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Behavior of Territorial Male Sea Otters (*Enhydra lutris*) in Prince William Sound, Alaska

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Abstract

Photo-identification and focal animal sampling were used to examine the daytime behavior of territorial male sea otters (*Enhydra lutris*) in Simpson Bay, Prince William Sound, Alaska, during the summer (June to August) of 2003. The average number of otters (all age classes of males and females) in the study area was 121 ± 12.1 SD (n = 5 surveys). The bout duration of six behaviors (resting, grooming, foraging, interacting with other otters, swimming at the surface, and patrolling), activity time budgets, and interactions with females were determined for territorial males. Ten males were observed during 183 focal follows (i.e., observation periods), representing 92 h of observation. More time was spent foraging (30%) than on any other activity, and foraging bouts were longer than all other activities. Males interacted with females with pups (59%) and with single females (41%). Two of three consortships (i.e., mating associations lasting ca. three days) were formed with single females. Sixty-seven percent of interactions between territorial males were aggressive and were longer than one min.

Key Words: sea otter, *Enhydra lutris*, behavior, territory, photo-identification, activity time budget, Alaska

Introduction

Several studies have examined the behavior of Alaskan sea otters (*Enhydra lutris*) (Estes, 1977; Estes et al., 1982; Garshelis et al., 1986; Gelatt et al., 2002; Kenyon, 1969), although some focused mainly on foraging behavior (e.g., Kvitek et al., 1993; Watt et al., 2000). The behavior of territorial male sea otters has been extensively studied in California (e.g., Jameson, 1989; Loughlin, 1980a; Vandevere, 1970) and, to a lesser extent, in Alaska (Calkins & Lent, 1975; Garshelis et al., 1984). One of the earliest descriptions of male sea otter behavior in Alaska was by Kenyon (1969); however, he described territoriality as being weakly expressed in sea otters, which was later shown to be incorrect (Calkins & Lent, 1975; Vandevere, 1970).

Sea otters are sexually segregated when not breeding, with adult males and females separated by distances of up to 150 km (Garshelis et al., 1984; Riedman & Estes, 1990). In expanding populations, male sea otters are the first to explore new, prey-rich areas (Garshelis et al., 1984). Females are more likely to remain in areas that are more protected and suitable for raising young, but often with decreased prey availability (Garshelis et al., 1984; Riedman & Estes, 1990). Male sea otters began to reoccupy eastern Prince William Sound (PWS) in the late 1970s after the population was decimated by commercial hunting prior to their protection under the International Fur Seal Treaty in 1911 (Garshelis et al., 1984; Kenyon, 1969; Lensink, 1962; Riedman & Estes, 1990). Simpson Bay remained a male area until the early 1980s (Garshelis et al., 1984, 1986; Monnett & Rotterman, 1988), but it is now an area used by females and pups. Adult males establish territories in Simpson Bay during the summer and autumn.

The purpose of this study was to assess activity patterns of territorial male sea otters. To accomplish this, we measured the bout duration of six behaviors—resting, grooming, foraging, interacting with other otters, swimming at the surface, and patrolling—and constructed activity time budgets. We also investigated whether differences existed among males with respect to female interactions. In contrast to previous studies that relied on radiotelemetry, flipper tags, and scan-sampling to assess behavioral patterns (e.g., Estes et al., 1986; Jameson, 1989; Ralls & Siniff, 1990), we used photo-identification (Würsig & Jefferson, 1990) and focal animal sampling (Lehner, 1996).

Materials and Methods

Study Site and Animals

Simpson Bay is a shallow fjord located in northeastern PWS (60.4° N, 145.5° W; Figure 1). Because of its location, Simpson Bay was not

