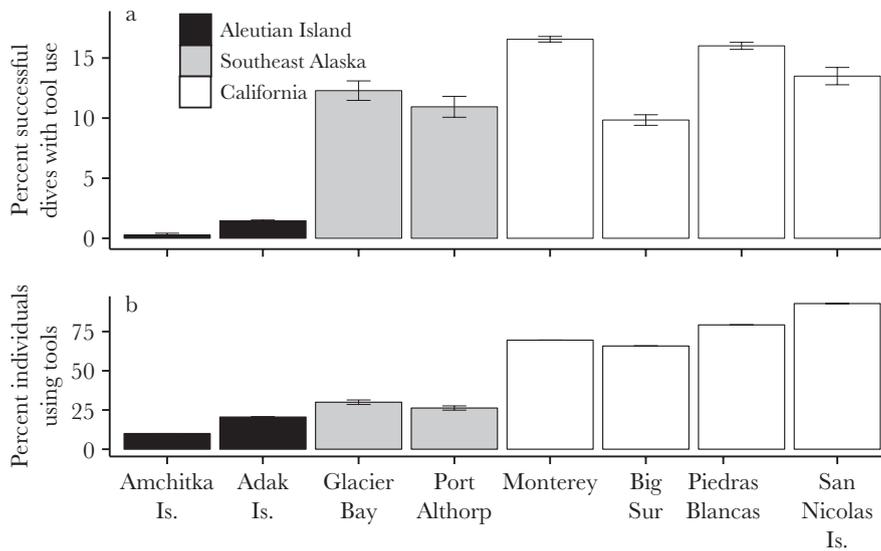


Figure 2 (a) Observed frequency of tool use (mean ± SE) across 8 study populations. Populations are in order along the coastline from north to south. (b) Percentage of tagged individuals observed to use tools at least once across 8 populations. Estimates were used for populations without known individuals.

Table 3
Summary of GLMMs examined

Fixed effects	Random effects	AICc	ΔAICc	χ^2
GLMM of main effects				
Region + prey + age + sex	Region/population/bout	14832.7	5.9	
Region + prey	Region/population/bout	14826.8	0	9.8
Individual effect between California and Aleutian Island regions ^a				
Region + prey + age + sex	Region/population/bout	13772.4	512.2	
Region + prey + age + sex	Region/population/otter/bout	13260.2	0	514.1
Interaction effect between prey type and geographic region ^b				
Prey + region	Region/population/bout	12345.2	7.4	
Prey × region	Region/population/bout	12337.8	0	19.3

^aSoutheast Alaska region was excluded due to lack of repeated samples among individuals.

^bDue to small sample size, we removed snails to explore interaction models.

2003; Sargeant et al. 2007; Macellini et al. 2012; Rutz et al. 2012), not all individuals in our studies used tools; however, at least some individuals in every population used tools. Two types of tool-use behavior, which may represent the extremes of a continuum, have been described: stereotyped tool-use behavior that occurs in every individual of a species and appears to be genetically “hard-wired” to emerge in response to certain stimuli and flexible tool use that does not occur in every individual but appears to be learned and develops in some individuals in specific ecological contexts (Biro et al. 2013; Call 2013; Hunt et al. 2013). Tool use in sea otters falls toward the flexible end of this spectrum. If tool use was a fixed-behavioral response to the morphology of the prey item (i.e., shell armoring) captured during a given dive, we would expect individuals in all regions to use tools with the same frequency on a given prey type.

Much like New Caledonian crows (*Corvus moneduloides*) and woodpecker finches (*Camarhynchus pallidus*), sea otters likely have a genetic predisposition to use tools (Tebbich et al. 2001; Kenward et al. 2005) but require the correct ecological context for this skill to become part of their regular foraging behavior. Captive sea otter pups have been observed to use tools without training or previous experience (Riedman and Estes 1990). In California, pups observed

in the wild played with objects such as empty shells, often pounding them on their chests, and first used a tool to open a prey item at about 14 weeks of age (Staedler 2011). Thus, although there does not appear to be a high cost for sea otters to learn to use tools, the benefit of doing so is likely only large enough under specific ecological conditions.

Much of the variation in the frequency of tool use was explained by a single ecological predictor: the type of prey being handled. Throughout their range, sea otters consume a wide array of invertebrate prey that encompass enormous taxonomic and morphological diversity: soft-bodied taxa such as worms and cephalopod mollusks, prey with chitinous exoskeletons such as decapods, prey defended with spines such as urchins, and prey with thick, calcium carbonate shells such as gastropods and bivalve mollusks. We found that tool use was overwhelmingly associated with handling and consuming prey with thick, calcium carbonate shells and was very rarely associated with the other classes of prey. Although there were also differences in tool-use frequency between individuals and among populations, the association of tool use with marine snails and bivalve mollusks was evident across all populations and explained the largest component (45%) of variation in tool-use frequency.

