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VARIATION IN THE FREQUENCY OF TOOL USE ACROSS AND WITHIN SEA OTTER (*ENHYDRA LUTRIS*) POPULATIONS

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF ARTS

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Jessica A. Perry

June 2012

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VARIATION IN THE FREQUENCY OF TOOL USE ACROSS AND WITHIN SEA OTTER (*ENHYDRA LUTRIS*) POPULATIONS

Jessica A. Perry

Abstract

Sea otters (*Enhydra lutris*) are well known and conspicuous tool users, but little is known about what drives the maintenance of this behavior in populations or individuals. I investigated how variation in the frequency of tool use across and within sea otter populations may be influenced by ecological factors such as age class, sex and reproductive status, geographic location, feeding habitat, and prey type. Additionally, I explored whether consistent inter-individual differences in tool use occurred and if the frequency of tool use occurrence was related to learned diet specializations. I used observed foraging and tool use data collected from nine sites across two subspecies of sea otters. Over 500 individuals were observed feeding and over 100,000 feeding dives were recorded between 1985 and 2011. Using binary generalized linear mixed effects models, I found the type of prey consumed the strongest predictor of the frequency of tool use across populations, although all factors contributed to the best fit model. In Monterey, California, I collected longitudinal data on sixty- three individuals for a minimum of one year. I found that individuals specializing in prey that required tools were more likely to carry-over this behavior to other prey consumed. My results suggest that the frequency of tool use in sea otter populations and individuals is influenced by ecological factors such as the

consumption of prey that is difficult to access, and the "behavioral inertia" of

individuals learning to use tools for particular prey items.

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Introduction

Although still considered a rare behavior, tool use has been identified in a wide range of animals including primates, non-primate mammals, birds, fishes, and insects (Bentley-Condit and Smith 2010). Tools are used for a variety of reasons including social display, defense, grooming, and foraging (Bentley-Condit and Smith 2010). Understanding why and how these animals develop and maintain tool using behaviors intrigues a range of disciplines including anthropology (McGrew 1987, van Schaik et al. 2003), psychology (Iwaniuk et al. 2009) cognitive biology (Stout and Chaminade 2007), evolution (Alcock 1972, Kenward et al. 2011), and behavioral ecology (Banschbach et al. 2006, Rutz et al. 2010).

The perception of tool use as a uniquely human capability persisted well into the 20th century (Oakley 1967, Gruber 1969) despite records of non-human tool use as early as the 1800s (Darwin 1871, Coues 1877). Some of this disparity stemmed from anthropocentric biases, but also from disagreements between what behaviors constitute tool use. The most commonly cited definitions come from van Lawick-Goodall (1970), Alcock (1972), and Beck (1980). Often considered the standard, Beck (1980) defines tool use as "… the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effecting orientation of the tool."

A universal definition of tool use continues to be debated (Hansell and Ruxton 2008, St Amant and Horton 2008, Bentley-Condit and Smith 2010, Seed and Byrne 2010); however, arguments over semantic distinctions can become a distraction and may be irrelevant for questions about the ecological relevance of tool use (Hansell and Ruxton 2008, Brown 2012). Whether an animal breaks a nut against a rock by holding the nut (not tool use) or the rock (tool use) seems to make little difference to individual fitness so long as the goal is achieved. Thus for many ecological studies of tool use, the ultimate goal is to identify the biological and adaptive significance. To do this, it is first necessary to identify what factors are most important in determining the likelihood that tool use behavior occurs in a given population.

Most tool using species only demonstrate tool use in a subset of populations or individuals. In these study systems, presence / absence comparison studies are an effective method for identifying key factors that may contribute to the maintenance of tool use after it has been invented (McGrew et al. 1997, Fox et al. 2004, Rutz and St Clair 2012). A variety of prospective determinants of tool use have been investigated, most of which can be classified into one of three broad categories: 1) genetics (Kenward et al. 2005, Langergraber et al. 2011, Teschke et al. 2011, Rutz et al. 2012), 2) ecology (Collins and McGrew 1987, Tyne et al. 2012), and 3) cognitive potential (i.e., individual learning or culture) (McGrew et al. 1997, van Schaik et al. 1999). In many cases all three types of drivers may play some role: for instance, tool use in most species likely originates from genetically predisposed behaviors which become further modified in response to ecological obstacles (Hall 1963). This new behavior

may then be transmitted to other individuals and populations through social learning or inheritance (Kenward et al. 2011, Rutz and St Clair 2012).

Some animals show instinctive (genetic) predispositions to manipulate objects as basic tools (Tebbich et al. 2001, Kenward et al. 2006, Macellini et al. 2012). Young, naïve woodpecker finches demonstrated tool use in the absence of a model tool user, and their development of these skills does not vary from young that were raised in the presence of a model tool user (Tebbich et al. 2001). Thus far, however, studies have failed to show a direct link between genetics and the variation of tool use across populations or individuals (Bacher et al. 2010, Lycett et al. 2010). These studies postulate that instinctive predispositions may lead to the origin of tool use, but ecological factors and social learning drive its persistence and variation.

One of the primary ecological drivers of tool use is the potential increase in foraging efficiency conferred upon tool users, and/or the broadening of niche breadth as otherwise inaccessible prey become accessible (Yamakoshi 1998, Tebbich et al. 2002, Banschbach et al. 2006, Bogart and Pruetz 2008, Rutz et al. 2010, Rutz and St Clair 2012, Tyne et al. 2012). For example, tool use in bottlenose dolphins, also known as "sponging" (in which a sponge is used as protection over an individual's rostrum while searching for prey along rocky substrate), provides access to a new niche of prey, but typically only occurs in habitats that support the preferred sponge (Patterson and Mann 2011, Tyne et al. 2012). Tool use by woodpecker finches occurs more frequently in arid versus humid zones of the Galapagos archipelago because of

the relative scarcity of easily accessible food in arid environments (Tebbich et al. 2002).

Other studies have found variation in tool use in similar environments (McGrew et al. 1997, van Schaik et al. 1999, Van Schaik and Knott 2001, Fox et al. 2004). The capacity for social learning may explain these observations. Social learning, sometimes referred to as cultural transmission, can be difficult to demonstrate (Lonsdorf and Bonnie 2010), but has been suggested as an important mechanism for the origination and spread of tool use in a population for a variety of animals including non-human primates (McGrew et al. 1997, van Schaik et al. 1999, Whiten et al. 1999a, van Schaik and Pradhan 2003, Melber et al. 2007, Lycett et al. 2010, Langergraber et al. 2011), birds (Tebbich et al. 2001, Kenward et al. 2006, Holzhaider et al. 2010), and bottlenose dolphins (Krutzen et al. 2005, Bacher et al. 2010).

In wild bearded capuchin monkeys (*Cebus libidinosus*), the frequency of tool use was influenced by both ecological and social behavioral factors (Spagnoletti et al. 2012). Under the "opportunity hypothesis", the frequency of tool use among different groups varied in response to the relative abundance of difficult to access prey in the diet, rather than seasonal changes in resource abundance (Fox et al. 2004, Spagnoletti et al. 2012). This suggests that given an ecological need, the frequency of tool use may vary depending on the frequency of exposure to tool using scenarios as individuals learn how to forage with or without tools on a regular basis.

One potential contributor to variation in tool use that has yet to be rigorously investigated is the existence of individual dietary specialization within a population (Smolker et al. 1997, van Schaik et al. 2003). Individual specialization has been reported for a range of taxa, including marine invertebrates, fish, birds, mammals, insects, reptiles and amphibians (Bolnick et al. 2003, Woo et al. 2008). Individual differences in diet can be attributed to a number of environmental or bio-physical variables (Schoener 1968, Grant and Grant 1996, Robinson et al. 1996, Smith and Skulason 1996, Svanback and Eklov 2002, Bolnick et al. 2003, Field et al. 2007, Woo et al. 2008), but it has also been reported in the absence of these factors (West 1986, 1988, Estes et al. 2003, Tinker et al. 2007, Tinker et al. 2008, Tinker et al. 2009). In the latter examples, diet specialization appears to be driven by behaviorally-mediated differences in prey choice between otherwise similar individuals, possibly related to variation in learned prey handling or capture skills. In one bottlenose dolphin population, the propensity for tool use varies between individuals and is apparently associated with dietary specialization on particular types of prey (Smolker et al. 1997, Hunt et al. 2007). Diet specialization also may relate to the "opportunity hypothesis" described above, by which individuals that specialize in difficult to access prey are more likely to use tools in response to increased opportunities to learn how to effectively use tools (Fox et al. 2004, Spagnoletti et al. 2012).

The number of tool using species continues to grow with detailed observations of animals in their natural environment. The sheer diversity of taxa now known to use tools may be one reason for the diversity of proposed explanations for this behavior.

Genetics, ecology, and culture have all been shown to play a role in the presence of tool use in at least some species. However, there is very little information on the costs of tool use or the costs of learning to use tools (either individually or via social learning), and no published reports of how such costs might influence individual diet specialization. Additionally, most tool use studies have focused on primates and birds. Little is known about the determinants of tool use in other tool using species.

Sea otters provide a model system for teasing apart the relative importance of ecological and social influences on tool use. Tool use in sea otters is unusually conspicuous and well developed for a non-primate mammal (Fisher 1939, Riedman and Estes 1990, Shumaker et al. 2011), and there have been extensive observations on foraging behaviors over the past 25 years. The first well described record of sea otter tool use was made in California by Fisher (1939) with subsequent reports in both Alaskan and Californian populations by Hall and Schaller (1964), Kenyon (1969), Houk and Giebel (1974) and Riedman and Estes (1990).

