Interannual assessment of territory quality for male sea otters (*Enhydra lutris*) in Simpson Bay, Prince William Sound, Alaska

Shannon E. Finerty, Heidi C. Pearson, and Randall W. Davis

Abstract: Territory quality and site fidelity were assessed for male sea otters (*Enhydra lutris* (L., 1758)) in Simpson Bay, Prince William Sound, Alaska, during the summer months (May–August) from 2003 to 2006. Territory quality was coded with a score of 0–2 for four attributes: territory size, shoreline enclosure, territory accessibility, and number of females observed feeding in each territory. Total quality scores ranged from 0.14 to 1.96 (0.9 ± 0.61, mean ± SD), with the highest quality territories having large areas, moderate to little shoreline enclosure, high accessibility, and many foraging females. A total of 13.1 km^2 (62.5%) of Simpson Bay was occupied at least once by a territorial male during the 4-year study, and 7.9 km^2 (37.5%) was never occupied by a territorial male. There were 7 ± 2.4 (mean ± SD) territorial males in Simpson Bay each year. Five males maintained territories for two consecutive years, with their respective territories having a 16%–34% overlap between years, indicating that repeat territory holders returned to the same area. The number of territorial sea otters, the size of territories, and whether or not a sea otter was a repeat territory holder did not significantly influence the size or quality of male territories.

Résumé : Nous avons évalué la qualité des territoires et la fidélité aux sites chez les loutres de mer (*Enhydra lutris* (L., 1758)) mâles dans la baie de Simpson, détroit du Prince-William, Alaska, durant les mois d'été (mai–août) de 2003 à 2006. Les territoires ont été dotés d'une cote de 0–2 d'après quatre critères, la taille du territoire, le repliement de la ligne de rivage, l'accessibilité du territoire et le nombre de femelles observées à s'alimenter dans chaque territoire. L'ensemble des cotes de qualité varient de 0,14 à 1,96 (0.9 ± 0,61, moyenne ± ET); les territoires de qualité supérieure ont une surface importante, un repliement moyen à faible de la ligne de rivage, une grande accessibilité et une forte présence de femelles qui s'y alimentent. En tout, 13,1 km^2 (62,5 %) de la baie de Simpson ont été occupés à au moins une occasion par un mâle territorial pendant les 4 années de l'étude et 7,9 km^2 n'ont jamais été occupés par un mâle territorial. Il y a 7 ± 2,4 (moyenne ± ET) mâles territoriaux dans la baie de Simpson chaque année. Cinq mâles ont maintenu des territoires deux années de suite et le recoupement de ces territoires respectifs était de 16 % – 34 % entre les années, ce qui indique que les propriétaires qui ont repris les territoires étaient retournés dans la même région. Le nombre de loutres de mer territoriales, la taille des territoires et le fait qu'une loutre utilise le même territoire à plusieurs reprises n'affectent pas significativement la taille ni la qualité des territoires des mâles.

[Traduit par la Rédaction]

Introduction

One of the earliest descriptions of male sea otter (*Enhydra lutris* (L., 1758)) behavior in Alaska was by Kenyon (1969). He described territoriality as being weakly expressed in sea otters, but later studies showed male territoriality to be a prominent behavior. Studies of territorial male sea otter behavior have since been conducted in California (Vandevere 1970; Loughlin 1980; Jameson 1989; Ralls and Siniff 1990) and Alaska (Calkins and Lent 1975; Garshelis et al. 1986; Gelatt et al. 2002; Pearson and Davis 2005; Bodkin et al. 2007). Prior to their protection under the International Fur Seal Treaty in 1911, the population of sea otters in Prince William Sound, Alaska, had been greatly reduced by commercial hunting. Currently, the population of sea otters in Prince William Sound is listed as stable or increasing under the Endangered Species Act (U.S. Fish and Wildlife Service 2005). In expanding populations, male sea otters are the first to explore new, prey-rich areas (Garshelis et al. 1984). Male sea otters began to re-inhabit eastern Prince William Sound in the late 1970s (Garshelis 1983; Rotterman and Simon-Jackson 1988). Simpson Bay remained exclusively a male area until the 1980s (Garshelis et al. 1984, 1986), but is now used by females and pups (Gilkenson 2004; Pearson et al. 2006) and territorial males.

Sea otters exhibit a form of territoriality, called resource defense polygyny, which is reported for most members of the family Mustelidae (Calkins and Lent 1975; Loughlin 1980; Garshelis et al. 1984; Jameson 1989; Pearson et al. 2006). Sea otters are sexually segregated when not breeding (Garshelis et al. 1984; Riedman and Estes 1990). In Alaska, adult males establish territories during the summer and autumn (Garshelis et al. 1984; Jameson 1989; Pearson et al. 2006). Female sea otters may be attracted to an area based on a number of factors, including prey availability, protection from waves or wind, accessibility, resting areas, and to-

Received 22 October 2009. Accepted 29 January 2010. Published on the NRC Research Press Web site at cjz.nrc.ca on 19 February 2010.

S.E. Finerty,[1] H.C. Pearson, and R.W. Davis. Department of Wildlife and Fisheries Sciences, Texas A&M University, 5007 Avenue U, Galveston, TX 77551, USA.

[1]Corresponding author (e-mail: shannonfinerty@yahoo.com).

tal area defended from harassment by other males (Garshelis et al. 1984; Pearson et al. 2006). Males will attempt to mate with females that rest or feed in their territories (Loughlin 1980; Riedman and Estes 1990). The peak of breeding occurs during the autumn in Prince William Sound, although evidence of copulations has been reported for all seasons (Garshelis et al. 1984).

Maintaining a territory can be energetically expensive for males (Kodric-Brown and Brown 1978; Pearson et al. 2006). Negative consequences of maintaining a territory may include (*i*) decreased time available for foraging and resting; (*ii*) increased energy expenditure owing to courtship, mating, and defense activities (e.g., patrolling boundaries); and (*iii*) risk of injury or death owing to agonistic encounters with conspecifics and predation (Clutton-Brock et al. 1988; Apollonio et al. 1989; Vehrencamp et al. 1989; Gosling and Petrie 1990; Isvaran and Jhala 2000; Pearson et al. 2006). However, territoriality increases access to females and therefore enhances reproductive success (Vehrencamp et al. 1989; Rosser 1992; Isvaran and Jhala 2000; Bro-Jørgensen and Durant 2003; Pearson et al. 2006). Males interact with both single females and females with pups (Pearson and Davis 2005). Males may copulate while guarding females during brief, opportunistic encounters, or during a consortship (Riedman and Estes 1990). Some mature males maintain year-round territories in female areas (Loughlin 1980; Garshelis et al. 1984), but most apparently switch between territorial and nonterritorial behavior during the year (Garshelis et al. 1984). It is still undetermined what factors influence a male sea otter's decision to switch between territorial and nonterritorial behavior, or what factors maximize the successful impregnation of females.

