RANGING PATTERNS AND HABITAT UTILIZATION OF NORTHERN RIVER OTTERS, *LONTRA CANADENSIS*, IN MISSOURI: IMPLICATIONS FOR THE CONSERVATION OF A REINTRODUCED SPECIES

by

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Abstract

I studied the spacing patterns and habitat utilization by reintroduced northern river otters, *Lontra canadensis*, at two sites in Missouri because previous studies of otters indicate, plasticity of a species social structure will likely be due to the tactics employed in acquiring resources in any given area. Seven hypotheses were tested by employing radio-tracking, habitat assessment and geographic information system approaches, these included: (1) home range (HR) and core area (CA) size differ by sex; (2) HR and CA size differ in breeding vs. non-breeding seasons; (3) percent range overlap differs by sex; (4) habitat utilization, as indicated by latrine use, differs seasonally; (5) primary prey type(s) found in scat differ seasonally; (6) environmental characteristics of areas used extensively by otters (latrines, dens, haul-outs) differ from adjacent, unused sites; and (7) stream-order effects and features associated with core area use are similar between two disjointed field sites, and can thus be used along with GIS-driven identifiers to generate predictions regarding suitable habitat for Midwestern river otter populations. Evidence is presented on differences in ranging patterns of otters by location, sex, and seasonality, as well as differences in core area use and accompanying habitat characteristics for the two populations. The following hypotheses were corroborated: (1) male otters had larger HRs and CAs than female otters; (2) female otters maintained small, non-overlapping home ranges; (3) males exhibit a greater percentage of inter- and intra-sexual HR and CA overlap than females; and (4) HR and CA size, and percent overlap differ between a large, riverine ecosystem and a small, meandering stream ecosystem. However, hypotheses examining temporal use of space by otters were not supported. In conclusion, this study suggested that northern river otters exhibit a variety of spacing patterns in different parts of their range, similar to those discovered in other solitary carnivores. Seasonal use of space was different from that typically found in solitary carnivores; differences may be related to habitat characteristics associated with stream order and wetland ecosystems. Overall, although introduced otters came from disjointed regions differing in habitat features and ecological pressures, reintroduced otters have done very well in Missouri.

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Dedication

For Josh, who waited patiently, and for Payton, who didn't. And for my Mom, who instilled in me my fascination, passion and respect for nature. Their encouragement and assistance made me persevere. My successful completion of this entire Ph.D. program from coursework to qualifying exams to field work, writing and defenses would literally not have been possible without them. I love you all so very much.

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Chapter 1

Introduction

Assessment of Two Reintroduced Populations of the Northern River Otter, *Lontra canadensis*, in Missouri, USA: a Review

"That portion of the continent watered by the Missouri and all its branches…is richer in beaver and otter than any country on earth…"

Captain Meriweather Lewis

Northern river otters, *Lontra canadensis*, have historically occupied almost all riparian drainage basins and aquatic habitats of the North American continent from 25º to 70ºN latitude and 53º to 166ºW longitude, with substantial populations existing in rivers, lakes, freshwater wetlands and marshes, and rocky sea coasts (Halbrook 1978; IUCN 1980; Hall 1981; Toweill and Tabor 1982; Jones et al. 1983; Melquist and Dronkert 1987; Lariviere and Walton 1998). During the late 1800s and early 1900s, the movement of European settlers into the interior of North America coincided with a drastic over-harvesting of river otters, beavers, *Castor canadensis*, and other furbearers for their valuable pelts (Erickson and McCullough 1985). Additionally, the degradation and fragmentation of suitable aquatic and riparian habitat, as well as the human population explosion and its associated consequences (i.e. pollution, roadway expansions, channelization of rivers, agricultural practices, runoff, habitat exploitation) further threatened the river otter throughout most of the contiguous USA (Hall 1981; Toweill and Tabor 1982; Melquist and Dronkert 1987). By the early 1900s northern otters were extirpated from many states with interior riverine habitats (Nilsson, 1980). In addition, conservation measures were already being considered for river otters and beavers in some areas of the USA (IUCN 1990). Restricted trapping regulations and wetland preservation were adopted as conservation measures in some parts of the otters' former range by the 1920s. But it was not until the 1970s that concerns about otter population declines and extirpations became increasingly evident (Endangered Species Scientific Authority 1978). And, although listed during 1973 in Appendix II by the Convention in Trade in Endangered Species (CITES), Jenkins (1983) still noted an almost complete absence of river otters from the Midwest and southwest states of the USA. In 1990, an IUCN Otter Specialist Group noted that it was illegal to harvest otters in 22 of 50 US states.

These aforementioned concerns, along with nation-wide attention to improving water quality, general ecology and habitats, and ethical furbearer management techniques, prompted many wildlife agencies to restore or enhance their river otter populations (Ralls 1990). About 20 years after the CITES listing, a 1994 survey revealed that 15 of the 50 United States, including Missouri, have reintroduced or restocked river otters (Reed-Smith 1995). By 1998, 4,018 otters were reintroduced to 21 states, the Canadian province of Alberta and one National Park (Raesly 2001). At present, otter populations are thriving in many parts of the USA, including Alaska, the Pacific Northwest, the Great Lakes, and most of the Gulf and Atlantic coast states, and most of Canada (Hall 1981). Twenty years ago, 17 states listed northern otters as threatened or endangered, whereas today only seven still provide their state-wide otter populations with legal protection (Melquist and Hornocker 1983; Kiesow and Dieter 2005).

In Missouri, northern river otters historically ranged among all watersheds throughout the state (Schwartz and Schwartz 1981). However, during the 1800s and early 1900s otter populations declined due to unregulated fur harvest and anthropogenic destruction of riparian and wetland habitats. While frontiersmen were lured to other parts of the North American continent in search of gold, farmland, or timber, their quest in the Missouri wilderness was for fur (Erickson and McCullough 1985). The Missouri Department of Conservation (MDC) estimated that only 35 to 70 river otters remained in the state in 1978 (Erickson and McCullough 1987), with the majority occurring in the south eastern "boot-heel" region, and the other concentration in the north western corner in the Big Creek of the Grand River watershed that drains into the Osage River (Choromanski and Fritzell 1982). In response to diminished numbers of river otters, and concerns that they might, in the near future, become completely extinct in the state, the MDC began a river otter restoration program to supplement the extant, but significantly truncated, population. From 1982 until April 1992, the MDC released 845 otters into 43 locations throughout the state of Missouri; these otters were primarily taken from large populations in coastal Louisiana (Erickson and Hamilton 1988; Hamilton et al. 1994).

The MDC assessed the success of experimentally translocated river otters by measuring survival rates of otters equipped with radio telemetric transmitters (Erickson and McCullough 1987). After being listed as endangered in 1985 in Missouri and following reintroduction efforts, northern river otters were watchlisted in 1992 (Reed-Smith 1995). In 1996, the population of river otters in Missouri was estimated at 8,000 to 9,000 individuals. Subsequently, trapping of river otters was reopened in the state (D. Hamilton, MDC, pers. comm.). During the first open trapping season for otters, a reported 1000+ individuals were taken (Leydig 1997; Uhlenbrock 1999; D. Hamilton, MDC, pers. comm.). The success of the MDC's reintroduction program, as well as those of neighboring states and the gradual expansion of extant populations, has resulted in river otters repopulating most of their historic range in Missouri, to the point where the current statewide status of the river otter population is excellent.