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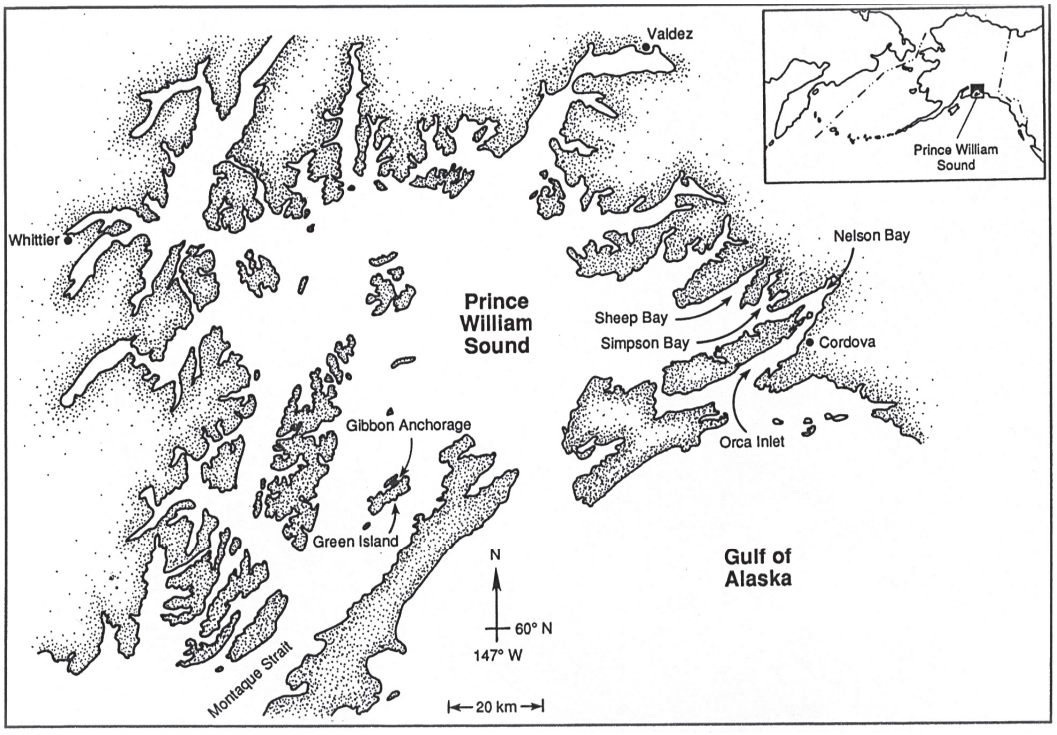

Figure 1. Map of Prince William Sound, Alaska, showing the study site in Simpson Bay during 2003 (used with permission from Riedman & Estes, 1990)

affected by the 1989 Exxon Valdez oil spill. Simpson Bay is composed of two arms (northwestern and southeastern), with a total area of ca. 13 km^2. The median width of Simpson Bay is 1.7 km, maximum length is 9.5 km, and maximum depth is 125 m. Summer sea surface temperatures range from 12° to 14° C. An extensive watershed, totaling 170 km^2 and reaching to heights of 1,500 m, strongly influences hydrographic processes in Simpson Bay by delivering large amounts of freshwater and sediment into the bay during the summer (Gay & Vaughan, 2001). Precipitation averages 415 cm/yr (Western Regional Climate Center, 2003), and average wind speed ranges from 4 to 14 km/h during the summer; however, strong westerly winds resulting from high pressure systems increase wave action that primarily affect the southeastern arm of the bay, while the northern arm is more sheltered (Gay & Vaughan, 2001). The seafloor of Simpson Bay is primarily soft sediment with occasional rocky outcrops, but it lacks large kelp such as *Nereocystis luetkeana* (Gilkinson, 2004). During the summer, Simpson Bay is used by female sea otters and their dependent pups, single females, and territorial males. The average number of sea otters in the study area during the 2003 field season (2 June to 31 August) was 121 ± 12.1 SD (n = 5 surveys), with pups representing about 24% (29 ± 7.0) of the population.

Focal Observations of Territorial Males

The summer field season was divided into six 8-day monitoring periods that coincided with groups of volunteers that assisted with data collection (Table 1). Focal animal observations were conducted from a 6-m skiff. Boat-based observers determined that a sea otter was a territorial male by its behavior (e.g., patrolling, copulatory behavior) and the presence of a penile or testicular bulge. Once a male's gender was confirmed, observers followed the otter at a distance of 50 to 100 m. Behavior (resting, grooming, foraging,

Table 1. Observation periods for territorial male sea otters in Simpson Bay, Alaska, during 2003

Session	Date
Session I	16 to 23 June
Session II	30 June to 7 July
Session III	14 to 21 July
Session IV	28 July to 4 August
Session V	11 to 18 August
Session VI	24 to 31 August

interacting with other otters, swimming at the surface, and patrolling) was recorded using instantaneous sampling (Lehner, 1996) at 1-min intervals for 30 min. Latitude and longitude were recorded every 5 min using a Global Positioning System (GPS). To determine the presence of other sea otters in the vicinity of the focal male, all sea otters that were visible to the unaided eye were counted before and after each focal follow. Females that interacted with males were classified as single or with a pup. Territorial males were observed on a regular schedule by dividing Simpson Bay into three sections—top of the northwestern arm, bottom of the northwestern arm, and the southeastern arm—and sampling each section evenly. Except for two instances, individual males were not followed more than once per day.

