

## SPACE USE AND SOCIALITY OF RIVER OTTERS (*LONTRA CANADENSIS*) IN MINNESOTA

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The river otter (*Lontra canadensis*) has a complex social system, which varies widely across its range. We examined patterns of space use and social interactions for a native population of river otters in southeastern Minnesota. We radiomarked 28 river otters and monitored annual home ranges and core areas, static and dynamic interactions, and site fidelity. We compared these characteristics and interactions between sexes and age classes. Annual home ranges of male river otters were 3.2 times greater than those of females ( $P = 0.042$ ), and annual core areas of males were 2.9 times greater than those of females ( $P = 0.083$ ). The static interactions among river otters were extensive, with 69% of the individuals exhibiting core-area overlap. Overall dynamic interactions were positive (i.e., animals were closer together than expected). Males used 74% of their year 1 home range during year 2, and females used 75%. Females on average used only 39% of their core area from year 1 during year 2, whereas males used 65%. In general, conspecifics were not excluded from home ranges or core areas and signs of cooperation were evident, suggesting that river otters in southeastern Minnesota were social rather than territorial.

Key words: core area, dynamic interactions, fidelity, home ranges, *Lontra canadensis*, river otters, sociality, static interactions, territoriality

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Knowledge of home ranges is used to understand the organization of animals through space and time (Kernohan et al. 2001). Home ranges of river otters (*Lontra canadensis*) are somewhat distinctive, because they are a semiaquatic mammal and are generally geographically confined to linear areas or edges associated with water bodies (Blundell et al. 2001). However, under some environmental conditions, such as large continuous marshes, home ranges of river otters can be polygon shaped (Melquist and Dronkert 1987; Reid et al. 1994). Home ranges of male river otters are typically larger than those of females (Melquist and Hornocker 1983; Melquist et al. 2003; Reid et al. 1994), possibly due to a polygynous breeding strategy or perhaps due to increased energetic demands from larger body size (Sandell 1989).

Space use by mustelids is often defined by intrasexual territoriality (Powell 1979). However, river otters are more social than many other mustelids (Blundell et al. 2002; Melquist and Dronkert 1987; Melquist et al. 2003) and may also exhibit more geographic variability in social systems. In coastal Alaska, river otters display multiple social systems ranging from social to solitary (Blundell et al. 2004), and social systems reportedly vary at a larger geographic scale as well (Blundell et al. 2004).

In Alberta, Canada, otters associate in known family groups (i.e., a female and her offspring), and males associate in “bachelor” groups (Reid et al. 1994). In contrast, only family groups were observed in Idaho, whereas males were solitary (Melquist and Hornocker 1983). In New York, a population of translocated river otters exhibited intrasexual territoriality between females, but not between males (Spinola 2003). Coastal river otters in Alaska either form family groups or large groups of males, presumably in an effort to more efficiently capture pelagic fish (Blundell et al. 2002), although some individuals of both sexes remained solitary (Blundell et al.

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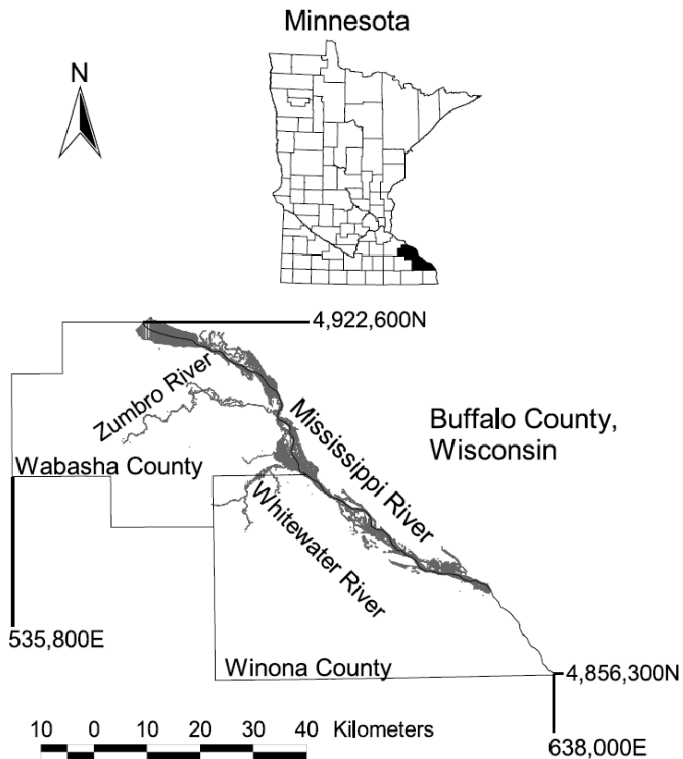


FIG. 1.—Study site where space use and sociality of 28 river otters (*Lontra canadensis*) were examined in southeastern Minnesota, 2002–2004.