Similar reintroduction undertakings and successes are reported for river otters in several other US states and Canadian provinces (Bluett et al. 1999; Johnson and Berkley 1999; Serfass et al. 1999; Pitt et al. 2003). Other states, such as Arkansas, Illinois, Iowa, Kentucky, New York, Pennsylvania and Tennessee have patterned their reintroduction programs after the MDC's in an effort to reestablish the North American river otter to its former range (Hamilton 1998). In a survey by Raesly (2001) conducted across the continental United States, most wildlife agency biologists reported that reintroduction efforts were successful in restoring otter populations. For example, from 1994 to 1997, Bluett et al. (1999) reintroduced 346 otters from Louisiana into three river basins in neighboring Illinois. Of these, 29 individuals were lost to diverse agents including hoop nets, vehicles, incidental trapping, and stress. However, overall evidence indicated that otter populations in Illinois, both introduced and extant, are persisting, reproducing and expanding their ranges, some as a result of releases during the 1980s in Missouri (Bluett et al. 1999). Likewise in Iowa, 261 otters were reintroduced from 1986-2001. A subsequent study in Iowa of 81 otters was conducted to document the characteristics of the reestablished population; and after high survival rates, widespread distribution and healthy reproductive characteristics were found to be present, a limited harvesting season was suggested (Pitt et al. 2003).

However, aside from a few post-release survival and movement studies of reintroduced otters (Serfass and Rymon 1985; Erickson and McCullough 1987; Serfass et al. 1993; Johnson and Berkeley 1999), few long-term reports exist on the success, persistence and status of river otters following reintroduction efforts. In addition, it is difficult to tease apart potential reintroduction success from that due to environmental improvements and habitat remediation, particularly along corridors (Ben-David et al. 1998, 2005; Blundell et al. 2002b). It was not until recently that the implications for natural recolonization of extirpated populations of river otters have been evaluated, shedding light on the importance of genetic implications and environmental factors (Blundell et al. 2002b).

The two populations evaluated in this dissertation resulted from natural expansions following a statewide reintroduction project initiated in 1982 by the state of Missouri. Animals released by state agencies in most US reintroduction efforts came primarily from wild-stock in Louisiana, although some states also released individuals considered to be from different subspecies (Reed-Smith 1995). For example, individuals used for restocking in Missouri came primarily from Louisiana. However some animals also came from Canada, Arkansas and Alaska. Thus, six different subspecies were released in Missouri which had been formerly occupied by only one subspecies of river otter, *Lontra canadensis* *lataxina* (Reed-Smith 1995). Currently the state-wide population is expanding its range into historic areas from which it had been absent. Reintroductions, as well as a concomitant increase in beaver, resulting in additional suitable otter habitat, are believed to be primarily responsible for the success of this project in Missouri. Increasing demand for river otter pelts in the world fur market, primarily in Asia, as well as concerns about depredations of game-fish by otters in Missouri, have contributed to the re-opening of trapping seasons in this, and most other US states (Reed-Smith, 1995; Leydig 1997; Bluett et al. 1999; Uhlenbrock 1999; Raesly 2001; Pitt et al. 2003; D. Hamilton, MDC, pers. comm.).

Although debate continues about the pros and cons of using reintroduction versus habitat restoration as tools for saving threatened and endangered species, reintroduced northern river otters are once again found in almost all aquatic habitat types from freshwater rivers, lakes, wetlands, and marshes to coastal marine and brackish environments (Toweill and Tabor 1982; Melquist and Hornocker 1983). Patterns of space use by otters may differ seasonally, particularly in northern portions of their range, and are often related to sex and age class differences, with pronounced geographic differences for these two variables (Melquist and Hornocker 1983; Serfass & Rymon 1985; Anderson and Woolf 1987; Erickson & McCullough 1987; Erickson & Hamilton 1988; Hamilton et al. 1994; Reid et al. 1994; Bowyer et al. 1995; Serfass 1994; Ben-David et al. 1998, 2005; Johnson & Berkley 1999; Serfass et al. 1999; Blundell et al. 2000, 2001, 2002a, 2002b).

While factors related to predation, demography and population density should certainly not be discounted as contributors to distributional ranges and abundance of fauna, space use and ranging patterns of animals are most often described as a component of resource dispersion (Sandell 1989; Hobbs and Hanley 1990; Bernstein et al. 1991; Lima and Zollner 1996; McIntyre and Wiens 1999). Essential resources for northern otters, like those of most animals, include food, shelter, and conspecific interactions (Gittleman 1989; Dunstone and Gorman 1998). However, until recently the potential differences in the behavioral ecology of otter populations living in different types of aquatic habitats in relatively close proximity (i.e. small versus large Midwestern stream systems, marine coastal regions with varying topography and resource distribution), as well as those from latitudinally distinct regions of the North American continent, were not well documented nor fully understood (Bowyer et al. 1994, 1995; Ben-David et al. 1998, 2005; Blundell et al. 2000, 2002a, 2002b, 2004). For example, in boreal Alberta, Reid et al. (1994) found the year-round availability of water (i.e. unfrozen during winter seasons) to be one of the major determinants in the distribution and dispersion of otters in a sub-arctic region. In coastal Alaska, primary predictors of northern river otter sociality and ranging patterns differ according to local dietary preferences, such as those found in the occasional presence of schooling pelagic fishes and running-salmon streams (Bowyer et al.1994, 1995; Ben-David et al. 1996, 1998; Blundell et al. 2000; 2002a, 200b). Such habitat determinants, however, have obviously not been reported for southern populations of northern river otters, such as those studied in Alabama, Arkansas, Florida and Texas (Lauhachinda 1978; Humphrey and Zinn 1982; Foy 1984; Karnes and Tumlison 1984). Studies of other Lutrinae have shown within population differences in the diets of individuals specializing on, for example, lake versus river prey when alternatives are available, suggesting the need for proper incorporation and prioritization of suitable foraging habitats to be included in immediate protection efforts of endangered or threatened species (Medina 1998; Perrin and Carranza 2000; Perrin and Carugati 2000).

Conservation efforts must be geared not only toward acquiring the aquatic habitats and natural conditions in which river otters have been found to range, but also to make certain that these areas offer an adequate supply of food to satisfy the trophic requirements of the river otters living in that region, taking into account potential future population growth (Dunstone and Gorman 1998; Blundell et al. 2000, 2002b). In addition, habitat available to otters for, and conducive to, the essential activities of denning and scent marking also often vary by location and season. Northern river otters are opportunistic denners (Melquist and Hornocker 1979*a*, 1979*b*, 1983; Serfass 1994; Blundell et al. 2000, 2002a, 2004), and both males and females deposit spraints at latrine sites situated typically on higher-elevation substrate or points of land found along riverbanks, lakeshores, coastlines and/or cross-over paths (Newman and Griffin 1994; Trusso 1997; Ben-David et al. 1998, 2005; Rostain et al. 2004). Sites visited in spraint surveys, as measures of the species distribution, relative population size and prey type selected, are oftentimes only visited once, and therefore should be carried out in the months when the sprainting activity is the greatest (for *Lontra canadensis* this is in the Spring), when ground cover is low or absent, and in all counties in a given region, even those with no evidence of otters for some years (Madsen and Gaardmand 2000).

