



Original Article

Food abundance, prey morphology, and diet specialization influence individual sea otter tool use

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Sea otters are well-known tool users, employing objects such as rocks or shells to break open invertebrate prey. We used a series of generalized linear mixed effect models to examine observational data on prey capture and tool use from 211 tagged individuals from 5 geographically defined study areas throughout the sea otter's range in California. Our best supported model was able to explain 75% of the variation in the frequency of tool use by individual sea otters with only ecological and demographic variables. In one study area, where sea otter food resources were abundant, all individuals had similar diets focusing on preferred prey items and used tools at low to moderate frequencies (4–38% of prey captures). In the remaining areas, where sea otters were food-limited, individuals specialized on different subsets of the available prey and had a wider range of average tool-use frequency (0–98% of prey captures). The prevalence of difficult-to-access prey in individual diets was a major predictor of tool use and increased the likelihood of using tools on prey that were not difficult to access as well. Age, sex, and feeding habitat also contributed to the probability of tool use but to a smaller extent. We developed a conceptual model illustrating how food abundance, the prevalence of difficult-to-access prey, and individual diet specialization interacted to determine the likelihood that individual sea otters would use tools and considered the model's relevance to other tool-using species.

Key words: dietary specialization, *Enhydra lutris*, food abundance, foraging behavior, sea otter, tool use.

INTRODUCTION

As the list of species observed to use tools in the wild continues to grow, repeated patterns are emerging in the factors that contribute to the invention and maintenance of tool-using behaviors. Particularly for tools used while foraging, numerous studies have shown that ecological factors (e.g., prey morphology or tool availability) play a key role in providing context for a species to evolve tool use (Teblich et al. 2002; Sargeant et al. 2007; Mann et al. 2008; Rutz et al. 2010; Gumert and Malaivijitnond 2012; Tyne et al. 2012; Visalberghi et al. 2015). Once an ecological context for tool use is established, social learning or culture may act to increase or decrease the likelihood of tools being used (Van Schaik and Knott 2001; Lycett et al. 2010; Macellini et al. 2012; Mann et al. 2012; Koops et al. 2013, 2014; Eshchar et al. 2016).

Researchers on primates have developed a 3-part conceptual model that depicts the interacting ecological, cognitive, and social factors thought to influence and constrain the probability of tool use at the species, population, or individual level (van Schaik et al. 1999; Humle 2010; Koops et al. 2014). Ecological constraints include resource availability and the degree to which a species is terrestrial. If a species is gregarious and forages in a social group, opportunities for tool use may be influenced by the degree of social tolerance shown by dominant individuals and the availability of tools that were previously used by another individual. Finally, the cognitive capacities of a species determine whether or not individuals are able to develop tool-use behavior through individual and/or social learning.

Even in species well known for tool-using behaviors, such as chimpanzees (*Pan troglodytes*), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), New Caledonian crows (*Corvus moneduloides*), and sea otters (*Enhydra lutris*), the type and frequency of tool use varies across populations (Collins and McGrew 1987; McGrew et al. 1997;

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Smolker et al. 1997; Hunt and Gray 2003; Sanz et al. 2014; Dutton and Chapman 2015; Fujii et al. 2015). Fox et al. (1999) proposed 2 nonmutually exclusive hypotheses to explain differences in the presence of tool use in populations of orangutans (*Pongo pygmaeus*). The opportunity hypothesis posits that encounter rates with tool materials and prey resources requiring tool use for efficient exploitation will determine the likelihood of tool use, whereas the necessity hypothesis posits that tool use is a response to scarcity of preferred foods. Studies of nonhuman primate species, including orangutans, bearded capuchin monkeys (*Cebus libidinosus*) and chimpanzees have tended to support the opportunity hypothesis (Fox et al. 2004; Emidio and Ferreira 2012; Spagnoletti et al. 2012; Koops et al. 2013, 2014). These hypotheses have received relatively little attention from researchers studying nonprimate tool users.

Most studies of the factors influencing the development of tool use have focused on variation among populations, perhaps due to difficulties in identifying and following known individuals. However, extensive variation among individuals occurs in some species. In Indo-Pacific bottlenose dolphins, only some individuals within 2 near-by populations have been observed using tools (Smolker et al. 1997; Koppes et al. 2014). By using marine sponges to protect their rostrum, these dolphins are able to hunt for fish that live among rocks on the ocean floor, which opens up a new food niche (Patterson and Mann 2011; Krützen et al. 2014). Extensive variation in the frequency of tool use among individuals also occurs in some populations of sea otters (Fujii et al. 2015) and may be related to whether or not all individuals in a population eat a similar diet.

Sea otters provide an excellent model system for examining factors influencing tool-use variation across individuals under naturally varied ecological conditions. Sea otters are near-shore foragers and always carry their prey to the water surface, allowing researchers to directly observe what and how prey is consumed (Riedman and Estes 1990). Sea otters consume a wide variety of invertebrate species with varying degrees of defensive armoring. To overcome the protective shells, sea otters sometime use rocks, shells, human debris (such as bottles), and other prey items as either hammers or anvils to crack open invertebrate prey (Hall and Schaller 1964; Riedman and Estes 1990).

The near-extinction of sea otters during the fur trade and their subsequent recolonization of much of their former range has enabled researchers to characterize a variety of differences between populations that are and are not food-limited, such as body condition, dietary breadth, and foraging effort (Monson and Bowen 2015). Comparative studies of sea otter foraging behavior at multiple sites in California where sea otter populations occur at differing densities (Figure 1) have revealed a clear pattern of density-dependent variation in diets (Tinker et al. 2008a, 2012). When sea otters first move into an area where they have been absent for many years, they forage almost exclusively on the most abundant, large, and calorically rich invertebrates such as sea urchins, large clams, or abalone, which can be characterized as “preferred prey.” Over time, these preferred prey become depleted and the diet of the population diversifies to include smaller, lower-calorie prey, which we term “alternative prey” (Ostfeld 1982; Laidre and Jameson 2006).