The Pearson et al. (2006) study of territory costs and benefits determined the territory quality of 10 adult male sea otters in a single season (2003). In this study, we used the territory assessment criteria originally developed by Garshelis et al. (1984), and modified by Pearson et al. (2006), to examine the total territory quality of Simpson Bay, Alaska, over a 4 season period (2003–2006). We predicted that the quality of male territories would change from year to year, depending on the number of males holding territories, the size of territories, and whether the male had previously held a territory in the area.

Materials and methods

Study area

Simpson Bay (ca. 60.6°N, 145.9°W; Fig. 1), located in northeastern Prince William Sound, Alaska, was selected as the study site because of its reasonable size, protection from rough seas, and reliable presence of sea otters. Simpson Bay is composed of two arms and has a surface area of ~21 km^2. The North and West bays together are 7.5 km long, the East Bay is 5 km long, and the entrance is 2.5 km wide. The mean depth of the bay is ~30 m and the maximum depth is 125 m. The benthos is mostly glacial clay, silt, and gravel with some rocky hard reefs (Gilkenson 2004). There are no large-bodied kelps (e.g., genus *Nereocystis* Postels & Ruprecht) that form canopies, but large fronds of sugar kelp (*Laminaria saccharina* (L.) Lamouroux) cover the benthos in many areas of the bay from the subtidal to a depth of ~10 m (R. Davis, unpublished observations).

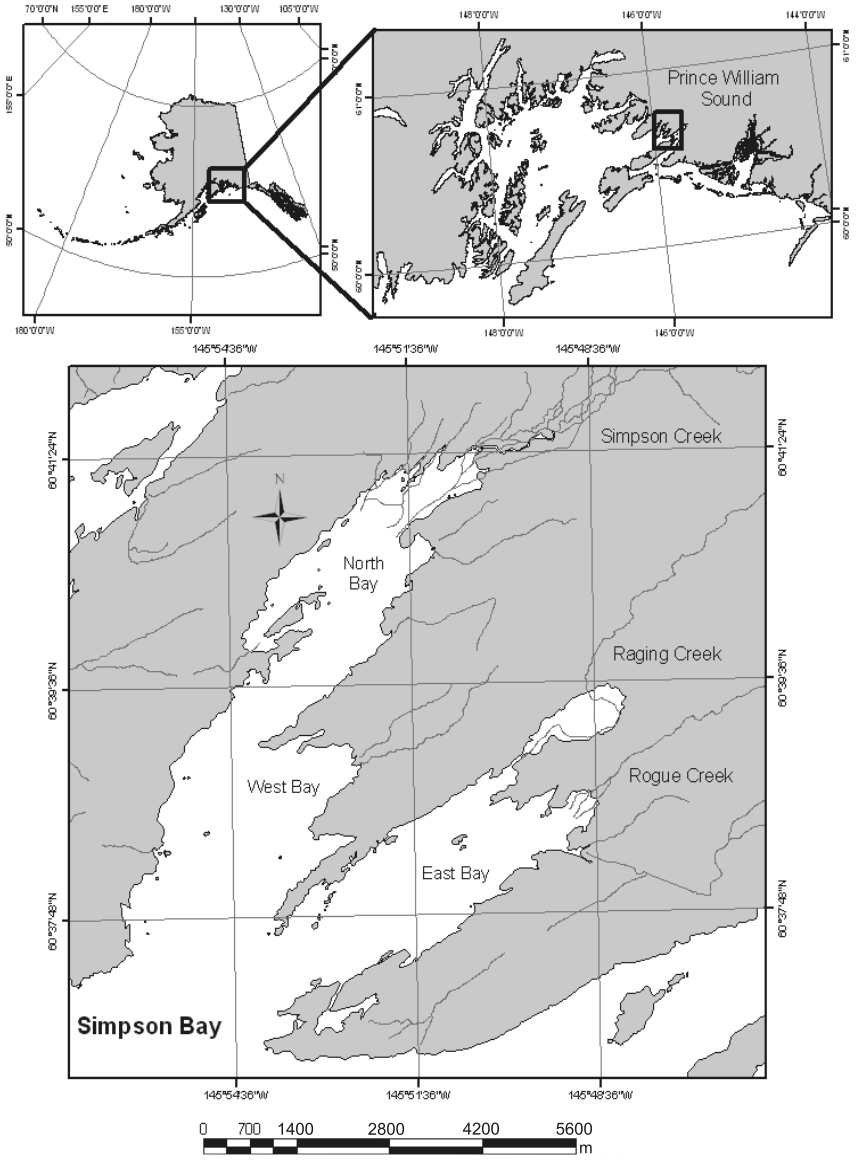
For the past 8 years, Simpson Bay has been occupied during the summer by 119 ± 9.3 (mean ± SD) sea otters, including adults and subadults (91 ± 6.8) and pups (28 ± 3.8) (R. Davis, unpublished observations). Gilkenson (2004) found significant correlations between the distribution of sea otters in Simpson Bay and bathymetry, sediment type, and location within the bay (peripheral vs. central). Significantly more sea otters were observed feeding over mud and mud mixed with gravel and sand in shallower areas (<30 m) along the shore, and significantly more otters were observed resting towards the center of the bay over deeper (approximately 30–60 m) water. During the winter, the number of otters in the bay decreases to ~50 individuals, although where they disseminate is poorly understood.

Focal observations

Field observations of sea otter behavior were conducted during the summers (early May through late August) of 2004–2006, and combined with Pearson et al. (2006) data from 2003, using individual follows (Mann 1999) and instantaneous sampling (Altmann 1974; Lehner 1996; Mann 1999; Pearson and Davis 2005). The research team, composed of a driver, recorder, and observer, conducted surveys from a 6 m skiff. A regular schedule was followed by dividing Simpson Bay into three sections: North Bay, West Bay, and East Bay (Fig. 1). Each day, one of these areas was selected for conducting observations, and another area was selected as an alternate should logistical problems occur. Boat-based observers determined if an otter was male by the presence of a penile ridge or testicular bulge (visible through binoculars), or by observing copulatory or patrolling behavior. Patrolling is a form of locomotion whereby a male swims belly-down with its head out of the water while scanning the surface, presumably for receptive females or other territorial males. Female sea otters primarily float on their backs or swim submerged, making patrolling a conspicuous male behavior (Pearson et al. 2006).