Photo-Identification

Scar tissue from wounds to the nose by conspecifics creates natural and unique marks in male and female sea otters (Foott, 1970). We identified territorial males using photo-identification of nose scars (possibly obtained during fights), other facial features (e.g., skin pigmentation around the mouth, pelage color, broken or worn teeth, and/or vibrissae characteristics), and general location in the study area. Identifiable nose scars were present in 45% of individual sea otters (113/251), including 63% (19/30) of males. Digital images were taken at distances of < 50 m using a Nikon D1X camera with 80-400 mm image-stabilized lens. The best images (i.e., proximity, angle, brightness, contrast) for each sea otter were assigned a unique identification number, cataloged, and compared with images from every other individual. Two experienced observers independently matched all images in the catalog. If no matches were found for an individual, it was considered a new animal.

Data Analysis

Non-parametric statistics were used due to non-normal distributions and small sample sizes. Kruskall-Wallis and Mann-Whitney U tests were used for analyses of bout duration according to activity, and for analyses of differences in activity bout duration and activity budgets according to time of day (morning, 0900-1200 h, versus afternoon, 1200-1830 h) and month (June, July, or August). A Wilcoxon signed rank test was used for analysis of interactions by female type (single or with a pup); a Kruskall-Wallis test was used to analyze differences in male-female interactions according to month; and a Mann-Whitney U test was used to analyze differences in the number of sea otters present during focal observations that did and did not involve interactions between males. Means are presented ± SD. All data were analyzed using *SPSS, Version, 12.1*, statistical software (SPSS, Chicago, IL). The two-tailed alpha level for all tests was set at 0.05.

Results

Research Effort

One hundred eighty-three focal observations (30 min each) were conducted for a total of 92 h; 99% ($n = 181$) of these occurred between 0900 and 1830 h local time. Only males with at least four focal follows ($n = 10$ males) were used in the analysis. In addition, 15 nonrandom focal follows (7.5 h) of the male sea otter named Je were analyzed separately. These data were used only for purposes of analyzing the consortship formed between Je and a female. Thus, random focal observations of 10 males represented 69% ($n = 127$) of the total focal observations and 69% ($n = 63$) of the total observational hours.

Bout Durations

Bout duration among the 10 territorial males differed according to activity (DF = 5, $X^2 = 87.341$, $p < 0.001$; Table 2). Mean foraging bouts (10.6 min) were significantly longer than all other activities (mean groom, 3.7 min: Z = -7.103, $p < 0.001$; mean interact, 6.2 min: Z = -3.992, $p < 0.001$; mean swim, 2.5 min: Z = -8.367, $p < 0.001$; mean patrol, 4.2 min: Z = -6.144, $p < 0.001$; and mean rest, 6.7 min: Z = -3.772, $p < 0.001$). Mean swimming bouts were shorter than bouts of mean interacting (Z = -2.843, $p < 0.01$), patrolling (Z = -3.725, $p < 0.001$), and mean resting (Z = -4.653,

Table 2. Mean bout durations in min ± SD (n) according to activity for 10 territorial male sea otters in Simpson Bay, Alaska, during 2003

Feed	Groom	Interact	Swim	Patrol	Rest
10.6 ± 9.2 A[a] (87)	3.7 ± 4.8 BD (121)	6.2 ± 8.4 BC (55)	2.5 ± 2.6 D (112)	4.2 ± 4.9 BC (121)	6.7 ± 8.0 C (83)

[a] Bout durations followed by the same letters are not different at $p < 0.05$ (Mann-Whitney U test). For example, since feed is the only activity followed by "A," it is different from all other activities; groom, interact, and patrol are all followed by "B," therefore they are not different; groom and rest do not share any common letters, therefore they are different.