2004). The composition of individuals in these male groups of coastal river otters was not a function of kinship or age; rather, familiarity (regardless of relatedness) from previous contact may be what determines the specific composition of individuals within groups (Hansen 2004). Likewise, Blundell et al. (2004) documented no preference or avoidance for closely related individuals, suggesting it was not the determinant of group composition.

Interactions between 2 individuals can influence space use of both individuals (Kernohan et al. 2001). A high degree of spatial overlap among animals suggests that key resources are not limiting, or the cost of maintaining exclusive territories is not greater than the benefit that would be gained by excluding others, or both. However, quantifying home-range overlap does not take into account the possibility of temporal avoidance. Dynamic interactions between 2 individuals provide information on attraction or avoidance by animals that are in proximity (Powell 2001) at a time. Individuals may be attracted to cooperate in raising young, foraging, or other activities leading to improved fitness (Clutton-Brock 2002). Possible reasons for territoriality may include protection of resources or competition for mates (Macdonald 1983).

Fidelity to home ranges and core areas provides insight into how animals use an area over the course of multiple periods of time (Kernohan et al. 2001). As with other mustelids, fidelity to home ranges and core areas likely is beneficial to river otters because it allows animals to become familiar with resources in the area (Phillips et al. 1998). However, some changes in space use over the course of multiple years are likely because of

competition, spatiotemporal variability in resources, or both (Powell 2001). Fidelity by individuals to an area over the course of multiple years provides stronger evidence of both stable resources and social systems (Powell 2001).

Previous investigations of space-use dynamics and social systems of river otters have focused primarily on coastal populations (Blundell et al. 2002, 2004) or reintroduced populations (Spinola 2003). Investigations have been conducted in the interior of North America (Melquist and Hornocker 1983; Reid et al. 1994), but there has been no detailed investigation of the behavioral ecology of river otters in the upper midwestern United States.

Our objectives were to document river otter home-range and core-area characteristics by sex and age class, to describe spatial and temporal interactions among individuals, and to assess annual fidelity to home ranges and core areas for river otters by sex. Understanding the space use and interactions of river otters provides insight into the behavioral ecology of this native species.

## MATERIALS AND METHODS

**Study area.**—We conducted this study along the Mississippi River watershed in Winona and Wabasha counties of southeastern Minnesota (Fig. 1). The study area included the backwaters of the Mississippi River and the major tributaries of the region (primarily the Zumbro River and the Whitewater River) that flow into the Mississippi River from the west. The entire Zumbro River watershed was 4,296 km<sup>2</sup>, composed of 89% cropland, 6% grassland pasture, 3% forest, and <1% aquatic wetland. The Whitewater River watershed was 829 km<sup>2</sup>, composed of 58% cropland, 8% grassland and pasture, 13% forest, 14% wetland, and 7% other (Minnesota Department of Natural Resources, in litt.). The Zumbro and Whitewater rivers were fast-moving streams, and a majority of the Whitewater River was a designated trout stream, whereas only a few small tributaries of the Zumbro River were designated as such. The region was devoid of natural lakes, but some small man-made ponds were present. Conversely, the Mississippi River was an expansive aquatic system with vast marshes (both emergent and submergent) and a wide range of channels with a range of slow- to fast-moving currents. This research was conducted on McCarthy Lake Wildlife Management Area, Whitewater Wildlife Management Area, the Upper Mississippi River National Wildlife and Fish Refuge, and private land.

The topography of the study area was predominantly bluffs with up to 183 m elevation. The bluffs were a bedrock plateau covered with a windblown layer of silt that was significantly eroded by rivers. The terrestrial portion of the study area was dominated by hardwood forest with some component of pine on poorly drained slopes, bottomland hardwoods in the deep valleys, and tallgrass prairie on the ridges and in the drier valleys. Annually, southeastern Minnesota receives 88 cm of precipitation with an annual mean temperature of 8°C, and minimum and maximum annual temperatures of 3°C and 13°C, respectively (Garogian 2000).