Individual follows occurred approximately twice a day, during one of four 6 h time periods corresponding with astronomical dawn (0500–1100), day (1100–1700), dusk (1700–2300), and night (2300–0500). Each individual follow took place at a distance of not less than 30 m from the target animal to minimize the risk of altering the animal's behavior or influence the animal's movement. Observation of an individual lasted 31 min (minute 0 to minute 30), and instantaneous samples (Altmann 1974; Lehner 1996) were taken every 1 min during which the latitude and longitude were recorded using a global positioning system (GPS; Garmin, Olathe, Kansas, USA). Photo-identification was used to identify individual sea otters according to distinctive patterns on the nose or other facial regions (Finerty et al. 2007). At the conclusion of the observation period, a high-resolution digital image was taken of the head. Images were taken with a Nikon D1H digital camera with an 80–400 mm image-stabilized telephoto lens. Data from individuals that could not be reliably identified or were not sampled ≥3 times were dropped from further analysis in this study.

Fig. 1. Simpson Bay, Prince William Sound, Alaska (modified from Noll et al. 2009, p. 2, and reproduced with permission of Geo-Mar. Lett., vol. 29, issue 1, © 2009 Springer Science and Business Media).



Assessment of territory quality

We used the same four attributes of territory quality used by Pearson et al. (2006) as adapted from Garshelis et al. (1984): size, shoreline enclosure, accessibility, and prey availability. Ranks of each attribute were coded within a range of 0–2, with higher ranks coding for higher quality (Table 1). Territory size was calculated from minimum convex polygons (Odum and Kuenzler 1955) in ArcMap version 9.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) using locations obtained during focal observations of territorial males. Pearson et al. (2006) modified the shoreline enclosure attribute criteria from that used by Garshelis et al. (1984) because our study site was a bay on the mainland rather than coves on an island (Table 1). Shoreline enclosure on two sides was scored as high quality, as opposed to the "three side" criteria defined by Garshelis et al. (1984). Accessibility was ranked based on the number of entrances blocked by the territories of other males (Table 1). A territory located at the "dead end" of the arm of a bay had a lower accessibility rank than one located at the "mouth of the arm". Males tended to intercept females entering at the mouth of the arm.

Because the distribution and abundance of benthic macroinvertebrates has not been determined for Simpson Bay (Gilkenson 2004), prey availability was estimated using an approach similar to that of Garshelis et al. (1984) and Pearson et al. (2006). Pearson et al. (2006) assigned a score for "food availability" (Table 1) based on the number of females observed feeding within each territory. In this study, we used female observations that were gathered by a concurrent study (R.C. Wolt, F. Weltz, F.P. Gelwick, and R.W. Davis, unpublished data). While making observations of fe-

Table 1. Adaptation of criteria for assessing relative quality of sea otter (*Enhydra lutris*) territories in Prince William Sound, Alaska (Pearson et al. 2006).

Attribute	Adapted criteria (Pearson et al. 2006)	Original criteria (Garshelis et al. 1984)	Rank value
Size (km^2)	>1.0	>0.3	2
	0.5–1.0	0.15–0.3	1
	<0.5	<0.15	0
Shoreline enclosure	Land on two sides	Land on three sides	2
	Land on one side	Land on two sides	1
	Mainly open	Mainly open	0
Accessibility	Entrance(s) not blocked by another territory	Entrance(s) not adjacent to another territory	2
	Entrance(s) partly blocked by another territory	Entrance(s) partly blocked by another territory	1
	Entrance(s) mostly blocked by another territory	Entrance(s) totally blocked by another territory	0
Prey availability	Number of females feeding in territory divided by 10*	Number of females feeding in a territory divided by 20† (values ranged from 0 to 2.1)	na

Note: na, not applicable.

*The number of females we observed was half as many as that observed by Garshelis et al. (1984).

†The prey availability attribute was divided by 20 to scale with the other three attributes.

male behavior, R.C. Wolt, F. Weltz, F.P. Gelwick, and R.W. Davis (unpublished data) also recorded the GPS coordinate sets for each feeding female encountered. We then plotted those coordinate sets in ArcMap to estimate the number of feeding females in each territory. The number of feeding females from 2004 to 2006 were similar to those recorded in 2003 by Pearson et al. (2006). We assumed that female sea otters would aggregate where food resources were plentiful, being "better samplers" than researchers (Garshelis et al. 1984; Pearson et al. 2006). We also assumed that the number of females feeding within each territory was a good indication of prey availability because the foraging success rate was 89% in Simpson Bay during the summer of 2003 (R.C. Wolt, F. Weltz, F.P. Gelwick, and R.W. Davis, unpublished data).

Sea otters have great potential to be influenced by their habitat because of their diet of benthic invertebrates, which requires them to dive through the entire water column and excavate bottom sediments. Thus, as another way to describe territories, we used sediment data collected by Gilkenson (2004) who determined the habitat characteristics of Simpson Bay by measuring water depth and taking sediment samples with an Eckman grab, as well as visually examining the seafloor with a black-and-white video camera at 198 separate data stations throughout the bay. Sediment type was then classified in gravel–sand–mud categories based on grain-size distributions of each sediment sample. Sediment categories were recorded as gravel, mixed gravel (including sandy gravel and muddy gravel), sand, mixed sand (including gravelly sand and muddy sand), mud, or mixed mud (including sandy mud and gravelly mud). In the present study, we overlaid maps of territories of sea otters with Gilkinson's (2004) sediment-type maps to determine the bottom type for each territory.

Data analysis

A summary quality score was calculated for each territory because the four attributes of quality were intercorrelated (Table 2). For example, territories located in the heads of the bays were ranked low for accessibility and high for shoreline enclosure. In addition, these territories also tended to be smaller in size than those territories located at the mouths of each bay (Pearson et al. 2006). Summary scores for territories found in 2004–2006 were calculated following the procedure of Pearson et al. (2006) and Garshelis et al. (1984), which allowed the 2003 data set to be combined with the 2004–2006 data set. A linear combination of variables was selected to best describe the orthogonal variation in the data. Principal components analysis (PCA) was used to transform the set of intercorrelated variables into a set of uncorrelated linear combinations of these variables (Dunteman 1989; Stevens 1992; Bryant and Yarnold 2003).

Territory overlap was assessed by comparing the minimum convex polygons of each individual within each year (Figs. 2*a*–2*d*). To understand the relationship between territory overlap and physical interactions between males, ad libitum sampling (Altmann 1974) was conducted to record all instances of aggression between males.

Analysis of covariance (ANCOVA) was conducted to test the influence of number of territorial males (as the covariate) on (*i*) territory quality among individual males and (*ii*) territory size among individual males. Univariate and multivariate analysis of variance (ANOVA and MANOVA, respectively) was used to test relationships between the following: (*iii*) territory quality and otter category (males that held a territory in consecutive years versus males that held a territory in only 1 year), (*iv*) territory quality and year, (*v*) territory size and otter category, and (*vi*) territory size and year. All statistical analyses were calculated using SPSS version 15 (SPSS Inc., Chicago, Illinois, USA). For all tests $\alpha = 0.05$.

