

Summer Foraging Tactics in Sea Otters (*Enhydra lutris*): Maintaining Foraging Efficiencies in a Stable Population in Alaska

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Abstract

Foraging specializations in large populations can reduce intraspecific competition for food. When individuals do not specialize on particular prey species, resource partitioning might occur as different search strategies at the sex and age group levels. This study focused on the foraging tactics of sea otters in a stable population in Alaska by testing cost-minimizing, energy-maximizing, and efficiency-maximizing models. Canonical Correspondence Analysis (CCA) was used to analyze the boat-based behavioral observations of 119 foraging bouts for adult males and females, females with pups, and juveniles. Observations were conducted during one summer breeding season. A foraging efficiency ratio was calculated using the gain variable—estimated mean energy values from captured prey—and the cost variables—inter-dive distances traveled and dive depths. Foraging efficiency ratios were not significantly different between all adults, including females with pups. Juveniles had significantly lower foraging efficiency ratios related to low mean energy gains and a higher proportion of unsuccessful dives. A cost-minimizing strategy was identified in females with pups that minimized travel costs and obtained low prey energy per dive. Adult males and females without pups used an energy-maximizing strategy of high travel costs and high prey energy gains per dive. The ability of adult females to change foraging strategies with the demands of raising a pup indicate female adult sea otters can have flexible foraging strategies while maintaining high foraging efficiencies.

Key Words: sea otter, *Enhydra lutris*, optimal foraging, niche partitioning, foraging tactics

Introduction

Partitioning resources through foraging specialization is one way that populations at carrying capacity can decrease intraspecific competition

for food. Prior to reaching carrying capacity, a generalist predator might experience relatively low intraspecific competition for food, allowing individuals to choose their preferred prey. The prey model of optimal foraging theory predicts that the most profitable prey species will be targeted until the abundance of the preferred prey reaches a critical value below which prey switching will occur (Stephens & Krebs, 1986). This has been observed in sea otters (*Enhydra lutris*), for which diet changes occurred as individuals began to rely on less profitable prey with increasing sea otter densities in reoccupied areas (Ostfeld, 1982; Garshelis, 1983; Kvitek et al., 1992; Watt et al., 2000). However, when prey density is low or the dietary variety is limited, foraging specializations could result in different search strategies.

The patch model can be used to describe search strategies by modeling when the predator should abandon a food patch that is no longer profitable (Stephens & Krebs, 1986). This model has empirical support from field studies (Krebs et al., 1974; Cowie, 1977; Stephens & Krebs, 1986), although certain assumptions such as negligible search and handling costs are not representative of real foraging behavior. Alternate foraging models build on aspects of the patch model by including other factors that could constrain foraging behavior such as the spatial and temporal scales of patches (Ritchie, 1998; de Knegt et al., 2007), patch predictability (Klaassen et al., 2006), foraging under predation pressure (Krebs & Kacelnik, 1991), prey handling costs (Holling, 1959), and social influences on foraging behavior (Gompper, 1996; Galef & Giraldeau, 2001). Most models treat the individuals within a species as behaviorally equivalent when foraging, but this fails to account for any differences in foraging strategies within a population as a result of high intraspecific competition.

The Niche Variation Hypothesis (NVH) predicts that large, generalist populations might actually consist of individuals with highly variable intraspecific foraging adaptations (Van Valen,

1965). An assumption of this hypothesis is that due to differences in prey handling costs, individuals may choose to specialize on particular prey. The occurrence of different foraging strategies increases the species niche width and reduces intraspecific competition.

Several models have also shown that the coevolution of competing species or individuals within a species can result in several phenotypes with different foraging strategies (Slatkin, 1980; Taper & Chase, 1985). The maintenance of these phenotypes can be achieved through disruptive selection (Rueffler et al., 2007) or population frequency dependence (Roughgarden, 1972). However, not all foraging specializations occur as a result of morphological differences. Differences in foraging behavior related to ontogenetic changes (Olson, 1996; Takimoto, 2003), differences between sexes (Gremillet & Wilson, 1999), and individual specializations (Bolnick et al., 2003) have also been proposed with support provided by observations in a wide range of taxa (Bolnick et al., 2007).

Such behavioral specializations are most likely to occur in apex predators with low interspecific competition and high intraspecific competition where a single species can act as two (or more) ecological species (Estes et al., 2003). The degree of foraging strategy heterogeneity within a species could explain how large populations of predators avoid intraspecific competition. While differential resource use among individuals, sexes, and age classes has been reported (Estes et al., 2003; Tinker et al., 2007), few studies include the cost factor of different foraging tactics, making it hard to compare the efficiency of various foraging tactics within a species. For species with high metabolic rates such as the northern sea otter (*E. l. kenyoni*) (Costa & Kooyman, 1984; Davis et al., 1988), efficient foraging strategies become especially important for populations at carrying capacity.

In southern sea otters (*E. l. nereis*), prey specializations have been identified in predominantly hard substrate habitats (Reidman & Estes, 1990; Estes et al., 2003; Bentall, 2005; Tinker et al., 2006), where most of the prey consist of nonburrowing species such as mussels, crabs, and abalone, and less than 50% of the prey caught by a particular foraging specialist consists of burrowing species such as clams (Estes et al., 2003; Tinker et al., 2006). In contrast, clams (including butter clam [*Saxidomus gigantea*], Pacific littleneck clam [*Protothaca staminea*], stained macoma [*Macoma inquinata*], bent-nose macoma [*M. nasuta*], truncate softshell clam [*Mya truncata*] and Arctic hiatella [*Hiatella arctica*]) often comprise between 70 to 80% of sea otter diets in soft-sediment environments (Calkins, 1978;

Kvitek et al., 1992; Doroff & DeGange, 1994; Davis, unpub. data). This lack of dietary specialization in soft-sediment environments, even with the high prey capture cost of excavating clams (Estes et al., 1981), is contrary to previous hypotheses that indicate foraging specializations occur as a result of differential prey-handling costs (Estes et al., 1982; Tinker et al., 2007).