Table 3. Mean bout durations in min ± SD (*n*) for each activity according to time of day and month for territorial male sea otters in Simpson Bay, Alaska, during 2003

Activity	Time of day		Month		
	AM (0900-1200 h)	PM (1200-1830 h)	June	July	August
Feed	11.7 ± 8.7 A[a] (35)	9.8 ± 9.5 A (52)	11.3 ± 10.0 A (12)	12.3 ± 10.7 A (30)	9.2 ± 7.8 A (45)
Groom	4.1 ± 5.3 A (65)	3.2 ± 4.2 A (56)	3.0 ± 2.3 A (14)	4.4 ± 6.2 A (44)	3.3 ± 4.1 A (63)
Interact	5.3 ± 7.2 A (36)	8.0 ± 10.2 A (19)	3.2 ± 4.3 A (13)	8.4 ± 8.8 A (9)	6.8 ± 9.3 A (33)
Swim	3.0 ± 3.1 A (61)	2.0 ± 1.7 A (51)	2.3 ± 2.5 A (28)	3.3 ± 2.7B (37)	2.1 ± 2.5 A (47)
Patrol	4.0 ± 3.9 A (68)	4.5 ± 6.0 A (53)	2.9 ± 2.2 A (29)	4.1 ± 4.7 A (31)	4.9 ± 5.8 A (61)
Rest	5.3 ± 5.8 A (49)	8.8 ± 10.2 A (34)	4.2 ± 4.3 A (10)	7.3 ± 9.6 A (36)	6.9 ± 7.0 A (37)

[a] Mean bout durations within each row followed by the same letters within each grouping (time of day, month) are not different at $p < 0.05$ (Mann-Whitney U test).

$p < 0.001$); and mean resting bouts were longer than mean grooming bouts ($Z = -3.077$, $p < 0.01$). Mean bout duration did not vary significantly throughout the daytime for any activity; however, mean swimming bout durations varied significantly according to month ($DF = 2$, $X^2 = 11.142$, $p < 0.01$), with longer bouts during July (3.3 min) than during June (2.3 min; $Z = -2.371$, $p < 0.05$) or August (2.1 min; $Z = -3.126$, $p < 0.01$; Table 3). When mean bout duration was examined individually, six males (Cu, Ha, Je, Li, Os, and Ot) exhibited significant differences in bout duration according to activity (Table 4).

Activity Budgets

An average daytime activity budget was created for the 10 territorial males (Figure 2), which may be compared with activity budgets from previous studies (Table 5). Approximately one-third of their time was spent foraging, while resting (18%), grooming (15%), and patrolling (17%) combined for one-half of the activity budget. Interacting (11%) and swimming (9%) occupied the smallest portions of the activity budget. Activity did not vary significantly throughout the daytime hours. The amount of time spent interacting varied significantly according to month ($DF = 2$, $X^2 = 7.338$, $p < 0.05$). Significantly more time was spent interacting during July than during June ($Z = -2.001$, $p < 0.05$), and more time was spent interacting during August than during July ($Z = -2.584$, $p < 0.05$). Separate activity budgets were created for each individual male (Table 6).

Interactions with Females

There was no difference in male-female interactions according to female type or month. Three males formed consortships (i.e., mating associations lasting ca. three days) with females. Two of these were with single females. Interactions involving one territorial male (Je) with a female and pup (ca. 16 wks in age) were of particular interest because of its long duration. The male and female were observed together for 39 days from 15 July to 29 August. They displayed typical pair-bonded behavior such as synchronous swimming, diving, and grooming (Kenyon, 1969); however, copulation was never observed.

Aggressive Interactions Among Males

Sixty-seven percent of interactions between territorial males were aggressive. Two interactions occurred during the first study session (on 20 June and 22 June), while the remaining four occurred during the last two study sessions (on 11 August, 13 August, 17 August, and 27 August). The two interactions that were not aggressive consisted of two males swimming towards each other while patrolling. One male departed the area without displaying aggressive behavior. Of the four aggressive interactions, all were longer than one min in duration, but only one may have involved physical contact (blood was observed on the male's head). Based on sea otter counts before and after each focal observation, a mean of 5.2 ± 4.7 individuals were within an approximate 100-m radius at the time of each male-male interaction; however, there was no significant difference in the number of sea otters present in counts conducted before

Table 4. Mean bout durations according to activity for individual territorial male sea otters in Simpson Bay, Alaska, during 2003