Results

Over the 4-year period, male territories in Simpson Bay were 0.95 ± 0.10 km^2 (mean ± SD) (range 0.35–2.57 km^2), with a maximum depth of 56 ± 7.40 m (range 30–90 m). Territories occupied 48% of Simpson Bay in 2003, 35% in 2004, 16% in 2005, and 28% in 2006. In total, 13.1 km^2

Table 2. Variation in territorial attributes (Table 1) for territorial male sea otters (*Enhydra lutris*) in Simpson Bay, Alaska, during the summers of 2003–2006.

	Territorial attribute				Quality score (PCA)	
Male ID. (year)	Size	Shoreline enclosure	Accessibility	Prey availability	Component 1*	Component 2†
Ch (2003)	2	1	1	1.3	1.96	0.10
Je (2003)	2	2	1	0.7	1.72	1.37
Ot (2003)	2	2	1	0.5	1.62	–0.42
Li (2003)	2	0	1	0.2	1.30	0.74
Wi (2003)	1	1	2	0.1	0.83	0.74
Os (2003)	1	1	0	0.1	0.69	–0.52
Cu (2003)	1	0	1	0.1	0.68	0.68
Jb (2003)	0	1	1	0	0.15	0.06
De (2003)	0	0	2	0	0.14	1.26
Ha (2003)	0	0	2	0	0.14	1.26
Ch (2004)	2	1	1	0.7	1.64	0.14
Cu (2004)	2	1	1	0.4	1.48	0.16
Em (2004)	2	1	1	0.3	1.43	0.16
Wi (2004)	1	1	1	0.3	0.87	0.10
Ot (2004)	1	0	1	0.4	0.84	0.67
Td (2004)	0	1	0	0.5	0.35	–0.60
Bj (2004)	0	1	0	0.1	0.13	–0.58
Mu (2005)	2	1	2	0.4	1.55	0.79
Ja (2005)	1	0	2	0	0.70	1.32
Be (2005)	0	1	1	0.2	0.26	0.05
Pu (2005)	0	1	1	0	0.15	0.06
Ni (2006)	2	0	1	1.1	1.77	0.68
Dr (2006)	2	1	1	0.6	1.59	0.14
Ri (2006)	1	1	1	0.8	1.13	0.07
Gr (2006)	1	0	2	0.6	1.02	1.28
Pe (2006)	1	0	1	0.5	0.90	0.66
Be (2006)	0	1	1	0.1	0.20	0.05
Qu (2006)	0	1	1	0.1	0.20	0.05

*Component explaining 43% of total variance; used to calculate summary scores, and weighted to size and prey availability.
†Component explaining additional 32% of total variance; weighted to shoreline enclosure and accessibility.

(62.5%) of Simpson Bay was occupied at least once by a territory during the 4-year study (Fig. 3), and 7.9 km^2 (37.5%) was never occupied by a territory. In addition, 23% of the total area occupied by individual territories was over sand or mixed sand sediment types, 28% was over gravel or mixed gravel, and 49% was over mud or mixed mud.

Individual territories in Simpson Bay overlapped by 6.9% in 2003, 2.9% in 2004, 0% in 2005, and 14.4% in 2006. Males Ch, Cu, Ot, and Wi held territories in 2003 and 2004, and their respective territories overlapped by 26.6%–34.2% between years (Fig. 4*a*). Between 2005 and 2006, the territory of male Be overlapped by 16.4% between years (Fig. 4*b*).

Recognition methods involved boat-based observations, and therefore the potential for observer effects on movements of sea otters may have slightly increased. However, the 30 m minimum distance between the boat and target animal, as permitted by the U.S. Fish and Wildlife Service, was strictly adhered to in order to minimize the risk of altering the animal's behavior or movement.

Territory quality

The first principal component of the PCA (eigenvalue of 1.73) accounted for 43% of the total variance among the four attributes of territory quality and was used to calculate the summary scores for each territory based on the weights of the coefficients for each variable: $y = 0.56_{size} + 0.08_{enclosure} + 0.07_{access} + 0.53_{prey}$.

Large territories with many prey resources scored high for this index. Territory quality ranged from 0.14 to 1.96 (0.9 ± 0.61) (Table 2). For example, male Ch held the highest quality territory in 2003, located near the mouth of West Bay, whereas males De and Ha (also in 2003) defended the lowest quality territories, located in the northern portions of the West Bay (Fig. 2*a*).

The second principle component, explaining an additional 32% of the total variance among attributes of quality, was negatively related to the degree of enclosure and positively related to the degree of accessibility ($y = 0.06_{size} - 0.57_{enclosure} + 0.63_{access} - 0.06_{prey}$). Therefore, highly enclosed territories that were primarily obstructed by other territories scored low for this index. High-quality territories had (*i*) large areas, (*ii*) some feeding sites for females, (*iii*) moderate to little shoreline enclosure, and (*iv*) more entrances away from other territories (Table 2).

Territory correlations

A Kolmogorov–Smirnov test found both territory quality

Fig. 2. Territories of male sea otters (*Enhydra lutris*) in Simpson Bay, Alaska, during summers of (*a*) 2003, (*b*) 2004, (*c*) 2005, and (*d*) 2006.