Paradoxically, this population-level pattern of diet diversification in response to prey depletion is not evident at the level of the individual: to the contrary, the diets of individual sea otters in these food-limited populations often become even more specialized. The population-level increase in diet breadth is thus achieved by among-individual, rather than within-individual, diversification

(Figure 2). Previous studies have shown that individual diet specialization is neither a function of age or sex differences, nor is it explained by differences in prey availability: Individuals of the same age and sex class foraging in the same area at the same time show distinct selection patterns for specific types of prey that are consistent over years (Estes et al. 2003; Tinker et al. 2007; Novak and Tinker 2015). Individual diet specialization is observed at long-established or high-density sites that are food-limited but is not observed at low-density, food-rich sites; thus, researchers believe that diet specialization by sea otters is a behaviorally mediated response to intraspecific competition for limited resources (Tinker et al. 2008a, 2012). Similar density-dependent increases in diet specialization have also been reported for a variety of other taxa (e.g., Svanbäck and Bolnick 2007; Araújo et al. 2011). The existence of within-population dietary variation in sea otters provides an opportunity to explore the ecological factors affecting tool-use behavior: By comparing tool-use behavior of marked individuals with known diets, we can examine the role of prey type while controlling for demographic and environmental factors.

We developed a series of statistical models to explore the factors that predict the frequency of tool use by individual sea otters, using long-term observational data on foraging behavior of 211 tagged sea otters in California. Our choice of factors to include in these models was influenced by previous work on other species (Smolker et al. 1997; Fox et al. 1999; Spagnoletti et al. 2012; Koops et al. 2014; Patterson et al. 2016), previous work on sea otters (Tinker et al. 2008a; Fujii et al. 2015) and the data that were available on our study populations. In particular, we sought to build on previous studies of nonhuman tool use by investigating whether individual differences in diet specialization are reflected by predictable differences in tool-use behavior.

We focused particularly on the ecological factors likely to be influencing individual variation in tool use, rather than social or cognitive factors. Unlike many primates, sea otters are solitary foragers whose access to foods is not directly constrained by other individuals; so, social influences may be less important in sea otters. Nothing is known about individual variation in sea otter cognitive abilities; however, all sea otters appear to have the cognitive abilities to learn to use tools. Staedler (2011) showed that all wild pups exhibit proto-tool behaviors (such as repetitive pounding of shells or other objects on their chests) and the age at which they first successfully used a tool to open prey does not vary with the mother’s diet specialization. Additionally, captive sea otter pups orphaned at a young age use tools without training or previous experience (Payne and Jameson 1984; Riedman and Estes 1990; Nicholson et al. 2007). The frequency with which a mother uses tools may influence the probability that her offspring will become a frequent tool user but we did not have sufficient data on diets and tool-use behavior of known mother–pup pairs to include maternal tool-use frequency as a separate factor. However, Estes et al. (2003) found that individual diet specializations in sea otters were often passed on, at least in female pups, by matrilineal transmission. Therefore, by including each individual’s diet specialization in our models, we indirectly and implicitly included maternal influences on both diet and the frequency of tool use.

Other ecological factors important in primates, such as food and tool abundance, may be important in sea otters as well. We were unable to include direct measurements of prey abundance. However, the presence or absence of individual diet specialization reflects prey abundance because diet specialization develops only in populations that are food-limited (Tinker et al. 2008a, 2012;