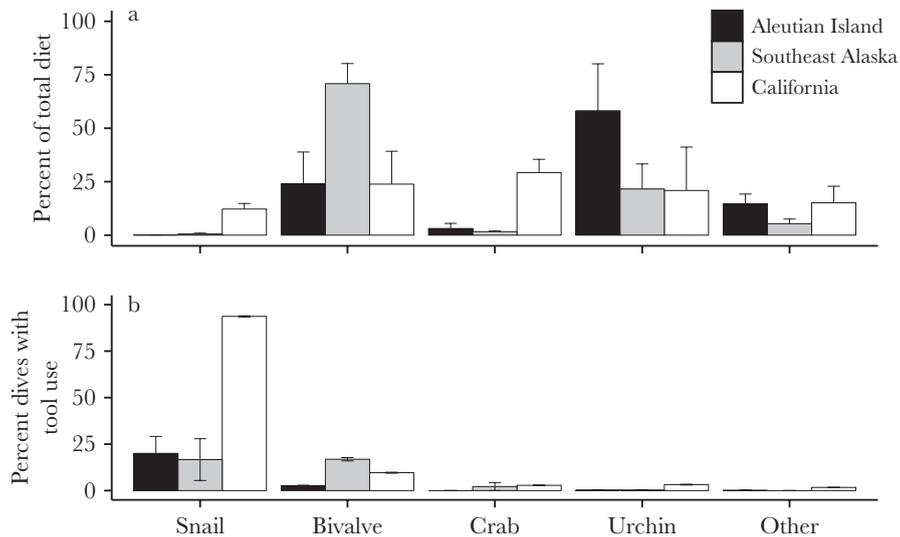


Figure 3

(a) Percentage of 5 prey types (mean \pm SE) in sea otter diets by region. The relative contribution of each prey type was calculated by frequency of occurrence. The Aleutian Island populations had a diet dominated by urchins, those in southeast Alaska a diet dominated by bivalves, and the California populations had a diet that was more evenly distributed across the 5 prey groups. (b) Percentage of successful foraging dives observed with tool use (mean \pm SE) for 5 common prey types by each region.

The adaptive benefits of using a tool to handle and consume well-armored marine snails and bivalve mollusks are intuitively rather obvious. The bivalves most commonly associated with tool use were horse mussels (*Modiolus modiolus*), giant rock scallops (*Crassadoma gigantea*), and Washington/butter clams (*Saxidomus* spp.), all species with thick shells that cannot be easily broken but that have calorically rich meat inside (Ofstedal et al. 2008). The most common snail species consumed was turban snails (*Chlorostoma* spp.), which are abundant and relatively easy to capture but which have thick, compact shells and small, well-protected opercular openings. Although it is possible for sea otters to break through these defenses using bite force alone, breaking into hard-shelled prey with a tool such as a rock can reduce both the risk of damage to teeth and the time required to handle hard-shelled prey, thereby increasing the realized rate of energy gain. Previous studies (Tinker et al. 2008, 2012) have shown that even very small increases in handling efficiency of prey can lead to substantial increases in foraging success, particularly with small prey such as turban snails (2–5 cm) that provide a low per-capita energy return. Tool use is likely a key factor in making these smaller prey items energetically profitable to sea otters by increasing handling efficiency.

Although the relationship between tool use and prey type was consistent across all populations, the absolute frequency of tool use varied considerably between populations. Sea otters in the Aleutian Islands rarely used tools, even when they were consuming prey such as snails or clams that were frequently associated with tool use in other populations (Figure 3b). Sea otters in California used tools most frequently. Sea otters from southeast Alaska used tools at an intermediate frequency although when consuming clams their rate of tool use was identical to that of otters in California (Figure 3b).

We considered several explanations for the patterns we observed: differences in the availability of tools, latitudinal variation in shell thickness of some mollusks, genetic differences between Alaska and California populations, and differences in diets of the populations. Although we were unable to test explicitly for tool availability, patterns of tool-use frequency were inconsistent with the prediction

that tool use should be least frequent in areas with fewer potential tools (i.e., the sandy and muddy-bottom areas prevailing in southeast Alaska). Furthermore, California and Aleutian Island regions had very different tool-use frequencies despite similar overall habitats (both regions are dominated by rocky kelp forests), whereas the frequency of tool use in southeast Alaska was more similar to that in California, despite different overall habitats in the 2 regions (soft sediment in southeast Alaska and rocky substrate in California).

Although latitudinal variation in the shell thickness of some mollusks (as reported by Vermeij and Veil 1978 and Vermeij and Currey 1980) may contribute to the pattern of increased tool use on hard-shelled prey in California, it is unlikely that this alone explains the large differences in tool-use frequency across regions. Diets in the Aleutian Islands, where otters used tools least frequently, are dominated by sea urchins (Figure 3a), which can be opened without using a tool, rather than bivalves with thinner shells than those in southeast Alaska.