Animal code	Number of focal observations	Mean bout duration ± SD in min (*n*)					
		Feed	Groom	Interact	Swim	Patrol	Rest
Ch	5	5.2 ± 1.79 A (5)	4.0 ± 6.87 A (6)	6.3 ± 5.03 A (3)	2.7 ± 3.30 A (7)	8.8 ± 9.64 A (6)	8.0 A (1)
Cu	18	9.8 ± 8.14 A[a] (13)	3.1 ± 2.92 BC (16)	6.9 ± 8.37 AB (10)	2.5 ± 2.43 B (22)	3.9 ± 6.20 BC (14)	8.6 ± 9.63 AC (19)
De	4	2.0 ± 1.41 A (2)	1.7 ± 1.15 A (3)	5.5 ± 5.50 A (10)	3.3 ± 1.50 A (4)	2.9 ± 2.35 A (14)	1.5 ± 0.71 A (2)
Ha	7	9.2 ± 6.51 A (14)	1.7 ± 1.34 B (10)	1.9 ± 1.21 B (7)	1.0 ± 0.00 B (4)	3.1 ± 3.74 B (15)	0[b] AB
Jb	4	0[b] A	2.9 ± 1.76 A (9)	27.0 A (1)	2.1 ± 2.42 A (8)	3.0 A (1)	5.2 ± 4.74 A (9)
Je	34	15.3 ± 6.11 A (3)	1.9 ± 1.51 B (19)	24.9 ± 10.62[c] AC (30)	2.6 ± 3.00 B (20)	4.54 ± 2.73 D (13)	4.4 ± 4.10 D (16)
Li	16	13.1 ± 10.93 A (14)	4.5 ± 0.42 B (22)	1.3 ± 0.58 BC (3)	1.3 ± 0.71 C (8)	3.0 ± 3.40 BC (20)	8.6 ± 9.95 AB (14)
Os	13	15.4 ± 11.22 A (10)	2.5 ± 2.46 B (11)	15.8 ± 16.46 AB (4)	3.3 ± 2.40 B (14)	5.3 ± 8.36 B (7)	4.8 ± 6.92 B (13)
Ot	22	9.7 ± 9.94 A (24)	5.8 ± 7.83 AB (21)	5.2 ± 8.95 AB (10)	2.3 ± 2.24 B (21)	4.9 ± 5.02 A (27)	11.8 ± 12.40 AB (6)
Wi	4	8.0 ± 9.90 A (2)	8.8 ± 9.60 A (4)	13.0 A (1)	4.5 ± 6.35 A (4)	6.3 ± 1.26 A (4)	4.3 ± 2.52 A (3)

[a] Mean bout durations within each row followed by the same letters are not different at $p < 0.05$ (Mann-Whitney U test).
[b] No bouts of this activity were observed for this individual.
[c] The long bouts of interaction by this individual were due to the formation of a consortship.

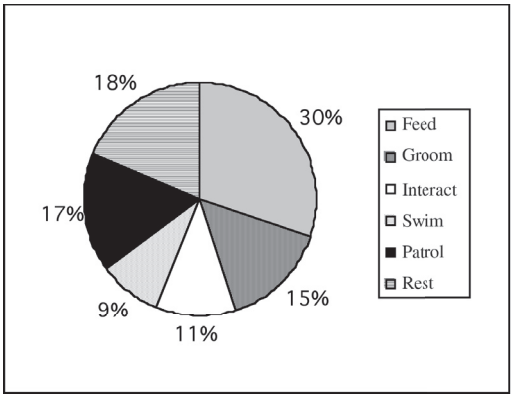

Figure 2. Activity budget for 10 territorial male sea otters in Simpson Bay, Alaska, during 2003

and after focal follows that did or did not involve male-male interactions.

Discussion

Sea otters have large energy requirements due to an elevated metabolic rate (Costa & Kooyman, 1982), and Kenyon (1969) estimated that they consume up to 25% of their body mass in food each day. As a result, sea otters spend much of their time foraging. Foraging bouts of male sea otters in Simpson Bay were longer than all other activities and represented 30% of the daytime activity budget. Previous studies also reported foraging to constitute a large portion of the activity budget for male sea otters (Garshelis et al., 1986; Gelatt et al., 2002; Loughlin, 1980b; Ralls & Siniff, 1990). In our study, a similar amount of time was allocated to resting (18%), grooming (15%) and patrolling (17%), which together represented 50% of the daytime activity budget. Interacting with other sea otters, including females, occupied less time than feeding, resting, grooming, or patrolling; however, the average duration of an interaction (i.e., bout duration) was only second to feeding, indicating that these interactions were of moderate duration but relatively infrequent. Swimming bouts were shorter than all other activities, occupied the least amount of the activity budget, and often occurred between feeding dives and other activities. For example, individuals frequently

Table 5. Comparison of adult male sea otter activity budgets in Alaska and California

Study location (source)	*n* individuals	% time spent[a] Foraging	Resting	Swimming
Prince William Sound, Alaska (this study)[b]	10[c]	30	18	9
Amchitka, Alaska (Gelatt et al., 2002)[d]	17[e]	38	46	N/A
Santa Cruz to San Simeon, California (Ralls & Siniff, 1990)[d]	4[e]	40	46	N/A
Prince William Sound, Alaska (Garshelis et al., 1986)[d]	6[c]	47	50	3
Monterey, California (Loughlin, 1980b)[d]	3[e]	33	13	N/A