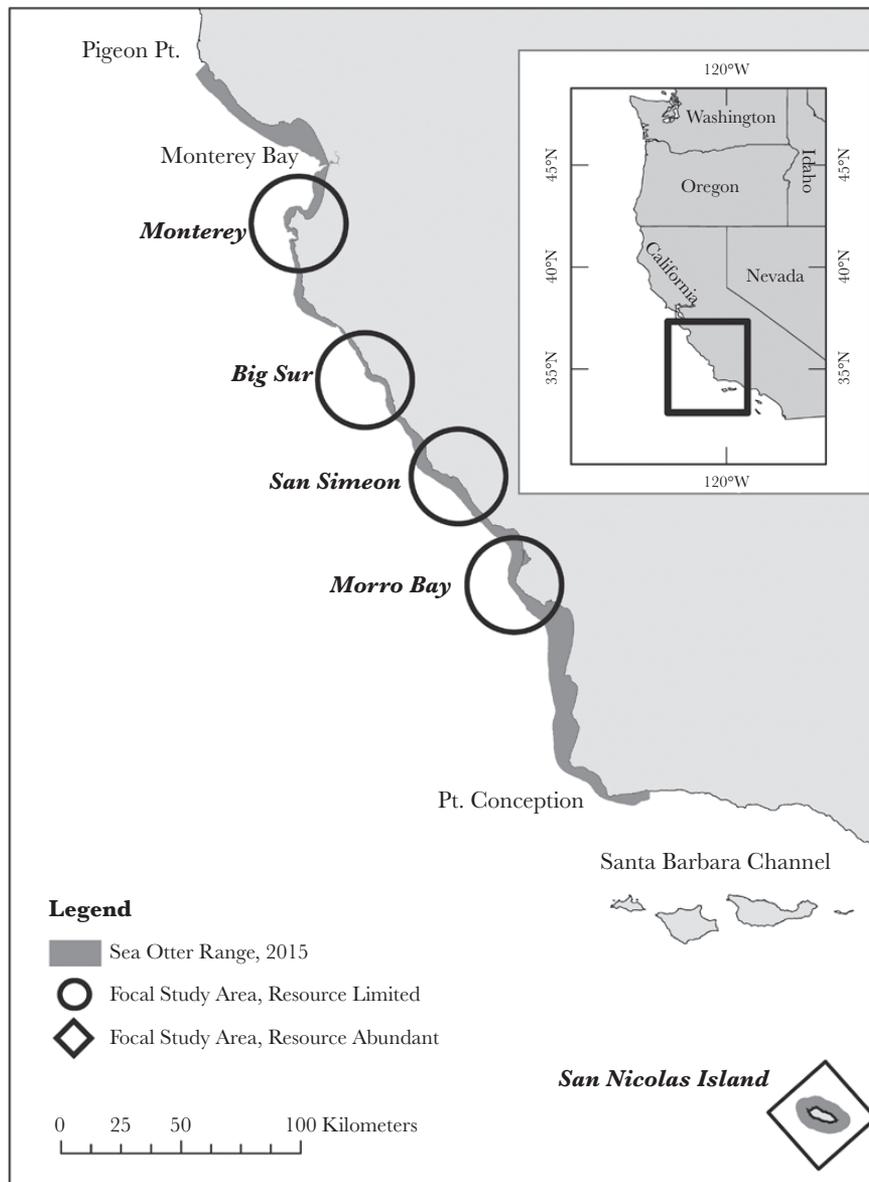


Figure 1

Current sea otter range in California showing locations of study areas. Four food-limited study areas are indicated by circles and one food-abundant study area indicated by a diamond.

Newsome et al. 2015). Moreover, because individuals with different diet specializations at a given study area experienced the same conditions of prey abundance (because they foraged in the same habitats), we were able to examine the effects of diet differences while controlling for resource availability. We did not expect access to tools to limit sea otters as rocks are common in rocky-bottom habitats and in sandy or muddy-bottom habitats, otters readily will use other objects. However, as the availability of rocks that are suitable for tool use varies across habitats, the type of habitat in which a dive occurs should reflect tool availability and thus was included in our models.

The factors explored in our models were sex, age, diet specialization of each individual, the habitat type where each foraging dive occurred, and the morphology of the prey type captured after each successful dive. We predicted that variation in the frequency with which individual otters used tools would be related to

the morphology of the prey being consumed by each individual (as seen at the population level in Fujii et al. 2015) as well as to individual diet specialization, which can lead to variation in prey handling techniques in both dolphins and sea otters (Riedman and Estes 1990; Smolker et al. 1997; Mann et al. 2008; Tinker et al. 2009). We summarize our findings on the ecological factors influencing sea otter tool-use frequency patterns in a conceptual model and discuss its relevance to other tool-using species.

METHODS

Study sites

We examined foraging data collected on tagged sea otters between 2000 and 2014 from 5 study areas spread out across the sea otter range in California (Figure 1). Previous work (Tinker et al. 2006, 2008b; Tarjan and Tinker 2016) indicated that these study areas

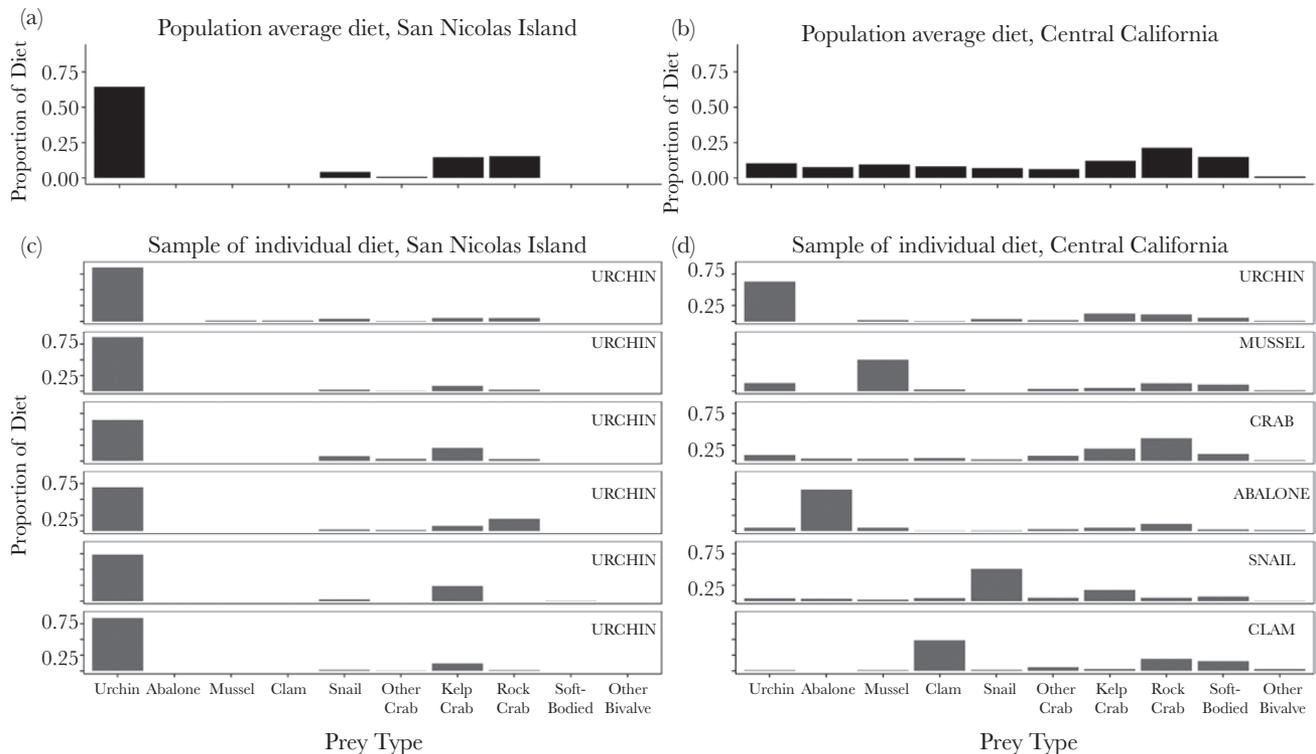


Figure 2

Population level and individual diet histograms for sea otters at San Nicolas Island (SNI) (a) and Central California (b), illustrating differences in diet diversity and individual diet specialization between food-abundant and food-limited populations. The vertical axis of each graph indicates the proportion of total prey capture events. Panels a and b show the mean diet composition for populations, whereas c and d show examples of 6 individuals at SNI and Central California, respectively. Each individual from Central California represents 1 of 6 individual diet specializations and are labeled by the core prey item on the left side of each graph.

