Exxon Valdez Oil Spill
Restoration Project Final Report

Communication in River Otters:
Creation of Variable Resource Sheds for Terrestrial Communities

Restoration Project 02593
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COMMUNICATION IN RIVER OTTERS: CREATION OF VARIABLE RESOURCE SHEDS FOR TERRESTRIAL COMMUNITIES

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Abstract. Movements and behavior of animals can result in transfer of nutrients between discrete spatial patches, leading to spatial and temporal variability in resource sheds, modification of nutrient cycling, changes in productivity and in community structure and function, and increases in landscape heterogeneity. In this study, we explored the function of scent-marking at latrines by coastal river otters (*Lontra canadensis*), through investigating spatial distributions of otters with respect to gender, sociality, and the distribution of their food resources. We then calculated the amounts of nitrogen (N) and phosphorus (P) transported to latrine sites based on otter foraging behavior and the function of scent-marking at latrines. Locations of 55 radio-tagged otters in Prince William Sound, Alaska, USA, were obtained through aerial telemetry over a period of four years. Data on fish densities and marine habitat features were concurrently obtained from scuba transects and aerial surveys. A plastic social organization in river otters resulted in different foraging strategies and scent-marking behaviors. Social otters were more closely associated with schooling fishes and used latrines for intra-group communication, whereas nonsocial otters, which concentrated on intertidal and subtidal fishes, probably signaled mutual avoidance. In contrast, females appeared to use latrines for the defense of territories. Social otters used fewer sites with greater intensity, whereas nonsocial otters used more sites with lower intensity. These different functions of scent-marking and associated behaviors of otters resulted in high variability in nutrient inputs to different latrine sites. Although some sites may receive 2.7 g $N \cdot m^{-2} \cdot yr^{-1}$ and 0.4 g $P \cdot m^{-2} \cdot yr^{-1}$, others may be fertilized with up to 47.6 g $N \cdot m^{-2} \cdot yr^{-1}$ and 6.7 g $P \cdot m^{-2} \cdot yr^{-1}$. This spatial variability and the temporal changes in resource sheds is likely to result in the creation of heterogeneous landscape at the land margin.

Key words: Alaska; intertidal and demersal fishes; latrine; Lontra canadensis; *mutual avoidance; nutrient transfer; river otter; scent-marking; schooling fishes; social organization; territorial defense.*

INTRODUCTION

Resource sheds (source areas for resources assimilated by individual organisms during their lifetime; Power and Rainey [2000]) of coastal terrestrial communities extend beyond the boundary of the land margin. Predation of pelagic fishes in nearshore environments by nesting seabirds and coastal river otters (*Lontra canadensis*) provides a pathway for nutrient transport from sea to land (Anderson and Polis 1998, Ben-David et al. 1998*a*, Hobson et al. 1999), extending the resource shed of the terrestrial community into the ocean (Power and Rainey, 2000). Such nutrient transfers in this and other similar systems (e.g., predation of spawning Pacific salmon, *Oncorhynchus* spp.) may lead to modification of nutrient cycling, changes in productivity and in community structure and function, as well as increases in biodiversity and landscape heterogeneity (Hobbs 1996, Ben-David et al. 1998*a*, *b*, Helfield and Naiman 2001, 2002, Hocking and Reimchen 2002, Reimchen et al. 2003). The extent of resource sheds and relative contribution of nutrients will vary with movements and behavior of the transporting animals (McNaughton 1988, Anderson and Polis 1998, Frank and Groffman 1998, Hilderbrand et al. 1999, Kie et al. 2002).

Resource dispersion and availability are major determinants of space use and behavior of animals, although they are not the sole factors (Hobbs and Hanley 1990, Bernstein et al. 1991, Lima and Zollner 1996, McIntyre and Wiens 1999). Other factors, such as those related to population density, demography, and social interactions, or to avoidance of predation, may alter patterns modeled solely on resource distribution (Erlinge and Sandell 1986, Sandell 1989, Hobbs and Hanley 1990, Johnson et al. 2000). Furthermore, the relative importance of resources, and thus the patterns of landscape use by individuals, may vary seasonally with

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changes in availability of an important food resource, or as a function of the mating system for that species (Powell 1979, Sandell 1989, Hilderbrand et al. 1999, Johnson et al. 2000). Such seasonal changes in movements and behavior are likely to further enhance the effects of animals on ecosystem processes and landscape heterogeneity.

As specialized piscivorous predators (Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994), coastal river otters are dependent on the abundance and availability of fishes in the intertidal and subtidal zones (Dean et al. 2000). River otters inhabiting marine environments frequently occur and forage in social groups (Testa et al. 1994, Blundell et al. 2002*a*). Blundell et al. (2002*a*) reported that large groups of river otters in Prince William Sound (PWS), Alaska, were composed mainly of males, and occurred concurrently with the nearshore migration of Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*; Brown et al. 1999), and Pacific salmon (Groot and Margolis 1991). When those schooling pelagic fishes were absent from the system, river otters consumed more intertidal and demersal fishes, and the degree of sociality declined (Blundell et al. 2002*a*). Although some females briefly joined mixed-gender groups, most females and some males remained solitary year-round (Blundell et al. 2000, 2002*a*).

Similar to other mustelids, and as part of their activity on land, river otters scent-mark at specific locations along the coast, known as latrine sites (Durbin 1989, Kruuk 1992, 1995, Bowyer et al. 1995, Ben-David et al. 1996). At these sites, river otters deposit feces and urine, as well as excretions from their anal glands (Bowyer et al. 1995, Ben-David et al. 1998*a*), thus fertilizing terrestrial vegetation with marine-derived nitrogen (N) and phosphorus (P). Such transport of marine-derived N and P to terrestrial latrine sites may reach levels that are several orders of magnitude higher than other sources in the system (Ben-David et al. 1998*a*).

Several hypotheses have been proffered to explain the function of scent-marking by otters. One hypothesis suggests that scent-marking signals the use and depletion of food patches (Kruuk 1992, 1995). Other hypotheses propose that scent-marking is territorial in nature (Gosling 1982, Kruuk 1992), or may facilitate mutual avoidance (Hornocker et al. 1983, Gorman and Trowbridge 1989). Yet others implicate male–female communication for the advertisement of reproductive status (Kruuk 1992), or alternatively, male–male intra-group communication (Durbin 1989) among social animals (Rostain et al. 2004). Whether scent-marking by river otters is a function of territoriality, advertisement of the depletion of food patches, advertisement of reproductive status, or intra-group communication will greatly influence the spatial distribution of latrines on the landscape as well as the intensity and temporal use of those sites by otters. Thus, resource sheds of coastal forests may vary in time and space. For example, terrestrial organisms inhabiting a latrine that is used by solitary males to signal mutual avoidance are likely to assimilate nutrients from their terrestrial surrounding, but also those derived from the inter- and subtidal zone, throughout the growing season. In contrast, the resource shed of terrestrial organisms inhabiting a latrine that is used for intra-group communication will extend far beyond the subtidal zone during the migration of schooling pelagic fishes and will contract to the subtidal at the end of this migration. This otter-dependent spatial and temporal variability in resource sheds of the land margin probably will result in variable inputs of N and P to the terrestrial community and will yield increased landscape heterogeneity.

In this study, we examined several hypotheses that explore the function of scent-marking in coastal river otters in Prince William Sound, Alaska, through investigating spatial distributions of otters with respect to gender, sociality, and the distribution of their food resources. We began by determining whether fishes occur in association with specific features of marine habitats, and then explored predictions of otter distribution based on fish distributions and the different hypotheses for scent-marking. Specifically, we tested the following predictions. (1) Because scent-marking may signal the use and depletion of food patches (Kruuk 1992, 1995), fishes will occur in higher densities at latrine sites, where scent-marking occurs, than at random sites. (2) Latrines will be characterized by marine habitat variables predictive of intertidal and demersal fishes if they signal resource use, but will not exhibit this relation if they function in intra-group communication (Rostain et al. 2004). (3) Under the latter, social otters will exhibit higher affinity to latrines than will nonsocial individuals. (4) Also, because nonsocial otters in PWS prey more on intertidal and demersal fishes, whereas social otters cooperatively forage on schooling pelagic fishes (Blundell et al. 2002*a*), locations of social otters will be more closely associated with fish schools than will locations of nonsocial animals. (5) Nonsocial otters will be associated with higher densities of intertidal and demersal fishes, or with marine habitat features that predict locations of these prey (Blundell et al. 2002*a*).