Tool use by sea otters occurs when foraging animals acquire a rock, empty shell, or other hard object while feeding and use it to crack open their prey as either a hammer or an anvil. Additionally, individuals will often keep the same tool for multiple dives. This behavior qualifies as tool use under most definitions because individuals pick up the object along with their prey and are responsible for proper orientation of it on their chest. Although Shumaker et al. (2011) have argued that this is not "true" tool use, but rather "borderline" or "proto" tool use, because the object is

not modified for use, the distinction does not change the potential ecological or evolutionary significance of the behavior.

Sea otters consume a wide array of invertebrates, some of which have soft bodies and others whose body is surrounded by shells, spines, or chitinous-exoskeletons. Tool use associated with processing prey is easily observed since sea otters return to the surface to consume captured prey, floating on their backs while processing and handling prey items. Historically, tool use has been reported while sea otters were consuming mussels (Hall and Schaller 1964), abalone (Ebert 1968), and clams (Calkins 1978).

Unlike many other tool using species, tool use in sea otters is not limited to a small number of individuals or populations (Kenyon 1969), although there is some suggestion that the frequency of occurrence of the behavior may be lower in the northern subspecies (Riedman and Estes 1990). Hypotheses advanced to explain such geographical variation in tool use frequency include differences in the strength of the individuals (Kenyon 1969), diet composition (Riedman and Estes 1990), and prey armoring (shell thickness) across latitudes.

Lensik (Hall and Schaller 1964) commented that in the Aleutians, tool use was more common in younger animals because they were less skilled in handling the prey. On the other hand, Jones (1951) noted that tool use in the Aleutians occurred in older sea otters because their teeth were worn and eroded. Aleutian sea otters also consume more fish than California populations and so may not use tools as frequently because their diet does not require it (Kenyon 1969). The thickness of mollusk shells

can also vary across latitudes, with thinner shells found in northern latitudes in response to changes in predators and environment (Vermeij 1976, Vermeij and Veil 1978, Palmer 1979, Vermeij and Currey 1980). It is therefore possible that the difference in the frequency of tool use between southern or northern populations occurs in response to the variation in the prey's defensive capabilities (Riedman and Estes 1990). However, none of these hypotheses have been rigorously tested.

The fundamental goal of my study was to compare frequencies of tool use both across and within sea otter populations, and to identify factors that were associated with observed variations in tool use frequency. Following historical descriptions, I expected that Alaskan populations would use tools less frequently than Californian populations. I tested whether site source alone explained the differences in frequency of tool use, which would provide support for a hypothesis of a genetic or social learning driver. I also investigated the relative contributions of age class, sex and reproductive status, feeding habitat, and prey type to the probability of tool use. I explored tool use variation across individuals, asking specifically whether consistent inter-individual differences in tool use occurred and if the frequency of tool use occurrence was related to learned diet specializations. Finally, I presented a conceptual model of how the factors influencing tool use in sea otters may interact to produce difference in the frequency of tool use among populations.

Methods

Study sites

My study utilized foraging data collected between 1985 and 2011 at eight

locations (with one location sampled over two time periods) across the sea otter's

range in the Northeast Pacific Ocean (Figure 1). Study populations encompassed two

of the three subspecies, the southern sea otter (*Enhydra lutris nereis)* and the northern

sea otter (*Endydra lutris kenyoni*), both of which have been previously reported to use

tools while foraging (Kenyon 1969). Within each subspecies, study sites were

geographically distinct with only occasional movement of individuals across

populations.

Each study site encompassed a variety of habitats including rocky intertidal

and sub-tidal substrates; kelp forests dominated by kelps *Macrocystis pyrifera* (in

California) or *Eualaria fistulosa* (in Alaska) surface canopies*,* sandy bottom areas,

and mixed substrates of mud and silt. These diverse habitats provided a rich prey-base

for sea otters, with over 60 species of consumable benthic invertebrates (Riedman and

Estes 1990). At each site, detailed data on sea otter foraging behavior were collected.

Standardized methods of data collection were used across the different sites with only

a few small differences, as described below.

California

Five studies took place along the California coast and within the southern sea

otter (*Enhydra lutris nereis)* range (Table 1). They included San Nicolas Island (SNI),

Piedras Blancas (PBL), Big Sur (BSR), and two studies in Monterey (MB1:1985-

1993 and MB2: 2000-2011). The density of sea otters ranged from well below carrying capacity (approximately 0.8 otters*km^{-1} ±0.13 otters at San Nicolas Island) to at or near carrying capacity (approximately 5.7 otters*km^{-1} ±1.24 in Monterey; Tinker 2008).

A recently described feature of sea otter diets in California is the existence of pronounced individual diet specialization, whereby individual otters utilizing the same habitat at the same time show distinct prey selection patterns that are consistent over years (Estes et al 2003). Individual diet specialization occurs at sea otter high-density, resource-limited sites such as Piedras Blancas, Big Sur, and Monterey, but not at the low-density, food-rich site at San Nicolas Island, and thus specialization is believed to be a behaviorally-mediated response to intra-specific competition for limited resources (Tinker et al. 2008, Tinker et al. 2012). The population at San Nicolas was established by translocation from the central California coast in the late 1980s (USFWS 1987).

Alaska

Studies of foraging and tool use were conducted at four sites within the northern sea otter (*Enhydra lutris kenyoni*) range of Alaska (Table 1). Sites included Glacier Bay (GLB), Port Althorp (SEA) Adak Island (ADK), and Amchitka Island (AMC). These four sites were further grouped into two regions, southeast Alaska (GLB and SEA) and the Aleutian Islands (ADK and AMC) (Figure 1). Sea otters in southeast Alaska were descendants from approximately 400 translocated otters originating from Amchitka Island and Prince William Sound in the 1960s (Jameson

1982). These studies were conducted between the summers of 1994-2011 with each study lasting 1-3 field seasons. During these studies, ADK and AMC populations were declining at approximately 25% per year (Estes et al. 1998). The sea otter populations at GLB and SEA were increasing at 20 and 6.6% per year, respectively (Esslinger and Bodkin 2009).

Individual sea otter captures

In all California study sites, individual sea otters were captured, tagged, and instrumented with VHF radio transmitters to aid in their identity (Ralls et al. 1995, Tinker et al. 2006). A variety of body measurements were taken on captured individuals and the age and sex of the animal was recorded at the time of capture while the animal was under anesthesia (Dean et al. 2002). Age was estimated in years based on body size, grizzle, and dental condition. Age estimates were then categorized into one of three groups: juvenile (6 months-1 year), sub adult (1-3 years) and adult (greater than 3 years) (Ralls et al. 1995). All work was performed in accordance with the protocols specified under the US Fish and Wildlife Permit #MA-672624-15. After release from capture, each tagged individual was located on an opportunistic basis in order to collect a minimum of 300 foraging dives (spanning multiple feeding bouts: see below) over the course of the subsequent 2-5 years (Ralls et al. 1995, Tinker et al. 2008).

At the Aleutian study sites, otters were also captured and radio-tagged following the methods described for Californian studies, and thus longitudinal data were available from tagged individuals. In contrast, data from the southeast Alaska

sites were collected from untagged individuals, and so longitudinal data from marked

individuals was not available. Untagged individuals were observed during one forage

bout, from which a maximum of twenty dives were observed and recorded, and then

another individual was selected for observation. Physical appearance and relative

location was used to minimize the chance that individuals were re-sampled.

Information on the otter's location, age class, sex, and reproductive status were also

recorded using the same classifications as above.

Foraging and tool use

Observational data on diet and foraging behavior were obtained with the aid

of 10 X 40 binoculars and Questar 50 X 80 power spotting scopes (Questar

Corporation, New Hope, PA), following methods previously described by Kvitek

(1993), Estes (2003), and Tinker et al. (2008). 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. After locating a

feeding animal, a standardized series of data were recorded for each feeding dive

including feeding habitat, dive and surface interval durations, dive outcome (whether

or not prey were captured), prey identification, number and size of the prey items,

prey handling times, tool use (yes or no) and tool type. A contiguous series of these

recorded dives in one day, for a single individual, was considered a forage bout.

Prey items were identified to the lowest possible taxon during data collection.

However, to avoid biases introduced by differences in taxonomic resolution among

study sites, all prey species were collapsed into eight prey classes for data analysis

(Table 2). Additionally, whenever possible, prey items were visually assigned to categorical size classes (1 to 4) based on the maximum prey diameter relative to the otter's paw width (Kvitek et al. 1993). Based on an average paw width of 5cm, size classes thus corresponded to 5 cm groups between 0 and 20 cm. Feeding habitat was categorized into one of four classes: kelp canopy, open water (unknown substrate), rocky intertidal and sandy bottom. Habitat classifications were only recorded in Californian populations and so could not be included in inter-population analyses.

The presence or absence of tool use was recorded for each foraging dive (see Appendix A for tool type descriptions). An otter was considered to be using a tool if it was observed at the surface using an external object (such as a rock) to aid in prey consumption (Figure 2). Typically, this included holding one object (prey or tool) between its paws and pounding it against the second object (prey or tool) placed on its chest until the prey item broke open. Occasionally, individuals pounded their paws on the prey item, or pounded the prey item on their chest without an additional object. These two behaviors were not categorized as tool use because they lacked the implementation of an external object and so do not follow conventional definitions of tool use (Bentley-Condit and Smith 2010). Tools were 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 with abalone (Ebert 1968), but because the frequency of underwater tool use could not be consistently determined, abalone captures were not included in prey specific analyses.