For example, in the upper Great Lakes region, Flaspohler et al. (2002) found that brook char (*Salvelinus fontinalis*) as well as several aquatic macroinvertebrate orders (Ephemeroptera, Plecoptera, and Trichoptera), were highly sensitive to the anthropogenic disturbance of logging. They found a significant positive correlation between the age of riparian stands and a standard index of habitat quality for coldwater streams (more brook char, and more dominant aquatic macroinvertebrates). The changes in local animal abundance and diversity, along with ground cover and its positive correlation with bird species richness, brought about by selective logging of riparian forests appear to persist in this region for over 30 years (Flaspohler et al. 2002). White et al. (2003) used a logistic regression model to relate fish density, physical characteristics of the river and surrounding vegetative cover to the presence or absence of otter spraints. They found that fish density and the physical characteristics of the river were the most important factors related to otter presence. Such factors need to be considered when evaluating the present and future availability of suitable habitat for reintroduced populations of carnivores (Hobbs and Hanley 1990; Breitenmoser et al. 2001; Gittleman et al. 2001).

Likewise, the potential interactions with heterospecific populations in a habitat being considered for reintroduction efforts should be addressed. A recent study on the interactions of beaver and otter in Delaware found a highly significant positive relationship between presence of beaver activity (active or inactive) and otter use ($\chi^2 = 24.8$, $P < 0.001$) of the same surveyed riparian habitat reaches (Swimley et al. 1999). Given that the preferred management goal for beaver throughout most of its range is economic gain through fur trapping, substantial incidental captures of otters and other non-target species, can be substantial. Thus, when selecting reintroduction sites or designing habitat refuges for otters, attention must be paid to other riparian species present in those areas that are actively managed using programs permitting non-releasable trapping methods. Management programs in such areas could instead utilize water level control devices and/or education and enforcement of non-lethal capturing techniques to minimize the impacts such practices have on otters (Swimley et al. 1999).

Understanding the effects of habitat structure on otter movements is critical to conservation management, especially in those parts of its range where it is most vulnerable (i.e. riverine habitats). For example, over a four year period in India, Hussain and Choudhury (1997) found a 12% decrease in the number of sites found with positive smooth-coated otter (*L. perspicillata*) signs. During the same time period, this area was subject to extensive human disturbance along the river (i.e. construction of road bridges and mining activities) which may have put pressure on the otter population, thus causing the decline. Monitoring of such otter populations should be done regularly as a measure of pre-emptive conservation, and restrictions, strictly enforced within refugia, should be imposed on cultivating, grazing and mining along banks extensively used by otters (Hussain and Choudhury 1997; White et al. 1997).

Finally, spatially explicit dispersal models should be incorporated into conservation programs and reintroduction efforts whenever possible, especially when pre-release data are sparse. The connectivity of suitable patches in heterogeneous landscapes should be given serious consideration, particularly in regions with considerable numbers of roads. In Germany, Kramer-Schadt et al. (2004) found the presence of dense transport systems and the associated road mortality risks to play a critical role in isolating modeled populations of Eurasian lynx (*Lynx lynx*). The connectivity of patches was limited more so by the high mortality of dispersers than it was by the distribution of dispersal habitat. As such, reintroduction and management efforts for species in such regions should not only focus on habitat restoration, but also on the careful selection of release points with particular concern paid to road-crossing management options (i.e. road culverts, highway tunnels, highway overpasses).

As evident in the preceding paragraphs, reports regarding northern river otter social structure and behavioral ecology are very variable. Otters are opportunistic, top carnivores, able to at times be selective in extracting what is needed from their local community to support their basic requirements (Dunstone and Gorman 1998). However, the habitat and community bases, off which they must forage and persist, differ geographically, even at the somewhat local scale (i.e. southeastern coastal Alaska; Blundell et al. 2000, 2002a, 2002b, 2004; Ben-David et al. 2005). With the continued interest in reintroduction efforts for this and other species, the smaller-scale, more localized ecological requirements and differences present in non-disjointed, but varying systems warrants further investigation (White et al. 2003). Therefore, identification of northern river otter spacing patterns, localized habitat use and thus implications for conservation of this reintroduced species were addressed in this study.

At present not much is known about ranging patterns and habitat use by reintroduced and expanding populations of any carnivore, much less otters in

Missouri. Therefore my goal in this dissertation was to assess issues related to the conservation of reintroduced river otters in two areas of Missouri. I evaluated the ranging patterns and habitat use of two reintroduced populations of northern otters at two sites in Missouri, separated by land but contiguous by waterways and characterized by streams of significantly different order (Murphy and Willis 1996), in order to determine which aspects of these watersheds and their surrounding riparian/wetland habitats are most critical in fulfilling the seasonal requirements for river otters in these regions. In Chapter II, I estimated the home range (HR) and core area (CA) sizes of male and female otters in two different stream-order systems (Strahler 1964). I specifically tested the following hypotheses: (H_1) male otters will have larger home ranges and core use areas; (H_2) HR and CA size will be positively correlated with morphological size; (H_3) HR and CA size will be larger for both genders during the breeding vs. non-breeding season; (H_4) percent HR and CA overlap will be greater for males than for females; (H_5) HR and CA size will differ for both sexes by site; and (H_6) percent HR and CA overlap will differ by site.

In Chapter III, I estimated seasonal use of core areas by otters through calculating visitation rates at latrine sites, and evaluating microhabitat variables in used versus unused portions of otter home ranges (i.e. riparian vegetation, riverine geomorphology, water quality measures, prey selection, and presence of beaver activity). These data were combined with additional geographic information system layers defining basic land use/land cover, distance to paved roads and human population centers greater than 1,000 individuals in size in an effort to determine which habitat variables are important in core area selection for northern river otters in Missouri and similar Midwestern states. I tested the following hypotheses: (H_1) otter latrine site revisitation rates will differ seasonally, with otters avoiding latrines in portions of their HRs (a) in summer when shallow, man-made impoundments run dry, and (b) in winter when non-moving, shallow impoundments are frozen; (H_2) otter core use areas will be associated with (a) older-growth vegetation (trees >30 cm in diameter), (b) points of land (i.e. log piles, large rocks on shore, man-made water control structures, elevated bank tree root systems), (c) presence of moving water, (d) water quality factors, and (e) presence of beaver activity; (H_3) heavily utilized portions of otter CAs (latrine and denning sites) will differ in the aforementioned variables from neighboring "unused" areas; and (H_4) centers of otter home ranges will occur more often (a) in land use areas not designated as being associated with human activity, (b) > 1 km from paved roads, and (c) > 10 km from human population centers numbering > 1,000 individuals in the 2000 US census.