Alternatives are presented by the following predictions. (6) In solitary carnivores, female dispersion is determined by resources and male dispersion is determined by that of females (Sandell 1989, Kruuk 1992); thus, distribution of male otters will be positively associated with the dispersion of females and this association will be stronger than the association with the dispersion of fishes. (7) Because solitary males may have a reproductive advantage (Blundell et al. 2004), the distribution of solitary males will be more closely associated with that of females than the distribution of social males. (8) If scent-marking at latrines serves as a passive defense of territories (Powell 1979, Gosling

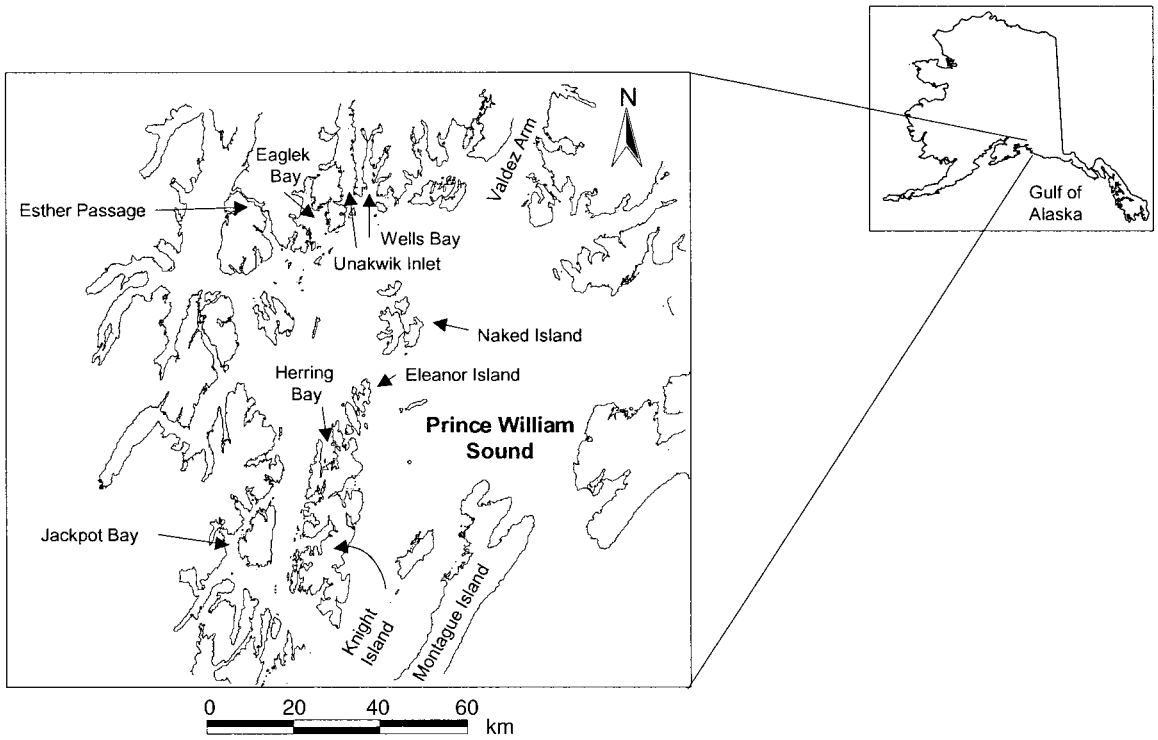

FIG. 1. Study areas in Prince William Sound, Alaska, USA. Herring Bay and Eleanor Island were heavily oiled by the *Exxon Valdez* oil spill. Although river otters were initially injured by the spill, their population recovered by the time we conducted our studies (Bowyer et al. 2003).

1982, Kruuk 1992), latrine sites will occur near the boundaries of otter home ranges. (9) Nonetheless, if latrines serve to facilitate mutual avoidance (Hornocker et al. 1983), latrines will occur throughout the otter home ranges, nonsocial otters will scent-mark more often than social ones, and nonsocial otters should be found more often than social otters in association with terrestrial habitat features that indicate scent-marking.

After determining the function of scent-marking in coastal river otters, we present examples of potential variation in the amounts of N and P transported to latrine sites, based on the behaviors of otters. Finally, using that information, we develop a scenario depicting spatial variability in resource sheds of terrestrial organisms, based on the amounts of N transported to known latrines in Prince William Sound.

METHODS

Study areas

Study areas were located in western Prince William Sound, Alaska, USA (PWS; Fig. 1). Detailed descriptions of the study areas are provided in Ben-David et al. (1998*a*), Blundell et al. (2002*b*), and Bowyer et al. (2003). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage (60°20′ N, 148°10′ W) and in Herring Bay and surrounding areas on northern Knight Island (60°23′ N, 147°40′ W). In 1998, our study areas included Herring Bay and Eleanor Island (60°32′ N, 147°37′ W).

Live capture of otters

We captured 79 individual river otters at Jackpot and Herring bays from May through July in 1996 and 1997 and at Herring Bay and Eleanor Island from mid-April through May in 1998. Otters were live-captured with Number 11 Sleepy Creek double-jaw leg-hold traps (Sterling Fur and Tool, Sterling, Ohio, USA) or with Hancock traps (Tomahawk Live Traps, Tomahawk, Wisconsin, USA; Blundell et al. 1999). Otters were anesthetized with Telazol (9 mg/kg; A. H. Robins, Richmond, Virginia, USA) administered by Telinject darts (Telinject USA, Saugus, California, USA) with a blowgun, or hand injection. Further details on capture and handling are provided in Blundell et al. (1999, 2000).

Radiotelemetry

Fifty-five otters were surgically implanted with radio transmitters (Blundell et al. 2000, Bowyer et al. 2003) and radio-tracked, mostly from a plane, from 1996 through 1999 at Jackpot Bay, from 1997 through 1999 at Herring Bay, and from 1998 to 1999 at Eleanor Island. Radio locations (n = 2230 total locations) were recorded using Global Positioning System (GPS) and data were recorded in Universal Transverse Mercator

(UTM) coordinates. Tracking occurred year-round, but locations were obtained with greater intensity during spring and summer (every 4–7 days), when weather was more conducive to regular flights. Location error was estimated at ~100 m from retrieval of carcasses (Bowyer et al. 2003). Further details on radio tracking are provided in Blundell et al. (2001, 2002*a*).

Intertidal and demersal fishes and marine habitat characteristics

Intertidal and demersal fishes were quantified by scuba divers at latrine ($n = 50$) and random sites ($n = 62$) at Herring and Jackpot bays in 1996 and 1997. Each year, the most active latrines (i.e., those with ≥10 fresh fecal deposits) were selected for prey assessment in each study area. Because prey were quantified at the most active latrine sites each year, some of the same latrine sites were sampled in both years ($n = 12$), but new random sites were selected each year. Random sites were systematically located approximately every 500 m along the shoreline beginning from a randomly selected starting point. After preliminary selection of random sites, the area above the tide line was inspected for scent-marking activity by otters. Sites with otter activity were discarded.

In 1996, each site was sampled only once during the month of July. In 1997, to assess changes in prey composition over time, 12 sites ($n = 6$ latrine sites; $n = 6$ random sites) were sampled twice (May and July) in Jackpot Bay and 30 sites ($n = 15$ latrine; $n = 15$ random) were sampled five times (June through August) in Herring Bay. An additional 18 sites in Jackpot Bay ($n = 9$ latrine; $n = 9$ random) were sampled only once that year (in July). In total, we collected data from 256 scuba transects (129 latrine, 127 random sites). To control for the effects of pseudoreplication in analyses, data were weighted by the number of samplings per site.