Analysis

Comparisons among study sites were potentially confounded by large discrepancies in the sample sizes of recorded foraging bouts observed and differences in dive numbers observed within bouts. To address this concern, I how many dives within a forage bout were needed to reliably detect tool use, if it was occurring. I re-sampled data from those feeding bouts with the largest sample sizes, calculating the average and standard error in the estimated frequency of tool use for sample sizes of 1-100 dives per bout and 1-100 forage bouts, with 1000 bootstrapped samples per sample size. I determined the minimum number of feeding dives and forage bouts required for subsequent analyses by examining where the variance in estimated values reached an asymptote (Appendix B), as this represented the sample size necessary to ensure consistent estimates.

To determine how tool use varied across populations, the mean percentage of forage dives observed with tool use was calculated for each study site. I used a single factor ANOVA to assess statistically significant variation among sites and Tukey's Honestly Different (HSD) test for specific treatment comparisons. The mean percentage of dives with tool use by each prey type and region was also calculated.

Diet composition was calculated for each site and region based on the relative frequency of occurrence of each prey type during recorded forage dives. To explore the degree to which differences in tool use frequency among sites might be explained simply by differences in diet composition, I statistically "equalized" the diet composition across study sites using a bootstrap resampling approach. Specifically, I

randomly drew (with replacement) 10,000 dives from the available dataset at each study site such that each prey category (Table 2) was equally represented across study sites (the relative frequency of each prey type corresponded to the average observed frequency across all sites). I then calculated the frequency of tool use for this diet-normalized sample. If variation in diet across sites was sufficient to explain differences in tool use frequency, I would expect those differences to disappear when the diets were thus statistically equalized.

I next developed a series of generalized linear mixed effects models (GLMMs) to examine the relative contributions of various potential explanatory factors to variation in tool use frequency across populations. The occurrence of tool use on each dive was treated as a binomial response variable (1= occurrence of tool use and 0= absence of tool use). Categorical, fixed-effects that were considered for inclusion in GLMM models included study site, sex and reproductive status, age class, and prey type. A nested model structure was used to account for potential autocorrelation among dives, with dives nested within forage bouts (the nesting term was treated as a random effect). Table 3 summarizes models that were tested. I limited consideration to those models that seemed biologically plausible. I used variance components analysis (calculated using REML) 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. AICs were then calculated and compared to determine the best-supported model (Burnham and Anderson 1988).

Sea otters at some California sites demonstrated strong individual variation in diet and feeding behaviors (Estes et al. 2003, Tinker et al. 2007, Tinker et al. 2008), and this individuality tended to aggregate into clusters, or modules (Tinker et al. 2012). The existence of modularity in the binary network describing individual use of prey resources was determined by weighted network analysis, as described by Tinker et al. (2012). Individuals were grouped into diet modules based on shared utilization of prey types in core diets (defined as those prey types, ranked in descending order of utilization, which together comprised 60% of all consumed biomass for an individual). Sixty-three individuals had adequate data to reliably determine diet specialization, among which the number of observed dives ranged from 310 -1345. Four dietary modules, or specialist types, were categorized from this sample of individuals. Type I individuals had core diets comprised predominantly of kelp crabs, sea urchins, and mussels; Type II specialists' diets were comprised mostly of clams and worms; Type III specialists consumed mostly *Cancer* crabs and abalone; and the core diets of Type IV individuals were dominated by small gastropods (hereafter snails).

To examine the relative contributions of various potential explanatory factors to variation in tool use frequency among individual animals, I developed a second set of binomial GLMMs. Data sets for these models were limited to the Monterey II study site, where there were sufficient sample sizes available for large numbers of marked individuals. Fixed effects evaluated included foraging habitat, prey type captured on a given dive, and diet specialization module. For these models, dives

were nested within foraging bouts and bouts were nested within individuals, with both of these nested terms treated as random effects. Interactions between feeding habitat, prey type, and diet specialization module were also explored (Table 3). The best supported model was selected using the same criteria described above.

The interaction between prey type and diet module was further explored by comparing the probability of tool use by prey type for each diet module to the population mean. Diets were standardized using the same methods described above for population comparisons, and the mean frequency of tool use was calculated for each prey type and diet module.

All data manipulation and statistical analyses were completed using R.2.13.2 (R Development Core Team 2010) with the exception of the power analysis and diet standardization, which were completed in Matlab (ver 7.13).

Results

A total of 7,532 forage bouts and 111,659 dives were recorded for 633 individuals over 25 years (Table 1). An analysis indicated that a minimum of twenty forage bouts with five dives per bout were necessary to reliably observe tool use (Appendix A). Under these criteria, 4,486 forage bouts and 104,893 dives for 574 individuals were included in analyses.

Overall dietary composition varied substantially among Aleutian Islands, Southeast Alaska, and California (Figure 3). By occurrence, Californian populations had the highest percentage of marine snails in the diet (10.46±1.02 % of feeding dives) while the Aleutians had the lowest (0.11±0.06%). Conversely, sea urchins

were most prevalent in the Aleutian diet (55.65±19.34%) and least prevalent in Californian populations (19.03±9.2%). Southeast Alaskan populations had core diets composed of clams (53.2±20.67%).

Frequency of tool use across populations

The mean ± SE frequency of tool use varied significantly across the nine sea otter study sites, from 21.02 ± 1.23% of forage dives in MB1 to 0.33 ± .19% of forage dives in AMC (Figure 4a). The Aleutian Island populations had the lowest frequency of tool use (0.33-1.37%) compared to southeast Alaska and California (10.06-21.02%). Each population had individuals that were never observed using tools.

Within California, the five sites showed significant variation in the frequency of tool use (χ^2= 766.0, p<0.001). Otters at the resource-limited sites (PBL, BSR, MB1, and MB2) showed a wide distribution of individual rates of tool use, while otters from the non-resource limited site (SNI) had a more narrow distribution of tool use rates (Figure 5). Two studies were conducted in Monterey, separated by 7 years (MB1 and MB2). Although the geographic location, habitat, and population genetics remained relatively constant between these samples, the frequency of tool use decreased from 21.0± 1.23% of forage dives to 16.3 ±0.71 % (Figure 4).

The frequency of tool use also differed across prey types and geographic regions (Figure 6). Marine snails and bivalves (including clams and mussels) were the most likely to be accessed with the aid of a tool. Crabs and urchins were only occasionally associated with tool use in California and vary rarely in Alaska. In

southeast Alaska, mussels were the prey most likely to be consumed with tools

(43.24±2.71% of dives).

Sources of Variation in tool use

Among populations

The GLMM indicated that site source and prey type explained 22.06% and 26.5% of the total variation in tool use across sites, respectively. In contrast, sex (.67%) and age class (.01%) explained little of this variation, thus leaving 50.75% of the total variation in tool use unaccounted for. Although sex and age class did not appear to explain much of the variation, the full model was the best fit model.

Prey type, site, and sex significantly influenced the frequency of tool use (Table 4). Compared to unidentified prey, snails were the most likely to be consumed with the use of a tool (Odds Ratios (OR) ± SE: 595.9 ± 1.13, p<0.001) while soft bodied prey were the least likely to be consumed with a tool (OR=0.23 ±1.13, p<0.001). By statistically standardizing diets across populations, I explored the remaining variation across populations (Figure 4b). MB1 still had the highest probability of tool use and AMC the lowest, however the variation across California populations was no longer statistically significant while variation within southeast Alaska and Aleutian Islands regions increased (Figure 4b).

Females without pups had the highest likelihood of tool use (OR= 1.70 ± 1.22, p-value= 0.01) compared to females with pups and males. The frequency of tool use did not vary significantly among age classes; juveniles and sub-adults appeared to have the same likelihood of tool use as adults (OR: 3.13 ± 3.32, p-value=0.34).

Among Individuals in California

Among individuals from MB2, prey type was responsible for 56.41% of the variance in tool use followed by diet specialization (13.51%) and feeding habitat (5.12%), thus leaving 24.96% of the variance attributable to between- and within-individual variation. The probability of tool use for any particular prey type was strongly influenced by the dietary specialization module (interaction $\chi^2 = 181.2$, p=0.00; Table 5). In general, individuals from specialization modules characterized by prey that required tool use tended to use tools more frequently on all other prey as well. For example, type IV specialists (snail consumers) were more likely to use a tool while foraging than other type of specialists regardless of the prey consumed and urchin specialists were less likely to use a tool regardless of the prey consumed (Figure 7). Of the three models compared, the full model had the lowest AIC score (Table 3).

Discussion

In its most basic form, tool use is the manipulation of an external object for the purpose of achieving a goal. Although a relatively rare behavior in the animal kingdom, tool use can play an important biological role in certain animals by improving their ability to attract mates, defend themselves or their kin against threats, or meet their nutritional requirements (Yamakoshi 1998, Tebbich et al. 2002, Banschbach et al. 2006, Rutz et al. 2010, Patterson and Mann 2011). The nature and extent of tool use in animals is likely dictated by a combination of genetic, ecological, and social factors. The influence of genetics and social learning in tool using

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behaviors is difficult to conclusively demonstrate because of numerous confounding effects (Whiten et al. 1999b, Lycett et al. 2010, Langergraber et al. 2011). Ecological influences are often easier to assess through comparative examinations of factors such as diet, habitat, age and gender within and among populations.