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Chapter 2

Ranging Patterns and Space Use in Northern River Otters, *Lontra canadensis*, at Two Sites in Missouri

ABSTRACT

Solitary living in carnivores is typically seen as a consequence of the lack of selection pressures for cooperation. The use of space by solitary female carnivores is usually determined by the abundance and biomass of their food resource. Therefore when food resources are stable and evenly distributed females should maintain small, non-overlapping home ranges. Whereas, when food availability varies spatially and/or temporally, overlapping home ranges should be expected. The use of space by solitary males is often dependent upon two resources, access to food and females, and seasonal shifts should be more pronounced. Thus, solitary male carnivores should maintain larger, more overlapping home ranges unless females are concentrated and evenly distributed. Dispersion patterns and mating systems of solitary carnivores are inherently interconnected; therefore an examination of one must include an analysis of the other. Several studies report evidence of plasticity in the social systems of northern river otters, *Lontra canadensis*, due to tactics employed in acquiring resources, the abundance of which can vary both spatially and temporally. However, very few studies examined differences in use of space by this wide-

ranging, riparian carnivore at two or more sites separated by land but ultimately connected by watersheds. Seasonal spacing patterns, home ranges (HR) and core use areas (CA) of two reintroduced populations of northern river otters in Missouri were studied using radiotelemetry and geographic information technologies. An evaluation of three home range analysis methods, the fixed kernel (fxK), minimum convex polygon (MCP) and Jennrich-Turner (JT) ellipse, was done to determine which method provided the most parsimonious results for a riverine species most often traveling by use of linear pathways. The fixed kernel method for HR size estimation suggested significant sexual differences when sites were pooled, with adult males occupying larger annual HRs and CAs than adult females. Extensive inter- and intra-sexual range overlap was documented for males at both sites. Neither sex maintained larger HRs or CAs during the breeding compared to the non-breeding season. During the non-breeding season (May – January), males' HR and CA sizes showed less overlap, however no significant seasonal differences were discerned between the two populations. The amount of HR overlap by males with females was significantly greater during the non-breeding season than during the breeding season. Accounts of the social ecology found in mid-western otter populations vary. Overall, annual HR and CA sizes of males showed significant location differences; larger ranges were evident for the lower-order stream system (Grand River site) than in the higher-order stream system (Mississippi River/Ted Shanks site). This variation appears to be in part dependent upon the presence of large riverine, diverse backwater habitats contrasting with meandering stream habitats. Although often overlooked, habitat characteristics other than food distribution and abundance may also influence mating system structures, and thus determine use of space by individuals in a region. Differences among stream order and wetland ecosystems seem to have pronounced effects on habitat use, spacing patterns and social structure in this riparian species. In conclusion, the following hypotheses were corroborated: (1) male otters had larger HRs and CAs than female otters; (2) female otters maintained small, non-overlapping home ranges; (3) males exhibit a greater percentage of inter- and intra-sexual HR and CA overlap than females; and (4) HR and CA size, and percent overlap differ between a large, riverine ecosystem and a small, meandering stream ecosystem. However, hypotheses examining temporal use of space by otters were not supported, that is, neither sex exhibited larger HR or CA sizes, or greater degrees of range overlap during the breeding and non-breeding season, regardless of site examined. This study suggested that northern river otters exhibit a variety of spacing patterns in different portions of their range, similar to those discovered in other solitary carnivores. Seasonal use of space is different from what is typically found in other solitary species of carnivores; and differences may be related to varying habitat characteristics associated with stream order and wetland ecosystems.

INTRODUCTION

The spatial organization of solitary carnivores is typically reported as resource dependent (Sandell 1989), with female distribution corresponding to den site and food availability, and males, particularly during the mating season, superimposed on and overlapping the dispersion of females. Males therefore have larger home ranges and travel greater distances than females, except perhaps during winter seasons in northern habitats when movements of both genders are significantly hampered by snow and ice cover (Sandell 1989; Blundell et al. 2000; 2002a). With some notable exceptions such as spotted hyena, and lion, members of the order Carnivora are not commonly found living in groups or aggregations, particularly outside of breeding seasons (Bekoff et al. 1984; Gittleman 1984, 1989). Animal species with visual-hunting predators in habitats with sparse cover may reduce predation pressure by living in groups to either defend themselves aggressively, or use the group as cover, employing the "selfish herd" tactic (Hamilton, 1971). In contrast, those species living in habitats with heavy cover pursue a solitary tactic. When found in social groups, the spatial organization in carnivores is most often associated with cooperative foraging or anti-predator defense strategies, with home range size, regardless of gender, typically dictated by prey distribution and abundance (Gittleman 1989). Spatial studies of semi-aquatic carnivores should address the dual and connective nature of their habitat usage, with prey resources being almost entirely aquatic, and shelter, resting and reproduction requirements being primarily terrestrial (Melquist and Dronkert 1987; Reid et al. 1994).

Northern river otters, *Lontra canadensis*, have historically occupied almost all riparian drainage basins and aquatic habitats of the North American continent from 25º to 70º N latitude and 53º to 166º W longitude, including freshwater wetlands, marshes, rivers, and lakes and coastal intertidal habitats (Halbrook 1978; IUCN 1980; Hall 1981; Toweill and Tabor 1982; Jones et al. 1983; Melquist and Dronkert 1987; Lariviere and Walton 1998). In geographically different parts of their range otters have been shown to use different spacing mechanisms and ranging patterns, utilizing and concentrating their activities in different parts of their available habitat and thus ultimately displaying varying degrees of sociality. For example, in southeastern Alaska, river otters exhibit a range of social organization primarily related to prey availability and distribution, and associated foraging strategies. In Alaska, individuals that inhabit marine environments have smaller home ranges and they tend to forage cooperatively in large social groups on schooling pelagic fishes. When specializing on numerous, rich salmon runs, males in this area (sometimes solitary, sometimes in small groups) must travel great distances and thus have very large home ranges. Whereas in this same region, some individuals, typically female with or without young, have medium-sized home ranges and are most often observed foraging on freshwater and/or intertidal systems with fewer prey (Bowyer et al. 1994, 1995; Ben-David et al. 1998, 2005; Blundell et al. 2000, 2002a, 2004).

Similar low levels of intrasexual range overlap were found for northern river otters in other coastal regions (Humphrey and Zinn 1982; Foy 1984; Erlinge 1968, in *Lutra lutra*). Other studies of river otters found that large male home range size, with little overlap, is influenced by local topography and/or seasonal climatic conditions, particularly in mountain streams and lakes, or at northern latitudes. Populations in these areas typically exhibit polygynous or promiscuous mating systems (Hornocker et al. 1983; Melquist and Hornocker 1983; Griess 1987; Serfass 1984, 1994; Reid et al. 1994; Serfass et al. 1999). Conversely, Midwestern otter populations possess relatively small home ranges with significant intra- and intersexual overlap among males. Moreover, their social structure appears to be dependent in part upon the type of habitat they use. The spaces utilized by otters in the Midwest are typically diverse backwater, wetland areas or meandering, stream habitats (Anderson 1982; Anderson and Woolf 1984; Erickson et al. 1984; McDonald 1989; Newman and Griffin 1994; Johnson and Berkley 1999).