One possibility for the lack of prey specialization is that prey diversity is lower in soft-sediment environments. However, sea otters have been observed to take mussels (*Mytilus trossulus*), dungeness crabs (*Cancer magister*), graceful rock crabs (*C. gracilis*), Helmet crabs (*Telmessus cheiragonus*), reddish scallops (*Chlamys rubida*), orange sea cucumbers (*Cucumaria miniata*), purple sea stars (*Pisaster ochraceus*), Alaska falsejingles (*Pododesmus macroschisma*), nuttall cockles (*Clinocardium nuttallii*), North Pacific giant octopus (*Enteroctopus dofleini*), red octopus (*Octopus rubescens*), fat innkeeper worms (*Urechis caupo*), and skate egg cases (*Rajiformes* sp.), albeit always in smaller proportions relative to clams (Kvitek et al., 1992; Davis, unpub. data). Svanback & Bolnick (2005) present a different explanation related to the level of competition. Their model predicts that as competition increases, foraging specializations occur; however, if competition continues to increase, individuals tend to become more generalist.

More subtle foraging specializations may occur to partition resources, and foraging specializations may instead occur at the level of sex and age classes (Polis, 1984). Within large, stable populations with unknown individual foraging specializations, it is hypothesized that different sex and age groups display different foraging strategies. In this study, behavioral and environmental factors were used to differentiate the foraging strategies between adult males, adult females, females with pups, and juveniles using (1) a travel cost-minimizing model of distances traveled and depth of dives, (2) an energy-maximizing model using estimated gross energy gained (sum of mean energy values of prey caught after each dive), and (3) an overall foraging efficiency model incorporating both costs (distance traveled) and gains (estimated energy values of prey captured).

Although field studies cannot truly test the marginal value theorem because of the inability to control prey density in patches, we tested models that looked at aspects of patch foraging strategies. The cost-minimizing model assumed that travel costs between patches were significant and could be used to distinguish when different sex and age groups chose to leave a patch. The energy-maximizing model looked at whether the gross rate of energy gain on a per dive basis

determined foraging strategies, and the foraging efficiency model estimated both the patch foraging costs and gains in the patch model of optimal foraging theory.

The efficiency of the different foraging strategies was also examined, and it was further hypothesized that large adult male sea otters would require the most efficient foraging strategies, whereas juveniles learning to forage would be the least efficient foragers. The occurrence of foraging specializations in northern sea otters was also tested by comparing within-individual variation to between-individual variation. It was hypothesized that higher between-individual variation would indicate individual foraging specializations similar to the behavior of southern sea otters, whereas higher within-individual variation would indicate broader foraging tactics with less specialization.

Materials and Methods

Study Site and Behavioral Observations

Simpson Bay is a fjord located in eastern Prince William Sound, Alaska (*ca.* 60.4° N, 145.5° W). The bay has a surface area of approximately 21 km², an average depth of *ca.* 30 m, and a maximum depth of 140 m (Figure 1). Over 50% of the benthos is classified as soft sediment or mud, but mud mixed with gravel and sand occur more commonly in shallow to intermediate depths

(Gilkinson, 2004). The area has been occupied by sea otters for over 30 y and was initially a male-only region (Garshelis, 1983; Garshelis et al., 1984). It is now predominantly a female or breeding (mating and pup-rearing) area with a few territorial males and large numbers of females and female-pup pairs.

We counted the number of sea otters in Simpson Bay every 2 wks between May and August and opportunistically during the rest of the year between 2002 and 2009. During the winter months, Simpson Bay is less accessible, and research crews were not available to conduct counts as frequently. The counts were conducted from two boats traveling 4 to 5 km h⁻¹ that stayed spaced 400 to 600 m abreast while sea otters were counted. The boats started in the upper end of East Bay and traveled toward the mouth of Simpson Bay. The sea otter counts then continued northward through West Bay and ended in the upper end of North Bay. Observers in both boats counted the number of single sea otters and females with pups between the boat and shore, but observers in only one boat counted the number of sea otters between both boats.

The population of sea otters in the bay has been stable since 2002, with the greatest number of individuals recorded during the summer months (91 ± 3.4 SE adults and subadults; 28 ± 1.9 SE pups; Davis, unpub. data, 2010). We assumed a similar level of competition between our study site and the studies of prey specialization in southern sea otters based on sea otter densities. In the studies of southern sea otter foraging, the average yearly sea otter density was approximately 2.1 sea otters per km² (Tinker et al., 2006), whereas the adult sea otter density in our study area (measured to the 150-m contour) was approximately 4.3 per km² (Davis, unpub. data, 2007).

We divided the bay into three regions for survey effort: (1) North Bay, (2) West Bay, and (3) East Bay (Figure 1). Behavioral observations of foraging sea otters were conducted between 22 May and 13 August 2007 during daylight hours (0800 to 2200 h). An average of 2 ± 3 behavioral observations were conducted on opportunistically encountered foraging sea otters each day. Observations were made from a 6-m long skiff at a distance of 50 to 150 m in an attempt to avoid altering sea otter behavior. Boat-based observations were used to reduce the distance bias in dive durations to which shore-based observation methods are prone (Reidman & Estes, 1990). Five different observers assisted with recording information and spotting sea otters, but only one observer identified the prey type and estimated the distance of the sea otter from the boat for foraging dives. Each day, one region within Simpson Bay was arbitrarily selected, with

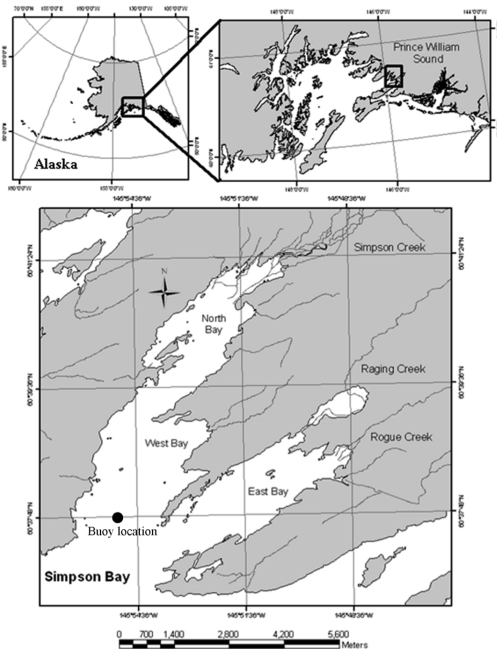


Figure 1. Simpson Bay study area divided into three areas used for behavioral surveys (Noll et al., 2009)

focal follows conducted on a foraging sea otter from the time it was first observed until we could no longer locate it, or it interrupted its foraging behavior for at least 5 min. Behavioral observations were terminated if the sea otter appeared to avoid the boat during the first 5 min of an observation or if weather conditions became unsuitable for boat-based observations. At such times, a different sea otter was followed if available or observations were terminated for the day. Examples of avoidance behavior included rapidly swimming away from the boat and diving increasingly farther from the boat. All foraging observations lasting more than 10 min were included in this study, including observations terminated because of weather conditions.