Sea otters are an excellent model system for teasing apart the relative importance of ecological influences on tool use. Tool use in sea otters is both conspicuous and common (Fisher 1939, Riedman and Estes 1990, Shumaker et al. 2011). Furthermore, detailed studies of sea otter foraging behavior over the past 25 years employing similar methods allowed for comprehensive comparisons among individuals and across populations.

To examine the patterns of tool use across and within populations, I used a large sample of feeding dives from nine sites across two subspecies. Collecting such a large sample simultaneously was not feasible, so data from previous studies were utilized. The time scale of these studies meant slight variations in the data collection protocol. While such inconsistencies placed some limitations on the types of inferences that could be made, the resulting analyses nonetheless represent the first rigorous, quantitative look at ecological drivers of tool use in sea otters.

Genetic similarity among populations was not a good predictor of the degree of similarity in tool use behavior, suggesting a relatively minor role for genetics as a determinant of tool use behavior in sea otters. For example, the frequency of tool use differed substantially between sea otters in southeast Alaska and the Aleutian Islands even though the southeast Alaskan population was descended from the Aleutian stock

less than fifty years earlier (Jameson et al. 1982, Bodkin et al. 1999). The frequency

of tool use was similar for southeast Alaska and California, despite the fact that these

two groups of animals are genetically distinct (Cronin et al. 1996, Larson et al. 2002,

Aguilar et al. 2008). These results are consistent with findings from other study

systems, where relationships between phylogenetic history and tool use have been

difficult to demonstrate (Bacher et al. 2010, Lycett et al. 2010). Exceptions to this

pattern include some avian species that show inherited predispositions for tool-

oriented behaviors (Tebbich et al. 2001, Kenward et al. 2011), and Rutz et al. (2012)

suggests that New Caledonian crow tool use could be preserved or diverge due fine

scale gene flow and population structuring.

Most studies agree that an ecological context is required for tool use to

develop in a population (Yamakoshi 1998, Van Schaik and Knott 2001, Tebbich et al.

2002, Fox et al. 2004, Banschbach et al. 2006, Bogart and Pruetz 2008, Rutz et al.

2010, Patterson and Mann 2011). Environmental variation in such features as tool

availability, prey availability, and prey morphology (e.g. shell thickness and

architecture) may lead to differences in the presence or frequency of tool use across

populations. Like many other tool using animals, the type of prey consumed strongly

influenced the presence of tool use both across and within sea otter populations. The

ability to access more, better (in terms of calories, size or ease of digestion), or novel

prey can have large fitness effects on an individual tool user compared to non-tool

users (Shumaker et al. 2011). Many studies have found that the high caloric reward of

prey consumed with the aid of a tool can be a compelling driver of the behavior

(Yamakoshi 1998, Bogart and Pruetz 2008, Ottoni and Izar 2008, Liu et al. 2009, Rutz et al. 2010). Resource competition can also drive tool use by providing access to new prey (Tebbich et al. 2002, Patterson and Mann 2011).

In sea otters, the prey classes most likely to be associated with tool use were snails, other bivalves, and mussels (Figure 6). Though these prey items are relatively easy to capture, they have heavily calcified exoskeletons without accessible openings to the meat. In California, the most common snail species consumed were turban snails (*Chlorostoma* (*Tegula*) spp). These small (2-5cm) snails have thick, compact shells and small openings. Turban snails have a low per-capita energy return, and yet individual sea otters that specialized on snails were just as likely to reach their daily caloric demands as those in other specialist groups (Oftedal et al. 2008). Tool use is likely the key factor in making snails and other "low value" prey energetically profitable to sea otters.

Regional and local differences in prey characteristics may also influence tool use variation. Variation in prey shape and predator defenses may alter the need for an animal to use tools to access the prey (Tebbich et al. 2002, Sanz et al. 2012). Between central California and British Columbia, Frank (1975) found that the size of *Chlorostoma* (*Tegula*) *funebralis* increased in size as latitude increased (and thereby increased ease of access to prey meat). Additionally, Vermeij and Currey (1980) demonstrated that gastropod shell thickness decreased in response to decreased crab predation with increasing latitude. Thus, California sea otters may need tools more frequently than Alaskan otters to overcome the heavier predatory defenses in snail

species. The lack of a clear latitudinal pattern in tool use frequency across all sites suggests that this effect is not a dominant influence. However, the effect of latitudinal changes in shell morphology on the frequency of tool use could not be conclusively determined within the parameters of this study.

In sea otters, foraging habitat did not appear to play a large role in dictating the frequency of tool use. Soft sediment habitats (such as Glacier Bay) did not vary in the frequency of tool use from rocky sub-tidal habitats (such as Monterey). Habitat may not play as large of a role in tool use as other ecological factors because a range of different prey species occur in both habitats, and sea otters are not limited by the presence of potential tools in the environment. For instance, sea otters often use other shelled prey as hammers or anvils in the place of a rock (Calkins 1978).

Individual Learning and Diet Specialization

Several prior studies have demonstrated a strong pattern of dietary specialization among individual sea otters in the apparently resource- limited environment of central California (Riedman and Estes 1990, Estes et al. 2003, Tinker et al. 2007, Tinker et al. 2008, Tinker et al. 2012). In as much as this individuality cannot be attributed to either genetic factors or ecological context, it is likely influenced to a significant degree by experience and learning (Tinker et al. 2009). These patterns and their presumed explanations provided an opportunity to explore the importance of prey type (environmental factors), feeding behaviors (learned behavioral factors), and their interaction in relation to tool use. The interaction

between prey type and diet module (Table 5) demonstrates how tool use can potentially be dependent on both ecological and learned behavioral factors.

Although the rate of tool use varied by prey type within each specialist group, snail specialists were more likely than other specialists to use tools on almost all other prey types (Figure 7). One explanation for this pattern is the transference of tool using skills to new prey, or "behavioral inertia". Tinker et al. (2009) explored situations under which behavioral specialization should arise and be maintained. A key component of this study suggested that as individuals spend more time and energy learning specific handling skills for a particular prey type, the cost of switching to new prey increases and specialization is favored. Snail specialists tend to be the most specialized feeders and have the most complex strategy to learn. Tinker et al. (2012) showed that snail specialists in central Californian were approximately twice as efficient at handling snails as non-specialists, and since snail specialists almost always use tools to handle their prey (Figure 7), it can be inferred that effective tool use is required for efficient prey handling. The transference of tool-use behavior to non-snail prey by snail specialists could conceivably reduce their handling efficiency for those other prey types, a phenomenon known as interference (Hughes and O'Brien 2001). Although it is unclear whether (and how much) such interference occurs in sea otters, it is very possible that learned tool use behavior is one of the mechanisms contributing to diet specialization, by increasing the cost of switching to alternate prey in resource limited areas.

Social Learning

Dietary differences were not sufficient by themselves to explain differences in the frequency of tool use among sea otter populations. When genetic and ecological factors do not fully explain tool use variation, social learning has often been suggested as a key contributor for primates, dolphins, and crows (van Schaik et al. 1999, Whiten et al. 1999a, Krutzen et al. 2005, Lonsdorf 2006, Melber et al. 2007, Holzhaider et al. 2010). There is evidence that sea otters learn foraging behaviors through matrilineal transmission (Riedman and Estes 1990, Estes et al. 2003), but it is currently unknown if they also learn via horizontal transmission.

Sea otters in the Aleutian island used tools less frequently than all did otters in the other study populations, even after accounting for regional differences in diets (Figure 4b). If the frequency of tool use was determined largely or exclusively by prey type, then the expected rate of tool use in the Aleutians would have been 2.76% rather than the 0.85% observed. Aleutian otters, which have a diet primarily consisting of crabs and sea urchins that do not require tools, may not have a need to use tools often enough for this behavior to spread through the population via either vertical or horizontal transmission. Moreover, behavioral inertia (see above) may reduce the tendency of otters to use tools on those infrequent dives that snails or large mussels are captured. Finally, the investment of time and energy required to learn tool use behavior may outweigh the potential benefits in the Aleutian environment, because the prey for which a tool would be needed is so uncommon.

If tool use in sea otters is a learned behavior, then individuals should increase their frequency of tool use over time as they become more proficient at the behavior. In this study, age did not show a significant effect on the probability of tool use. However, the sample sizes for juveniles and sub-adults were much lower than adults and unevenly distributed across populations and diet specialist groups (Appendix C). Future studies would benefit from a larger sample of individuals from each diet specialist group that could be followed from pup to adult.

In sea otters, the propensity for tool use varied by sexual status. Sexual differences in tool use tendency have not been studied in detail for most systems. However, researchers have found sexual biases in chimpanzees, capuchin monkeys, and bottlenose dolphins (Mann et al. 2008, Gruber et al. 2010, Moura and Lee 2010). Explanations for these sex-specific differences range from energetic constraints (McGrew 1992), curiosity and innovation (Lonsdorf 2004), sexual display (Moura 2010), and social learning (Mann 2010). I also found a female bias in tool use in sea otters, although this effect was barely significant and only apparent when the females were not caring for a pup (Table 4). Further work is needed to elucidate why tool use may be more frequent among female sea otters.