Another possible explanation is that southern sea otters (*Enhydra lutris nereis*) are more genetically predisposed to tool use than northern sea otters (*Enhydra lutris kenyoni*); however, our results are inconsistent with this simple subspecies-level explanation suggested by Hall and Schaller (1964), Kenyon (1969), and Calkins (1978). Tool-use frequency in southeast Alaska (*E.l. kenyoni*) was more similar to that in California (*E.l. nereis*) than other populations within *E.l. kenyoni*. Furthermore, the southeast Alaskan population is descended from sea otters reintroduced in the 1960s. The founding population included individuals from the Aleutian Islands (Bodkin et al. 1999), and it seems unlikely that such large differences in a “tool-use gene” would evolve in so few generations.

A more likely explanation for the region/prey type interaction is suggested by the correlation between frequency of tool use and the prevalence of bivalves and marine snails in the diet: for example, sea otters in California (where snails comprise around 20% of the diet) had a much higher probability of tool use when consuming snails than those in southeast Alaska and Aleutian Islands, where snails were not a major proportion of the diet. Such a pattern

might be expected if tool use in sea otters has not only a strong ecological basis but also a learned component (Holzhaidner et al. 2010; Macellini et al. 2012; Mann et al. 2012). Individual learning of the benefits of tool use for accessing a given prey type, such as hard-shelled bivalves, would be more likely if that prey type was frequently encountered and utilized.

Furthermore, in California, it has been shown that diet preferences can be transmitted matrilineally between mothers and their female offspring (Estes et al. 2003), and it is possible that vertical transmission of learned skills such as tool-use contributes to this pattern. Tool use might also be facilitated by other means of transmission of learned skills, whereby otters specializing on marine snails or clams learn to use tools by observing this behavior in nonrelated conspecifics. In either case, a learning component would predict that a higher frequency of animals utilizing prey such as snails or thick-shelled clams (where tool use has the potential to increase foraging efficiency) would lead to a higher frequency of individuals using tools.

One caveat in the interpretation of our results is that we use prey consumption rather than environmental prey availability as a predictor variable. We have limited independent data on environmental prey abundance that were collected simultaneously with sea otter foraging observations. At one site in southeast Alaska (Glacier Bay), inter- and subtidal surveys were conducted simultaneously with foraging observations (Weitzman 2013) and showed that sea otters focused on the prey species with the greatest biomass (e.g., large clams and large horse mussels) and ignored species that had highest numbers but small biomass (small clam species and small urchins), consistent with patterns reported elsewhere (Ostfeld 1982; Estes et al. 2003). However, we would argue that invertebrates found in the environment but that are not consumed would not influence observed tool use. As diets change over time in response to changes in the relative abundance of various prey species (e.g., the inclusion of low calorie prey that are ignored when preferred prey are abundant) we would expect corresponding changes in tool-use frequency, depending on the nature of prey added to or dropped from the diet.

Individual differences in tool-use behavior accounted for approximately one-third of the total variation in tool-use frequency in our data set. These results are consistent with the previously reported individual variation in foraging behavior and diet (Estes et al. 2003; Tinker et al. 2008). Earlier studies have shown that individual-level variation in foraging behavior is strongly affected by ecological context: when per-capita prey resources are abundant, most individuals in a population have similar diets, but when they are limited, individual sea otters in the same area develop specialized diets, with some individuals eating mainly large prey such as abalones and crabs, some consuming mainly urchins and mussels, and others feeding primarily on marine snails (Tinker et al. 2007, 2008, 2012). Our current study suggests that individuals that specialize on different types of prey may use tools at different frequencies, depending on the relative costs and benefits of using a tool to access their preferred prey. Such a pattern would be expected to lead to a greater degree of individual variation in tool use in resource-limited populations. At the same time, individual variation in tool-use skills may be one of the factors that contribute to the emergence of dietary specialization in this species. Further research will be needed to elucidate the complex causal relationships between dietary specialization and tool-use behavior.

Interestingly, our results suggested that age and sex were not significant contributors to tool-use prevalence. The lack of a sex effect was not surprising as diet is not strongly related to sex in sea

otters (Tinker et al. 2007). Although we did not find an age effect, it is likely that any age effect would occur in juvenile otters between 6 months (approximate weaning age) and 3 years of age (beginning of adulthood, Riedman et al. 1994) as this is likely the period in which individuals are establishing survival strategies (Burns 1999). Our data set had few individuals within this age range, limiting our power to detect any effect of age. Future studies are needed to specifically examine the ontogenetic development of tool-use behavior in pups and juvenile sea otters.

This first, quantitative examination of sea otter tool-use behaviors showed that the frequency of tool use varied within and across sea otter populations in response to the prevalence of difficult-to-access prey in the diet. The use of tools to facilitate handling of marine snails and thick-shelled bivalves is likely a learned strategy to increase foraging efficiency on these prey types. The degree of variation in tool use within populations suggests that a more thorough examination of longitudinal data on foraging behavior and tool use by tagged individuals (focusing in particular on younger animals) will be needed to better understand how individuals develop and maintain tool-using strategies and how these strategies contribute to individual diet specialization in this species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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