While observing a sea otter, we recorded the location of the boat using a global positioning system (GPS) after each feeding dive. A compass direction and estimated distance between the sea otter and the boat were recorded to correct for the actual dive location. The accuracy of distance estimates were later quantified in the West Bay by recording GPS locations of the boat and estimating the distances between the boat and a single fixed-location buoy with a known GPS location (Figure 1). The actual distances were later measured using *ArcView 9.2* software (ESRI Inc, Redlands, CA, USA). Dive and surface durations were recorded to the nearest second, and 8×50 binoculars were used to identify prey and estimate prey size classes when the sea otter surfaced. Prey were identified to the lowest taxonomic level possible and classified as greater than 5 cm or less than or equal to 5 cm by comparing prey size relative to the size of the sea otter's paw (approximately 5 cm wide; Kvitek et al., 1993; Laidre & Jameson, 2006). Unsuccessful foraging dives were also recorded. Additional environmental data collected included tidal state (rising or falling), cloud cover (sunny weather was recorded if there was less than 10% cloud cover; overcast was recorded for greater than 10% cloud cover), and Beaufort sea state (0 – no

waves; 1 – light wind, small waves; and 2 – moderate wind, white caps seen). At the end of each foraging observation, the observed animal was approached to confirm its sex and to obtain high resolution digital images of the sea otter's face and any nose scars using a Nikon D1H camera with a 400-mm image stabilized lens. We later identified individuals from the digital images of facial and nose-scar patterns (Gilkinson et al., 2007). Adult males were identified by the presence of a penile ridge, and juveniles (sex unknown) were identified by their smaller size and darker pelage.

Environmental and Behavioral Data Analyses

Corrected dive locations were obtained using GIS software by entering the boat GPS locations into *ArcView 9.2* and finding the corrected coordinates with the associated distance and direction data. Dive depths were assumed to be the same as water depth as all prey were benthic. Therefore, we overlaid the corrected dive locations on detailed bathymetry maps of Simpson Bay to estimate dive depths (Gilkinson, 2004; Noll et al., 2009). The distances traveled at the surface between dives and minimum convex polygon (MCP) areas in km² were calculated using the *Hawth's Tools* extension for *ArcGIS 9.x* (Beyer, 2004). The surface area covered during a foraging bout (period of observation from first observed foraging dive to last observed foraging dive) was quantified by creating 100-m-wide circular buffers around each dive location and calculating the sum of the buffer areas for each foraging bout. The 100-m buffer size was chosen as the maximum area a sea otter could cover during a single dive. When prey items were identified after each dive, we were able to estimate the mean energy value of prey from published values of energy content (Garshelis, 1983; Tinker et al., 2006) (Table 1). To assign an estimated energy value to unidentified prey, a relationship between the amount of prey captured and the surface duration was assumed (see Laidre & Jameson, 2006, for a description of

Table 1. Estimated energy gain from prey

Prey	Size class	Source	Mean energy value (kJ)	Units of energy gain used
Clam	< 5 cm	1	12.6	Per item
	> 5 cm	1	83.8	Per item
Crab	< 5 cm	1	41.9	Per item
	> 5 cm	1	1,709.0	Per item
Mussels	< 5 cm	1	2.5	Per 3 s
Scallop	> 5 cm	2	85.1	Per item
Sea star	> 5 cm	2	35.8	Per item
Unidentified	< 5 cm	1, 2	28.0	Per 30 s

Energy gain is a function of number of individual items seen eaten and time spent eating prey item at the surface (Source 1: Garshelis, 1983; Source 2: Tinker et al., 2006).

relationships between surface durations and prey caught). Unidentified prey items were given an energetic value (kJ) that was a function of the mean value of the most commonly seen small prey items (i.e., clams, mussels, and crabs) and proportional to the surface duration. The estimated gross energy gained from this method was not used as an accurate estimate of energy consumption but, rather, as an approximate index value indicating relative success after a dive.

The inter-dive distance traveled was associated with the behavioral and environmental conditions of the dive immediately preceding it (i.e., each dive was assigned a distance value related to the dive depth, estimated prey energy, dive duration, and prey type from the last observed dive). A foraging efficiency ratio for this study was also calculated for each individual foraging bout by dividing the estimated energy gained (E) by the sum of horizontal surface distances traveled (inter-dive distance) between dive locations (I) and dive depths (D):

$$R_i = \sum_1^n E_i / (I_i + D_i)$$

where R_i is the efficiency ratio for the i th foraging bout; n is the total number of dives in the i th foraging bout; and E_i , I_i , and D_i refer to the estimated prey energy gained, inter-dive distances traveled, and dive depths for each dive in the i th bout, respectively. Although a complete dive cycle involves traveling twice the dive depth (distance to bottom and return to surface) to obtain benthic prey, only the distance to the bottom was included when calculating travel costs due to the positive buoyancy of sea otters when surfacing. We assumed that the reduced underwater traveling costs relative to surface traveling costs would make the calculation of this ratio more reasonable (Williams, 1989; Yeates et al., 2007).

Statistical Analyses

The data were compared for dive and surface durations (inter-dive intervals), maximum dive depths, distances traveled, and the foraging efficiency ratios among four sex-age classes (adult males, adult females, females with pups, and juveniles) using a Kruskal-Wallis test for significance and pairwise Mann-Whitney U post-hoc tests using SPSS, Version 15.0 (Chicago, IL, USA). The Spearman's rank coefficient was calculated to quantify the association between observed foraging bout durations and total surface areas calculated using the 100-m buffer and MCP methods.

Travel Cost-Minimizing Model

The cost-minimizing model was tested using a Canonical Correspondence Analysis (CCA)

(CANOCO software, Version 4.5). The CCA is a direct gradient analysis that uses the weighted averages of samples and multiple linear regression to find a linear combination between the explanatory variables that maximizes the dispersion in the species data (Jongman et al., 1995). A value for inertia was calculated which describes the amount of variation in the data set comparing the different sex and age classes. Eleven foraging bouts that included dives ($N = 190$) with missing data were excluded from the analysis. Using the inter-dive distances as a cost parameter required the assignment of the distance traveled to either the preceding dive (i.e., as a post-dive distance) or the next sequential dive (i.e., as a pre-dive distance). In the analysis of post-dive distances, the distance traveled after each dive observed was associated with the prey captured in the previous dive. Therefore, after the last observed dive within the foraging bout, there was no associated distance value. The post-dive distances traveled were hypothesized to be related to the patch success from the previous dive. We chose to associate distances traveled with past success rather than anticipated success at a patch and used only post-dive distances for the analysis.