Conceptual model of tool use frequency

The results of this study suggest that patterns of tool use in sea otter populations and individuals are driven by multiple factors interacting together. A conceptual model summarizing the various ecological contexts under which tool use behavior is expected to be rare or common is presented in Figure 8. This model is

based on the premise that tool use occurs when there is at least one commonly utilized prey type for which performance can be enhanced (e.g., increased handling efficiency or ease of digestion). However, the social context is likely to mediate these patterns somewhat: for example, the exposure to "difficult to access" (DTA) prey must be sufficiently high that the behavior will spread through the population, either by individual or social learning. Such a model is similar to the "opportunity hypothesis" for tool use maintenance presented by Fox et al. (2004). However, in contrast to the conclusions of Spagnoletti (2012), resource limitation ("necessity hypothesis") can also play a role in the frequency of tool use in sea otters, in this case by influencing the degree of individual diet specialization.

Conclusions

This study has demonstrated significant relationships between prey types, learned feeding behaviors and the occurrence of tool use by sea otters. The morphology of various prey appears to be influential in determining the benefit of using a tool, but there may be trade-offs in terms of the cost of learning to use a tool (either individually or socially) and the transference of that behavior to other prey. Variation in the frequency of tool use across populations is likely dictated by the changes in diet composition and opportunity to learn effective tool use behaviors. Within populations, variation in tool use among individuals is largely explained by differences in prey use among individual diet specialists. Learning to use tools apparently benefits certain prey specialist types, particularly snail specialists, but transference of those behaviors to non-snail prey could inhibit an individuals' ability

to prey-switch effectively, thus reinforcing specialization in resource-limited populations.

My study is the first to rigorously document the patterns of tool use in sea otters. As such, there are many aspects of this behavior that warrant further research. Future study might help clarify how sea otters learn tool use (i.e. vertical or horizontal transmission, or individual learning) by following animals from early life to adulthood. Additionally, our understanding of why this behavior has developed in greater frequency in some populations would benefit by quantifying the energetic costs and benefits of tool use.

Tables

Table 1 Summary of sample sizes for each study site.

Study site	Years	# Males	# Females	# Juvenile	# Sub-adult	# Adult	# Forage Dives
San Nicolas Island, CA	2003-2006	5	8	0	2	11	2703
Piedras Blancas, CA	2001-2004	16	34	0	8	42	25698
Big Sur , CA	2008-2011	6	31	2	4	30	7971
Monterey, CA	1985-1993	14	44	0	0	58	11531
	2000-2011	28	80	7	8	93	34727
Glacier Bay, AK	2011	21	110	0	33	98	1886
Whale Bay, AK	2011	17	65	2	11	69	1214
Adak Is, AK	1995-2008	7	29	2	0	34	11337
Amchitka Is, AK	1992-1994	10	50	11	0	49	7826
Total		*124*	*450*	*24*	*66*	*474*	*104893*

Table 2 Summary of common prey items consumed by sea otters

Common Name	Latin Name or Taxonomic Group	Prey Category
Abalone spp.[a]	*Haliotis spp.*	Abalone
Gaper clam	*Tresus nuttallii*	Clam
Butter clam	*Saxidomus gigantea*	Clam
Cockle	*Serripes sp., Clinocardia sp.*	Clam
Cancer crab	*Cancer spp*	Crab
Kelp crab	*Pugettia spp*	Crab
Helmet crab[b]	*Telmessus cheiragonus*	Crab
California mussel[a]	*Mytilus californianus*	Mussel
Horse mussel	*Modiolus modiolus*	Mussel
Blue mussel[b]	*Mytilus trossulus*	Mussel
Octopus	*Octopus spp.*	Soft bodied
Sea star	*Various spp*	Soft bodied
Fat Innkeeper worm	*Echiuris caupo*	Soft bodied
Unidentified fish[b]	*Various spp*	Soft bodied
Sea cucumber	*Various Holothurian spp*	Soft bodied
Giant rock scallop	*Crassodoma gigantea*	Other Bivalve
Rock jingle	*Pododesmus macroschisma*	Other Bivalve
Snail spp.	*Tegula spp* , *Calliostoma sp.* , and *Lithopoma sp.*	Snail
Purple urchin	*Strongylocentrotus purpuratus*	Urchin
Red urchin	*Strongylocentrotus franciscanus*	Urchin
Unidentified prey	*Various spp.*	Unknown

[a] Not consumed in Aleutian diets

[b] Not consumed in California diets

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Table 3 Binary logistic generalized linear mixed effects models showing the relationship between the probabilities of occurrence of tool use with factors Site, Prey, Sex, Age, Habitat, and Diet Module. Forage bouts were random effect nested in site and individual for inter-population and inter-individual models, respectively.

| Model	AIC
Inter-Population	
Site	38404
Site + Prey	26588
Site +Prey + Sex	26450
Site + Prey+ Sex + Age	26335
Inter- Individual	
Prey + Habitat + Diet Module	7369
Prey + Diet Module+ Prey*Diet Module	7299
Prey + Habitat + Diet Module+ Prey*Diet Module+ Prey*Habitat	6299

Table 4 Binomial generalized linear mixed effects model parameters showing the relationship between the probability of tool use being used during a dive with site source, age class, sexual status, and prey type. Superscripts represent populations that are significantly different

	Factor	β	β S.E.	χ^2	P-value
	Intercept	-9.35	1.25		<0.0001
Site:				79.5	<0.0001
Reference=	ADK[a]	0.15	0.86		0.86*
AMC[a]	SEA[ab]	2.84	0.90		0.002
	BSR[b]	3.35	0.79		<0.0001
	GLB[b]	3.68	0.85		<0.0001
	MB2[b]	3.78	0.76		<0.0001
	PBL[b]	3.99	0.76		<0.0001
	SNI[b]	4.75	0.82		<0.0001
	MB1[b]	5.33	0.77		<0.0001
Age Class:				0.79	0.67*
Reference=	Sub-Adult	0.74	1.25		0.55*
Juvenile	Adult	1.14	1.20		0.34*
Sexual Status:				1.8	0.4*
Reference=	Female w/ pup	0.21	0.22		0.34*
Male	Female w/o pup	0.53	0.20		0.01
Prey Type:				2502	<0.0001
Reference=	Other prey	-1.46	0.12		<0.0001
Unknown	Crab	-0.66	0.07		<0.0001
	Urchin	-0.43	0.09		<0.0001
	Mussel	0.47	0.10		<0.0001
	Clam	1.64	0.09		<0.0001
	Other Bivalve	1.95	0.10		<0.0001
	Snail	6.39	0.12		<0.0001

**Table 5** Parameter effects for best fit model of tool use variation across individuals in MB2.

| Predictor	df	χ^2	P-value
Diet Specialist Group	3	157.3	0.00000
Prey type	4	66.2	1.4e-13
Habitat	3	14.0	0.003
Prey* Group	12	181.2	0.00000
Prey*Habitat	12	159.8	0.00000