**Animal capture and monitoring.**—We captured river otters in autumn and spring beginning in autumn 2001 and ending in autumn 2003. We trapped otters at areas of intense use such as crossover trails (i.e., trails traveling across land between 2 bodies of water) and latrine sites. We used Sleepy Creek #11 double-jaw foothold traps (Sleepy Creek Manufacturing, Berkley Springs, West Virginia) to capture otters (Blundell et al. 1999; Shirley et al. 1983). To reduce capture-related injury, traps were equipped with an inline shock spring and

multiple swivels, which resulted in a chain length of approximately 56–66 cm. After capture, we transferred otters from the trap to a transport tube, and transported them to Plainview Veterinary Clinic (Plainview, Minnesota) for surgical implantation of a radiotransmitter (models 1245 2-stage or 1250 2-stage or 3-stage; Advanced Telemetry Systems, Inc., Isanti, Minnesota; or model FH-3; Global Tracking Systems, Coleman, Alberta, Canada).

Before surgery for transmitter implantation, otters were administered a combined intramuscular injection of ketamine ( $\bar{X} = 16.8$  mg/kg) and xylazine ( $\bar{X} = 10.2$  mg/kg). A veterinarian surgically implanted radiotransmitters into the peritoneal cavity through a paralumbar incision. While under anesthesia, an upper premolar was extracted for aging by counts of cementum annuli (Kuehn and Berg 1984). We submitted teeth to Matson's Laboratory, LLC (Milltown, Montana) for cementum annuli aging and combined this data with other morphological data to group individuals as subadults (<2 years old) or adults (>2 years old). Age classes were defined this way because otters do not typically breed successfully until >2 years old (Hamilton and Eadie 1964). We ear-tagged otters with number 1 Monel ear tags and web-tagged otters with number 3 Monel web tags (National Band and Tag Company, Newport, Kentucky). To minimize the likelihood of infection, we injected otters with 2 ml of long-acting penicillin, 1 ml of enrofloxacin, and 2 ml of clostridium antitoxin. Otters were allowed to recover naturally from anesthesia and were released at the site of capture between 6 and 74 h after capture. We followed guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and all capture and handling procedures were approved by the Minnesota State University, Mankato Institutional Animal Care and Use Committee (project 01-3).

We radiotracked river otters 2 days per week (i.e., 2 locations/week) from the ground using an ATS R4000 scanning receiver and a 3-element Yagi antenna (Advanced Telemetry Systems, Inc.) via triangulation and homing methods during both night and day. Triangulation was used to estimate locations of otters with  $\geq 2$  bearings recorded from known locations (Zielinski et al. 2004) within a mean time period of 6 min (median = 6 min). Also, homing was used to navigate toward many animals until a location could be verified. In addition, radiotracking was conducted at approximately 7- to 10-day intervals via Cessna Skylane 182 fixed-wing aircraft equipped with a 4-element Yagi antenna on each wing. We collected locations of river otters during all seasons for the duration of the study.

We computed the bias and precision of our telemetry equipment and triangulation techniques by placing test transmitters at georeferenced locations unknown to the observer ( $n = 23$ ). Test transmitters were placed in the water, under debris, and on the ground. We assessed accuracy of the bearings by comparing the estimated bearings to the true bearings. The mean difference between these bearings was used to quantify bias ( $\bar{X} = -1.5^\circ$ ), whereas the *SD* of errors was used to quantify the precision of our techniques ( $SD = 5.5^\circ$ —White and Garrot 1990). Locations obtained using triangulation were computed using maximum-likelihood estimator in program Locate II (Nams 2000).

*Home-range characteristics.*—To describe home ranges of river otters, researchers have previously used 95% minimum convex polygons (Reid et al. 1994), adaptive kernels (Johnson and Berkley 1999; Sauer et al. 1999), total length of shoreline or river used (Bowler et al. 1995; Melquist and Hornocker 1983), or length of shoreline within a fixed kernel (Blundell et al. 2001). Although each of these methods may be appropriate in some portions of the otter's geographic range, none seemed appropriate for our data.

In this study, otters used linear stretches of river as well as the surrounding expanses of backwater sloughs and wetlands. We

estimated annual 95% home ranges and 50% core areas using a fixed-kernel estimator (Worton 1987, 1989) with least-squares cross-validation (Seaman et al. 1998, 1999; Worton 1995) in the Animal Movement extension (Hooge and Eichenlaub 2000) for ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). We used this method rather than length of river to minimize the loss of information on the size and shape of aquatic areas used and to allow for inclusion of islands and uplands used for natal denning (Gorman et al., 2006), resting, and latrine sites.