Energy-Maximizing Model

The energy-maximizing model was used to distinguish between total energy values of prey captured by individual sea otters of different sex-age classes. This model was tested with a Canonical Variates Analysis (CVA) and a CCA with stepwise addition. The CVA is similar to a discriminant functions analysis and is commonly used to determine the variables that best characterize differences (discriminate) among species groups in a community (Leps & Smilauer, 2003). The four different species groups in this model were adult males, adult females, females with pups, and juveniles. The CVA uses ordination to compare the multivariate correlations between two matrices for a set of observations; one matrix contains the value of the dependent variable (i.e., prey energy value) for each observation (a dive) identified by a species group. The second matrix contains the potential explanatory (independent) variables associated with each dive. The explanatory variables included behavioral data (e.g., scale variables: dive duration, inter-dive intervals, and dive depth), number of each prey type eaten (categorical variables: clams, crabs, scallops, mussels, and unidentified), area used (scale variables: MCP areas and total of the 100-m buffer areas around a dive point), foraging bout duration (scale variable), physical factors (e.g., categorical variables: Beaufort sea state; tidal state: rising or falling tide; and scale variable: Julian date), month (categorical variables:

May, June, July, and August), sub-bay location (categorical variables: east, northwest, and southwest bay), time of day (categorical variables: 0500 to 1100 h = dawn, 1101 to 1700 h = day, and 1701 to 2200 h = dusk), and weather (categorical variables: sunny, overcast, and rainy). Only one bout per individual per day was used for ordination. Forward selection was used to select only variables that significantly explained the variance in each model. Removing nonsignificant variables also reduced the multicollinearity (variance inflation factor [VIF] > 3) among variables. Collinear or nonsignificant variables were removed in the CCA analysis, whereas the CVA was used only to identify the relationships between variables. The total amount of energy (kJ) from prey captured after each foraging dive was estimated from the prey type, prey size, duration of the surface interval observed, and published energy values of various prey types (Garshelis, 1983; Tinker et al., 2006) (Table 1).

Overall Foraging Efficiency Model

Foraging efficiency with respect to costs, gains, and recorded environmental variables were analyzed using a CVA with stepwise addition into the final model. The final model of foraging efficiency incorporated both the cost (inter-dive surface distances and dive depths) and gain (estimated energy value of prey) parameters as variables to determine differences in foraging tactics among sex and age classes. The significance of the ordination axes for the overall foraging efficiency model was tested by Monte Carlo simulations to determine the validity of the model's relationships.

Individual Foraging Specializations

Individual foraging specializations were tested using a CCA of estimated energy gained using only foraging bouts of individuals observed at least twice on different days and at different times. The energy-maximizing model was chosen to test whether individuals in soft-sediment environments had foraging specializations similar to southern sea otters. This test determined whether there was greater within-individual variation compared to between-individual variation.

Results

A total of 4,646 min were spent observing 1,354 foraging dives in 119 bouts. An average of 12 dives (SD = 6.2) were observed in each foraging bout. Foraging bout observations lasted between 7 to 101 min, with an average bout duration of 39.8 min (SD = 20.6). The average time spent observing adult males ($n = 16$) was 56 min (SD = 22.4), adult females without pups ($n = 35$) was

45.6 min (SD = 20.4), adult females with pups ($n = 32$) was 33 min (SD = 15.4), and juveniles ($n = 13$) was 32 min (SD = 11.7). Although survey effort for the three sub-bays was similar (North Bay = 6,370 min, West Bay = 7,560 min, and East Bay = 6,010 min), most foraging observations occurred in the West Bay (64 bouts), with approximately equal numbers of observations in North Bay (28 bouts) and East Bay (27 bouts). The resighting rate of individuals was relatively low, with only six individuals positively identified more than once using nose-scar patterns. A total of 88 different individuals were identified in this study. During data collection, 24 animals were observed for whom sex was not determined because of avoidance behavior or poor picture quality; thus, these individuals were not included in the analyses.

The estimated distances between the fixed-location buoy and the location of the boat were within 30 to 80 m of the actual measured distance. Accuracy was higher when estimating distances less than 50 m; however, given the error associated with this method, any difference in distances traveled between sex and age classes that were less than 80 m were not assumed to be significantly different.

The estimates of total area used during a foraging bout differed between the MCP and the 100-m buffer methods. The foraging area estimated with the 100-m buffer method ranged between 0.044 and 0.43 km² (mean = 0.135 km², SD = 0.074), whereas the MCP method yielded slightly smaller areas ranging between 0.0005 and 0.32 km² (mean = 0.05 km², SD = 0.06). However, both estimates of total surface area used during a foraging bout were positively correlated with the total duration of the foraging bout observed ($p < 0.001$), with a slightly higher correlation using the buffer method (Spearman's coefficient = 0.7) than the MCP method (Spearman's coefficient = 0.6).

Dive Variable Comparisons

The surface distances traveled between dives among adult males, adult females, and juveniles were not significantly different (DF = 2, $X^2 = 0.82$, $p = 0.665$); however, females with pups ($n = 324$) traveled significantly shorter distances than adult males ($n_{\text{males}} = 209$, $n_{\text{femalepup}} = 324$, Mann-Whitney U = 26,611, $p < 0.001$), adult females ($n_{\text{males}} = 361$, Mann-Whitney U = 46,138, $p < 0.001$), and juveniles ($n_{\text{juveniles}} = 136$, Mann-Whitney U = 18,388, $p < 0.005$) (Table 2). Adult females and adult males displayed the most similar dive behavior, with no significant differences between estimated dive depths ($n_{\text{males}} = 223$, $n_{\text{females}} = 394$, Mann-Whitney U = 43,475, $p = 0.83$), gross energy gained ($n_{\text{males}} = 200$, $n_{\text{females}} = 355$, Mann-Whitney