Transects were situated 20 m apart and extended perpendicular from the shoreline for a distance of 30 m, or until 15 m depth was reached, whichever occurred first. On the first transect, dominant substrate by physical size (rock reef, boulder, cobble, gravel, sand, or mud) was recorded at 0 m, 15 m, and 30 m. At those same points on each transect, dominant vegetation was also recorded: ''leafy brown'' (sieve kelp *Agarum clathratum*, split kelp *Laminaria bongardiana*, sugar kelp *L. saccharina*, bull kelp *Nereocystis luetkeana*, and three-ribbed kelp *Cymathere triplicata*); ''turf'' (rockweed *Fucus gardneri*, other brown algae [Phaeophyta], red algae [Rhodophyta], and green algae [Chlorophyta]); ''eelgrass'' (*Zostera marina*); and ''none.''

The first diver counted fish in the water column that extended over a 2 m wide swath along the bottom of both transects. A second diver counted all benthic (demersal) fishes along a 1 m wide swath on both transects, by moving aside algae or other vegetation; no rocks were moved, which could have introduced a slight bias in our results. Fish were identified to family level (Gadidae, Cottidae, Pholidae, Stichaeidae, Hexagrammidae, Bathymasteridae, Scorpaenidae, and other) and were divided into three size classes (<8 cm, 8–15 cm, and >15 cm). The category ''other'' consisted of fishes that were rarely sighted, including schooling fishes such as herring, sandlance, and capelin.

Schooling pelagic fishes

From 1995 to 1999, visual aerial surveys were used to map the distribution and abundance of schooling pelagic fishes (Pacific herring, Pacific sandlance, and capelin) occupying nearshore (<1 km from shore) habitats in PWS. Methods are described in detail by Brown et al. (1999). In short, aerial-survey line transects were flown approximately parallel to shore in a Cessna 185 float plane at ~203.7 km/h (110 knots) over much of PWS. Detection error was modeled using a truncated beta curve (Quang and Lanctot 1991) that accounted for the blind spot immediately under the plane and a sharp drop-off in detection, due to the incident angle of reflected light at the far edge of the sighting swath. Other sources of error, introduced from surveyor bias, species misidentification, and repeatability or short-term variability in school counts, were also estimated. Total error in school densities at each location was <20% of the mean (Brown et al. 1999); because we used only school location, rather than fish counts, in this study, we felt that error would have little impact on further analysis.

Flight path, distinctive features along path, and fish schools were recorded during the survey. From 1995 to 1997, a resolution along the transect line of 500 m with a 95% confidence interval between 492 and 508 m was achieved (Brown et al. 1999). In 1998–1999, due to improvement in computerized logging capabilities, the mean location error was 83 m with a 95% confidence interval between 81 and 85 m (Brown et al. 1999). Because our analysis included data collected from 1996 to 1999, we used a conservative resolution of 500 m in the location of fish schools.

Terrestrial habitats

Terrestrial habitat characteristics were assessed for latrine and random sites in the areas of Jackpot and Herring bays in 1996 and 1997. Based on the model developed by Bowyer et al. (1995) and Ben-David et al. (1996), each site was characterized by aspect, tidal slope, vegetated slope, proportion of old-growth trees, intertidal substrate, and exposure to wave action. Terrestrial and intertidal characteristics were assessed for a 10-m arc with its pivotal point at mean high tide. For latrine sites ($n = 61$), the pivotal point was aligned with the most obvious entrance to the latrine; for random sites ($n = 62$), the point location as determined by the GPS unit was used. Relative cover of old-growth trees was estimated with a Likert scale that ranged from

0 to 4 (Bowyer et al. 1995). Intertidal substrate (sand, gravel, small rock, large rock, and bedrock) also was rated from 0 to 4 for each type of substrate. Vegetated and intertidal slopes were measured with a hand-held clinometer (to the nearest 5°). The aspect of the latrine site was recorded in eight compass directions (e.g., N, NE, E, SE, etc.), and exposure to wave action was ranked into exposed (code 1), moderate (2), and protected (3). At each site, the number of underground burrows was recorded.

Food habits

In 1996, fresh fecal samples were collected from latrine sites where scuba-diving transects were conducted in Herring and Jackpot bays. Samples were collected within two weeks of the dates in which prey assessment occurred, thus representing the diets of otters for the same period. In total, 100 fecal samples (50 samples from Herring Bay collected from 29 latrines and 50 samples for Jackpot from 19 latrines) were submitted to Pacific Identifications (Victoria, British Columbia, Canada) for an identification of prey remains. The samples were washed and strained in an elutriator (Beckman Coulter, Fullerton, California, USA; Olesiuk 1993) and dried. Fish remains were compared with reference specimens of fishes of known size housed at the University of Victoria, British Columbia (S. Crockford, *personal communication*) to identify fish to the highest taxonomic category (species level when possible). Each identified individual fish was classified according to the three size categories (<8 cm, 8–15 cm, and >15 cm) recorded in our scuba-diving transects.

Data analysis

Radiotelemetry and sociality.—For each otter location, we determined whether the animal was alone (nonsocial; $n = 367$ locations) or occurred with at least one other radio-tagged individual (social; $n = 124$ locations, representing between five and eight groups each year for a total of 27). For two animals to be considered as being together, the telemetry signal had to originate at the same location, as verified by repeated flights over that location. In 4.2% of locations, visual observations were also obtained (Blundell et al. 2002*a*). Our designations of sociality based upon telemetry data, however, may constitute underestimates, because marked animals could have associated with unmarked ones. Nonetheless, we estimated that 40–55% of all resident animals were tagged and therefore believe that our estimates of sociality are representative (Blundell et al. 2004).

Our previous analyses indicated that, excluding associations of females with young of the year where a female is the only forager, ~47% of females and 24% of males were nonsocial (Blundell et al. 2002*a*). Among social otters, males were social in 46% of their locations, and, during 63% of that time, occurred in all-male groups. Females were only social in 26% of locations and were in mixed-sex groups 78% of that time (Blundell et al. 2002*a*). Thus, adult males dominated social groups of river otters in this system. Females, usually those that failed to reproduce, joined male groups for brief periods of time (Blundell et al. 2002*a*).

In different years, otters potentially were in different reproductive condition, which could influence their sociality, and at any given point in time, an otter could choose to be social or nonsocial based on the cost or benefit of sociality. Therefore, we used otter locations as the sampling unit. Although this could lead to bias as a result of pseudoreplication, ignoring the biologically significant decisions made by individual otters would mask the very process that we were interested in exploring. In following analysis, we controlled for the effects of such pseudoreplication by using randomization and weighting of data by the number of repeated observations (Manly 1991).

We determined the location of otters relative to random and latrine sites by querying Geographic Information System (GIS) ArcInfo (ESRI 2004) for otter locations within 100 m of either type of site. Although foraging may occur anywhere along the shoreline, otters are not known to go ashore at random sites (i.e., random sites were those that did not have otter sign). Given the measurement error of GPS (≤100 m) when these data were collected, we could not determine with certainty that a location within 100 m of a site necessarily constituted a visit to the exact site for purposes of either foraging or scent-marking. Nonetheless, locations recorded near latrine sites constitute a high probability of a visit to a site.

Characteristics of latrine and random sites.—We identified those variables that distinguished between otter latrines and random sites, similar to previous analyses conducted by Bowyer et al. (1995, 2003), but also included marine habitat characters obtained from dive data. To test for differences in terrestrial and marine habitat features between latrine and random sites, we used logistic regression with site type (latrine or random) as the dependent variable and habitat features as independent variables (Manly et al. 2002). We controlled for multicolinearity by excluding one of each pair of variables that were significantly ($P < 0.05$) correlated at $r = |0.4|$. We ensured that the data did not depart from a logistic-regression model with Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989), and used AIC (Akaike information criterion) scores to guide model selection (Burnham and Anderson 2002). We evaluated the statistical significance of each independent variable using a general linear test procedure (SAS Institute 2000, Neter et al. 1996). In these analyses, observations were weighted by the number of dives at each site. For those variables that were correlated, we performed univariate analyses

to evaluate their effects on separation between latrine and random sites.