Home ranges and core areas were calculated only for animals with data on >30 locations/year ( $\bar{X} = 80.0$ ,  $SE = 3.9$ ), provided the locations were spread out over a period of  $\geq 120$  days of total tracking/year ( $\bar{X} = 290.2$ ,  $SE = 12.5$ ). We used a paired *t*-test to test for differences in home-range and core-area sizes between years for the 11 (5 females and 6 males) river otters that we sampled for both years (i.e., year 1 = June 2002–May 2003 and year 2 = June 2003–May 2004). Given a lack of difference between years, we used the average home-range size for these 11 animals to avoid temporal pseudoreplication in subsequent analyses. We then used a univariate general linear model to evaluate differences in home-range size between sexes and ages (i.e., subadults and adults) as well as in differences in core areas between sexes and ages. Parametric assumptions of general linear models were evaluated with a modified Levene's test to evaluate equality of variance and a Lilliefors test to evaluate normality (Neter et al. 1996). We log-transformed data if assumptions were not met (Neter et al. 1996).

*Static interactions.*—Static interaction measures the amount of spatial overlap between 2 animals without reference to time (Kernohan et al. 2001). It is possible for the percentage of space-use overlap to be 0. In some cases this is meaningful (e.g., 2 adjacent animals with exclusive territories), whereas in other cases it is not meaningful (e.g., 2 animals living 30 km apart). There were few instances where individuals were in close proximity but had no overlap at the 95% home-range scale. At the home-range scale, 94.9% of all otters had some overlap with another individual (Gorman 2004). Furthermore, the degree of overlap in 50% core areas may be a more accurate descriptor of social tolerance than overlap in 95% home ranges. To address both points, we restricted our overlap analysis only to pairs of animals with 95% home range overlap > 0. For these pairs, we then quantified core-area overlap. Overlap measurements for years 1 and 2 were pooled for this analysis. The amount of overlap in core areas was calculated using ArcView 3.3. We used the equation:

$$CA_{i,j} = \frac{A_{i,j}}{A_i}$$

where  $CA_{i,j}$  is the proportion of the core area of otter *i* overlapped by the core area of otter *j*,  $A_i$  is the area of the core area of otter *i*, and  $A_{i,j}$  is the area of overlap (Kernohan et al. 2001) between the 2 core areas. The degree of overlap is specific to the individual (i.e.,  $CA_{1,2} \neq CA_{2,1}$ ). We assigned each static interaction into pairwise groups defined by either sex (i.e., male–male, male–female, or female–female) or age (i.e., adult–adult, adult–subadult, or subadult–subadult). We examined differences among groups using randomization tests (Manly 1997) with 1,000 replicates.

*Dynamic interactions.*—Dynamic interactions differ from static interactions by maintaining the serial correlation in location data, therefore explaining both the spatial and temporal aspects of 1 animal's influence on a 2nd individual (Kernohan et al. 2001). Static and dynamic interaction analyses complement one another, because it is possible for static interactions to occur, but for animals to temporally avoid each other. Dynamic interactions between 2 individuals were calculated if some portion of their 95% fixed-kernel home range overlapped with another animal. We assumed that there were no

**TABLE 1.**—Home-range and core-area sizes of 28 river otters (*Lontra canadensis*) in southeastern Minnesota, 2002–2004.

Group	n	Home range (km <sup>2</sup> )		Core area (km <sup>2</sup> )	
		$\bar{X}$	SE	$\bar{X}$	SE
Age class <sup>a</sup>					
Adult	14	15.71	3.45	2.43	0.83
Subadult	14	25.72	9.66	3.31	1.22
Sex class					
Male	15	30.38	8.76	4.12	1.23
Female	13	9.56	2.14	1.43	0.44

<sup>a</sup> Adults were river otters  $\geq 2$  years old and subadults were river otters  $< 2$  years old.

interactions between individuals if home ranges did not overlap. We computed the distance between locations of otters obtained within the same sampling period ( $\bar{X} = 67$  min,  $SE = 1$  min, median = 16 min). Based on guidelines from Kernohan et al. (2001), we calculated the observed distance ( $D_O$ ) as:

$$D_O = \frac{1}{n} \sum_{j=1}^n \sqrt{(x_{1j} - x_{2j})^2 + (y_{1j} - y_{2j})^2},$$

where  $x_1$  and  $x_2$ , and  $y_1$  and  $y_2$  are the universal transverse mercator coordinates for animals 1 and 2, respectively. Expected distance ( $D_E$ ), assuming random interaction, was calculated as:

$$D_E = \frac{1}{n^2} \sum_{j=1}^n \sum_{k=1}^n \sqrt{(x_{1j} - x_{2k})^2 + (y_{1j} - y_{2k})^2}.$$

For all interactions pooled, and for interactions pooled by sex or age, we compared the difference between observed and expected pairs using a Wilcoxon signed-rank test (Zar 1996). Individual interactions were either positive (observed distance  $<$  expected distance), which suggests that the 2 individuals were attracted to each other and may benefit from the presence of the other, or negative, which suggested that the 2 individuals temporally avoided each other.