Table 2. Mean dive variables and SD of different sex and age classes

Sex	Inter-dive distance (m)	Dive duration (min)	Estimated dive depth (m)	Surface duration (min)	Estimated energy gain (kJ dive ⁻¹)	Foraging efficiency ratio*
Male	107.8 ± 102.8 ^a	2.3 ± 0.79 ^b	35.6 ± 21.2 ^a	1.32 ± 0.75 ^a	85.9 ± 39.9 ^a	0.9 ± 0.83 ^a
Female	97.4 ± 83.0 ^a	2.2 ± 0.63 ^c	31.8 ± 17.7 ^a	1.39 ± 0.75 ^a	110.3 ± 144.9 ^a	1.4 ± 1.45 ^a
Female & pup	73.7 ± 69.1 ^b	1.6 ± 0.81 ^a	21.9 ± 19.9 ^b	1.10 ± 0.83 ^b	75.4 ± 101.3 ^b	0.9 ± 0.81 ^a
Juvenile	91.7 ± 75.4 ^a	1.5 ± 0.54 ^a	13.5 ± 14.4 ^c	0.82 ± 0.70 ^c	53.5 ± 29.8 ^c	0.53 ± 0.34

Mean values with the same exponents (e.g., a, b, c) within a category (column) are not significantly different from each other. (*See “Materials and Methods” section for details on how this was calculated.)

U = 32,462, $p = 0.087$), and surface durations ($n_{\text{males}} = 201$, $n_{\text{females}} = 368$, Mann-Whitney U = 35,580, $p = 0.45$). There was a significant difference in dive duration between adult males and females ($n_{\text{males}} = 216$, $n_{\text{females}} = 384$, Mann-Whitney U = 37,088, $p = 0.031$), with males diving approximately 6 s longer than females. No significant difference was found in dive durations between females with pups and juveniles ($n_{\text{femalepup}} = 344$, $n_{\text{juveniles}} = 141$, Mann-Whitney U = 23,714, $p = 0.701$), but significantly longer surface durations ($n_{\text{femalepup}} = 329$, $n_{\text{juveniles}} = 137$, Mann-Whitney U = 16,641, $p < 0.001$), deeper dive depths ($n_{\text{femalepup}} = 355$, $n_{\text{juveniles}} = 148$, Mann-Whitney U = 19,699, $p < 0.001$), and higher estimated prey energy values ($n_{\text{femalepup}} = 311$, $n_{\text{juveniles}} = 133$, Mann-Whitney U = 15,993, $p < 0.001$) occurred in females with pups compared with juveniles. There was no significant difference among the foraging efficiency ratios of adult males (0.9), adult females (1.4), and females with pups (0.9) (DF = 2, $X^2 = 1.55$, $p = 0.462$), but juveniles ($n = 13$) had a significantly lower foraging efficiency ratio (0.53) than all adult sea otters ($n = 81$) (Mann-Whitney U = 333, $p = 0.038$).

Travel Cost-Minimizing Model

The CCA of distances traveled consisted of 70 foraging bouts with 736 total dives. There was no clear differentiation among sex and age classes, with 31.1% of the total variation explained by the canonical axes and a total inertia of 69.0. When the model was modified to remove nonsignificant and collinear variables, separating the sex and age classes as supplemental variables, it explained less (17.0%) of the total variation. The sex and age classes fell mostly in a gradient along the first axis, with females with pups and single adult females behaving most similarly (Figure 2). The shortest distances were traveled by females with pups and were indicated in the CCA plot by their location near the origin (where axes 1 and 2 meet). The other sex and age class variables occurred farther from the origin, indicating longer inter-dive distances traveled. The only significant correlation in

axis 1 of the modified CCA model was between adult males and increasing Beaufort sea state, with males traveling longer distances when wave height increased. Axes 3 and 4 showed significant correlations between distances traveled by males and increasing dive durations ($p = 0.002$), distances traveled by females and increasing MCP areas ($p = 0.002$), distances traveled by juveniles and the North Bay ($p = 0.002$), and distances

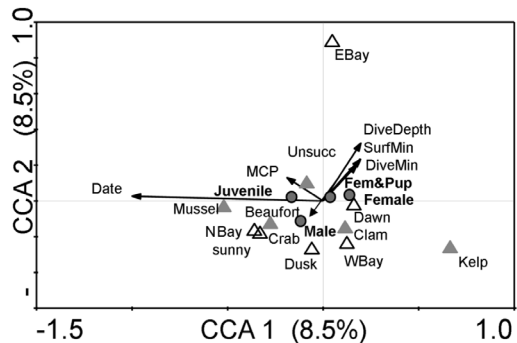


Figure 2. Canonical Correspondence Analysis (CCA) of inter-dive distances traveled by individual sea otters excluding nonsignificant, collinear variables; percent variance explained by each axis is indicated in the parentheses. Filled grey circles refer to the supplemental “species” classes (Male, Female, Fem&Pup = female with pup, and Juvenile). Categorical variables are displayed as open triangles for environmental variables (WBay = West Bay, NBay = North Bay, EBay = East Bay, sunny, dawn, and dusk) and filled triangles for different prey types (crab, clam, kelp, mussel, and unsucc = unsuccessful dive). Short distances between a categorical variable and a species variable show a greater correlation between the two. Arrows indicate the direction of increasing response of a scale variable. The magnitude of the response is indicated by the length of the arrow (DiveMin = dive minutes, SurfMin = surface minutes, MCP = minimum convex polygon area, Date, and DiveDepth). Greater correlation to a particular canonical occurs when there is an acute angle between the arrow and the axis.

traveled by females with pups and foraging on mussels ($p = 0.044$).

Energy-Maximizing Model

The CVA of estimated energy gained during foraging bouts showed the greatest similarity in foraging behavior between adult males and adult females without pups. Increased energy intake was mostly correlated with foraging on clams; increased bout duration; and, to a lesser extent, increased dive duration and the MCP area (Figure 3). Females with pups showed the majority of their energy gains were from foraging on crabs and kelp, probably covered with epiphytes (which have a very low energy content). Females with pups also showed increases in energy gained with date (i.e., more energy gained later in summer). Foraging behavior in juveniles was most associated with unsuccessful dives, sunny weather, and foraging in North Bay. The total inertia was 4.0, and 30.6% of the variation was explained from the initial stepwise CVA. High variance inflation factor (VIF) values were observed between bout number (VIF = 455) and date (VIF = 595), buffer area (VIF = 14) and MCP area (VIF = 12.7), and rising (VIF = 2,123) and falling tidal states (VIF = 2,119). After excluding collinear, nonsignificant variables, the total amount of variation explained decreased to 13.0% with a total inertia of 107.