were demographically distinct, with only occasional movement of a few individuals between adjacent sites (Tinker et al. 2008b). One study (Morro Bay) overlapped another (San Simeon) in some locations but occurred 10 years later and did not include any individuals from the earlier study and so was treated as a distinct study area. Each study area included a variety of habitats, including rocky intertidal and subtidal substrates, kelp forests, and sandy bottom areas. These diverse habitats provide a rich prey base for sea otters, with more than 100 species of consumable benthic invertebrates (Riedman and Estes 1990).

Individual sea otters were captured, tagged with colored-plastic cattle tags on the hind flippers (Ames et al. 1983; Siniff and Ralls 1991) and implanted with VHF radio transmitters (Ralls et al. 1989). Thus, observations were collected on known individuals that could be located by radiotelemetry, identified visually by their flipper tags, and followed over time. Age and sex of each animal were determined at the time of tagging. Age was categorized as subadult (<3 years) or adult (≥ 3 years) based on body size, grizzle (i.e., lightening of fur color over the body, which generally increases with age), and dentition (tooth wear increases predictably with age). All fieldwork was conducted with authorization by the US Fish and Wildlife Service under permits issued to M.T.T. and with oversight by the Institutional Animal Care and Use Committee at the University of California Santa Cruz. Standardized methods of data collection were used at all study areas, as described below.

Foraging

We used focal animal sampling (Altmann 1974) to opportunistically record foraging data on individual otters for the duration of each

study. 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 minutes (Ralls et al. 1995). For each feeding dive, we recorded a standardized series of data: dive outcome (whether or not prey was captured), prey identification, time (seconds) spent handling prey, and the presence or absence of tool use (refer to Tinker et al. 2012 for detailed methods). We identified prey items to the lowest possible taxon but collapsed them into 8 prey classes for data analysis (clams, mussels, other bivalves, rock crabs, kelp crabs, snails, urchins, and soft-bodied prey).

We also recorded the type of feeding habitat (kelp canopy, rocky intertidal, sandy, and unknown substrate in open water) for each dive as an individual could change habitats within a single forage bout. Habitat was identified visually by presence or absence of kelp canopy, rocky coast line, and sandy beaches (Laidre et al. 2001). These habitats potentially varied in the availability of stone tools, although sea otters in all habitats would still have access to other potential tools such as shells and other prey items. Although the abundance of prey in different classes varied among habitat types, all prey classes were observed being consumed in each feeding habitat.

Tool use

A sea otter was considered to be using a tool if it was observed at the surface using an external object to aid in prey consumption. Tool objects included loose rocks, empty shells, other prey items,

and anthropogenic litter (such as bottles or various plastic objects). Additionally, sea otters sometimes used fixed objects such as emergent rocks or the hull of boats in harbors as anvils. Sea otters also used tools underwater 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.); however, we excluded abalone captures from prey-specific analyses because we could not consistently determine the frequency of underwater tool use (Ebert 1968; Houk and Geibel 1974).

Diet specialization

Four study areas along the central California coast supported high densities of sea otters (Figure 1) and have been shown to be food-limited (Tinker et al. 2008a; Newsome et al. 2015). Individuals in these 4 study areas were grouped into diet specialist groups based on shared utilization of prey types in core diets, which are defined as those prey types, ranked in descending order of prevalence, which together comprise 60% of all consumed biomass for an individual, as described by Tinker et al. (2012). We were able to reliably determine the diet specialization for 211 individuals. We classified each individual into 1 of 6 diet specialization types, referred to by their principle core prey item: ABALONE, CRAB, MUSSEL, CLAM, URCHIN, and SNAIL (note that we henceforth use block capital letters to designate diet specialist types and thus avoid confusion with the prey type captured on a given dive, which we designate with lower case letters).

A fifth study area, San Nicolas Island, was a translocated population that had a low density of otters and abundant food resources; thus, individuals did not develop or maintain diet specializations (Tinker et al. 2008a). Instead, all individuals had similar diets composed predominately of sea urchins (*Strongylocentrotus* spp.), the most energetically profitable and preferred prey type in this habitat (Tinker et al. 2008a).

Analyses

To determine how tool use varied across individuals, we developed a series of generalized linear mixed effects models (GLMEs) fitted by Laplace approximation to examine the relative contributions of potential explanatory factors to the probability of tool use (Bolker et al. 2009). We used prey capture events—defined as one or more individuals of a given prey class brought to the surface for handling and consumption after a feeding dive—as the basic statistical unit for our analyses. In the majority of dives only one prey type was captured but in approximately 25% of dives there were multiple prey types captured: In the latter instances, prey capture events were still treated as independent (in terms of tool use) because individuals were frequently observed to switch between using a tool and not when consuming different types of prey during a single dive. A GLME model with number of prey types per capture (single or multiple) treated as a categorical fixed effect confirmed that the prey-specific probabilities of tool use did not differ significantly between captures that consisted of a single prey type and those that contained multiple prey types (Supplementary Table S1). We then fit a series of GLME models to examine factors that did affect the likelihood of occurrence of tool use during a prey capture event (tool use was treated as a binomial response variable: 1 = presence of tool use; 0 = absence of tool use). The fixed effects we considered for inclusion in the GLMEs were study area, sex, age class, habitat, prey type, and type of individual diet specialization (Supplementary Table S2). These categorical main effects were

considered statistically independent as all possible combinations of effect levels were represented by prey capture events. However, because we expected that different specialist types might exhibit different handling behavior for core and noncore prey types, we also evaluated models including an interaction term for diet specialization and prey type. An interaction between age and sex was also evaluated to explore potential sex-based differences in learning or social influences. Finally, to account for unexplained inter- and intraindividual variation in tool-use frequency, our models included random effects for individual and forage bout, with forage bouts nested within individuals.