These studies of northern river otter spacing patterns have revealed significant plasticity in social structure, varying both geographically and/or seasonally. This plasticity is attributable to the varying means by which individuals acquire resources, be this food, shelter, conspecifics, or a combination thereof (Ben-David et al. 2005). Few studies of otters, however, have evaluated the potential differences in space use by individuals at two or more sites locally separated by land, but continuous by varying watersheds. As can be gleaned from the preceding discussion, the northern river otter is a popular model species among biologists interested in answering questions about habitat utilization, use of space, and other aspects of their conservation biology. This accrues primarily because of its once threatened status, and the popularity of reintroduction programs as a restoration tool. In addition, there are several other characteristics that contribute to northern river otter's popularity as a study species: 1) relative ease of capture in live traps; 2) adults are large enough to tolerate implantation of relatively large radios; 3) tolerate stress of capture and implantation surgery well; and 4) relatively easy to radio track on foot, from terrestrial and aquatic vehicles, and from the air.

The specific objectives of this study were to assess the use of space by populations of reintroduced *L. canadensis*, including gender-specific differences in home range size and patterns of range and habitat use. I also evaluated whether reintroduced Missouri populations of this species conform to the typical spatial organization of solitary carnivores. Specifically, in solitary carnivores, females have smaller, resource dependent ranges with a greater percentage of their home range comprised of core areas. Additionally, their ranges seldom overlap those of other females'. The spacing patterns of male solitary carnivores are more expansive. Consequently, their home ranges encompass those of several females and also potentially overlap those of other males, particularly during the mating season (Sandell 1989). Accordingly, I estimated the home ranges (HR) and core areas (CA) used by otters of both sexes. I assumed that the home ranges and core areas provide the seasonal needs of food, shelter and intraspecific interaction in two different Strahler (1964) stream-order systems (Murphy and Willis 1996). Specifically, I tested the following hypotheses: H_1 male otters will have larger home ranges and core use areas than females; H_2 home range and core area size will be positively correlated with morphological size; H_3 home range and core area size will be larger for both genders and degree of intersexual overlap will be greater during the breeding vs. non-breeding season; H_4 percent home range and core area overlap will be greater for males than for females; H_5 home range and core area size and percent overlap will differ by site. Specifically, I predicted that a big river system (stream orders > 8) and its associated backwater, wetland ecosystem will provide rich habitats that resulted in smaller home range and core use area sizes, than those observed in a smaller river system (stream orders 3-7). It is likely that features associated with stream order and wetland ecosystems could have pronounced effects on the habitat use, and thus on spacing patterns and social structure of a riparian species, such as the river otter (Strahler 1964; Cowardin et al. 1979; Frayer et al. 1982; Murphy and Willis 1996).

MATERIALS AND METHODS

Study species.—Otters belong to the subfamily Lutrinae (Carnivora; Mustelidae Swainson 1835), and include the genus *Lontra*, a monophyletic group including four species of New World river otters, to which the northern river otter, *Lontra canadensis* Schreber (1776) belongs (van Zyll de Jong, 1972, 1987). According to Hall and Kelson (1959) and Toweill and Tabor (1982), there are 19 subspecies of *Lontra Canadensis*. However, in 1981, Hall published a revision in which he proposed that there are actually only seven subspecies. More recently, Serfass (1994), using an electrophoretic analysis of liver tissue from 732 otters harvested in 18 states and three Canadian provinces, found the delineation of river otter subspecies to follow neither Hall and Kelson's (1959) nor Hall's (1981) classifications. Given that otters possess large home ranges and are able to disperse long distances over both terrestrial and aquatic habitats (Melquist and

Hornocker 1983, Serfass 1994), Serfass (1994) concluded that adjacent otter populations, other than those perhaps isolated on opposite sides of mountain ranges, likely have frequent opportunities for transmission of genetic material due to the extensive connectivity of major drainage systems. As such, Serfass (1994) designated only three subspecific categories for the northern river otter.

Northern river otters, also known as North American or Canadian river otters, are found in almost all aquatic habitat types from freshwater rivers, lakes, wetlands and marshes, to coastal marine and brackish environments (Toweill and Tabor 1982; Melquist and Hornocker 1983). Activity levels in northern river otters have been reported as nocturnal, crepuscular (especially active during the pre-dawn and morning hours), and diurnal, particularly during winter months (Melquist and Hornocker 1979; Toweill and Tabor 1982; Serfass 1994; D. Boege Tobin, pers. obs.). Similar to Eurasian otters (see Erlinge 1967, 1968; Kruuk and Hewson 1978; Jenkins and Burrows 1980; Green et al. 1984), northern river otters are opportunistic denners (Melquist and Hornocker 1979a, 1979b, 1983; Serfass 1994; Blundell et al. 2000, 2002a, 2004). Both males and females deposit personal identification scat, sometimes with anal gland secretions known as "spraints" near dens and feeding locations. Sprainting activity often produces "latrines" (areas with > 2 piles of scat) usually placed on higher-elevation substrate or points of land found along riverbanks, lakeshores, coastlines and/or cross-over paths (Newman and Griffin 1994; Trusso, 1997; Ben-David et al. 1998, 2005; Rostain et al. 2004).

The use of space by northern otters, including the size of home ranges and core areas of use, has been reported to differ seasonally and is often dependent upon the age or sex class being considered (Melquist and Hornocker 1983; Serfass & Rymon 1985; Anderson and Woolf 1987; Erickson & McCullough 1987; Erickson & Hamilton 1988; Hamilton et al. 1994; Reid et al. 1994; Bowyer et al. 1995; Serfass 1994; Ben-David et al. 1998, 2005; Johnson and Berkley 1999; Serfass et al. 1999; Blundell et al. 2000, 2002a, 2002b, 2004). Dispersers typically leave their natal range at about one year of age (Melquist and Hornocker 1979a, 1979b, 1983; Serfass 1994; Blundell et al. 2002b). Northern otters often travel significant distance in order to reach open water (Erlinge 1967; Park 1971; Bottorff et al. 1976; Anderson and Woolf 1987). However, unlike Eurasian otters, northern river otters generally exhibit little if any territoriality (Erlinge 1967; Serfass 1994; Blundell et al. 2000, 2002a, 2002b).

Study sites.—From 30 October 1999 to 24 May 2003 northern river otters and the habitats they occupied were evaluated at two sites in Missouri (Fig. 2.1): 1) Ted Shanks Conservation Area (TS) is located within the Eastern Glaciated Plains along the Mississippi River, a 12th-order river, north of and including its confluence with the Salt River, an 8th-order stream. TS encompass 2,794 ha of bottomland hardwood timber, marsh, wetlands, oxbow lakes and sloughs, borrow ditches, row crop and old field habitats. Most of these habitats have arisen due to the primary or secondary effects of human activities on the Mississippi River (channelization), and from management practices on parts of the associated floodplain using human impoundments (Thom and Wilson 1980); and 2) the Grand River site (GR) consists of several protected areas that together, along with private land, comprise our second field site. Located in north-central Missouri, the Grand River, an 8th-order stream, is the largest prairie river in Missouri that is relatively unaffected by impoundments or channelization. It has eight major tributaries (4th-7th-order streams) and several extensive marsh areas, including Fountain Grove Conservation Area, Swan Lake National Wildlife Refuge and many smaller wetlands. The Grand River Basin is located within the Western Glaciated Plains and contains in excess of 1,000 3rd-order streams, making it the most extensive network of streams of any of the sub-basins in Missouri. Areas specifically used in this study include: (i) Swan Lake National Wildlife Refuge (SLNWR), which consists of 4,446 ha of Grand River floodplain and contains wetlands, moist soil units, old growth bottomland hardwood habitats, and open water, as well as croplands and grasslands; (ii) Pershing State Park (PSP), 1, 212 ha in size, consists mostly of wet prairie interspersed with mature bottomland forest, and marshes, swamps and oxbow lakes created by Locust Creek, a 7th-order stream. Locust Creek is a rich, winding river system, which is a rare habitat of the Western Glaciated Plains, and one of the only sizeable streams in northern Missouri that has not been channelized, or reshaped, by humans; and (iii) Fountain Grove Conservation Area (FGCA), a 2,981 ha intensively managed wetland area, containing both the Grand River and Locust Creek, but primarily utilized for moist soil crop production.