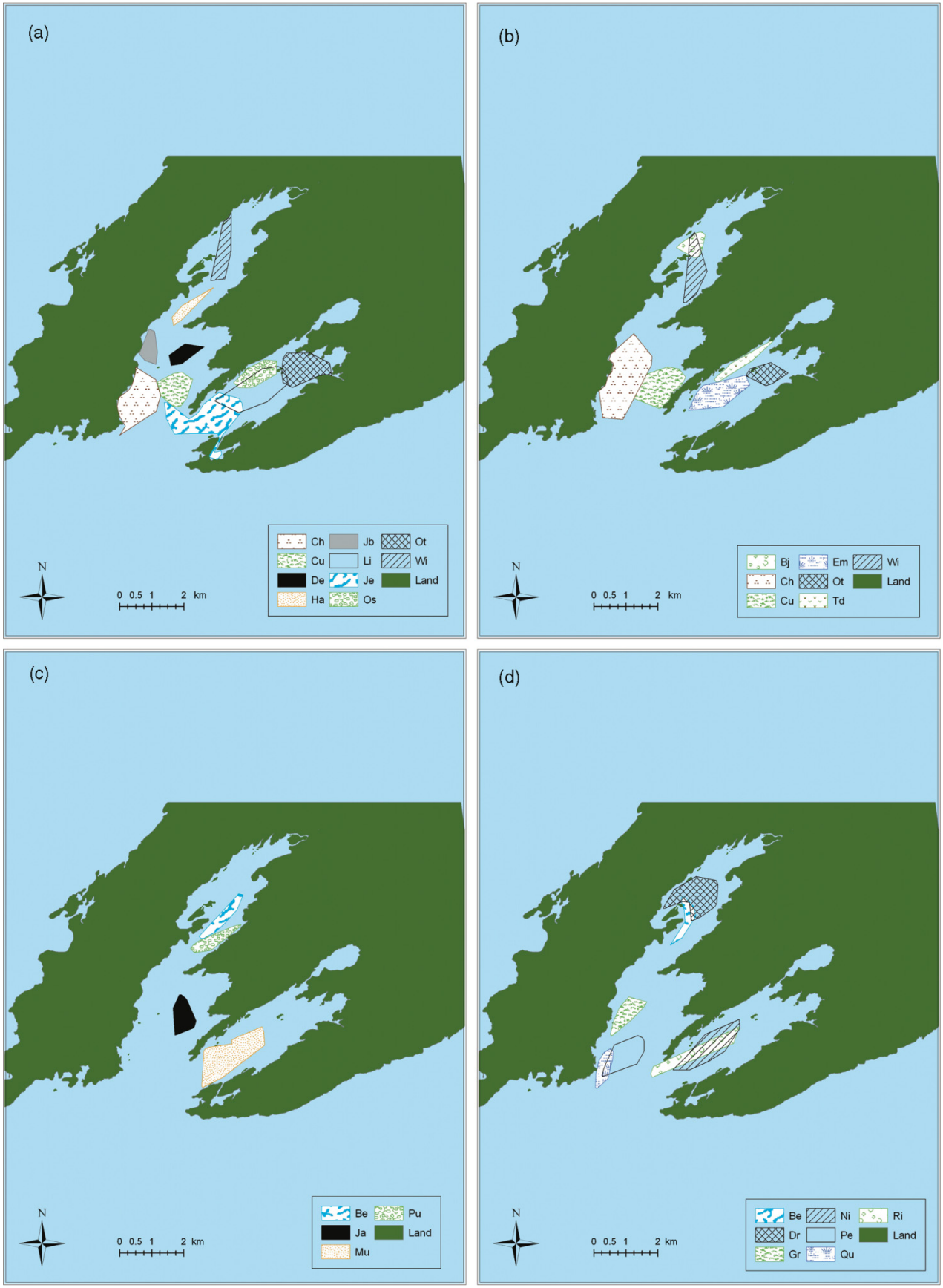
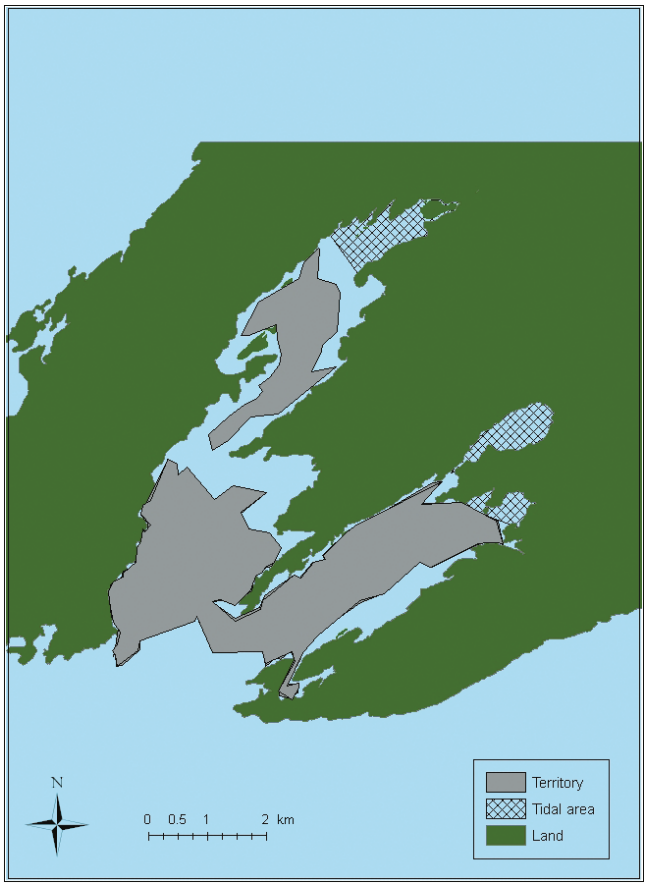


Fig. 3. Area of Simpson Bay, Alaska, that was covered by a male sea otter (*Enhydra lutris*) territory at least once from 2003 to 2006.



(p = 0.158) and territory size (p = 0.072) to be normally distributed. The ANCOVA showed that the total number of males holding a territory in Simpson Bay had no significant effect on the size (p = 0.845) or quality (p = 0.804) of the territories. The ANCOVA also found no interaction (year × total otters) effect on the size (p = 0.423) or quality (p = 0.177) of the territories. A two-way ANOVA showed that neither year (p = 0.639) nor otter category (p = 0.804) had a significant effect on the quality of the territories over the 4 years. In addition, there was no significant interaction (year × otter category) effect on the territory qualities (p = 0.177). The MANOVA also showed no significant effect of year (p = 0.898), otter category (p = 0.969), or their interaction (p = 0.166) on the quality or size of territories over the 4 years.

Male–male interactions

Two physically aggressive male–male interactions were observed in Simpson Bay during the 4-year period. In 2003, males Li and Ot held adjacent territories in the East Bay. On several occasions, male Ot invaded male Li's territory only to be chased out with no physical interaction. However, on 19 July, male Ot encroached upon male Li's territory. Male Li was observed patrolling its territory when it came upon male Ot, and a physically aggressive encounter ensued. Both males began lunging, hissing, biting, and scratching each other. The physical interaction lasted ~3 min. Male Li then chased male Ot back to its adjacent territory but abruptly stopped the chase at what appeared to be its territory boundary, while male Ot continued swimming and porpoising farther into its own territory.

The displacement of one territorial male by another was witnessed in 2004. Male Ch was displaced by a transient male (Ro) for ~12 days. On 13 August, male Ch was observed in a physically aggressive encounter (biting and scratching) with an unidentifiable male (later presumed to be transient male Ro). On 15 August, transient male Ro was observed in male Ch's territory. During this time, male Ch was not seen in any part of the study area. However, on 25 August, male Ch was observed resting back in its original territory. On August 28, transient male Ro was observed and monitored patrolling the outskirts of male Ch's territory, then leaving the study site. Transient male Ro was only observed twice and was therefore excluded from further analysis in this study.