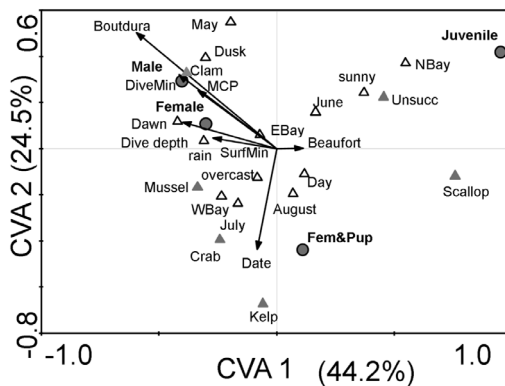


Figure 3. Canonical Variates Analysis (CVA) of energy obtained from prey after each dive by sex and age class; percent variance explained by each axis is indicated in brackets. Filled grey circles refer to the “species” classes (Male, Female, Fem&Pup = female with pup, and Juvenile). Filled grey triangles are prey types, and open triangles are categorical environmental variables (NBay = North Bay, WBay = West Bay, and EBay = East Bay). Arrows indicate the direction of increasing response of scale variables. The magnitude of the response is indicated by the length of the arrow (DiveMin = dive duration, SurfMin = surface duration, MCP = minimum convex polygon area, Date, Dive depth, and Boutdura = foraging bout duration).

The CCA also decreased the amount of separation between sex and age classes and changed the significance of the variables associated with the different sex and age classes. Juveniles were still significantly associated with foraging in North Bay and sunny conditions, but prey energy gained by adult females and males were only significantly related to increases in foraging bout duration. There were no significant correlations between increased prey energy gained by solitary adult males and females and the variables of prey type, dive depth, dive durations, and surface durations.

Foraging Efficiency Model

The final model incorporating both prey energy gained and distances travelled was selected after omitting nonsignificant and collinear variables. Excluding adults of unknown sex ($n = 24$) from the analysis increased the degree of separation between the sex and age classes. The total inertia of the CVA was 3.0, and the percent variation explained was 36%. The first canonical axis was significant ($p = 0.002$), and the test for all canonical axes was also significant ($p = 0.002$). The model showed the greatest similarity between solitary adult males and females when only significant variables were included (Figure 4). Juvenile foraging behavior occurred mostly in North Bay and was correlated with a higher proportion of unsuccessful dives. There was also a trend relating juvenile foraging success to sunny weather conditions, although this relationship did not contribute significantly toward explaining the group variation (Table 3).

Adult males and females without pups were significantly correlated with increases in dive depths, foraging bout durations, total 100-m buffer areas, surface durations, dive durations, and energy gained (Figure 4). The differences between adult males and females without pups occurred in canonical axes 2 and 3, which showed that adult females had higher prey energy gains, dive durations, and surface durations than males (Figure 5). The foraging behavior of females with pups was most correlated to foraging on kelp and mussels later in the summer, particularly in the month of July.

Individual Prey Specializations

Six individuals were identified at least twice, including two males, three females, and one adult of unknown sex. Because of the small sample size for observing individuals repeatedly, it was not possible to reliably characterize individual foraging specializations or preferences. However, the CCA analysis of estimated energy gain in three adult females, each observed twice, indicated that prey type explained less than 4% of the variation among individuals.

Table 3. Regression coefficients of variables included in the final model CVA; variables that significantly contributed to the variance have *t*-values $\geq |2.1|$.

Variable	Axis 1	Axis 2	Axis 3
Dive order	-1.2099	-3.8111*	-1.1757
Begin	-0.8561	-0.9796	-0.0325
End	-0.5113	1.8035	1.0543
West Bay	-4.4972*	-2.7133	0.8558
North Bay	11.425*	5.5492	2.9038
East Bay	0.0	0.0	0.0
Dawn	2.9586	-5.0756*	4.1266
Day	12.5535*	-4.1287	-2.6866
Dusk	0.0	0.0	0.0
May	4.5717	11.0979*	-1.6917
June	10.3256*	7.4575	4.1856
July	9.9773*	4.8774	2.7018
August	0.0	0.0	0.0
Rising tide	4.5418*	4.5358	-2.3618
Falling tide	0.0	0.0	0.0
Rain	-6.886	-7.4973*	3.686
Overcast	-6.6829*	-5.602	0.426
Sunny	0.0	0.0	0.0
Beaufort	-2.3038*	-1.1607	-0.0211
Buffer area	6.2548*	-4.7968	1.1413
Dive minutes	-1.5284	4.3306*	2.6441
Surface minutes	0.3984	-2.9882*	1.3695
Dive depth	-8.1014*	0.8198	-1.6465
Energy	0.7185	-1.3486	2.8051*
Clam	-0.4237	-0.4394	-1.6697
Crab	-0.9245	-0.5218	-0.1447
Unidentified prey	-0.9125	0.5822	-0.7229
Kelp	-2.1922*	-0.2909	-1.1241
Mussel	-5.4301*	-0.2925	3.2087
Scallop	2.204*	0.517	-0.2332
Other prey	-0.2095	-1.3452	2.1801
Unsuccessful dive	2.2397*	0.4258	-0.4584
Bout duration	-12.622*	11.0072	-2.6531
Distance traveled	0.2098	1.3571	-0.3537

* Indicates the most significant axis for each variable

Discussion

Several foraging strategies were observed among the different sex and age groups with adult males and females without pups behaving the most similarly. Adult females were able to maintain high foraging efficiency ratios despite changing foraging strategies while raising a pup. Only juveniles had significantly lower foraging efficiency ratios. The dive parameter analysis predicted some resource partitioning among the sex and age groups but only for dive depths. The most significant foraging strategies are discussed for the dive parameter analysis and the three foraging models tested.

Adult males and females without pups had the most similar dive parameters with no significant

differences in inter-dive distances traveled, dive depths, surface durations, and estimated prey energy gained. There was no resource partitioning between adult males and females without pups by water depth, although previous studies have found that males generally dive in deeper water than females (Bodkin et al., 2004; Tinker et al., 2006). However, there was a significant difference in the dive depths of females with pups and juveniles that preferred water that was approximately 10 and 19 m shallower, respectively, than the average estimated dive depths for adult males and females without pups. The differences in estimated dive depths could reduce competition among solitary adult males and females, females with pups, and juveniles through resource partitioning by water depth.