Further, we calculated a coefficient of association (Kernohan et al. 2001) for river otters that had interactions with another otter. Animals were considered “together” if their locations, based on homing, aerial tracking, or triangulation, had a separation of  $< 1$  m. We also examined association using only the direct observations (no locations based on triangulation or aerial tracking) of river otters  $< 1$  m apart, thereby eliminating potential concern over location accuracy.

**Fidelity.**—We evaluated site fidelity of otters to both home ranges and core areas. Fidelity was assessed for animals that were radio-tracked for 2 years, and thus for which we had sufficient location data to compute home ranges and core areas for 2 successive years. We calculated fidelity by measuring the amount of overlap between the year 1 and year 2 home range and core areas for each individual. We then divided the area of overlap between the 2 home ranges or core areas by the area of the year 1 home range or core area. We then used this proportion of individual fidelity to assess how the sexes as a group behaved from one year to the next. Mean values of male and female proportions of fidelity were compared using an independent-sample  $t$ -test (Zar 1996). We did not have sufficient replicates to compare age groups. For all analyses we evaluated statistical significance at  $\alpha = 0.05$ .

## RESULTS

**Home-range characteristics.**—For the 11 animals monitored throughout both years, we did not detect an annual difference

in the size of home ranges ( $t = 0.488$ ,  $P = 0.630$ ) or core areas ( $t = -0.288$ ,  $P = 0.777$ ). Therefore, we used mean home-range and core-area size for these 11 animals to avoid pseudoreplication. We combined these animals with the other 17 animals for which we had only 1 year of data for all subsequent analyses for a total of 28 otters (15 males and 13 females).

No sex  $\times$  age interaction was found in size of 95% home ranges ( $F = 0.640$ ,  $P = 0.432$ ). Hence, we proceeded with interpretation of age and sex effects. Male home ranges were 3.2 times greater than female home ranges ( $F = 4.63$ ,  $P = 0.042$ ; Table 1). No difference was found in size of home ranges between ages ( $F = 0.254$ ,  $P = 0.619$ ). Similarly, no sex  $\times$  age interaction was found for core areas ( $F = 0.449$ ,  $P = 0.509$ ), and the size of core areas did not differ between ages ( $F = 0.134$ ,  $P = 0.717$ ). Although we did not detect a difference between sexes at the core-area scale ( $F = 3.28$ ,  $P = 0.083$ ), male core areas were 2.9 times larger than female core areas (Table 1).

**Static interactions.**—Considering only animals with some degree of 95% home-range overlap with another radiomarked otter ( $n = 91$  combinations), overlap of 50% core areas occurred in 32% ( $n = 29$ ) of the interactions and 69% of individual otters overlapped with at least 1 other otter at this scale. Of the animals with overlap at the 50% core area, male–female (51.7%,  $n = 15$ ) static interactions occurred most frequently, with male–male interactions (27.6%,  $n = 8$ ) and female–female interactions (20.7%,  $n = 6$ ) being less common (Fig. 2). Across all otters with 95% home-range interactions (but not necessarily core-area interactions), females had an average of 22.2% of their core areas overlapping with another female and 15.8% of their core areas overlapping with a male otter (Fig. 2). On average 15.7% of a male otter’s core area overlapped with another male. However, these 3 percentages were not statistically different ( $P = 0.634$ ).

When core-area overlap occurred among age-class pairs, subadult–adult interactions (48.3% of pairs,  $n = 14$ ) were the most frequent (Fig. 2), followed by adult–adult (27.6%,  $n = 8$ ) and subadult–subadult interactions (24.1%,  $n = 7$ ). For all the individuals that had some overlap of their 95% home ranges, mean proportion of core-area overlap for adult–adult, subadult–subadult, and subadult–adult was 8.1%, 30.4%, and 18.7%, respectively (Fig. 2). Age differences in percentage of core-area overlap were statistically significant ( $P = 0.003$ ), with pairwise comparisons indicating that the amount of area in common was greater for subadult–subadult pairs than for adult–adult pairs ( $P = 0.003$ ). Also, a difference was detected in the amount of overlap that occurred between adult–adult and subadult–adult overlap ( $P = 0.043$ ). No difference was detected between the amount of overlap between subadult–subadult and subadult–adult pairs ( $P = 0.057$ ).