Figures
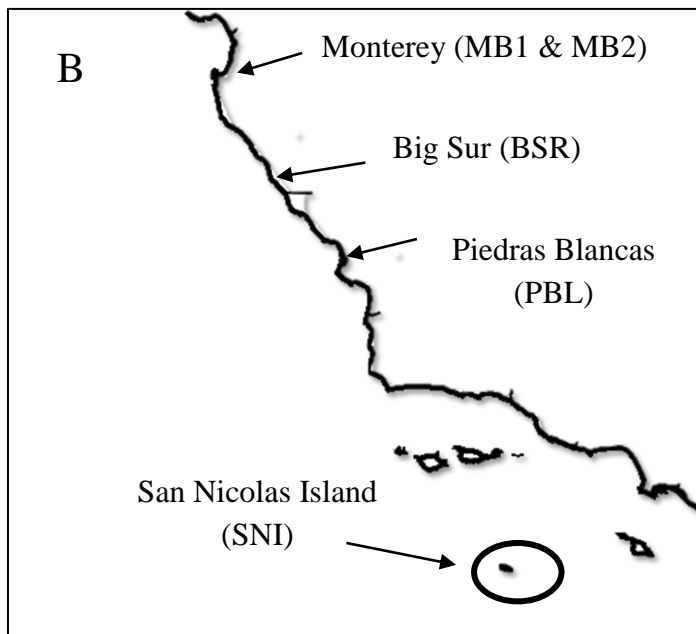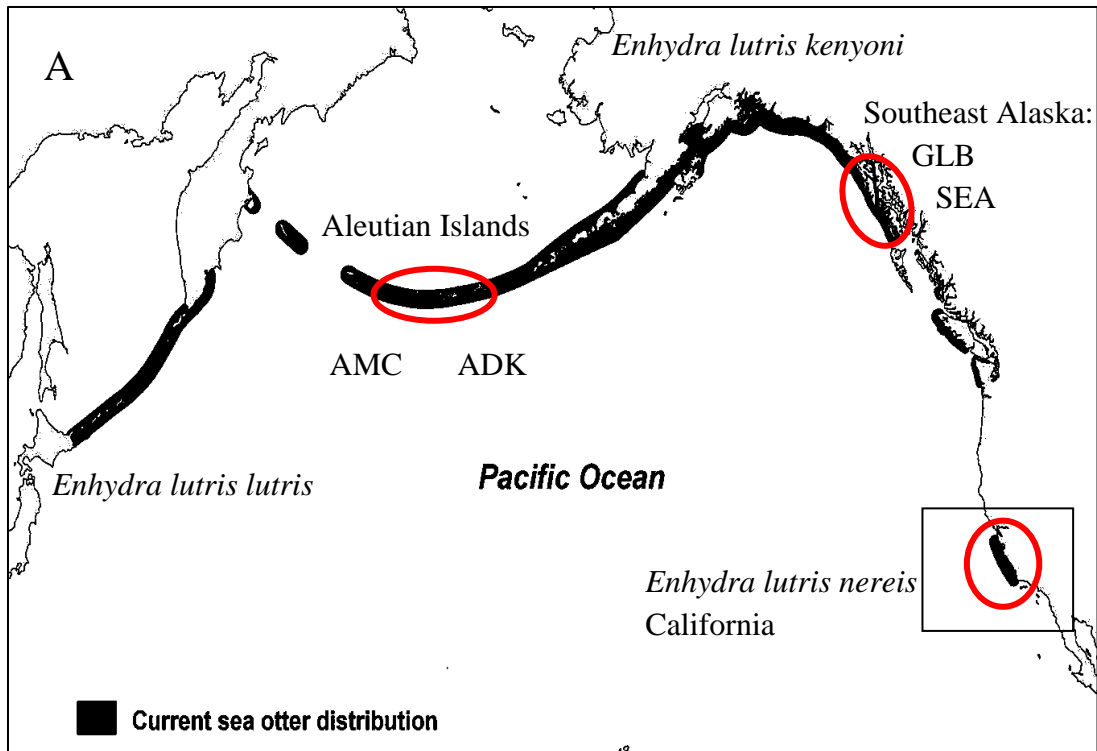
Figure 1 Map of study populations. A) Map of sea otter range with relevant study regions circled in red. B) Close up map of relevant study areas in California.
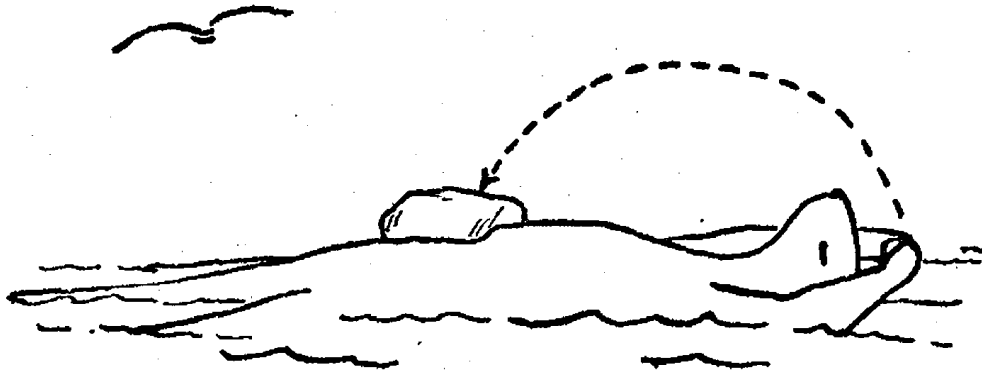
Figure 2 Drawing of a sea otter about to use a rock as an anvil in order to break open a small prey item. Sea otters also use rocks, shells, and other prey as hammers to achieve the same goal. Recreated from Fisher (1939).
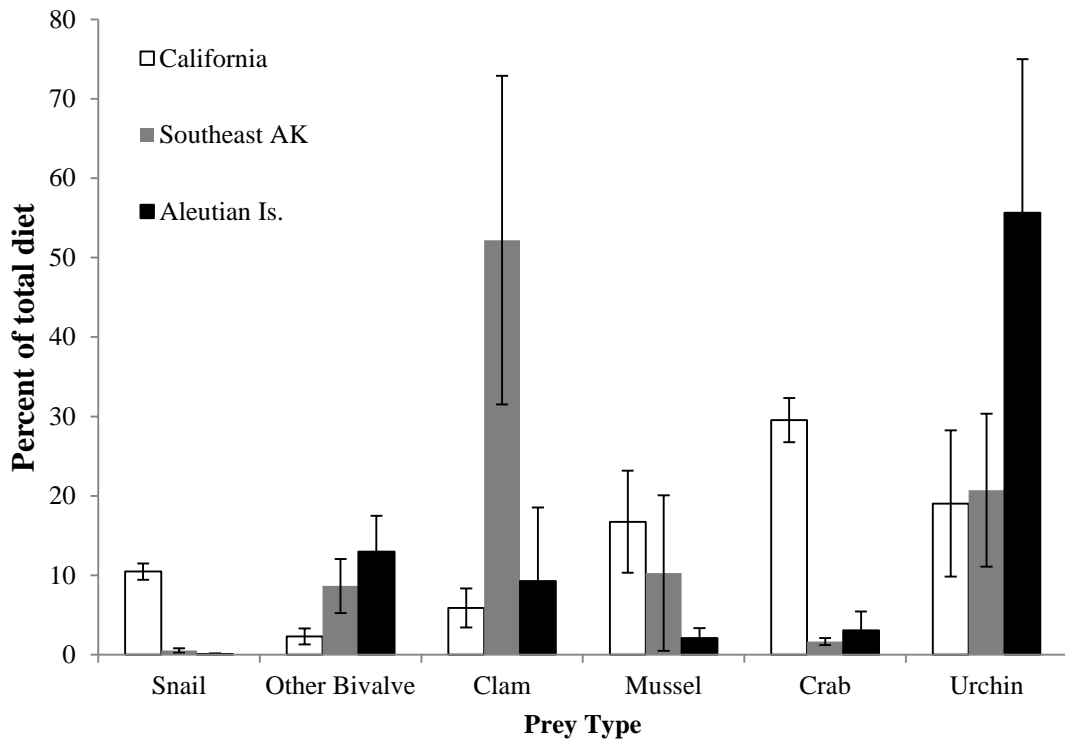
Figure 3 Summary of diet by region. The relative contribution of each prey type was calculated by occurrence. White bars represent Californian region; grey is southeast Alaska; and black is Aleutian Islands.
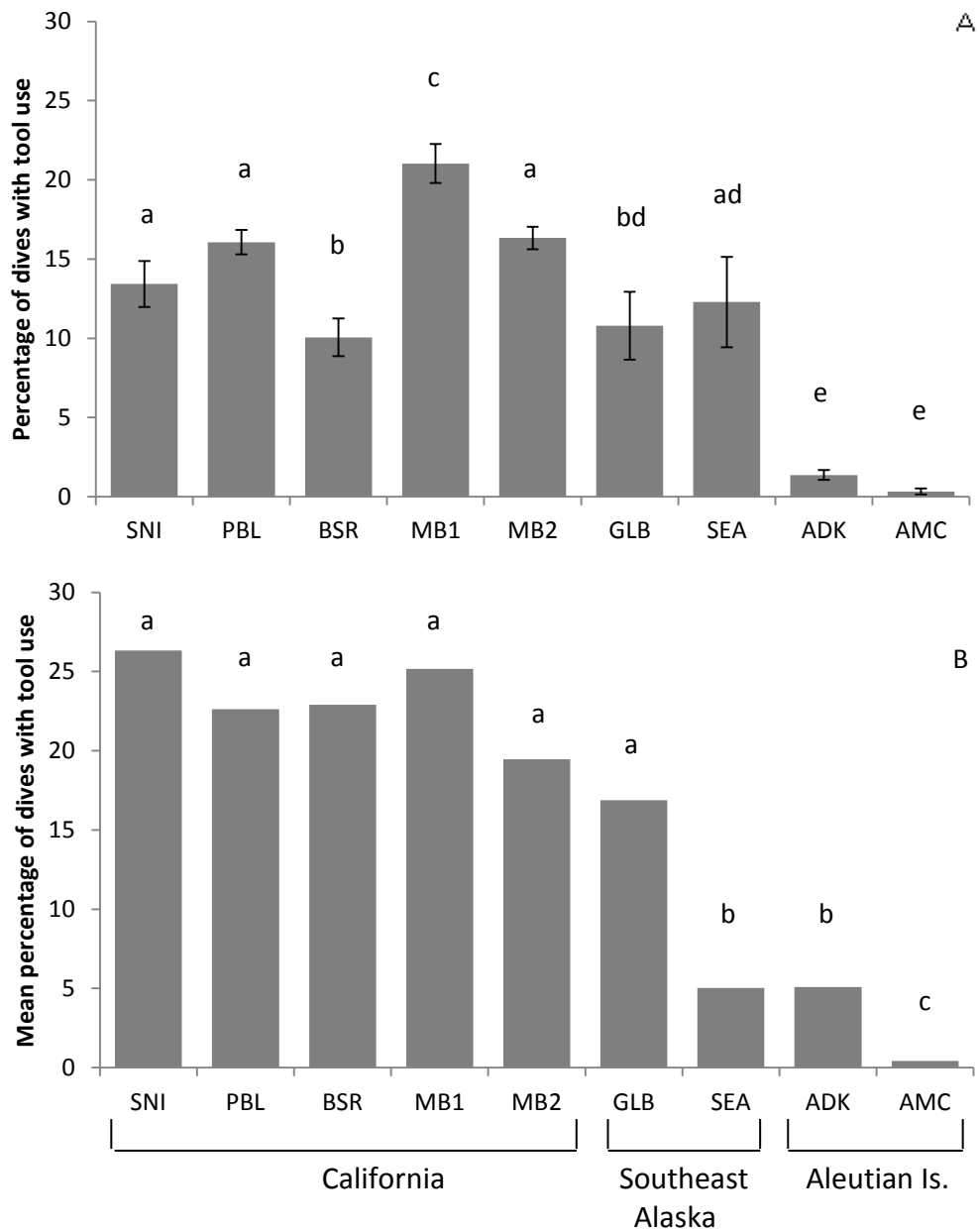
**Figure 4 a)** Observed frequency of tool use across nine study sites. Sites are in order of appearance along the coastline (See Figure 1). Letters represent significantly different means. Error bars represent standard error. **b)** Expected frequency of tool use across nine study sites with statistically equalized diets (see Methods for details). If diet alone explained all variation, all bars should be of similar height.
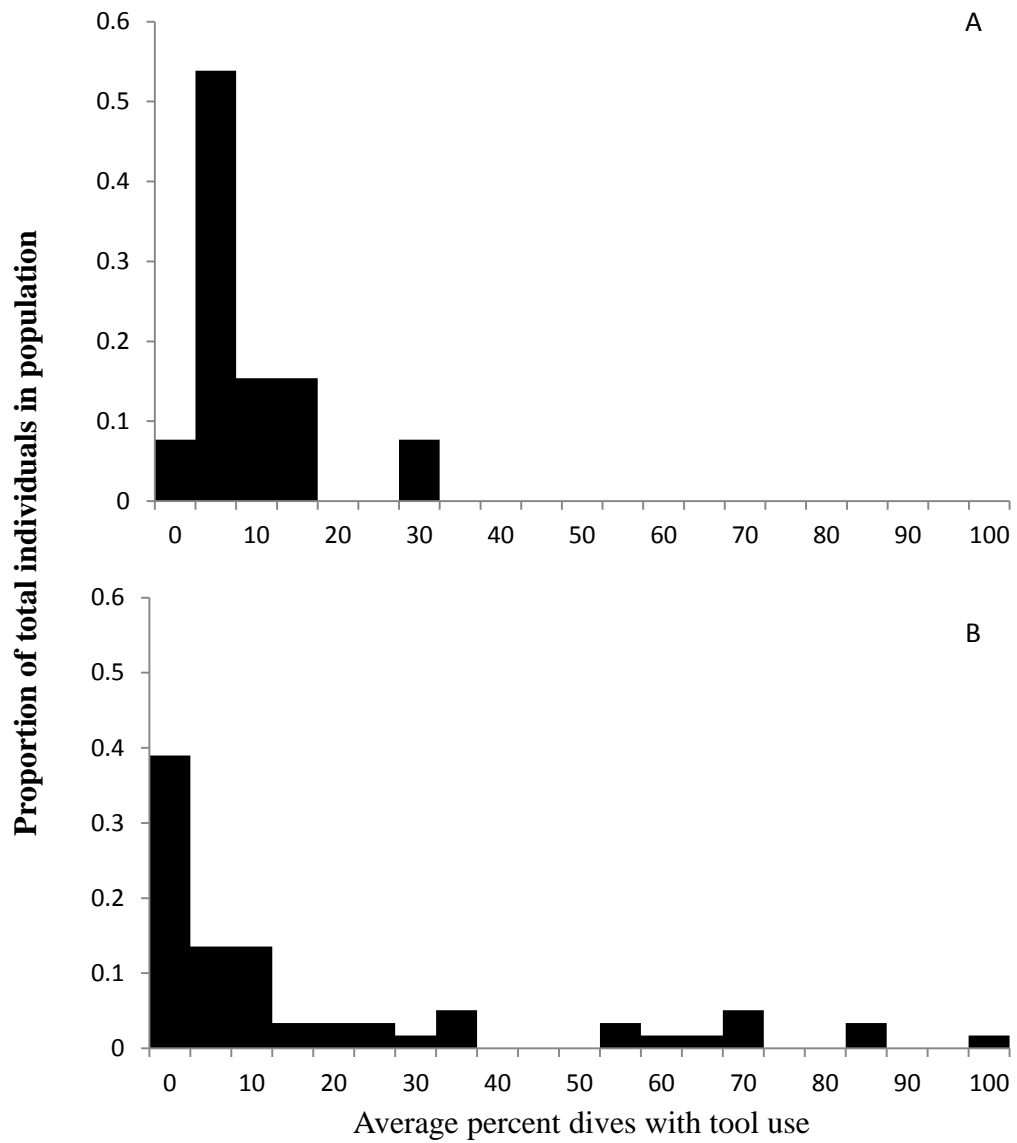