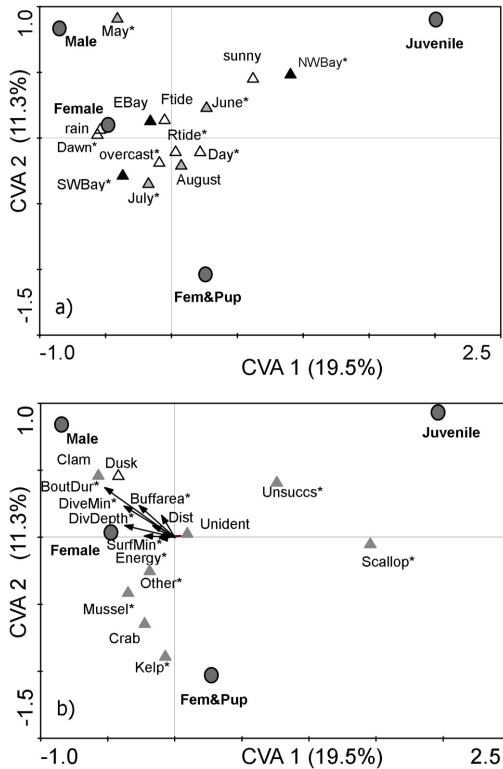


Figure 4. CVA results on axes 1 and 2 for individuals in each sex-age group; percent variance explained by independent variables on each axis is in parentheses. Filled grey circles refer to the “species” classes (Male, Female, Fem&Pup = female with pup, and Juvenile). An asterisk indicates variables that significantly contribute to the variance on the plotted axes. (a) Filled grey triangles are months, black triangles are sub-bay areas, and open triangles are environmental conditions (Ftide = falling tide, Rtide = rising tide, Dawn, Day, and Dusk). (b) Filled grey triangles are prey types (Unident = unidentified prey and Unsuccs = unsuccessful dive), and open triangles are time of day (Dusk). Arrows indicate the direction of increasing response of scale variables (DiveMin = dive duration, SurfMin = surface duration, Date, Divdepth = dive depth, BoutDur = foraging bout duration, BufArea = buffer area, and Dist = distance traveled between dives).

Females with pups and juveniles had more similar dive behavior compared to adult males and females without pups; however, juveniles had longer inter-dive distances traveled, shallower dive depths, shorter surface durations, lower estimated prey energy gained, and lower foraging efficiency ratios. The dive durations were not significantly different between juveniles and females with pups, even though juveniles typically foraged in shallower water. The shorter dive durations in juveniles showed shorter giving-up times (premature

ending of a foraging dive caused by the inability to find or capture prey) resulting in more unsuccessful foraging dives. This might be the result of immature hunting skills (Baker, 2007) or a shorter aerobic dive limit (Kooyman et al., 1980).

The similar foraging efficiency ratios of adult males and females without pups did not support the hypothesis of higher foraging efficiencies in adult males that are generally larger than females. The territorial behavior of males in Simpson Bay, however, may have affected their foraging efficiencies. Territorial males are known to occur in our study area during May through August (Pearson & Davis, 2005; Finerty et al., 2009), and our study probably included both territorial and nonterritorial males. Adult males were often observed terminating their feeding to pursue females, and males in Simpson Bay spend almost as much time interacting with females and patrolling as they do feeding (Pearson & Davis, 2005). These observations suggest that males in Simpson Bay are equally motivated toward mating behavior and foraging, which may not be the case in predominantly male areas.

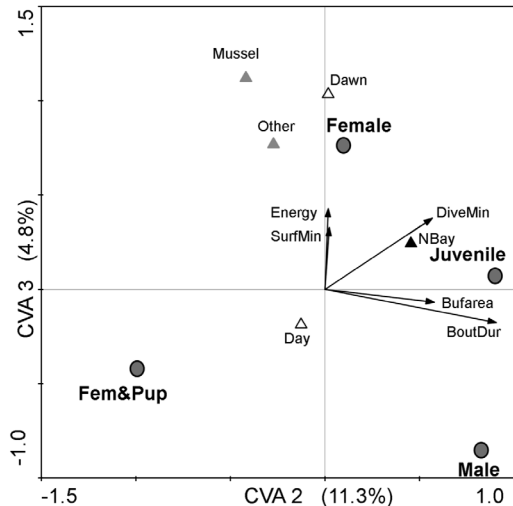


Figure 5. CVA of overall foraging tactics for sex and age classes in axes 2 and 3; percent variance explained by each axis is indicated in brackets. Filled grey circles refer to the “species” classes (Male, Female, Fem&Pup = female with pup, and Juvenile). Filled grey triangles are prey types (Unident = unidentified prey and Unsuccs = unsuccessful dive), black triangles are sub-bay areas (NBay = North Bay), and open triangles are time of day (Dawn, Dusk, and Day). Arrows indicate the direction of increasing response of scale variables (DiveMin = dive duration, SurfMin = surface duration, Date, Divdepth = dive depth, BoutDur = foraging bout duration, BufArea = buffer area, and Dist = distance traveled between dives).

Females with pups had foraging efficiency ratios that were slightly lower than females without pups. However, because net energy gain was not calculated, we were unable to determine whether the demands of feeding a pup actually reduced foraging efficiency. Changes in female foraging behavior included changing preferred dive depths to shallower water and decreasing dive durations when a pup was present. The shorter dive durations by females with pups could be caused by the shallower dive depths or the reluctance to leave pups unattended at the water surface. Predation events on sea otter pups are rare, but females still tend to be very protective of pups (Kenyon, 1969). The need to change foraging behavior while pups learn to forage or to potentially protect small pups from predation may play a large role in the foraging tactics of females with pups.

The cost-minimizing model found a strategy that reduced travel costs for females with pups and predicted a relationship between environmental factors and the foraging behavior of adult males. No obvious foraging strategies were identified for juveniles and females without pups using this model. The cost-minimizing strategy of females with pups predicted that shorter travel distances were associated with foraging on low energy prey items such as mussels and small epibenthic prey found on kelp. Foraging on easy to capture epibenthic prey may be especially important for females that have pups learning to forage. An earlier study by VanBlaricom (1988) showed that large mussel patches were less common in established areas compared to newly occupied areas. In VanBlaricom's maternal-care hypothesis, females with pups were hypothesized to be more likely to feed near mussel patches to allow pups to learn to forage on easily captured prey, but this tactic also minimized travel costs. Females without pups are not likely to maintain this cost-minimizing strategy as indicated by their higher foraging efficiency ratios, and adult females may switch foraging tactics at different stages of their reproductive cycle and with pup age (Reidman & Estes, 1990). The cost-minimizing model also predicted that adult males traveled longer distances with increasing wave height, suggesting that changes in sea conditions (e.g., rate of drift, orientation at the surface relative to shoreline features) influenced a male's foraging decisions.