Otter capture.—Otters were live-trapped from 30 October 1999 to 9 July 2000 and from 30 September 2000 to 9 April 2001 at TSCA. At FGCA otters were trapped from 25 March 2000 to 9 July 2000 by the PI, and from 15 September 2000 to 20 April 2001 and from 15 October 2001 to 7 April 2002 by the Missouri Department of Conservation (MDC) for a concurrent study. Trapping was conducted using primarily #11 Sleepy Creek double jaw, double long-spring traps and a few #1-½ coil-spring foot-hold traps (Minnesota Trapline Company, Pennock, MN). Soft-catch® traps were initially employed to try to minimize damage to the trapped foot. However, this type of trap proved ineffective at holding trapped individuals. Consequently, all traps had to be modified to prevent injury to trapped animals. Specifically, all traps were equipped with swivels (every 10-15 cm), springs, and trap wax, and were attached to short, swiveled leads (< 0.5 m). Additionally, the traps were hammered into the substrate with 1 m rebar stakes. All vegetation > 0.5 cm in diameter, was removed (Blundell et al. 1999). These steps were taken to ensure that captured individuals could not forcefully jump or become twisted, perhaps causing a dislocation or break in the captured limb (Blundell et al. 1999; Blundell, pers. comm.). Using these techniques, only two individuals suffered minor injuries to one toe. These minor injuries were treated by a veterinarian before the animals were released. Neither animal appeared to suffer any permanent consequences; both were radio-tracked for the duration of the study and their behavior was comparable to that of uninjured animals. Traps were primarily un-baited and blind-set along cross-over paths where recent otter sprainting evidence was detected. Care was taken to ensure that trap placement minimized incidental captures and was away from thick vegetation around which an entrapped animal could become tangled (Belfiore, pers. comm.; Blundell, pers. comm.).

Traps were kept active over a four day period, and were checked two times each day, approximately 2-3 h after sunset and again just prior to sunrise. When air temperatures exceeded 15º C, traps were monitored three times a day. At remote sites, traps were fitted with trap transmitters which change repetition rate at a given frequency whenever the trap-line was triggered. Remote radio monitoring of such traps occasionally required more frequent checks. Trapped animals were guided into a large-breed dog air-transport cage with a removable door (equipped at one end with a squeeze-box mechanism) (Serfass et al. 1996; Campbell Pet Company, Brush Prairie, WA). Following veterinary advice (see below) no sedatives or anesthesia were administered until the animals were prepared for surgery.

Knockdown and surgical radio-implantation procedures.—Animals were transported to St. Louis for surgeries performed by Jay King, D.V.M. Otters were anesthetized by immobilizing them using a squeeze-cage and then administering an intramuscular injection in the dorsal hindlimb region (Serfass et al. 1996). Thirty-four of 38 intraperitoneal radio implant surgeries were performed by J. King. For these procedures otters were anesthetized using Telazol® (Tiletamine hydrochloride and Zolazepam hydrochloride; conc. = 100mg/ml; mean = 1.1 mg/kg, range=0.5-3.6 mg/kg) with no reversal drug, and were maintained anesthetically recumbent using 1-1.5% Isoflurane gas (IsoFlo®, Abbott Laboratories, North Chicago, IL) with the O_2 flow rate at 2 L and endotracheal tube size of 3.5-4.0 (King, pers. comm.). In four cases alternative anesthetics [Domitor® (Medetomidine hydrochloride; 0.113 mg/kg), or Ketamine hydrochloride (4-5 mg/kg) with Domitor® (0.025-0.050 mg/kg), both requiring the use of the reversal drug Antisedan® (Atipamezole hydrochloride; 5.0 mg/ml; 0.3-2.5 mg)] were used by veterinarians at the Saint Louis Zoo's veterinary hospital, as suggested by the MDC, however neither proved as effective as the methods used by J. King, because as King asserted, surgeries on otters requiring an anesthetic plus a reversal drug may be more stressful to the animals.

Radio transmitters were sterilized in a cold sterilant (Protec-Top® Plus, Carlisle Laboratories, Rockville Centre, NY; Novasan® P, Ecolab® Center, St. Paul, MN) for at least 24 hr prior to implantation. Lithium battery-powered, coiled-antennae, hermetically sealed radio transmitters (Unit #17C, dimensions: 10.9 L X 3.3 W cm, 90 g; Advanced Telemetry Systems, Inc., Isanti, MN) were used, except in three instances when the small size of captured yearlings required the use of slightly smaller (9.7 L x 3.3 W cm, 85 g) transmitters of the same design (Unit #IMP/400/L; Telonics, Inc., Mesa, AZ). Both transmitters constituted less than 5% of an animal's mass. Surgical incisions were made in the abdominal region about 3 cm off the mid-lateral ventral line. All surgical procedures were performed under sterile conditions in veterinary operating facilities.

After surgery was completed, any recent or older injuries were medically treated and antibiotics (0.6-2.5 ml Procaine Penicillin-G + Benzothain pen-G; 300,000 units per ml) were administered subcutaneously into the thigh opposite that used for anesthetic injection. Based on the judgment of the veterinary surgeon, other ancillary medications were given to several otters during surgeries. For example, in a few cases, 0.6-1.5 ml Atropine or 0.1-1.0 ml Dopram was administered as respiratory stimulants. On two occasions Dexamethasone (4 mg/kg, a sodium-phosphate steroid which helps lessen the effects of shock), was given to elevate hydration and electrolyte levels (Kollias 1999; King, pers. comm.). Although normal temperature range is quite broad in otters, it can elevate or drop suddenly. Therefore, temperature was carefully monitored every five minutes during anesthetic procedures as a means of foreseeing potential problems associated with capture/stress myopathy (Hartup et al. 1999). (Hartup et al. 1999; Kollias 1999; Hernandez-Divers et al. 2001).

Otters were not given reversal anesthetic, but were allowed to naturally awaken from the surgical anesthesia under the direct supervision of the operating veterinarian. Otters were held only long enough to ensure their successful recovery (King, pers. comm.), and were returned to their capture site and released, to maximize the probability that they would maintain established home ranges and conspecific contacts. Otters were generally released within 12 h after capture.