Discussion

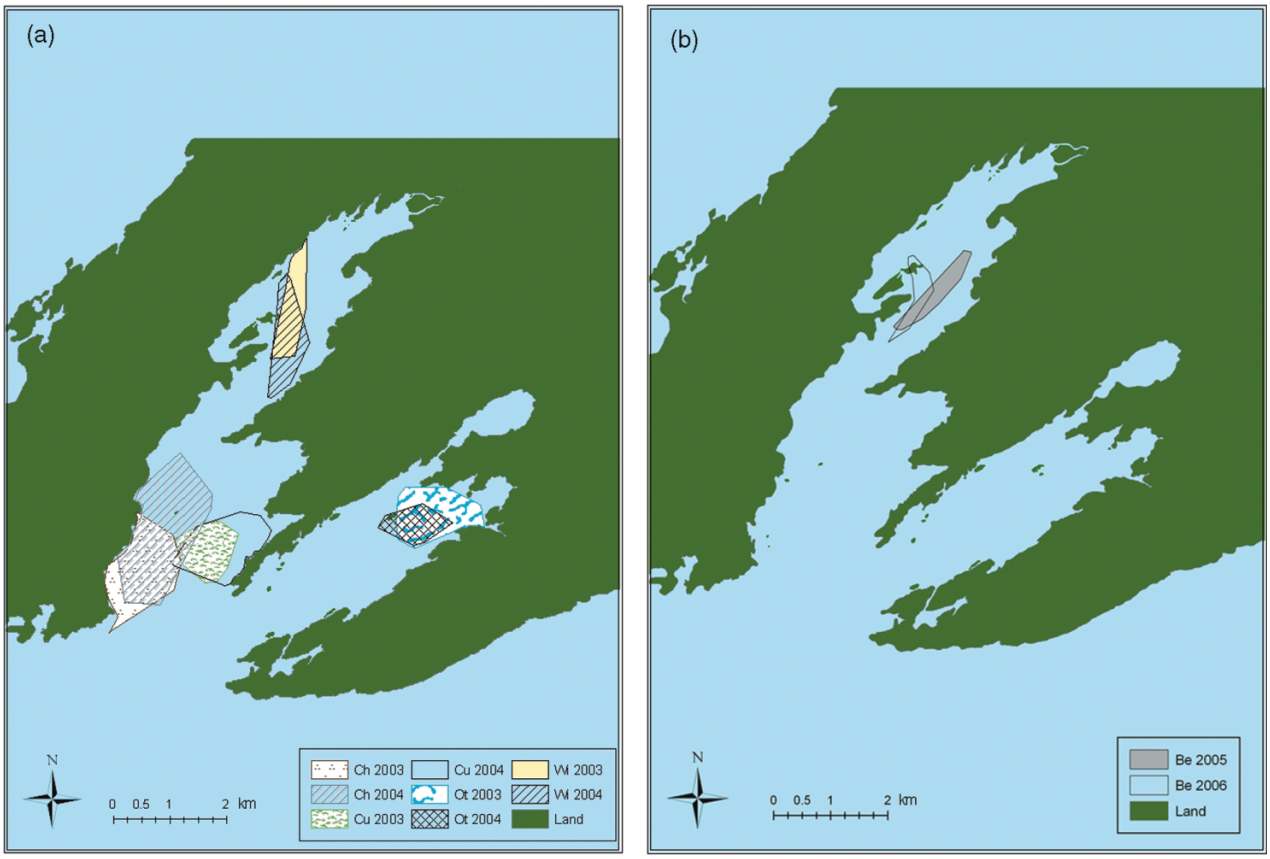
The results of this study imply a common finding: during 2003–2006, the quality and size of territories in Simpson Bay were not significantly different among years and not significantly influenced by the total number of otters holding territories, or whether or not an individual otter held a territory in the area during consecutive years.

Territory quality

The importance of the four major territorial attributes (size, shoreline enclosure, accessibility and prey availability) to overall territory quality was similar among this study, Pearson et al. (2006), and Garshelis et al. (1984). In each study, size was the most important territory quality, followed by prey availability. However, Pearson et al.'s (2006) study showed that higher quality territories had more entrances obstructed by other territories, while this study and that of Garshelis et al. (1984) showed the opposite. Territories with the higher quality scores were those that had boundaries away from other territories, moderate to little shoreline enclosure, large areas, and some feeding sites for females.

The mean (SD) size of Simpson Bay territories was 0.95 ± 0.1 km^2 (range 0.35–2.57 km^2). Previous studies have reported smaller territories. For example, Garshelis et al. (1984) conducted a study in Prince William Sound at Gibbon Anchorage from 1975 to 1984 and found the mean male territory area to be ~0.23 km^2 (range 0.04–0.50 km^2). Jameson (1989) conducted a study from 1978 to 1982 along the California coast from Santa Cruz to Pismo Beach and found the mean male territory area to be ~0.36 km^2 (range 0.23–0.62 km^2). Larger territory areas in Simpson Bay may result, in part, from its size and location. Gibbon Anchorage is ~3.5 km^2 in area and is considered to be a partially enclosed region (Garshelis et al. 1984). Jameson (1989) conducted his study on over 200 km of the California coastline, which contains few enclosed areas for protection from rough seas. Simpson Bay, which is located inside of Prince William Sound and protected from sea conditions in the Gulf of Alaska, is 21 km^2 in area and is almost entirely enclosed (except for the 2.5 km wide entrance to the bay). This offers much protection from rough seas, thus making it easier for males to patrol larger areas. However, both Gibbon Anchor-

Fig. 4. Territory locations for repeat territory holders between (*a*) years 2003 and 2004, and between (*b*) years 2005 and 2006.



age and the California coast have been occupied by sea otters for longer periods of time than Simpson Bay. It is possible that there is more competition for territories in those areas. It is also possible that other factors that we do not yet fully understand, such as food availability, might affect territory size.

Much the area in Simpson Bay that was unoccupied by territories was located at the mouth or head of each portion of the bay. The mouths of West and East bays, while having no shoreline enclosure (a positive attribute), are also located over deeper (60–125 m) water. Deep water may limit the number of feeding sites available (Gilkenson 2004). In contrast, the heads of North and East bays were very shallow and often included areas exposed at low tide. Because Simpson Bay has semidiurnal tides, this would considerably decrease the territory size twice during each 24 h period, depending on the time of the month. In addition, entrances to these areas were often blocked by other territories, which this study has shown to be an undesirable territory attribute.

Territory overlap and physical interactions

There was little territory overlap in Simpson Bay, indicating that male sea otters may avoid conflict by maintaining nonoverlapping territories. As in other studies (Calkins and Lent 1975; Loughlin 1980; Garshelis et al. 1984), territorial trespassing by other males, whether resident or transient, was not frequently observed, and therefore very little male–male aggressive behavior was observed. In the present study, only two aggressive interactions between males involved physical contact, and only one instance of territory displacement occurred. Most trespassers were deterred from entering a territory without physical interaction with the territory holder. Aggressive vocalizations such as hissing or growling, chasing, or simply the territory holder's presence in the area were often enough to discourage a trespasser from invading a territory.

Site fidelity and repeat territory holders

Fidelity by individuals to an area over multiple years provides strong evidence of stable resources and social systems (Powell 2001), as well as insight into how animals use an area over time (Kernohan et al. 2001). However, some changes in space utilization over the course of multiple years may occur because of competition for resources (Powell 2001). In the present study, 5 of 23 territorial male sea otters held a territory for two consecutive years. Territory overlap for a given male between years ranged from 16.4% to 34.2%. Although some shifting occurred, male sea otters occupied the same territory during consecutive years. This indicates stability of resources, as well as competition between males for those resources.