Fish distributions.—Data on abundance and location of intertidal fishes from Herring and Jackpot bays were pooled because earlier studies (Bowyer et al. 2003) noted no difference in fish density between areas. Because numerous sites had no fish observations in association with particular habitat characters, we collapsed substrate variables to include three categories: (1) rock reef and boulder; (2) cobble and gravel; and (3) sand and mud. Similarly, because leafy brown vegetation was the dominant feature on the marine landscape (57.6% of all observations, weighted for multiple counts on a single site), we reduced marine vegetation to include two categories: (1) leafy brown; and (2) other vegetation. For each scuba transect, dominant vegetation and substrates were those that occurred at two or three of the three sample points. In cases where the vegetation or substrate differed at each point, the category was assigned as mixed.

To test whether fishes were more likely to be associated with latrines than random sites, we used logistic regression on pooled data for density of all fish families. We conducted the analysis only for fish that were larger than 8 cm, because otters rarely consume smaller fish (Kruuk 1995). For each fish family analyzed separately, we used general linear models with Poisson error (i.e., Poisson regression; McCullagh and Nelder 1989) to model fish counts as a function of dominant types of marine substrate and vegetation. We evaluated the statistical significance of the test and each independent variable using the general linear test procedure (Neter et al. 1996). In all analyses, data were weighted by the number of dives performed at each site.

Food habits.—We determined diets of otters by calculating the frequency of occurrence of fishes in their feces (Kruuk 1995). We quantified the data using the same fish families assessed during our scuba transects, including a miscellaneous category for fishes that were identified in feces but did not occur on transects. We separated feces with >5 schooling pelagic fishes (herring, sandlance, or capelin) in a single sample, or >15 Gadidae (which occur in small schools), from all other feces because those containing a prevalence of schooling fishes (e.g., the remains of as many as 57 individual schooling fishes identified in a single sample) were probably deposited by social otters (Blundell et al. 2002*a*). We considered larger, more conservative, numbers of Gadidae to indicate feces of social otters because those fishes occur in large numbers throughout the marine system and are slower than herring, sandlance, or capelin. Thus, solitary otters not relying upon cooperative foraging may be able to opportunistically catch more Gadidiae than herring, sandlance, or capelin, although the numbers of such fish in their feces are likely to be limited, given the schooling behavior of these fish. We calculated the frequency of occurrence in those samples with and without a preponderance of schooling fishes as a representation of diets of social and nonsocial otters, respectively.

Sociality and schooling fishes.—The average distance of social and nonsocial otters to fish schools was assessed with a one-way ANOVA. The significance of differences was evaluated using randomization to control for pseudoreplication (Manly 1991). In that analysis, the average distance of each individual otter location to all schooling fish groups was determined with a query of GIS. Because of differences in location error (100 m for otters and 500 m for fish schools), we had to calculate the average distance to all fish schools rather than the distance to the nearest school. To explore temporal effects (i.e., the effects of time on spatial proximity between otter locations and fish schools), we conducted the same analysis in six time windows (3, 12, 18, 24, 36, and 48 hours between recorded location of schools and otter locations).

Otter distribution in relation to fish densities and habitat variables.—For each site (latrine or random), the number of otter locations within a 100 m radius was counted. The count was conducted separately for social and nonsocial otters. To evaluate the relation between otter distribution and fish densities or habitat variables associated with fish distribution, we modeled otter counts by the terrestrial habitat variables that significantly separated latrine from random sites and both marine habitat variables, but did not account for whether sites were latrines or random. A separate log-linear model (Poisson distribution; McCullagh and Nelder 1999) for social and nonsocial animals was constructed and models were then compared. In this analysis, gender (male or female) was ignored because we assumed that social and nonsocial animals would behave in the same manner regardless of gender (Blundell et al. 2002*a*). We repeated the analysis with the terrestrial habitats and fish density to explore whether fish densities, rather than marine habitat variables, were associated with otter counts.

Distribution of male otters in relation to fish densities and female counts.—To test whether male distributions were dependent on those of females, we modeled otter counts by fish densities and female counts, regardless of whether sites were latrines or random. A separate log-linear model (Poisson distribution; McCullagh and Nelder 1999) for social and nonsocial males was constructed and models were then compared.

Home range and distribution of latrines.—In this analysis, each year of telemetry data for each otter was considered an independent sample, resulting in a sample size of 51 home ranges from 35 individual otters (10 females and 25 males) with more than 25 locations. Home ranges were estimated with fixed-kernel analyses and the reference-smoothing parameter (Blundell et al. 2001). Home range contours were obtained for 95% isopleths for each otter in each year with RANGES V (Kenward and Hodder 1996). Because otters generally confine their movements to the shoreline (Blundell et

al. 2001), we considered the outermost intersections of the home range contour with the shoreline as the boundary of that home range.

To test whether scent-marking was associated with passive defense of territories, and the associated prediction that latrines should occur most often at the borders of home ranges, we measured the distance of latrines within the home range to the borders (i.e., the outermost intersections between home range contour and shoreline). We calculated the mean and median distance of latrines to the boundary of the home range for each otter with the GIS ARC/VIEW. We reasoned that scent-marking, as a mechanism for border defense, should occur within a distance equivalent to 5% of the average shoreline length of an otter home range ($\bar{X}$ = 20.3 km; Blundell et al. 2002*a*); in other words, within 1 km of a home range border. We used a one-sample *t* test (Zar 1999) to determine whether the mean distance of latrines was significantly closer to the home range boundary than 1 km; performing that test for all otters, males and females, and social and nonsocial otters. For this assessment of social otters, an otter was considered social if it was located with other otters on at least one occasion during a year of telemetry tracking; nonsocial otters were never located with other otters.

Results

Food habits

Schooling fishes were the most prevalent fishes identified in otter feces (39.9%, Fig. 2), followed by Cottidae (15.4%) and Pholidae (14.8%). Schooling fishes included 22.7% herring, 16.2% sand lance, and 1.1% capelin (Fig. 2). In feces of otters that probably were socially foraging (i.e., those samples with a high incidence of schooling fishes), schooling fishes constituted 62% of the identified prey remains, followed by Gadidae (10%), Pholidae (8%), and Cottidae (7.6%). Prey remains identified in feces of otters that probably foraged as solitary individuals were dominated by Cottidae (26.3%) and Pholidae (24.1%; Fig. 2).

Otter locations relative to latrine and random sites

In an analysis with site (latrine or random) as the sampling unit, social otters were located near fewer individual latrine sites (n = 25) than were nonsocial otters (n = 123 sites potentially visited). Of those sites, 103 were potentially visited only by solitary animals, 20 were potentially visited by both social and nonsocial otters, and five were probably used by social animals only. We recorded no otter locations near 62 additional latrine sites.

In a total of 491 occurrences of otter locations within 100 m of latrine and random sites (with otter location as the sampling unit), both social otters and nonsocial otters were located less often near random sites (n = 38 and 105 observations, respectively) than latrine sites

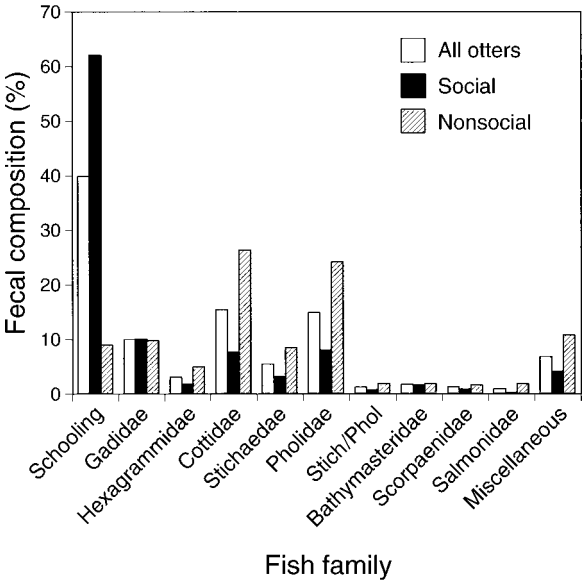

FIG. 2. Diet of coastal river otters in Prince William Sound, Alaska, represented as the percentage of each fish family in the diet (i.e., the number of fish in each fish family divided by the total number of fish identified in feces) in all fecal samples analyzed for prey content (all otters). In those cases in which remains of Pholidae could not be distinguished from those of Stichaeidae, they are reported as a mixed group (Phol/Stich). The percentage of fish in the diet also was calculated for those samples that contained a prevalence of schooling fishes (>15 Gadidae or >5 schooling pelagic fishes) as representative of diets of social otters, and those samples without a prevalence of schooling fishes were quantified as being representative of the diet of nonsocial otters.