Figure 5 Distribution of individual average rates of tool use for resource rich (**A**) versus resource limited populations (**B**).
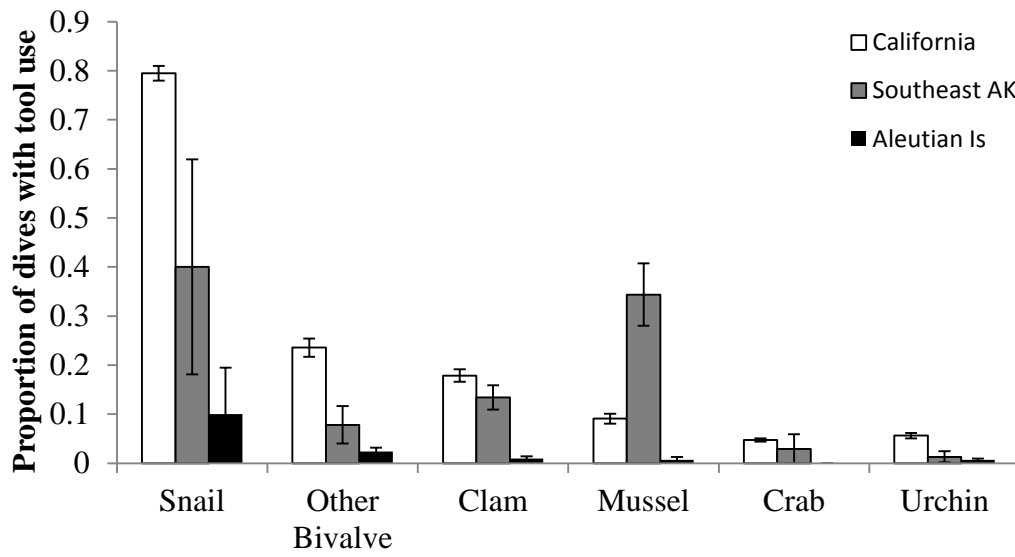
Figure 6 Rates of tool use for six common prey types by each region. Error bars represent standard error. White bars represent Californian region, Grey is southeast Alaska and Black is Aleutian Islands.
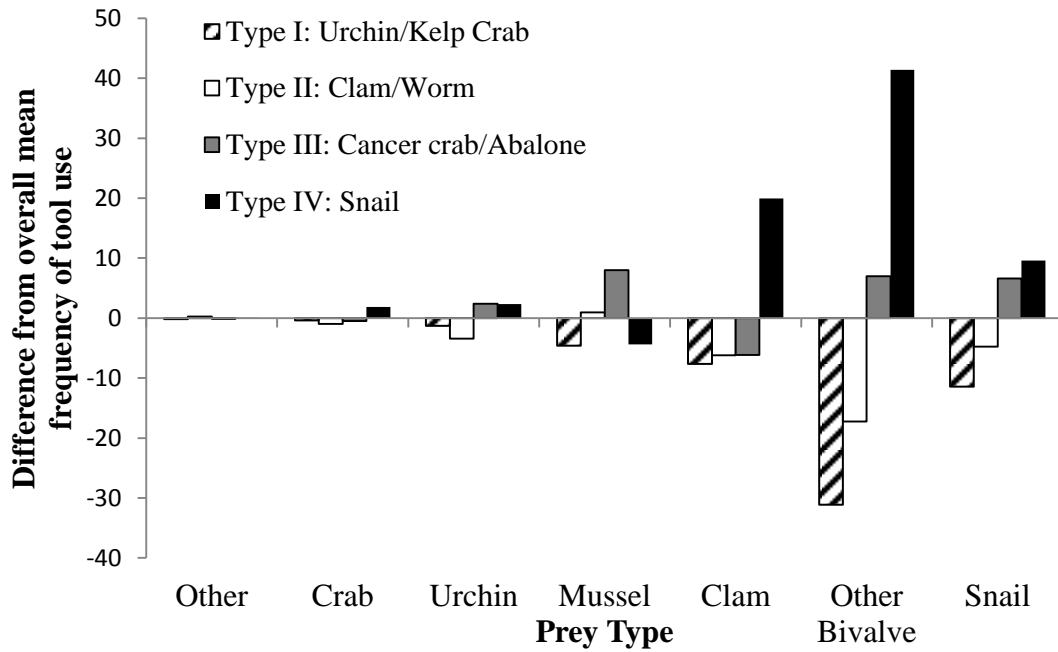
Figure 7 The deviation from mean tool use for common prey items by four diet specialist modules. Population mean frequency of tool use for each prey type standardized to 0. Positive bars represent a higher than average frequency of tool use while negative bars represent a less than average frequency of tool use. If diet specialist group Type I(Urchin/kelp crab) = black strips, Type II (clams/worms)= white, Type III(*Cancer* crab/abalone)= grey; Type IV (snails)= Black.
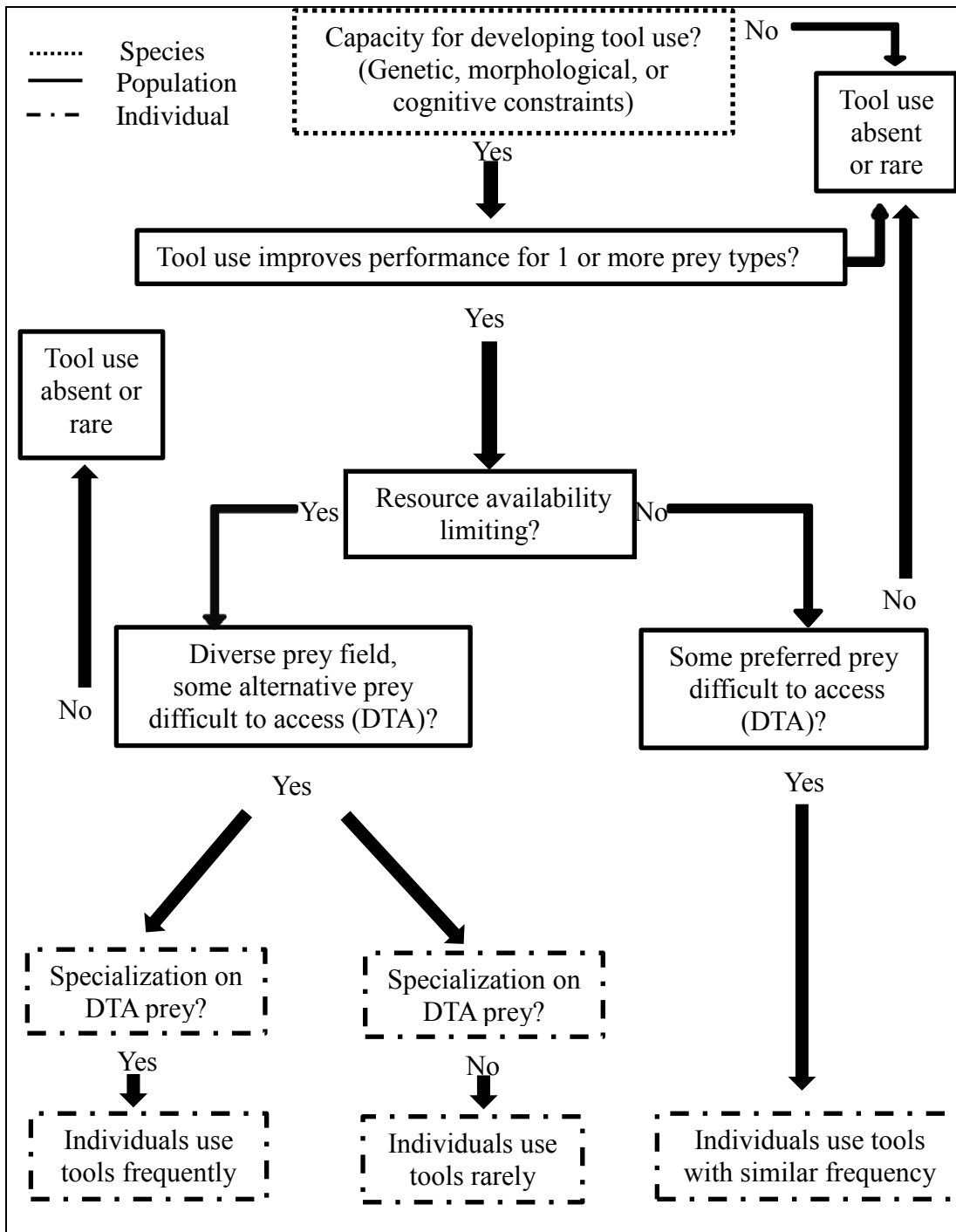
Figure 8 Decision tree for the expected presence/absence and relative frequency of tool use in sea otter populations and individuals. In cases where tool use is present, the population level frequency of tool use depends on the frequency of "difficult to access" (DTA) prey in the individual diets.