We compared models of varying complexity ranging from a null model (constant only) to a saturated model including all terms (Supplementary Table S3). Corrected Akaike Information Criterion (AICc) statistics were computed for each model and compared to select the best-supported model (Burnham and Anderson 1998). Fixed-effect coefficients in the final model were also tested for significance using Wald tests (Burnham and Anderson 1998; Bolker et al. 2009). We used variance components analysis, calculated using Reduced Maximum Likelihood (REML) estimation, to determine which factors explained the most variation in tool use (Noh and Lee 2007), and calculated a pseudo- R^2 (McFadden 1974) to evaluate overall model efficacy in explaining variation in tool use. The best-supported model was used to predict marginal probabilities of tool use for different combinations of main effects (e.g., by prey type and individual diet specialization). All data processing and statistical analyses were completed using MATLAB programming language and MATLAB statistics toolbox (Mathworks Inc., Natick, MA).

RESULTS

A total of 3374 forage bouts and 48 206 prey captures were recorded for 211 individuals. Each individual was categorized into 1 of 6 diet specialist groups, with CRAB specialists being the most common ($n = 80$ individuals), followed by CLAM ($n = 46$), MUSSEL ($n = 25$), SNAIL ($n = 22$), ABALONE ($n = 16$), and URCHIN specialists ($n = 22$), with all 11 individuals from San Nicolas Island considered URCHIN specialists (Figure 2c and d). Individuals from food-limited sites had overall greater diversity of prey types in their diets compared to the nonfood limited site (Figure 2a and b).

The mean \pm standard error frequency of tool use varied across the 5 study areas, ranging from $9.18 \pm 0.43\%$ of successful forage dives in Big Sur to $26.75 \pm 0.65\%$ at Morro Bay. San Nicolas Island had less variation in individual average tool-use frequency (4–38% of prey captures) compared to all other study areas (0–98% of prey capture events). These estimates should be considered underestimates because we were unable to quantify underwater tool use.

The best supported model explained almost 75% (pseudo- $R^2 = 0.74$) of the observed variation in tool use and included effects for age, sex, prey type, diet specialization, study area, habitat, as well as interactions between age and sex and between diet specialization and prey type (Supplementary Table S4). The prey type being handled on a given dive and the individual otter's diet specialization accounted for 28.9% and 15.9% of the total variation in tool use, respectively and their interaction an additional 7.1%. Study area (7.8%), age class (<0.01%), sex (3.0%), age/sex interaction (6.2%), and habitat type (2.2%) explained much less variation. Random effects associated with interindividual differences and within-individual variance across bouts accounted for 12.5% and 16.4% (respectively) of the total variation in tool use.

Adult females used tools with greater frequency than did subadult females and were also more likely to use tools than adult males. In contrast, tool-use frequency for subadult males was greater than for adult males (Supplementary Table S5). Marine snails and bivalves were most likely to be accessed with the aid of a tool across all study areas. However, some diet specialists were more likely to use tools than were others and the interaction between diet specialization and prey type implied that the probability of using a tool on a given prey type depended upon an individual's diet specialization (Figure 3, Supplementary Table S6). SNAIL specialists were most likely to use a tool when consuming snails (Probability₉₅ of tool use = 96.14–98.83%) and were also more likely than non-SNAIL specialists to use a tool when handling all other prey types (Figure 3). In contrast, for individuals specializing on non-snail prey, tool use was much less likely for all prey types except snails. However, tool use was relatively common when handling snails irrespective of diet specialization (e.g., CLAM specialists rarely used tools for most types of prey but when handling snails their probability₉₅ of tool use was 30.45–62.77%; Figure 3).

DISCUSSION

As with many complex behaviors, the frequency of tool use in sea otters cannot be attributed to a single factor. We have previously shown that the morphology of the prey being handled, specifically whether or not it is difficult to access, is an important predictor of differences in the frequency of tool use in sea otter populations ranging from California to the Aleutian Islands in Alaska (Fujii et al.

2015). In the current study, we examined the causes of variation in the frequency of tool use by individual sea otters in California. Although the morphology of the prey being handled remained an important factor at the individual level, the development of dietary differences between individuals when food resources declined also played an important role.

The likelihood that an individual otter uses a tool to process a particular prey item also depends on its sex (females > males) and age (older > younger for females). Although our model showed that subadult males were more likely to use tools than other age and sex classes, this finding is somewhat suspect because only 3 subadult males were included in our study. Sex-based differences in tool use have also been reported for capuchin monkeys (Moura and Lee 2010), chimpanzees (Lonsdorf 2005), and dolphins (Smolker et al. 1997; Mann et al. 2012). Our finding that older females use tools more frequently than younger females is similar to results for dolphins (Patterson et al. 2016) and crows (Kenward et al. 2006). These demographic trends may reflect disparate physical capabilities of different age or sex classes or age/sex-based variation in opportunities for social learning. But they could also reflect differences in skills arising from accumulated experience. The limited amount of variation explained by age in our model probably reflects the fact that we have few animals less than 3 years of age in our sample.