**Dynamic interactions.**—The majority (72.4%) of dynamic interactions between river otters were positive (i.e., observed distance  $<$  expected distance;  $Z = -4.596$ ,  $P < 0.001$ ). Under the null hypothesis of no attraction or avoidance, the observed distance between male–male locations was not different from expected (62.5% were positive;  $Z = -1.543$ ,  $P = 0.123$ ,  $n = 24$ ). In contrast, the observed distance between female–female

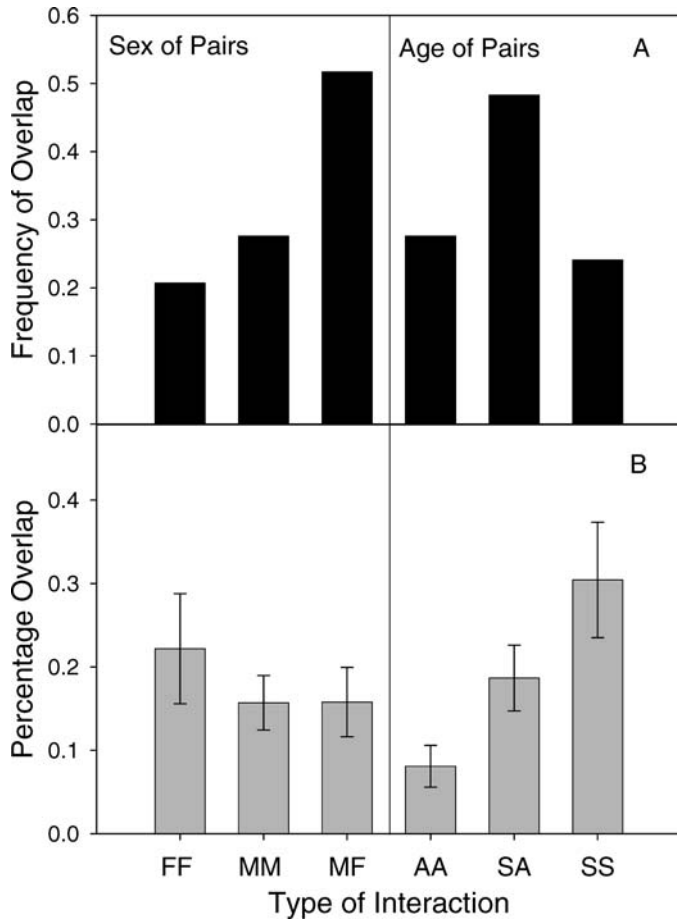


FIG. 2.—A) Frequency of core-area overlap between otters in southeastern Minnesota, 2002–2004. B) Percentage core-area overlap for pairs of individuals exhibiting some degree of 95% home-range overlap, shown as mean  $\pm$  SE. Pairwise interactions were grouped by their sex or age class. The type of interactions were categorized as: FF = female–female, MM = male–male, MF = male–female, AA = adult–adult, SA = subadult–adult, SS = subadult–subadult.

locations (78.5% were positive;  $Z = -2.542$ ,  $P = 0.011$ ,  $n = 14$ ) and male–female (75.5% were positive;  $Z = -3.815$ ,  $P < 0.001$ ,  $n = 47$ ) locations were closer than expected.

The observed distance between subadult–subadult locations was not different from expected values (55.6% were positive;  $Z = -0.719$ ,  $P = 0.472$ ,  $n = 18$ ). However, the observed distance between adult–adult locations (75.0% was positive;  $Z = -2.880$ ,  $P = 0.004$ ,  $n = 32$ ) and subadult–adult locations (77.1% were positive;  $Z = -3.538$ ,  $P < 0.001$ ,  $n = 35$ ) were closer than expected.