(n = 86 and 262; P = 0.06 and 0.003, respectively, Z test of two proportions; Zar 1999). Nonetheless, the number of visits per latrine (i.e., intensity of use) was greater for social otters (average of 3.44 visits per site; 86 visits to 25 latrines) than for nonsocial otters (average of 2.13 visits per site; 262 visits to 123 latrines).

Observations of male otters were more frequent within 100 m of latrines (n = 216) than random sites (n = 115), but this trend was more pronounced for females (latrines n = 132, random sites n = 28). Of those observations, male otters were found in association with latrine sites with burrows in 31 observations (14% of locations), and females occurred near sites with burrows on 35 occasions (27%).

Terrestrial and marine habitat features at latrine and random sites

As in previous studies (Bowyer et al. 1995, Ben-David et al. 1996), latrine sites had a greater presence of old-growth trees (coefficient 0.97, $P < 0.001$), vegetated slopes that were significantly less steep (coefficient −0.09, $P < 0.001$), and more large intertidal rock (coefficient 0.99, P = 0.007) than did random sites. The dominant marine substrate did not differ between latrine and random sites (P = 0.15), although

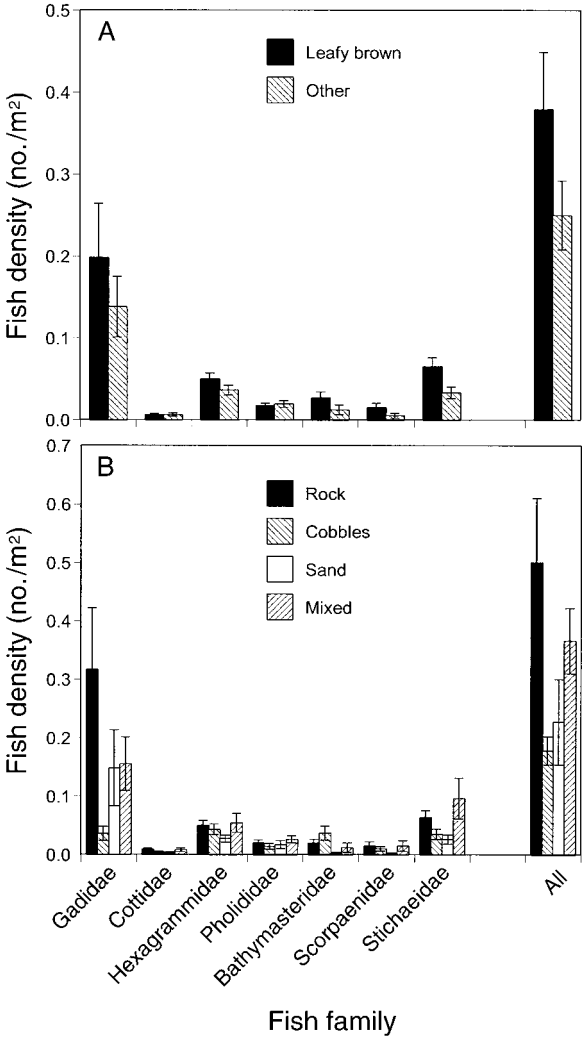

FIG. 3. Densities of fish by fish family, and for all fish families combined (number per square meter for fish >8 cm), that were identified in association with (A) dominant marine vegetation and (B) dominant marine substrate in Prince William Sound, Alaska. Key: leafy brown includes multiple *Laminaria* spp. and constituted the most prevalent marine vegetation, occurring on ~58% of all sites surveyed; rock, rock reef and boulder; cobbles, cobbles and gravel; sand, sand and mud; mixed, no dominant substrate (i.e., a different substrate identified at each of three points sampled on the transect).

this may be a result of the correlation between intertidal rock and dominant substrate ($r = -0.26$, $P = 0.005$, where rock reef/boulders is coded 1, cobbles/gravel 2, sand/mud coded 3, and mixed is coded 0). Marine vegetation and tidal slope were highly correlated with large intertidal rock ($r = 0.47$, $P < 0.001$, and $r = 0.4$, $P < 0.001$, respectively), and thus were excluded from the overall model. Univariate logistic regression indicated that latrines were characterized by high prevalence of leafy-brown vegetation compared with random sites (coefficient 1.34, $P = 0.006$), and steeper tidal slopes (coefficient 0.03, $P = 0.025$).

Fish as a function of marine substrate and vegetation

When all intertidal and demersal fishes were considered collectively, there were more fish associated with latrine (0.39 ± 0.1 fishes/m^2; mean ± 1 SE) than random sites (0.24 ± 0.05 fishes/m^2; $P = 0.049$). This probably was due to the higher density of Gadidae and Scorpaenidae at latrine sites (for Gadidae, 0.22 ± 0.1 fishes/m^2 at latrines vs. 0.1 ± 0.05 fishes/m^2 at random sites, $P = 0.066$; for Scorpaenidae, 0.02 ± 0.005 fishes/m^2 at latrines vs. 0.005 ± 0.002 fishes/m^2 at random sites, $P = 0.039$). For all other fish families, densities did not differ between latrine and random sites.

In a model describing densities of all intertidal and demersal fishes as a function of both marine habitat variables, fish densities were positively associated with the presence of leafy brown vegetation ($P = 0.049$; Fig. 3A) and rock reef substrate ($P = 0.001$; Fig. 3B). The lowest overall fish densities were associated with cobble substrates (Fig. 3B). For individual families, however, fish densities in relation to vegetation and substrate composition varied. Several fish families were positively associated with leafy brown vegetation (Bathymasteridae, $P = 0.044$; Hexagrammidae, $P = 0.057$; Scorpaenidae, $P = 0.026$; and Stichaeidae, $P = 0.0001$; Fig. 3A). Similarly, several fish families were found in higher densities in rock reef and mixed habitats (Fig. 3B). These included Gadidae (rock reef, $P = 0.042$), Cottidae (rock reef, $P = 0.007$; mixed, $P = 0.04$), Stichaeidae (rock reef, $P = 0.056$; mixed, $P = 0.001$), and Hexagrammidae (rock reef, $P = 0.052$; mixed, $P = 0.047$). Bathymasteridae occurred more often in association with rock reef ($P = 0.062$) and cobbles/gravel ($P = 0.004$) than with sand/mud. Scorpaenidae were found less frequently in sand/mud substrates than in mixed ($P = 0.08$), rock reef ($P = 0.114$), and cobbles/gravel ($P = 0.18$) substrates. Pholidae were found in similar numbers across all substrates ($P = 0.208$; Fig. 3B).

Otter distribution as a function of schooling fishes

There was no difference in distance from otters to schooling fishes between social and nonsocial animals at intervals (hours between locating fish schools and otters) spanning 24–48 hours (Fig. 4). At shorter intervals (3, 12, and 18 hours), social otters were located significantly closer to fish schools than were nonsocial otters ($P = 0.03$, ANOVA by randomization; Fig. 4).