The energetic benefits of tool use are likely to increase with age as individuals learn and practice tool-using skills, a process that appears to take several years in dolphins (Patterson et al. 2016). In both dolphins and sea otters, male individuals have larger home ranges and more generalized diets than females (Gibson and Mann 2008; Krützen et al. 2014; Smith et al. 2015), which may reduce

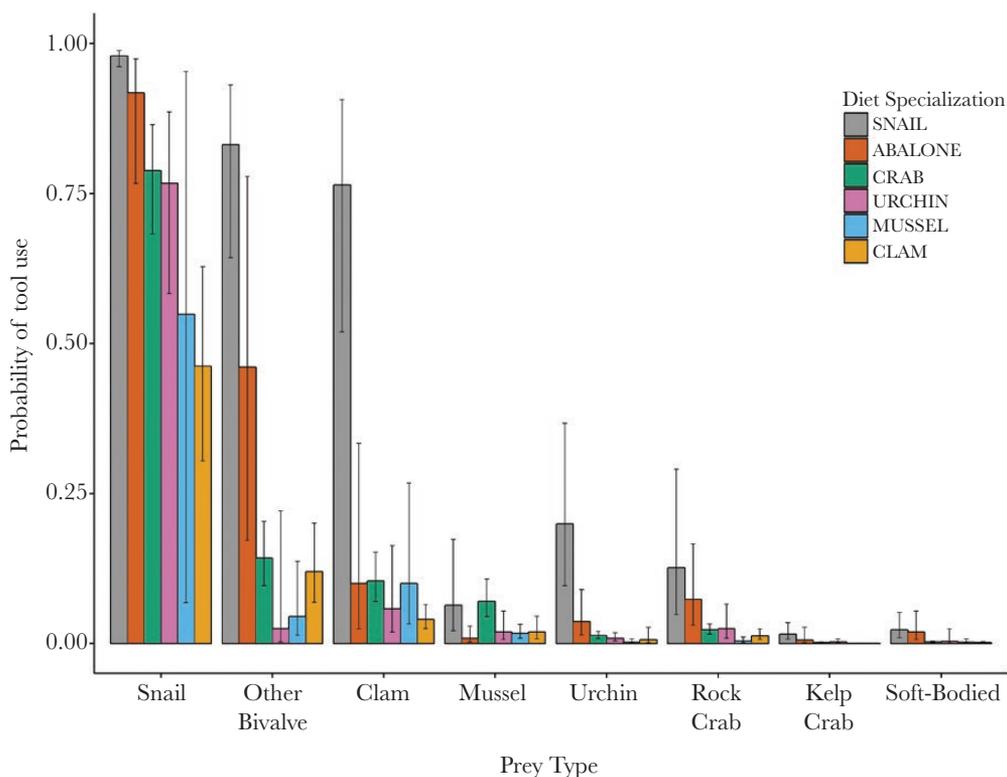


Figure 3

Predicted probabilities of tool use in food-limited study areas by prey type consumed on a given dive and the individual's diet specialization group. Sea otters that specialize on different types of prey differ in the probability that they will use a tool on the same prey type. Error bars represent 95% confidence limits.

the opportunities to learn and hone the specialized skills of effective tool use associated with repeated experience with a single difficult-to-access prey type.

Tool use and individual diet specialization

In addition to age, sex, and prey type being handled, an individual's diet specialization also impacted the probability of tool use. SNAIL specialists were the most likely to use tools, whereas URCHIN, MUSSEL, and CLAM specialists were least likely to use tools. Individual diet specialization emerges in sea otter populations as a facultative response to food resource limitation (Tinker et al. 2008a, 2012; Newsome et al. 2015): When preferred prey becomes depleted, sea otters begin to specialize on less-preferred prey and this pattern is most pronounced for females (Smith et al. 2015). Previous work has shown that individual specialization is predicted by an optimal foraging model that accounts for individual differences in prey-specific handling efficiencies (Svanback and Bolnick 2005) and that learned skills (such as tool use) are one possible source of such differences (Tinker et al. 2009). Diet specialization appears to be transmitted matrilineally to some degree in sea otters (Estes et al. 2003): a preference for particular prey types, as well as handling skills for those prey (including tool-use skills), may be acquired by female dependent pups via vertical transmission. Foraging skills and prey preferences continue to develop postweaning, as does the likelihood of tool use (as evidenced by the significant age effect in our model) and the diet specializations of adult females can deviate substantially from their mothers, although they are more likely to be similar than are nonrelated females (Estes et al. 2003). Although we could not include the diet specialization of each otter's mother in our models, the effect of maternal diet type is implicit in the individual's diet specialization. Moreover, some of the unexplained individual differences in tool-use frequency might also reflect maternally transmitted behaviors. Diet specialization accounted for about 14% and individual random effects accounted for 12.5% of the total variation in the frequency of tool use and thus the combined variance component (26.5%) represents an upper limit for the size of the maternal effect.

Cost of tool use

The cost of tool use can be considered in terms of time and energy spent acquiring a tool and measured in terms of the opportunity costs associated with missing easier-to-access foods while finding tools and/or learning to become a proficient tool user (Chappell and Kacelnik 2002; Seed and Byrne 2010; Teschke et al. 2013). In some species, tool use becomes less frequent when the opportunity costs exceed benefits: for example, capuchin monkeys use tools to dig for tubers in arid environments but not when surface foods are sufficiently abundant (Moura and Lee 2004). Although not directly measured in this study, there is little evidence to suggest that finding and carrying a tool is costly for sea otters in most areas. Tools can be obtained in a single dive and carried and used throughout an entire forage bout or dropped once no longer needed. Although differences in habitat type (and thus potential tool availability) did contribute to variation in tool use, this effect was relatively small compared to other factors (Supplementary Table S2). However, it is also worth noting that all of our study areas included substantial amounts of rocky substrate, and thus tool-sized rocks were rarely difficult to find. Future studies in exclusively soft sediment habitats such as tidal estuaries, where the time investment and potential opportunity costs associated with finding rocks would be more substantial, will provide