In previous studies, the time that an adult male sea otter held a territory ranged from 1 to 9 years (Garshelis et al. 1984; Jameson 1989). Garshelis et al. (1984) captured otters in floating nets, marked them with colored tags, and then monitored their movements with binoculars and spotting scopes. Eight tagged males held territories during the breeding season during each of two consecutive years, and one male held a territory for at least nine consecutive years (Garshelis et al. 1984).

As in the Garshelis study, Jameson (1989) captured otters and marked them with colored tags and then monitored them during daily surveys. Two otters maintained the same territory for five consecutive years, two for six consecutive years, and one for seven consecutive years. No tagged males changed territories within the study area, and it was noted that males frequently rested within a few metres of the same location during each survey (Jameson 1989).

Site-fidelity studies have been conducted on both aquatic and terrestrial animals including other mustelids (river otters, *Lontra canadensis* (Schreber, 1777); Gorman et al. 2006), pinnipeds (northern fur seals, *Callorhinus ursinus* (L., 1758); Kiyota 2005), and ungulates (guanacos, *Lama guanicoe* (Müller, 1776); Young and Franklin 2004). River otters exhibit strong annual site fidelity by both males and females. Gorman et al. (2006) conducted a 2-year study that showed male river otters used 74% of their year-1 home range in year 2, while females home ranges overlapped by 75% between years. As with sea otters, some shifting of home ranges of river otters occurred between years, but none of the river otters completely abandoned or relocated their home ranges during the study (Gorman et al. 2006).

Kiyota (2005) investigated territory acquisition and mating success of male northern fur seals on St. Paul Island (Pribilof Islands), Alaska, from 1993 to 1999. Adult female fur seals arrive at the breeding colony in early summer and tend to aggregate in "central breeding areas" (Kiyota 2005). Similar to adult male sea otters, one attribute for a high-quality territory for an adult male fur seal is the spatial and temporal concentrations of receptive females. Many prime male fur seals initiated their territory tenure in early summer (May or June). As with adult male sea otters, once adult male northern fur seals acquired breeding territories, they displayed strong tendencies to return to the same locations during the following breeding seasons (Kiyota 2005). Male fur seals can hold a territory for 1–5 years, with a mean of 2 years (Kiyota 2005).

Southern Chilean guanacos establish territories in the spring to prepare for the summer mating season (Young and Franklin 2004). Adult males are found in one of three social groups (Franklin 1982; Young and Franklin 2004). Similar to territorial male sea otters, solitary male guanacos establish nonoverlapping territories for a mean of 2 years (range 1–5 years). Family groups include a territorial male, several adult females, some yearlings, and other young. Lastly, male groups are composed of nonterritorial males, immature males, and old or injured males, and occur in distinct areas (Young and Franklin 2004) similar to rafts of nonbreeding male sea otters (Kenyon 1969; Garshelis et al. 1984; Pearson et al. 2006).

Bathymetry and sediment type

Gilkenson (2004) observed that significantly more otters were feeding over mud and mixed-mud sediments. The present study showed that nearly half (49%) of the total area in Simpson Bay covered by territories from 2003 to 2006 consisted of mud or mixed-mud sediments. The three main prey categories for sea otters in eastern and central Prince William Sound include mollusks, crustaceans, and echinoderms. Prey items collected during successful foraging dives in Simpson Bay include 75% clams, 9% Pacific blue mussels, 6% crabs, 2% reddish scallops, and a variety of other invertebrates that individually represented less than 2% of the diet (R.C. Wolt, F. Weltz, F.P. Gelwick, and R.W. Davis, unpublished data). This study has shown the availability of feeding sites to be a favorable territory attribute.

Sample size

Sample sizes in previous studies of territorial males have been small, ranging from 2 to 12 individuals (Jameson 1989; Pearson et al. 2006). Pearson et al. (2006) concluded that because of the physiography of Simpson Bay, the sample size was not likely to exceed 10 territorial males in any 1 year. This study supports that conclusion. Simpson Bay supported 7 ± 2.4 territorial males each year. At any one time from 2003 to 2006, there was a maximum of two territories in the North Bay and four territories in either the West Bay or the East Bay (Fig. 2).

Similar to previous studies, we used a combination of four variables to characterize the quality of male sea otter territories that include both physical aspects of their habitat, as well as variables related to female choice for residing in an area. Our results indicated that the best male territories in Simpson Bay had large areas (0.95 ± 0.1 km^2), moderate to little shoreline enclosure, were not blocked other male territories, and had food resources to attract foraging females. However, there are probably other variables that have yet to be identified. Ultimately, evaluating the quality of a territory will depend on the number of females that a male impregnates. This type of assessment will require new research techniques and technology for tracking and monitoring the long-term movements and behavior of sea otters and determining when impregnation occurs.

Acknowledgements

We thank A. Gilkinson, O. Lee, Y. Mitiani, H. (Briggs) Morin, F. Weltz, R.C. Wolt, T. Wright, the Texas A&M undergraduate students, and the Earthwatch volunteers for field assistance; F. Gelwick for statistical assistance; and the Earthwatch Institute and Texas A&M University for financial support. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, **49**(3): 227–266. doi:10.1163/156853974X00534. PMID:4597405.

Apollonio, M., Festa-Bianchet, M., and Mari, F. 1989. Correlates of copulatory success in a fallow deer lek. Behav. Ecol. Sociobiol. **25**(2): 89–97. doi:10.1007/BF00302925.

Bodkin, J.L., Monson, D.H., and Esslinger, G.G. 2007. Activity budgets derived from time-depth recorders in a diving mammal. J. Wildl. Manage. **71**(6): 2034–2044. doi:10.2193/2006-258.

Bro-Jørgensen, J., and Durant, S.M. 2003. Mating strategies of topi bulls: getting in the centre of attention. Anim. Behav. **65**(3): 585–594. doi:10.1006/anbe.2003.2077.

Bryant, F.B., and Yarnold, P.R. 2003. Principal components analysis and exploratory and confirmatory factor analysis. *In* Reading and understanding multivariate statistics. *Edited by* L.G. Grimm

and P.R. Yarnold. American Psychological Association, Washington, D.C. pp. 99–136.

Calkins, D., and Lent, P.C. 1975. Territoriality and mating behavior in Prince William Sound sea otters. J. Mammal. **56**(2): 528–529. doi:10.2307/1379387.

Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M., and Albon, S.D. 1988. Passing the buck: resource defense, lek breeding and mate choice in fallow deer. Behav. Ecol. Sociobiol. **23**(5): 281–296. doi:10.1007/BF00300575.

Dunteman, G.H. 1989. Principal components analysis. Series: Quantitative applications in the social sciences. No. 69. Sage Publications, Inc., Newbury Park, Calif.