[a] Row totals do not all equal 100% due to different categories of activity presented by each study.
[b] Daytime behavior
[c] Territorial male sea otters
[d] Behavior throughout the 24-h cycle
[e] Adult male sea otters, unknown if territorial or not

Table 6. Activity budgets (%) for individual territorial male sea otters in Simpson Bay, Alaska, during 2003

Animal code	Feed	Groom	Interact	Swim	Patrol	Rest
Ch	17	16	13	13	36	5
Cu	24	10	13	9	13	31
De	3	4	47	11	33	2
Ha	61	8	6	2	22	0
Jb	0	22	23	14	2	39
Je	6	4	71[a]	6	6	7
Li	38	21	1	2	13	25
Os	40	7	16	12	9	16
Ot	36	17	8	6	19	13
Wi	19	29	11	15	15	11

[a] The large amount of time spent interacting by this individual was due to the formation of a consortship.

swam when changing behavior from resting or grooming to foraging.

The only consortship we observed in which the female had a pup lasted at least 39 days. While Riedman & Estes (1990) reported the mean duration of a consortship to be three days, consortships have reportedly lasted 10 and 24 days in California (Riedman & Estes, 1990) and in Alaska (Garshelis et al., 1984), respectively. To our knowledge, our observations represent the longest reported consortship for sea otters.

Aggressive Behavior

Previous studies reported few aggressive interactions between territorial males (Calkins & Lent, 1975; Garshelis et al., 1984; Loughlin, 1980a). Although they did not provide the number of fights observed, Garshelis et al. (1984) reported that most aggressive interactions did not involve contact between the individuals and were < 5 s in duration. In contrast, most of the aggressive interactions observed in our study were ca. 1 to 2 min in duration.

On three occasions, we observed aggressive interactions (hissing and lunging by the male) between a male and a female. This behavior is typical of fighting males, but its function during an interaction with a female is unclear. Another aggressive encounter occurred when a male approached a pup floating on the surface while its mother was diving for food. The male forced the pup under water as if trying to drown it. When the female surfaced, the male stole her food (a clam), after which the female and pup quickly departed. This behavior also has been observed in California and is called "hostage behavior" (Riedman & Estes, 1990) because it appears that the male will not relinquish the pup until the female gives up the prey item.

Comparison of Methods

In contrast to previous studies of sea otter behavior which used radio telemetry and flipper tags to identify individuals, our study used photo-identification. This technique has been widely used in studies of cetaceans since the 1970s (Würsig & Jefferson, 1990; Würsig & Würsig, 1977), with manatees

(*Trichechus manatus latirostris*) (Langtimm et al., 1998), on Mediterranean monk seals (*Monachus monachus*) (Forcada & Aguilar, 2000), and on gray seals (*Halichoerus grypus*) (Vincent et al., 2001). To our knowledge, ours is the first study to use photo-identification with sea otters. Approximately 45% of the sea otters in Simpson Bay had identifiable nose scars, making photo-identification a reliable means of individual recognition for future sea otter studies.

Scan-sampling has been used to record sea otter activity data in several studies (e.g., Estes, 1977; Estes et al., 1982, 1986; Shimek & Monk, 1977); however, because there is an unequal probability of observing sea otters in various activities during scan samples, correction factors should be used to obtain accurate estimates of activities (Estes & Jameson, 1988). Additionally, due to overlap in activity within the broad activity states of groom, interact, and locomotion, Packard & Ribic (1982) reported that only three activity categories—feed, rest, and general—may be recorded reliably during instantaneous scan-samples. Our study followed their recommendation that focal animal sampling be used if data are to be collected on other activities such as grooming, resting, and swimming.

Conclusions

We used photo-identification and focal animal sampling to examine the daytime behavioral patterns of territorial male sea otters during the summer in Prince William Sound, Alaska. Territorial males spent more time foraging (30%) than in any other activity, and foraging bouts were longer than all other activities. A similar amount of time was allocated to resting, grooming, and patrolling, which together represented 50% of the daytime activity budget. Males sexually investigated females with and without pups. Aggressive interactions between males were rare and were generally 1 to 2 min in duration. More information is needed on territorial male behavior throughout the remainder of the year, and throughout the 24-h cycle.

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