further insights into how the costs of tool acquisition affect foraging decisions of sea otters. The interaction of prey type and individual diet specialization may shed light on less-obvious costs of tool use for sea otters. Our results show that otters specializing on heavily-armored turban snails are not only more likely than other individuals to use tools when handling snail prey but also when handling nonsnail prey (Figure 3). Conversely, those individuals specializing on prey such as clams, urchins, or crabs are much less likely to use tools either on their core prey or on other prey types. This suggests that it may take extensive experience before a sea otter becomes a proficient tool user for a given prey type and reflects an opportunity cost of learning: Specialists must forego easier-to-access prey as they develop the tool-handling skills needed to make their core prey profitable. Intriguingly, our results also suggest that the learning cost of tool-use behavior may in turn act to reinforce individual diet specialization. The interaction between diet specialization and prey type in determining the probability of tool use (Figure 3) implies a “behavioral spillover” effect, whereby tool-using SNAIL specialists also use tools on other prey such as urchins, for which tools do not improve handling efficiency (and may even reduce handling efficiency; Tinker et al. 2008a). In other words, if all you have is a hammer, everything looks like a nail; however, individuals with hammers do best if they stick with nails and avoid nuts and bolts.

This spillover suggests a form of behavioral inertia known as “interference” (Hughes and O'Brien 2001), which should act to reinforce individual diet specialization by reducing the profitability of feeding on prey types that are mismatched to an individual's tool use tendencies. Although non-SNAIL specialists are less likely to use tools, even when consuming snails, they are also likely to be less proficient in this behavior. Any energetic costs of obtaining a tool, as well as the opportunity costs of spending time attempting to use a tool rather than acquiring a different, easier-to-access prey item may be greater than any potential benefit in using tools occasionally.

Conceptual model

The cascade of ecological and individual contingencies influencing the probability of tool use by individual otters can be conceptualized as a dichotomous key (Figure 4). Four of the 5 possible outcomes of this model, representing different patterns of tool use, are found in sea otter populations: outcomes 1 and 2 at Monterey, Big Sur, San Simeon, and Morro Bay in California (this study); outcome 3 at Adak and Amchitka Islands in the Aleutians (Fujii et al. 2015); and outcome 4 at San Nicolas Island in California (this study), and Glacier Bay and Port Althorp in Southeast Alaska (Fujii et al. 2015). Some individuals in all populations do not use tools but to date no population is known to consist entirely of individuals that do not use tools (outcome 5). Our conceptual model for sea otters integrates 2 previous hypotheses on ecological determinants of tool use developed for primates: the “opportunity” hypothesis and the “necessity” hypothesis (Fox et al. 1999, 2004; Spagnoletti et al. 2012; Sanz and Morgan 2013; Koops et al. 2014). Tool use in sea otters provides support for both hypotheses. The necessity hypothesis finds support in that the depletion of preferred prey species leads to diet diversification and individual diet specialization on alternative types of “less-preferred prey,” some of which are difficult to access (i.e., they have very hard shells) and are more efficiently handled using tools (Figure 4, outcomes 1 and 2). The model also includes elements of the opportunity hypothesis (outcome 4): The key to whether outcome 3 or 4 occurs depends on the local availability of preferred prey with hard shells that are difficult

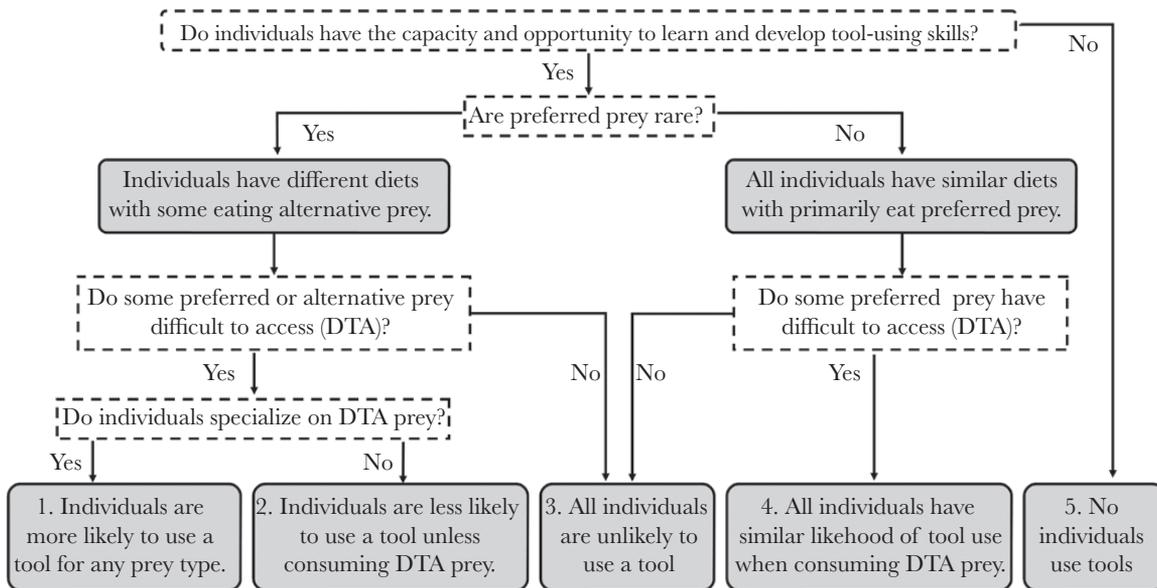


Figure 4

Dichotomous conceptual model of the ecological factors influencing the frequency of tool use by sea otters. Most variation among individuals and populations can be explained by the local abundance of preferred prey, the presence or absence of difficult-to-access (DTA) prey, such as heavily armored turban snails and whether or not individuals specialize on DTA prey. Questions outlined with dashed line. Outcomes outlined with solid line and shaded in gray.