We observed 14 (8 males and 6 females) individuals that were located  $<1$  m from  $\geq 1$  other otter. Coefficient of association ranged from 1% to 66% ( $\bar{X} = 30\%$ ,  $SE = 4\%$ ) for the 14 otters that were located within  $<1$  m of one another on 358 occasions. Restricting further analyses to only locations that were attained using homing (i.e., walk-in locations) we documented 44 occasions where  $\geq 2$  animals were located together (i.e., within  $<1$  m). The same 14 individuals were involved in these 44 interactions. On 23 occasions 2 females were observed together, on 9 occasions mixed male and female

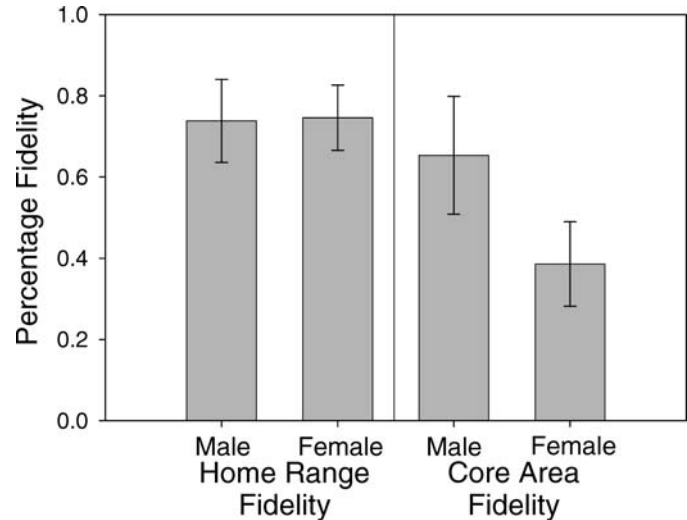


FIG. 3.—Fidelity of male and female otters to home ranges and core areas in southeastern Minnesota, 2002–2004, shown as mean  $\pm$  SE.

groups were observed (5 of which included 3 individuals), and on 12 occasions 2 or more males were observed together (5 occasions involved 3 males). The age composition of these groups included 14 occasions of 2 subadults, 18 occasions of subadults and adults (10 occasions involved 3 individuals), and 12 occasions between adults. Most instances were otters sharing resting sites in beaver bank dens or log jams, and a few were otters swimming together (i.e., potentially foraging).

**Fidelity.**—Male and female river otters both showed high annual site fidelity at the 95% home-range scale. No difference was found between males (73.8%) and females (74.6%) in the proportion of their year 1 home range used during year 2 ( $t = -0.058$ ,  $P = 0.955$ ; Fig. 3). Likewise, we did not detect a difference between the fidelity of males (65.3%) and females (38.6%) at the core-area scale ( $t = 1.440$ ,  $P = 0.184$ ; Fig. 3).

## DISCUSSION

River otters on our study area exhibited clear evidence of space sharing, suggesting that individuals in this population were neither solitary nor territorial. The majority of the animals in our study area shared space with at least 1 other animal at the core-area scale, and animals tended to be attracted to each other and were frequently located in close proximity to other otters. River otters are more social and exhibit varying and complex social structures compared to other carnivores (Blundell et al. 2004). The social structure of river otters is not well defined, but the structure appears to vary across the otter's geographic range. Based on our analyses of home-range characteristics using multiple techniques, river otters in the upper Mississippi watershed appeared to be social and appeared to socialize to some degree with any individual for which they had an encounter opportunity.

**Home-range characteristics.**—Consistent with our findings, it has been documented that home ranges of male river otters are larger than home ranges of females (Melquist and Hornocker 1983; Reid et al. 1994). Females are generally

thought to have smaller home ranges because they restrict their movements during spring (Gorman 2004; Melquist and Hornocker 1983), and it is likely that males have larger home ranges because of a polygynous breeding strategy or perhaps because of increased energetic demands of larger body size (Sandell 1989). River otter age was not a good descriptor of home-range or core-area size (the 2 largest home ranges we recorded were for subadult males).

*Static and dynamic interactions.*—Groups of male otters reportedly are not exclusive, but rather form loose bonds that likely allow for each individual to benefit from the others' presence (Blundell et al. 2002; Hansen 2004). Many studies have documented male groups (Blundell et al. 2002, 2004; Hansen 2004), but our results indicate that females also form small groups, possibly to help raise young and/or to forage cooperatively. This type of relationship, or group augmentation, does not require kinship, but rather allows both individuals to increase their fitness (Clutton-Brock 2002).