Otter distribution in relation to fish densities and habitat variables

The models describing otter distributions as a function of marine and terrestrial habitats identified the presence of old-growth forest as an important habitat variable for both social and solitary otters (Appendix A). High counts of social otters were associated with steep vegetative and tidal slopes, and were less asso-

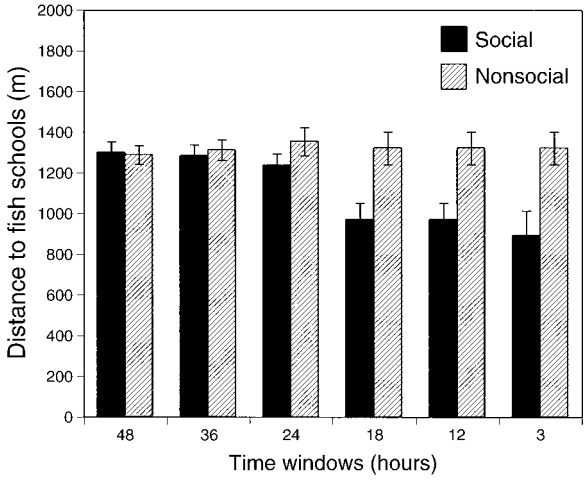

FIG. 4. Distance (mean ± 1 SD) between otter locations and location of fish schools, at various time intervals (hours between recorded location of schools and otter locations), for social and nonsocial otters in Prince William Sound, Alaska. Sample sizes were: for 48 h, $n = 56$ social otters, $n = 127$ nonsocial otters; for 36 h, $n = 54$ social, $n = 96$ nonsocial; for 24 h, $n = 47$ social, $n = 48$ nonsocial; for 18 h, $n = 11$ social, $n = 38$ nonsocial; for 12 h, $n = 11$ social, $n = 38$ nonsocial; for 3 h, $n = 7$ social, $n = 38$ nonsocial. Distances to fish schools were significant for time windows ≤18 hours.

ciated with cobbles/gravel and mixed habitats as dominant marine substrate (Appendix A). In contrast, high counts of nonsocial otters were associated with a high incidence of leafy brown vegetation as the dominant marine vegetation (Appendix A). Models assessing the effects of fish densities again identified the presence of old-growth forest as an important habitat variable for both social and solitary otters (Appendix B), but fish densities only influenced the counts of social otters (Appendix B). Models of individual fish families identified the densities of Gadidae (coefficient 0.11, $P = 0.08$), Bathymasteridae (coefficient 5.38, $P = 0.003$), Hexagrammidae (coefficient 6.04, $P < 0.001$), and Scorpaenidae (coefficient 8.37, $P < 0.001$) as positively associated with counts of social otters.

Distribution of otters in relation to gender and fish

In models in which the location of male otters was the dependent variable and the location of females and fish densities were the independent variables, social otters again were positively associated with fish densities (coefficient 0.17, $P = 0.004$) and negatively associated with female counts, although the latter was only marginally so (coefficient −0.33, $P = 0.087$). Nonsocial male otters were more negatively associated with female otters (coefficient −0.28, $P = 0.056$) and were not associated with fish densities (coefficient 0.002, $P = 0.98$).

Distribution of latrines within home ranges

The mean distance of latrines from home range boundaries was significantly greater than our expected value of 1 km for all otters, male otters, nonsocial male otters, and social and nonsocial otters (Table 1). Latrines were located closer to home range boundaries for females (all females and nonsocial females) than for males (Table 1). Females also had fewer latrines in their home ranges than did males (Table 1), but the number of latrines within home ranges was similar for social and nonsocial otters (Table 1). No difference in mean distance of latrines to home range boundary was detected for social compared with nonsocial otters.

Otter behavior and transport of marine-derived N and P to terrestrial latrine sites

A study on 15 wild-caught captive male river otters (Ben-David et al. 2000) determined that otters consume, on average, 1140 g of fishes/d (M. Ben-David, *unpublished data*), which is equivalent to nearly 10% of their body mass. Similar results were obtained for Eurasian otters (*Lutra lutra*; Kruuk 1995). Such a quantity of fishes will contain ~40 g of N because tissues of marine fishes are composed of 11.7% N in dry matter

TABLE 1. Distance (mean and median) between latrines and home range boundary for coastal river otters in Prince William Sound, Alaska, USA, and concentration of latrines within 1 km of boundary, which is likely to facilitate territorial defense through scent-marking.

Otter category	No. otters	Distance to boundary (km) Mean	(1 SE)	t†	P	Median distance (km)	No. latrines Mean	(1 SE)	t‡	P
All otters	51	1.46	(0.094)	4.85	<0.001	1.48	31.4	(2.6)		
Females	16	1.1	(0.076)	0.797	0.438	1.1	23.3	(2.5)	2.76	0.008
Males	16	1.6	(0.121)	5.25	<0.001	1.7	35	(3.5)		
Social	30	1.42	(0.099)	4.19	<0.001	1.42	31.8	(3)	−0.204	0.84
Nonsocial	30	1.52	(0.186)	2.77	0.012	1.57	30.7	(4.8)		
Nonsocial female	10	1.1	(0.115)	0.77	0.464	1.2	21.5	(3.1)	2.06	0.063
Nonsocial male	10	1.95	(0.303)	3.1	0.013	1.99	39.8	(8.3)		

Note: Because some distributions were skewed, we present both mean and median values (Zar 1999).

† One-sample t test to determine whether the mean distance of the latrines was significantly closer to the home range boundary than 1 km.

‡ The test statistic (t) and probability (P) are derived from one-sample t tests comparing mean number of latrines between males and females, and social and nonsocial otters. Equal variance is not assumed.

(M. Ben-David, *unpublished data*). Because river otters achieve adult size at an early age (~1 year) and do not hibernate (Melquist and Hornocker 1983), it is likely that most of the consumed N will be excreted in feces and urine. For example, non-hibernating brown bears (*Ursus arctos*) in Alaska excreted 99% of N derived from salmon through feces (3%) and urine (96%; Hilderbrand et al. 1999). Thus, assuming that N metabolism is similar in river otters, each otter may deposit ~39.6 g N/d at latrine sites. The same captive study (Ben-David et al. 2000) determined that each otter defecates, on average, 7.7 times/d. Because defecation is always accompanied by urination (M. Ben-David, *personal observation*), it is reasonable to assume that, at any visit to a latrine, an otter will excrete, on average, 5.15 g of N.

In this study, we monitored otters an average of 30 days per year, in which solitary animals visited each latrine 2.13 times and social otters visited 3.44 times. Extrapolation of these observations to an entire year (365 d) results in 26 visits to a latrine by solitary animals and 42 visits by social otters. We calculated N deposition at each site:

$$N_{\text{total}} = (5.15 \text{ g} \times V \times G)/A. \quad (1)$$

Here N_{total} is the annual amount of nitrogen deposited at the site in grams per square meter per year; V is the number of visits to the site per year; G is group size; and A is the area of the latrine in square meters.

Assuming that latrines are 50 m^2 in area (Swimley et al. 1998), N deposition at latrine sites will range between 2.7 and 47.6 g $N \cdot m^{-2} \cdot yr^{-1}$ for group sizes of 1–11 animals, respectively, at the average visitation rate of solitary and social otters. Using actual counts of otter visitation to 22 latrines in Herring Bay and representative group sizes of four and seven otters (Blundell et al. 2002*a*), estimates of N deposition vary from 1.3 to 76.5 g $N \cdot m^{-2} \cdot yr^{-1}$ (Fig. 5).

Similarly, the variation in otter activity at latrine sites may result in significant transport of phosphorous (P) to latrines. The daily fish diet of otters contains ~5 g P (0.5% of wet mass; Schreckenback et al. 2001). Assuming that adult otters excrete 99% of consumed P in feces (Robbins 1993) and using similar calculations, river otter latrines may receive 0.4–6.7 g $N \cdot m^{-2} \cdot yr^{-1}$ depending on group size (1–11 animals, respectively) and the difference in latrine use between solitary and social otters.

Discussion

Our investigation of the relationships among social organization, communication, and landscape use of coastal river otters resulted in some unexpected conclusions. As in previous studies, latrine sites had a greater presence of old-growth forest, significantly less steep vegetated slopes, and more large intertidal rock than did random sites. In addition, we were able to demonstrate that latrines had higher prevalence of leafy-brown marine vegetation (*Laminaria* spp) and higher densities of intertidal and demersal fishes. These higher densities of intertidal and demersal fishes were mostly driven by Gadidae and Scorpaenidae. Member species of these families such as Pacific cod (*Gadus macrocephalus*) and black rockfish (*Sebastes melonops*) frequently occur in small schools (Eschmeyer et al. 1983).