Data Collection

Morphometric Data and Processing.—During and following surgeries, morphometric measurements were taken on sex, age class, weight, total body length, tail length, right rear foot and leg lengths, abdominal girth, muzzle girth, distances between eyes and between ears, ear height, and baculum length in males (following methods in Serfass 1994; Baitchman and Kollias 2000). Colored ear tags (#893 Jiffy wing bands) were placed on each ear denoting the sex and identity of each individual, and #1-1005 Monel tags were secured onto each otter's left rear foot, in the webbing between the fourth and fifth digits (National Band and Tag Co., Newport, KY, 41072-0430, USA). Only one ear-tag was seen still intact on all future otter sightings, therefore this technique should only be repeated if smaller, less obtrusive colored tags are available. As tags are often difficult to see from a distance and/or are frequently lost, stenciled "freeze marks" were briefly frozen onto a shaved area in the dorsal, mid-scapular region using canned aerosol Freon (QuikFreeze® 134a; Rostain, pers. comm.; Russell, 1981). Locally freezing, or freeze-branding, a shaved area of mammalian skin for approximately five seconds destroys the melanocytes that produce pigment in the hair, thus permanently creating a stenciled patch of white hair in this area (Russell, 1981). In an evaluation of tagging techniques used for small odontocete cetaceans, Irvine et al. (1982) found that freeze brands were the easiest to locate from a distance, most long-lived and were the least harmful. Any additional obvious markings (i.e. from previous injuries) and overall body condition were noted. Toothwear was documented and assisted in determining age class of individuals (Serfass 1994; Baitchman and Kollias 2000).

Radio-Tracking.—Otters were radio-tracked from 23 November 1999 until 24 May 2003 year-round (mean = 3 d/wk during each spring and autumn trapping season; mean = 4 d/mo during the remaining parts of each year). Otters were radio-tracked primarily by Jeep® and on foot, and occasionally by motorboat, using both a 3-element collapsible and 5-element stationary Yagi antenna (Advanced Telemetry Systems, Minneapolis, MN) and a TR-2 VHF receiver with a frequency band of 150.000 to 152.000 MHz (Telonics, Mesa, AZ). Aerial radio-tracking surveys were conducted once or twice every month by Cessna® airplane or MDC helicopter equipped with strut-mounted 5-element Yagi antennas, one on each side of the aircraft. These aerial tracking surveys were conducted primarily to locate wide-ranging or ‘lost’ individuals for which no radio locations, or ‘fixes,’ could be acquired during the past month by terrestrial tracking.

Capture and release location represented the initial point of contact and, thus, the first radio fix for each study subject. Subsequently, each time a telemetered otter was found its precise locational coordinates were recorded either directly into a global positioning system (GPS) Garmin 12 unit (software version 4.02; MapSource® software version 6.5; Garmin International Inc., Olathe, KS, 66062, USA) or were plotted using United States Geological Survey (USGS) quadrangle county maps (1:24000-scale). Whenever visual contact was made with a telemetered otter, observations regarding group size and behavioral activities (i.e. foraging location) were recorded.

Data Analysis

Morphometric data.—Otter mass, total body length, tail length, right hind foot length and girth measurements were analyzed by reproductive class, gender and site employing either the parametric *t*-test, or the non-parametric, Mann-Whitney *U* test as appropriate (Zar 1996).

Home range size estimation.—Location data for otters were entered into a geographical information system (GIS) for analysis. GPS data entered in the Universal Transverse Mercator (UTM) Nad 1983 Zone 15N projection were converted into point shape files using DNRGarmin® v5.0.4software (Minnesota Department of Natural Resources 2001) which were then saved directly into the GIS ArcView 3.2® (ESRI, Redlands, CA, USA). USGS map location coordinates (latitude and longitude) were digitized into the GIS program GTM® v2.3.6 (Sartwell 2000; MDC, Columbia, MO, USA) using Microsoft Access® software (Microsoft Corporation, Redmond, WA) for cataloging data points, and were then reprojected into ArcView® 3.2 GIS also using the UTM Nad 1983 Zone 15N projection. In a few cases, locations had to be triangulated using multiple radio fixes, bearings, and Locate III triangulation software (Pacer Computing, Tatamagouche, Nova Scotia, Canada). All home range and movement estimates were calculated using the ArcView Animal Movement Analysis Extension® 2.0 (AMAE; Hooge and Eichenlaub 2000) for ArcView® 3.2 in kilometer map units.

Each otter's set of radio location points were first examined for site fidelity using a Monte Carlo simulation of random movement paths; H_0 = The observed movement is less or equal to random movement paths (n = 100 replicates; Hooge 1995, 1997; Worton 1995). Home ranges calculations were conducted for every otter whose location data rejected the null hypothesis of site fidelity.

Because of controversies regarding the best ways to measure home ranges, I used three different home range estimators: (1) fixed kernel (fxK); (2) minimum convex polygon (MCP); and (3) Jennrich-Turner ellipse (JT). As way of background for these analyses, it should be noted that Burt (1943:351) first defined the home range of an animal as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." The most commonly applied statistical definition of a home range is typically that area which describes the relative frequency distribution of an animal's locations over time, often referred to as a utilization distribution (UD; Worton 1987, 1989). Regardless of the method of calculation, most scientists estimate an animal's home range by defining 95% of its locations, thus eliminating outliers typical of exploratory activities (White and Garrott 1990).

Kernel home range estimators, whether fixed or adaptive, assess the probability of occurrence at each point in space for an individual, do not require assumptions regarding the underlying distribution of the data, and ultimately produce a UD for that animal based on its location points (Worton 1987, 1989). Many scientists (Worton 1987, 1989, 1995; Kie et al. 1996; Seaman and Powell 1996; Powell et al. 1997; Swihart and Slade 1997; Seaman et al. 1999; Blundell et al. 2001) currently hold that kernel estimation is a more accurate means of determining a home range size in comparison to earlier methods such as the MCP (Bekoff and Mech 1984; Worton 1987), the harmonic mean (Dixon and Chapman 1980; Worton 1987; Boulanger and White 1990; White and Garrott 1990), and the JT ellipse (JJennrich-Turner 1969; Boulanger and White 1990). For animals with primarily one-dimensional, linear movement pathways, such as river otters inhabiting areas at the aquatic-terrestrial interface, the MCP has little utility as it includes areas of land in home range estimation over which an otter is unlikely to travel, while at the same time excluding waterways that constitute likely paths (Sauer et al. 1999; Blundell et al. 2001; Fig. 2.2). The JT elliptical method is also not appropriate due to its dependence on a bivariate normal distribution of locations.

For these reasons, the fixed kernel (fxK) method for home range estimation was used in this study. So that comparisons can be made more readily to earlier studies (Green et al. 1984; Melquist and Hornocker 1983; Reid et al. 1994), I also present home range calculations for the MCP and the JT elliptical estimators when appropriate.

Therefore, in this study the overall home range (HR) of an individual was calculated from 95% fixed kernel analyses using the reference smoothing parameter (h_{ref}); each individual's core area (CA) was calculated from 50% fixed kernel density contours using least squares cross validation (LSCV) smoothing estimates (Worton 1987, 1989; Silverman 1986; Seaman and Powell 1996; Blundell et al. 2001). Finally, similar to the methods employed by Sauer et al. (1999) and Blundell et al. (2000, 2001), I also measured kilometers of "waterways" (e.g., stream and river banks; wetland, reservoir, slough and borrow ditch edges; lakeshores) that fell within the boundaries of each estimated home range and core area kernel polygon. These distances were calculated using ArcView® 3.2 and Missouri land use/land cover maps [see Sauer et al (1999) and Blundell et al. (2001) for detailed descriptions of these methodologies].