Finerty, S.E., Hillman, G.R., and Davis, R.W. 2007. Computer matching of sea otter (*Enhydra lutris*) nose scars: a new method for tracking individual otters. Aquat. Mamm. **33**(3): 349–358. doi:10.1578/AM.33.3.2007.349.

Franklin, W.L. 1982. Biology, ecology and relationship to man of the South American camelids. *In* Mammalian biology in South America, Spec. Publ. Ser. *Edited by* M.A. Mares and H.H. Genoways Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pa. pp. 457–489

Garshelis, D.L. 1983. Ecology of Sea Otters in Prince William Sound, Alaska. Ph.D. dissertation, University of Minnesota, St. Paul.

Garshelis, D.L., Johnson, A.M., and Garshelis, J.A. 1984. Social organization of sea otters in Prince William Sound, Alaska. Can. J. Zool. **62**(12): 2648–2658. doi:10.1139/z84-385.

Garshelis, D.L., Garshelis, J.A., and Kimker, A.T. 1986. Sea otter time budget and prey relationships in Alaska. J. Wildl. Manage. **50**(4): 637–647. doi:10.2307/3800974.

Gelatt, T.S., Siniff, D.B., and Estes, J.A. 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. J. Wildl. Manage. **66**(1): 29–39. doi:10.2307/3802868.

Gilkenson, A. 2004. Habitat associations and photo-identification of sea otters in Simpson Bay, Prince William Sound, Alaska. Master's thesis, Texas A&M University, College Station.

Gorman, T.A., Erb, J.D., McMillan, B.R., and Martin, D.J. 2006. Space use and sociality of river otters (*Lontra canadensis*) in Minnesota. J. Mammal. **87**(4): 740–747. doi:10.1644/05-MAMM-A-337R1.1.

Gosling, L.M., and Petrie, M. 1990. Lekking in topi: a consequence of satellite behavior in small males at hotspots. Anim. Behav. **40**(2): 272–287. doi:10.1016/S0003-3472(05)80922-4.

Isvaran, K., and Jhala, Y. 2000. Variation in lekking costs in blackbuck (*Antilope cervicapra*): relationship to lek-territory location and female mating patterns. Behaviour, **137**(5): 547–563. doi:10.1163/156853900502204.

Jameson, R.J. 1989. Movements, home range and territories of sea otters off central California. Mar. Mamm. Sci. **5**(2): 159–172. doi:10.1111/j.1748-7692.1989.tb00330.x.

Kenyon, K.W. 1969. The sea otter in the eastern Pacific Ocean. Dover Publications, New York.

Kernohan, B.J., Gitzen, R.A., and Millspaugh, J.J. 2001. Analysis of animal space use and movements. *In* Radio tracking and animal populations. *Edited by* J.J. Millspaugh and J.M. Marzluff. Academic Press, San Diego. pp. 125–166.

Kiyota, M. 2005. Site fidelity, territory acquisition, and mating success in male northern fur seals (*Callorhinus ursinus*). Mammal Study, **30**(1): 19–27. doi:10.3106/1348-6160(2005)30[19:SFTAAM]2.0.CO;2.

Kodric-Brown, A., and Brown, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology, **59**(2): 285–296. doi:10.2307/1936374.

Lehner, P.N. 1996. Handbook of ethological methods. 2nd ed. Cambridge University Press, Cambridge, UK.

Loughlin, T.R. 1980. Home range and territoriality of sea otters near Monterey, California. J. Wildl. Manage. **44**(3): 576–582. doi:10.2307/3808005.

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Mar. Mamm. Sci. **15**(1): 102–122. doi:10.1111/j.1748-7692.1999.tb00784.x.

Noll, C.J., Dellapenna, T.M., Gilkinson, A., and Davis, R.W. 2009. A high-resolution geophysical investigation of sediment distribution controlled by catchment size and tides in a multi-basin turbid outwash fjord: Simpson Bay, Prince William Sound, Alaska. Geo-Mar. Lett. **29**(1): 1–16. doi:10.1007/s00367-008-0120-8.

Odum, E.P., and Kuenzler, E.J. 1955. Measurement of territory and home range size in birds. Auk, **72**: 128–137.

Pearson, H.C., and Davis, R.W. 2005. Behavior of territorial male sea otters (*Enhydra lutris*) in Prince William Sound, Alaska. Aquat. Mamm. **31**(2): 226–233. doi:10.1578/AM.31.2.2005.226.

Pearson, H.C., Packard, J.M., and Davis, R.W. 2006. Territory quality of male sea otters in Prince William Sound, Alaska: relation to body and territory maintenance behaviors. Can. J. Zool. **84**(7): 939–946. doi:10.1139/Z06-083.

Powell, R.A. 2001. Animal home ranges and territories and home range estimators. *In* Research techniques in animal ecology: controversies and consequences. *Edited by* L. Boitani and T.K. Fuller. Columbia University Press. New York. pp. 65–110.

Ralls, K., and Siniff, D.B. 1990. Time budgets and activity patterns in California sea otters. J. Wildl. Manage. **54**(2): 251–259. doi:10.2307/3809038.

Riedman, M.L., and Estes, J.L. 1990. The sea otter (*Enhydra lutris*): behavior, ecology and natural history. U.S. Fish Wildl. Serv. Biol. Rep. **90**(14): 1–126.

Rosser, A.M. 1992. Resource distribution, density, and determinants of mate access in puku. Behav. Ecol. **3**(1): 13–24. doi:10.1093/beheco/3.1.13.

Rotterman, L.M., and Simon-Jackson, T. 1988. Sea otter. *In* Selected marine mammals of Alaska: species accounts with research and management recommendations. *Edited by* J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 237–271

Stevens, J. 1992. Applied multivariate statistics for the social sciences. 2nd ed. Lawrence Erlbaum Associates, Inc., Hillsdale, N.J.

U.S. Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants: determination of threatened status for the Southwest Alaska district population segment of the northern sea otter (*Enhydra lutris kenyonai*). Fed. Regist. **70**(152): 46366–46386.

Vandevere, J.E. 1970. Reproduction in the southern sea otter. *In* Proceedings of the Seventh Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, Calif., 23–24 October 1970. *Edited by* T.C. Poulter. Stanford Research Institute, Menlo Park, Calif. pp. 221–227.

Vehrencamp, S.L., Bradbury, J.W., and Gibson, R.M. 1989. The energetic cost of display in male sage grouse. Anim. Behav. **38**(5): 885–896. doi:10.1016/S0003-3472(89)80120-4.

Young, J.K., and Franklin, W.L. 2004. Territorial fidelity of male guanacos in the patagonia of southern Chile. J. Mammal. **85**(1): 72–78. doi:10.1644/1545-1542(2004)085<0072:TFOMGI>2.0.CO;2.