This phenomenon may explain the unexpected observation that social, rather than nonsocial, otters were more closely associated with intertidal and demersal fishes. It is important to note here that Hexagrammidae, Bathymasteridae, and Scorpaenidae, those families that (together with Gadidae) appeared to be closely associated with the distribution of social otters, compose a small and probably insignificant part of the diet of otters (Fig. 2). In contrast, Gadidae may compose up to 10% of the diet of social otters. Although their importance is lower than that of pelagic fishes (Fig. 2), Gadidae may comprise a significant part of the diet of social otters, especially when forage fishes such as herring, sandlance, and capelin are unavailable. Thus, it appears that the association of social otters with Gadidae is a function of their schooling behavior. The relation between social otters and Hexagrammidae, Bathymasteridae, and Scorpaenidae is likely to be a byproduct of the association between Gadidae and rock reef habitats; all of those fishes were more prevalent in that habitat (Fig. 4).

It is surprising that we found no association between nonsocial otters and fish densities even for Cottidae and Pholidae, which were the two most prevalent prey items in their diets (Fig. 2). That densities of Cottidae and Pholidae were not explained by any of our models may suggest that their distributions, and therefore those of nonsocial otters, are determined by other unmeasured factors. Alternatively, those fishes may occur ubiquitously on the landscape (Dean et al. 2000). This may be further supported by our observation that nonsocial otters were positively associated with *Laminaria* spp., which were recorded in 57.6% of all scuba transects.

That the distribution of social otters on the landscape may be influenced by the distribution of schooling fishes is further supported by our finding that social otters were located closer to schooling pelagic fishes than were nonsocial otters (Fig. 4). This is consistent with our earlier studies (Blundell et al. 2002*a*), in which social otters consumed higher quantities of schooling pelagic fishes than did nonsocial otters. The proximity of social otters to schooling fishes was only evident, however, within a short time window (≤18 hours). These short associations reflect the high mobility of both fish schools and foraging otters. Indeed, both herring and sandlance exhibited high temporal and spatial variability in staging within the study region in PWS (Brown et al. 1999). This high temporal fluidity in the association between social otters and schooling fishes

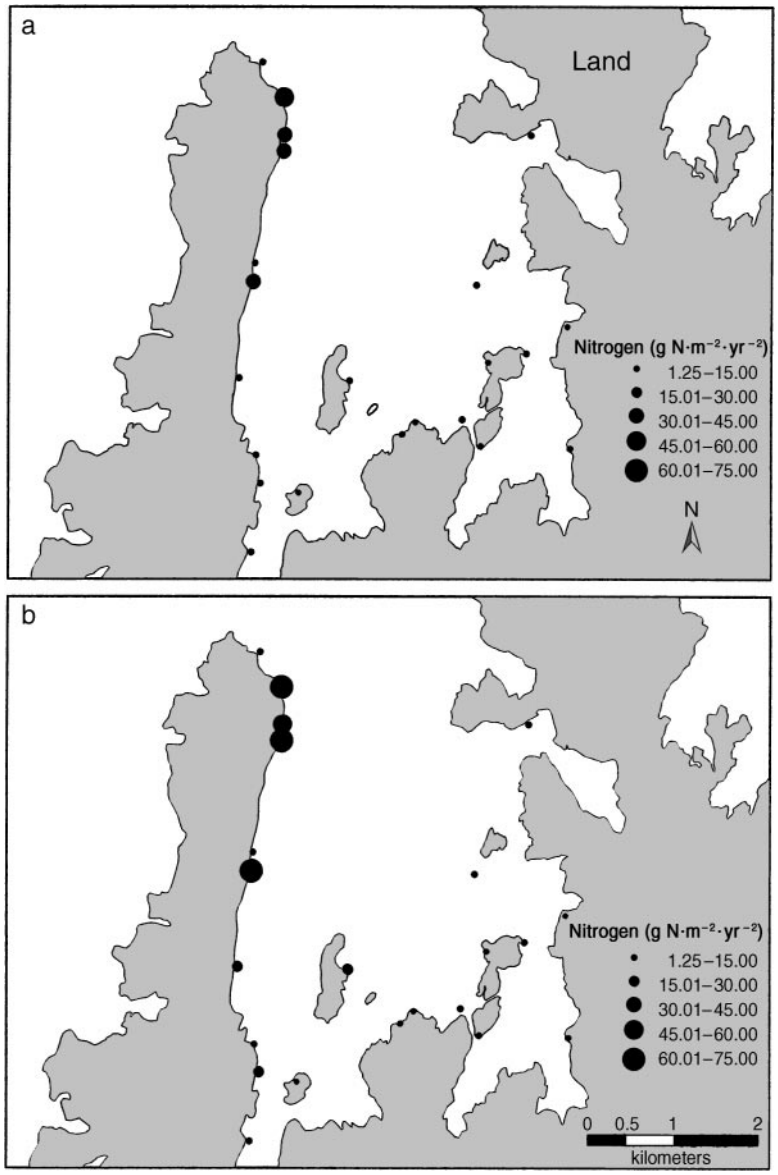

FIG. 5. Illustration of the variability in N inputs to river otter latrines in Prince William Sound, Alaska. The relative size of the circles indicates the amount of N deposition per year in each latrine. The amount of N deposition was calculated based on an average of 5.15 g N per visit per otter. For each site, the actual number of visits during our sampling period was used. The number of visits was extrapolated for the entire year, and the latrine area was assumed to be 50 m^2 (Swimley et al. 1998). N inputs were calculated assuming a group size of (a) four otters and (b) seven otters.

will, in turn, significantly influence resource sheds of terrestrial communities.

That some fishes occurred at higher densities at latrine sites may suggest that scent-marking in coastal river otters is associated with a claim to a foraging area (Gosling 1982, Kruuk 1992), or signaling the use of resources, similar to Eurasian otters (Kruuk 1992, 1995). Nonetheless, close examination of the data may lead to different conclusions. First, social otters, which were more closely associated with fish densities, visited fewer latrines than did nonsocial otters. Of these sites, only five of 25 were exclusively visited by social otters. Second, male otters were found less frequently near latrines than were females. Blundell et al. (2002*a*) reported that, in PWS, ~47% of females were nonsocial, compared with only 24% of males. Thus, it seems that social otters may be found less frequently near latrines than nonsocial otters. Third, the main marine habitat feature that separated latrines from random sites was the prevalence of *Laminaria* spp., which was significantly associated with counts of nonsocial otters, but was only associated with the densities of fish families that were less important in the diet of nonsocial otters (i.e., Bathymasteridae, Hexagrammidae, Scorpaenidae,

and Stichaeidae). It is likely that the association of nonsocial otters with this marine habitat feature is a by-product of the high correlation between *Laminaria* species and large intertidal rock. Thus, it is unlikely that latrines are used to signal the depletion of food patches.

What is the function of scent-marking at latrines for male otters? We predicted that if scent-marking facilitates mutual avoidance, nonsocial otters should be found more often than social otters in association with latrines and terrestrial habitat features that indicate scent-marking. Indeed, we found that nonsocial otters used 123 latrines compared to only 25 used by social otters. Nonetheless, social otters visited latrines with greater intensity than nonsocial otters, and both groups were positively associated with large intertidal rocks, which serve as scent-marking platforms (Bowyer et al. 1995, Ben-David et al. 1996), and with the presence of old-growth conifer forests that prevent the dehydration of scent-marks in the summer or their cover by snow in the winter (M. Ben-David, *personal observations*). The only explanation that we can offer to this discrepancy relates to the plastic social organization of river otters in PWS (Blundell et al. 2002*a*, *b*). It is likely that while solitary male otters use latrines to facilitate mutual avoidance, this behavior also serves as intra-group communication for social animals. Blundell et al. (2002*b*) observed that social males left their group and conducted long breeding migrations prior to the arrival of schooling pelagic fishes. These males reunited with their group members at the end of the breeding season (Blundell et al. 2002*b*). Such separation and reunion can also occur on shorter time periods such as several hours or days when individuals separate during foraging excursions (M. Ben-David, *unpublished data*). In studies performed in captivity, Rostain et al. (2004) noted that dominant male otters showed more interest in scent-marks than did subordinate individuals, suggesting that, indeed, among social otters, scent-marking at latrines serves for intra-group communication. Although additional manipulative experiments in the wild are warranted, our study indicates that the function of scent-marking for social otters may be to facilitate intra-group communication (Durbin 1989, Rostain et al. 2004), perhaps enabling otters that have separated from the group to reunite with their conspecifics for social foraging.