The energy-maximizing model showed similar foraging strategies between adult males and females without pups. Females with pups and juveniles did not appear to maximize prey energy gained, but females with pups did increase prey energy gained from May to August. It is likely that changes in foraging tactics occur over time, but

our results were only from the summer foraging tactics of sea otters.

The energy-maximizing model found some resource partitioning among adult males and females without pups on a temporal scale. Higher prey energy was obtained at dawn for females and at dusk for males. Diel peaks in crepuscular foraging behavior have been described in Simpson Bay before (Garshelis, 1983) but were not attributed to differences in male and female foraging behavior. Such crepuscular peaks have only been observed for sea otters foraging on fish in Amchitka (Estes et al., 1982), but there have been no studies suggesting that certain prey can be more easily captured at different times of day in soft-sediment environments.

The energy-maximizing model also predicted that increases in prey energy captured by females with pups occurred as summer progressed. This is also consistent with the maternal-care hypothesis (VanBlaricom, 1988). Earlier in the summer, most pups are relatively small, and females often did not have to give up a portion of their prey or spend as much time feeding smaller pups (Osterrieder & Davis, 2010). As summer progressed, the number of large pups learning to dive increased, and females were often observed giving up a portion of their food to their pups. This may have forced females with pups to obtain higher energy prey as summer progressed and more food sharing occurred.

The efficiency-maximizing model best summarized the foraging behavior for all sex and age groups and predicted similar foraging strategies that the cost-minimizing and energy-maximizing models identified. The foraging strategies identified in this model included behavior predicted by the marginal value theorem (Stephens & Krebs, 1986), foraging behavior expected in large stable populations (Van Valen, 1965), and foraging behavior consistent with the maternal-care hypothesis (VanBlaricom, 1988). The efficiency-maximizing model predicted that adult males and females without pups traveled longer distances between dives as dive duration increased, suggesting that as search effort increased, individuals were more likely to move to a different location. This is consistent with the behavior predicted by the marginal value theorem (Stephens & Krebs, 1986) and suggests some knowledge of prey availability in the area. Kruuk et al. (1990) found that river otters (*Lutra lutra*) often dive in areas in a nonrandom pattern that may be related to previous hunting success in the area. Kvitek et al. (1993) also determined that the high success rates of sea otters were related to enlarging existing sea otter-dug pits in previously chosen dive sites, which may indicate that sea otters do not travel long distances between dives until a patch has been depleted.

The efficiency-maximizing model also determined that both males and females without pups increased their per-dive energy intake by increasing foraging bout durations. The increase in foraging bout durations is similar to observations of other established populations where individuals foraged for longer periods of time to obtain equivalent prey mass compared to sea otters in more recently occupied areas (Estes et al., 1982; Garshelis, 1983; Doroff & Degange, 1994; Bentall, 2005).

The efficiency-maximizing strategy for females with pups included foraging in shallower water with significantly shorter dive durations than solitary females. This strategy was also observed in the dive parameter analysis and the energy-maximizing model that indicated these behaviors were related to decreases in prey energy gained. Foraging on epibenthic prey found on kelp and mussels was also related to decreased prey energy gained. However, this was a foraging strategy also observed in other soft-sediment environments (Kvitek et al., 1993). A trade-off for foraging on energy-poor prey (e.g., kelp and mussels) is that they are also easier to capture, thereby reducing handling time. This may subsequently affect net energy gains and play a role in determining whether a cost-minimizing, energy-maximizing, or efficiency-maximizing foraging strategy would be optimal. We observed a higher proportion of females with large pups feeding on energy-poor prey, which is consistent with the maternal-care hypothesis that it is easier to teach pups to forage on easy to capture prey (VanBlaricom, 1988).

The foraging behavior of juveniles did not indicate a cost-minimizing strategy or an energy-maximizing strategy, and their foraging efficiency ratios were lower than those of adult sea otters. The efficiency-maximizing model showed that juvenile foraging behavior was most related to foraging in the sheltered North Bay during sunny weather conditions, with a higher overall incidence of unsuccessful dives. Juveniles learning to forage independently appear to prefer optimal foraging conditions in sheltered areas (less turbidity), with maximum light penetration in the water column (Davies-Colley & Smith, 2001). The reduced foraging efficiency of juveniles is probably only a temporary condition (unless foraging inefficiencies cause mortalities), while they learn to specialize on more profitable prey (e.g., clams) that are harder to capture than smaller, more abundant prey (Tinker et al., 2006). The high occurrence of small, unidentified prey in juvenile sea otter diets also supports this hypothesis.

Individual foraging specializations were difficult to determine due to low resighting rates of individuals. Although dietary specializations may

occur among individuals in soft-sediment environments (e.g., at the species level for clams), our methods were unable to distinguish prey specializations. Based on our methods and the low sample size, the occurrence of individual prey specializations in soft-sediment environments is inconclusive.

Different foraging strategies at the sex and age group levels were detected in our study even though individual prey specializations were not observed. Adult sea otters displayed more similar foraging strategies than juveniles. The foraging efficiency ratios for adults were also significantly higher than for juveniles. The low foraging efficiencies of juveniles were probably a result of immature hunting skills that prevented them from having high success rates for capturing energy-rich prey. Adult males and females without pups had the most similar foraging strategies that included the deepest dive depths, largest travel costs, and high prey energy intake which was consistent with an energy-maximizing strategy. When pups were born, females changed strategies to minimize travel costs, forage at intermediate depths, and decrease prey energy intake. Females with pups may change their foraging strategies to minimize the time spent away from pups or to allow pups to learn to forage in shallower water. Nevertheless, despite having flexible foraging strategies, adult sea otters were able to maintain high foraging efficiencies.

Acknowledgments

We would like to thank P. Olivier, R. Wolt, and Texas A&M University students for fieldwork assistance; F. Weltz, G. Davis, I. Davis, S. Arms, D. Wentling, T. Wright, S. Finerty, and P. Canton for logistical and administrative assistance; and E. Mooney and L. Mooney for partially funding this study. This research was conducted under a Letter of Confirmation No. MA078744-2 from the U.S. Fish and Wildlife Service.

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