Male group composition in captive river otters in Alaska was based on encounter opportunity rather than on age or kinship (Hansen 2004). Thus, the social structure of this species may vary in part from an individual response to encounters with other otters. Such responses may ultimately be influenced by local conditions determining whether group formation is beneficial. For example, river otters in coastal Alaska formed groups to facilitate feeding on pelagic fishes (Blundell et al. 2002). Although pelagic fishes were not present on our study area, group formation may nevertheless have been related to potential benefits from cooperative foraging. Other mustelids such as American marten (*Martes americana*), fisher (*Martes pennanti*), and American mink (*Mustela vison*) defend intrasexual territories, presumably to limit access to resources by other individuals (Arthur et al. 1989; Katnik et al. 1994; Yamaguchi and Macdonald 2003). If food resources for river otters are not limiting, the territorial defense of food resources may not be cost-beneficial. Groups may thus form if individual foraging success is improved (Blundell et al. 2002), if food resources are patchily distributed (Johnson et al. 2000; Macdonald 1983), or both. Based on fish surveys conducted on several of the main rivers in our study area (Minnesota Department of Natural Resources, in litt.), fish distribution in our study area is clumped, specifically around pools and other habitat structures (e.g., woody debris).

The majority of individual otters in our study area, regardless of sex or age, experienced some core-area overlap. Core-area overlap indicates that these otters tolerated the presence of other individuals within the area of their home range they used most frequently, although it remains possible that fine-scale temporal exclusion went undetected in our study. Some of the core-area overlap could be attributed to family groups. Although we did not confirm genetic relatedness, examination of data on body mass and proximity of capture suggests that only 14% of interactions involving core-area overlap were for a female and her young. This may reflect a lack of female–young pairs in our capture effort rather than a lack of interaction. However, it supports the conclusion that core-area overlap regularly occurred among independent adult animals.

Core-area overlap occurred more frequently between males and females and was not restricted to any specific age class. Intersexual overlap is a common spacing strategy among carnivores (Macdonald 1983; Sandell 1989), but there were also occasions when either 2 female core areas ( $n = 15$  pairs) or 2 male core areas ( $n = 30$  pairs) overlapped, which suggests an inability to exclude others or a neutral or positive effect for both sexes from some degree of intrasexual overlap.

Considering temporal association as well, a higher ratio of positive interactions was found between male–female and female–female pairs than for male–male pairs. However, on several occasions we observed males resting together in groups of 2 or 3 individuals. Similarly, we observed pairs of females sharing resting sites and traveling together and we observed mixed groups of males and females ranging from 2 to 3 individuals. Although these observations were limited, they do corroborate our other analyses. This atypical strategy that is displayed by core-area overlap, positive dynamic interactions, and observed resting and traveling events may be explained by food resources being distributed patchily (Johnson et al. 2000), there being net benefits of cooperative foraging, because prey resources are nonlimiting (Powell 1994), or a combination of these factors.

*Fidelity.*—Annual fidelity to home ranges by river otters was high for both males and females (Fig. 3) on our study area. Interpretation of the fidelity metric we used could be confounded if home-range size changed noticeably across years. For example, if home-range shape and centroid remained constant but size increased 4-fold, fidelity would be 25%. However, if size decreased 4-fold, fidelity would be 100%. In both cases, the area of overlap (fidelity) remains constant. In our study, both size and shape of successive annual home ranges remained relatively constant, with only slight shifts in home-range centroids, and thus interpretation was straightforward. Both sexes had some movement between their successive home ranges, and in both cases approximately 75% of the year 1 home range was used during the 2nd year. Although there was some shift in home ranges and core areas, no otters completely abandoned or relocated their ranges. The high degree of site fidelity indicates that the dynamics governing space use by otters in southeastern Minnesota were stable during our study, and the slight shifts in home ranges that occurred may be a response to minor spatial variability in resources within an otter's range, rather than to competition with conspecifics.

*Conclusions.*—In southeastern Minnesota, conspecifics were not excluded from home ranges or core areas and river otters displayed intersexual and intrasexual overlap and attraction, suggesting that river otters were social rather than territorial or solitary. Although females used smaller areas than males, both sexes had high degrees of site fidelity. Despite the differences in the size of areas used, females shared with conspecifics of either sex a greater portion of their core areas than males and had a greater proportion of positive interactions. The reduced amount of intrasexual territoriality, atypical for carnivores, may be a result of nonlimiting resources, may indicate that the individual benefits from cooperative foraging may outweigh any

costs from various forms of potential competition, or both. Space-use patterns for river otter populations may involve territoriality in areas where food is limiting, if cooperative foraging is not cost beneficial, or both. Future research should focus on otter social dynamics in relation to availability of prey resources in interior systems.

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