Three lines of evidence suggest that females, but probably not males, may use latrines to signal territoriality. First, the location of latrines relative to the boundary of home ranges of females was not significantly different than the 1 km that we expected if latrines were used for territorial defense (Table 1). Second, as previously mentioned, females were more likely to be found near latrines than males. Finally, solitary males were less likely to be found near females compared with social males, a result consistent with our previous studies (Blundell et al. 2002*a*); when females were social, they associated with male groups, probably to obtain a better quality diet via cooperative foraging. The lack of association between females and solitary males may be a result of high competition for prey items captured by solitary foragers (the likely method of hunting for most females and nonsocial males), and thus a need for territorial defense. That females may use latrines to mark territories (Hornocker et al. 1983) is further supported by our previous observation that dispersal distances were significantly higher for females than for males (Blundell et al. 2002*b*). Blundell et al. (2002*b*) hypothesized that this difference resulted from the ability of new dispersing males to join neighboring male groups, whereas females were required to find exclusive home ranges (Blundell et al. 2002*b*).

Alternatively, latrines may provide greater cover for females and their young. Although females had significantly fewer latrines within their home range than males (Table 1), they were found more often near latrines, especially those with burrows (27% of the latrines for females and only 14% for males). Female otters are accompanied by young for up to a year after birth (Melquist and Hornocker 1983, Noll 1988). In the first several months, otter pups may be vulnerable to predation by aerial predators, such as Bald Eagles (*Haliaeetus leucocephalus*; Blundell et al. 2002*a*), and may benefit from the cover afforded by old-growth forests and burrows. Evaluating whether latrines are used by females for territorial defense against other otters, or more for protection of young from aerial predators, and the effects of these different behaviors on landscape use and nutrient transports will require further studies.

Can we conclude that scent-marking at latrines is not a function of male–female communication of reproductive status? We found that solitary males were less likely to be found near females than were social males, which is in contrast with our initial prediction. Our analysis, however, encompassed the entire year, rather than the breeding season. Unfortunately, for the period of the breeding season we have only two counts of females near our sampled sites. This small sample size precludes evaluation of the association between males and females during this period. We believe that, during this period, females attend to young sequestered in natal dens and are less likely to be detected with aerial telemetry (Blundell et al. 2002*a*).

The differing strategies in the social organization of coastal river otters and the emerging differences in the function of latrines probably affect the transfer of marine nutrients to the terrestrial community at the level of the landscape. Recall that nonsocial otters were located near 123 latrine sites with less intensity (each latrine visited, on average, 2.13 times), compared with the 25 latrines potentially used by social otters with greater intensity (on average, 3.44 times). Thus, nonsocial otters deposit lower amounts of N and P (2.7 g $N \cdot m^{-2} \cdot yr^{-1}$ and 0.4 g $P \cdot m^{-2} \cdot yr^{-1}$), at more sites, probably to facilitate mutual avoidance, whereas social ot-

ters deposit high amounts of these nutrients (up to 47.6 g $N \cdot m^{-2} \cdot yr^{-1}$ and 6.7 g $P \cdot m^{-2} \cdot yr^{-1}$) at fewer sites, probably for intra-group communication. In addition, although sites visited by males are distributed more evenly along the shoreline, female latrines are concentrated at the boundaries of their home ranges, probably for the defense of territories. Finally, the high temporal fluidity in the association between social otters and fish schools suggests that visits by social otters to specific latrines along the coast will be unpredictable. In concert, the function of latrines and the behaviors of otters create variable resource sheds in time and space for the terrestrial community of the land margin. Gaining a more complete understanding of the effects of otter behavior on resource sheds of terrestrial communities will require the development of spatially explicit, individual-based models (DeAngelis and Gross 1992). Such models will use the distribution of demersal and schooling fish, the number of otters, and the demography, group affiliation, and distribution of otters on the landscape as inputs. Based on the relations described here, the model will simulate visitation rates to specific latrines and will calculate nutrient deposition at specific sites.

Nutrient deposition by river otters could influence processes in the terrestrial community only if it is large relative to other sources. Recently, Helfield and Naiman (*in press*) developed a mass balance model for N deposition in riparian zones near Wood River, Alaska. They determined that leaching from upland forests was the main source of N inputs to riparian zones in their study. Wet atmospheric deposition, N fixation, and contributions from salmon accounted for the rest of the N inputs (Helfield and Naiman, *in press*). Developing a similar model for river otter latrines in the rain forests of coastal Alaska will require information that is currently unavailable. For example, unlike streams, which are found at the bottom of water catchments, river otter latrines frequently occur at points of land and are elevated relative to the surrounding landscape (Bowyer et al. 1995). Thus, in many cases, leaching may be responsible for loss of N and P from latrines rather than be a major source of these nutrients. Also, contributions from N fixation are difficult to assess because the distribution of alder is patchy and, in many cases, is limited to individual plants along sections of the coastline. The abundance of other N fixers such as legumes, lichens, or bryophytes is unknown, although Helfield and Naiman (*in press*) suggest that the relative contributions of these sources in riparian zones is probably negligible. The range in atmospheric wet N deposition in Alaska is 0.01–0.2 g $N \cdot m^{-2} \cdot y^{-1}$ (*available online* from the National Atmospheric Deposition Program)[7] (see Lilleskov et al. 2001). This represents a small fraction of N deposition relative to contributions from otter activity. Similarly, contribution of P from non-otter sources also may be limited. Information on P availability in our system is scarce, so as a comparison, we offer P content in heath soils in northern Alaska, which ranges between 0.007 and 0.01 g P/m^2 (Giblin et al. 1991).

That otter nutrient deposition could have significant effects on ecosystem processes in the land margin can be discerned from our recent data. Soil N at latrines was significantly higher (1.63% ± 0.07%) than at random sites (0.92% ± 0.02%; Mann-Whitney, $P = 0.003$; M. Ben-David and J. Gulledge, *unpublished data*), probably representing higher biomass of soil microorganisms. In addition, the difference in $\delta^{15}N$ between the same species of plants growing on river otter latrines and those growing at random sites ranged from ~5‰ in goose-necked moss (*Rhytidiadelphus triquetrus*) to 18‰ in red elderberry (*Sambucus racemosa*; Ben-David et al. 1998*a*). More importantly, the variance in both percentage N (M. Ben-David and J. Gulledge, *unpublished data*) and values of $\delta^{15}N$ (Ben-David et al. 1998*a*) was several times larger at latrines than at random sites. Ben-David et al. (1998*a*) hypothesized that this larger variance is a result of the variation in visitation rate of otters to specific latrines.

What would be the landscape consequences of such high variability in transport of marine-derived nutrients to land? Spatial and temporal variation in nutrient inputs may have significant effects on the structure and function of the plant community in coastal forests, because primary production in forests is often limited by the availability of N and P to plants (Nadelhoffer et al. 1995, Treseder and Vitousek 2001). In coastal forests of the Pacific Northwest, plants fertilized by piscivorous predators exhibited higher N concentrations (Ben-David et al. 1998*b*) and higher growth rates than their conspecifics elsewhere (Helfield and Naiman 2001, 2002). In addition, sites fertilized by river otters in PWS had higher plant diversity than random sites (M. Ben-David, *unpublished data*). Thus, the high variability in deposition of N and P at latrines may create a mosaic of patches that experience variable resource sheds (Fig. 5) and therefore differ in community composition, plant tissue stochiometry, and plant size. Such differences may, in turn, influence space use and behavior of primary consumers in this system. The effects of otter-dependent resource sheds on community and ecosystem processes merit further investigation.

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[7] ⟨http://nadp.sws.uiuc.edu/sites/siteinfo.asp?net=NTN&id=AK01⟩

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APPENDIX A

A table showing results of models describing the relation between otter counts and terrestrial and marine habitat variables for coastal river otters in Prince William Sound, Alaska, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-074-A1.

APPENDIX B

A table showing results of models describing the relation between otter counts and densities of intertidal and demersal fishes and terrestrial habitat variables for coastal river otters in Prince William Sound, Alaska, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-074-A2.