to access without tools. When heavily armored prey are rare, as at Amchitka and Adak Islands in the Aleutians (Fujii et al. 2015), tool use is also rare, as predicted by the opportunity hypothesis. Sea otters at San Nicolas Island also had abundant food resources so diets of individuals were similar. The diet at San Nicolas Island was predominantly urchins, but included some large, energetically rich, thick-shelled snails (a different genus than the smaller turban snails consumed on the mainland) and so, in contrast to the food-limited areas, all individuals used tools at a relatively similar rate. The novel insight here is that considerations of the ecological context of tool use should include not only environmental conditions (i.e., the morphological diversity and abundance of available prey) but also variation in individual responses to these conditions, particularly diet specialization. Diet specialization appears to increase the likelihood of tool use for certain individuals (through increased exposure to heavily armored prey as well as matrilineal transmission of prey preferences and tool using skills), and tool use in turn may act to accentuate selection for individual specialization.

Applications to other taxa

Our conceptual model provides a useful predictive tool for sea otters, but the degree to which it can be generalized to other taxa remains to be seen; however, there are some tantalizing hints of broader applicability. For example, 2 interconnected groups of New Caledonian crows demonstrate distinct patterns in tool selection, although it is currently unknown whether this variation reflects dietary differences between groups or individual specialization (St Clair et al. 2016). The association of tool use in sea otters with specialization on heavily armored prey such as marine snails and, to a lesser extent, large, thick-shelled bivalves (e.g., *Saxidomus* spp. and *Crassidoma* spp.) provides an interesting parallel to coastal Burmese long-tailed macaques (*Macaca fascicularis aurea*) in southeast Asia, which use rock tools to handle these same prey groups in intertidal habitats (Gumert and Malaivijitnond 2012). Marine mollusks such as larger snails and bivalves have evolved a degree of armoring that renders them

immune from most predators. Preliminary research on sea otter bite-force indicates that the armoring of turban snails (*Chlorostoma* spp.) gives them a hardness that is at the upper limits of what a typical sea otter can crush with its jaws (Law C, personal communication). However, this armoring is relatively ineffective against the tool-use behavior that has evolved independently in long-tailed macaques and sea otters. Because snails and bivalve mollusks tend to be extremely abundant in intertidal and subtidal habitats, the emergence of tool use in both cases would have opened a profitable and largely unexploited niche. Future comparative studies in these 2 groups will likely provide additional insights into the evolution of tool use.

Our conceptual model may also be applicable to the interesting case of “sponging” by bottlenose dolphins at Shark Bay, Australia. The use of sponges as tools is associated with a distinct foraging specialization (i.e., feeding on small cryptic fish in underwater trenches) that is exhibited by a small subset of individuals in the population (Smolker et al. 1997; Sargeant et al. 2007; Patterson and Mann 2011; Krützen et al. 2014). As with sea otters, this specialization on relatively unrewarding prey may be a response to resource limitation that occurs at high population density (Watson-Capps 2005; Patterson et al. 2016). Additionally, individual dolphins who develop this specialization forage almost exclusively with tools (Kopps et al. 2014). A key difference between dolphins and sea otters is that tool use in the former has a strong genetic component (Bacher et al. 2010; Kopps et al. 2014) and seems to be limited to 1 matriline, whereas tool use in sea otters is relatively ubiquitous among and within sea otter populations, with diet specialization affecting the relative frequency of tool use.

Further tests of the predictions of our conceptual model should be possible for other taxa, requiring in some cases minor changes in terminology (i.e., “food” might be substituted for “prey” and “energetically or nutrient rich” for “preferred”). We also recognize that other factors such as the availability of tools (Tyne et al. 2012), potential for social learning or the degree of terrestriality may play a far greater role in other species (Kopps et al. 2014) and would necessitate additional levels to our dichotomous key that are not

needed for sea otters. We expect that some primates such as chimpanzees, orangutans, and capuchin monkeys (Koops et al. 2014) and birds such as the New Caledonian crow (Rutz et al. 2010) may follow the pathway to outcome 4, because the foods they obtain with tools are often energetically rich. The tool-using dolphins may correspond to outcome 1 and the woodpecker finch (*Cactospiza pal-lida*) to outcome 2 (Tebbich et al. 2002). However, the presence and effects of diet specialization may be difficult to address in other tool-using species if individuals are not easily distinguished or difficult to observe and metrics to determine whether populations are food-limited have not been developed. The majority of the known cases of dietary specialization are vertebrates, and many are predators, suggesting that the potential for individual dietary specialization may increase with trophic level (Araújo et al. 2011). There appear to be no cases reported in primates to date.

CONCLUSION

In conclusion, the data and analyses we present here provide new insights into the ecological factors influencing the probability of tool use. We find mixed support for the predictions of both the opportunity and necessity hypotheses advanced based on studies of primates and dolphins; however, we also show that differing individual responses to ecological factors—especially individual diet specialization—can generate complex variation in tool-use patterns within populations. Our best statistical model was able to explain 75% of the variation in sea otter tool use using only ecological and demographic variables, although we note that because diet specializations can be transmitted from mother to offspring, our model implicitly included social factors in the form of matrilineal transmission: Future studies will be needed to tease apart the relative importance of maternal effects and individual learning.

We present a new conceptual model that advances on the most current model for primates by introducing the concept of individual dietary variation and making predictions about the frequency of tool use under specific ecological conditions (Koops et al. 2014). We find that most variation in the frequency of tool use among individuals and populations of sea otters can be explained by the local abundance of preferred prey, the relative frequency of difficult-to-access prey, and whether or not individuals specialize on such prey. Comparative studies that examine the ecological context for tool use, at both the population and individual level, promise to increase our understanding of the evolution and ecological predictors of tool use.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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