Appendix

Appendix A Five common tool use behaviors observed in sea otters

Tool Type	Description
Anvil	Rock, empty shell, or other hard item placed on abdomen before pounding prey on it
Hammer	Rocky, empty shell, or other hard item held in paws and hit against prey on chest
Prey on Prey	Two prey items pounded together as either anvil or hammer. Both prey items may be consumed, or one may be retained as tool for subsequent dives
Prey part on prey	Part of a prey item (e.g crab claw) removed and pounded against remaining prey (e.g crab carapace)
Dislodge	Rocky, empty shell, or other hard item used as a hammer underwater to dislodge prey from substrate
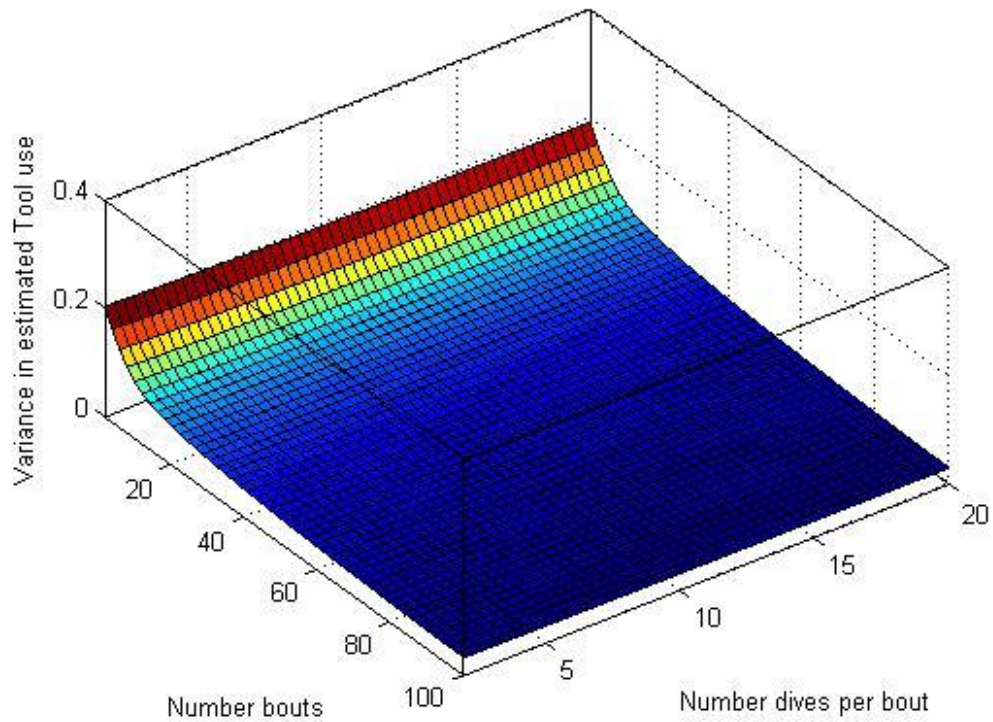
Appendix B The variance in estimated tool use as a function of the number of forage bouts and dives per bout in the sample. Cooler colors represent decreased variance in estimated tool use. Approximately twenty forage bouts with a minimum of five dives per bout are required for the variance to asymptote near 0.1.
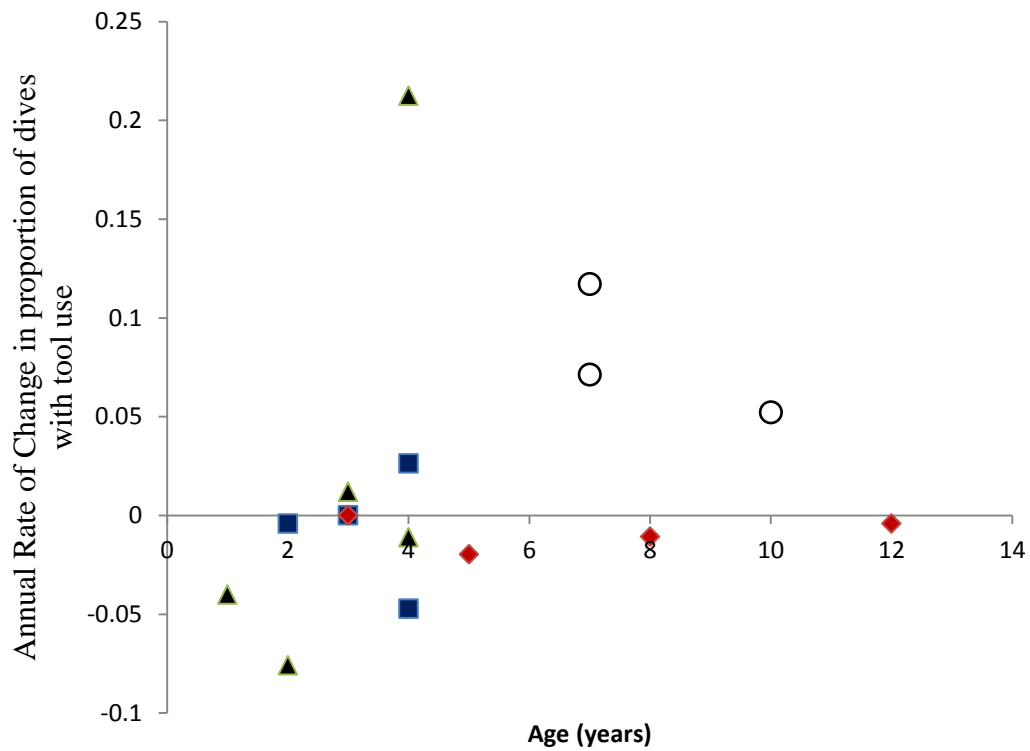
Appendix C Relationship between age and change in frequency of tool use for individuals with multiple years of data and known specialist modules (N=16). Red diamonds= Type I specialists; Blue squares= Type II specialists; Black triangles= Type III specialists; White circles= Type IV specialists. Positive change represented individuals increasing frequency of tool use over time. Only Type IV specialists (snail feeders) showed consistent positive change, but all animals were older. Other specialist groups showed zero or negative change in tool use frequency.

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