All three ranging measurements (i.e. HR; CA; and kilometers of waterways within each) were made for males and females using their entire set of radio-fixes (total use of space) and were also broken down according to breeding season (1 February - 30 April) versus non-breeding season (1 May - 31 January). Sexes were compared by combining data across sites; however only males provided large enough sample sizes to be compared between the two sites. Therefore, due to the small sample sizes obtained in live-trapping females ($n = 6$), they were included only in total range analyses when data from both sites could be pooled (by site: $n = 3$ for TS; $n = 3$ for GR). For temporal analyses, the number of females radio-tracked during the breeding season ($n = 4$) was too low for powerful statistical examinations by sex. However, all females ($n = 6$) were radio-tracked during the non-breeding season, thus comparisons with males could be made.

Age classes could not be compared in any home range analyses. Some non-reproductives (≤ 1 year old; Hamilton 1998) were too small for radio-transmitters to be implanted intraperitoneally (King, pers. comm..), thus producing a radio-tracking sample size that was too small for powerful statistical conclusions to be drawn

Statistical analysis of use of space.—Statistical tests were performed using JMP (v.5.1.2, SAS Institute Inc., Cary, NC) and GraphPad InStat (v.3.06, GraphPad Software, San Diego, CA) software packages. Whenever possible, parametric tests were used and unless otherwise noted, results are presented as mean ± 1 SD. Because the sizes of home ranges and core areas were typically not normally distributed, I used Mann-Whitney *U*-tests to discern median differences in home range size, core area size and space use overlap between: (i) sexes; (ii) the two field sites; and (iii) the two seasonal designations (breeding season and non-breeding season). Data were log transformed prior to non-parametric analyses when necessary (e.g., during examinations of percent home range and core area overlaps). I evaluated the consistency of the three range estimation methods (fxK, MCP and JT) by employing a repeated-measures ANOVA with Tukey-Kramer multiple comparisons post-hoc test to elucidate which pair wise comparisons contributed to overall significance. For all tests, $P < 0.05$ was used as the level of significance (Zar 1996).

All procedures were conducted in accordance with the ethical guidelines established by the Animal Care and Use Committee (1998) of the American

Society of Mammalogists (http://www.mammalogy.org/committees/index.asp), and were approved by the Institutional Animal Care and Use Committee of the University of Missouri-St. Louis (protocol #S99-2) and the Missouri Department of Conservation (Wildlife Collector's Permits # 10626 and # 11191).

RESULTS

Morphometric Data and Correlations

Table 2.1 lists the means ± SE or medians, *t*- or *U*-values, and α levels (*P*-values) for all otters trapped and measured during this study (n = 37) compared in the following pairwise fashions: (i) reproductive class [non-reproductives (n = 15) and reproductives (n = 22)]; (ii) sex [females (n = 9) and males (n = 28)]; and (iii) site [TS (n = 15) and GR (n = 22)]. Pair-wise comparisons by reproductive class revealed strongly significant differences between non-reproductives (≤ 1 year old; see Hamilton 1998) and reproductives for all size categories (Table 2.1). No size differences were detected among non-reproductives between the two sites, and only marginally significant differences were detected in mass and tail lengths among individuals of reproductive age between the TS and GR sites (Table 2.1). Unfortunately, due to their small size, non-reproductive individuals were too small to implant radio-transmitters, and therefore were excluded from the remainder of the study.

Comparisons between the sexes revealed strongly significant differences in sizes of males versus females in all but two measurements (tail length and hind foot lengths of females versus males at the TS site), whether compared within or between sites (Table 2.1). Conversely, no significant differences were observed in sizes of individuals between sites, regardless of whether sexes were combined or teased out (Table 2.1).

Since they are often reported in other studies, correlations between gross morphological measurements (mass, total length, and length:mass ratio) and home range and core area sizes were also computed. No significant correlations of morphological size and range sizes were found for comparisons among males at TS, among males at GR, among pooled males between sites, nor between sites when gender classes were pooled. Because the total sample size of females was small even when sites were pooled (n = 6), female versus male comparison were conducted by first randomly selecting six males from all males pooled from both sites. In each comparison of mass, total length, and length:mass ratio, females were significantly smaller than males (mass: $U = 0.00$, $P = 0.002$; total length: $U = 0.00$, $P = 0.002$; length:mass ratio: $U = 1.00$, $P = 0.004$). Reproductive age classes could not be compared across sites due to small sample sizes.

Home Range Size

Comparison of three home range analysis methods.—Thirty-three of 37 live-trapped otters were surgically implanted with radio-transmitters; four were too small for intraperitoneal placement. The total number of radio-locations acquired was 1, 666 (mean = 52.06, range = 8 - 134). Overall comparisons of male home ranges yielded significant differences in size for the three types of estimators (i.e., fxK, MCP, JT) regardless of whether all males were pooled (n = 27) or examined separately by site (n = 10 at TS, 17 at GR; repeated measures ANOVA — Pooled: $F_{[2,25,50]} = 16.04$, $P < 0.0001$; TS: $F_{[2,9,18]} = 3.62$, $P = 0.05$; GR: $F_{[2,15,30]} = 13.90$,

$P < 0.0001$; Fig. 2.3 a-c). In every case, multiple comparisons post-tests revealed significant differences due to pairwise comparisons between either the fxK and/or the MCP methods vs. the JT method.

When compared within seasons, similar results were obtained for males whether pooled or analyzed by site (repeated measure ANOVA; **BS**-Pooled: $F_{[2,23,46]} = 5.23$, $P = 0.009$; TS: $F_{[2,9,18]} = 8.65$, $P = 0.002$; GR: $F_{[2,13,26]} = 3.56$, $P = 0.04$; **NBS**-Pooled: $F_{[2,26,52]} = 9.76$, $P = 0.0003$; TS: $F_{[2,9,18]} = 5.75$, $P = 0.01$; GR: $F_{[2,16,32]} = 6.50$, $P = 0.004$). However, in every seasonal comparison the MCP vs. JT pairwise post-hoc comparison was the only set which contributed significantly to overall results. No significant differences were found when comparing the three analysis methods for female home range size estimations, whether considering the entire data set or separated by seasons.

Home range distributions.—As described above, post-hoc comparisons revealed the MCP and JT analysis types to be the primary contributors to the different home range sizes calculated for males in all cases (Fig. 2.3 a-c). The fixed kernel (fxK) method and the length of waterways (km) within the kernels appear to be the most appropriate methods to use in calculating and describing the ranges of animals that move in primarily linear pathways. Consequently, the remaining calculations presented here were determined using the fixed kernel method, as well as the total kilometers of waterways within home ranges (defined as 95% of the fixed kernel areas) and core areas (defined as 50% of the fixed kernel areas). In some cases, results are also presented from MCP and JT analyses for comparisons with previous studies that have utilized these methods.

Female versus male range comparisons were made after individuals from both sites were pooled. In all cases, female range sizes were significantly smaller than those of males (Fig. 2.4 a-d): home ranges (t-test: $t_{30} = 4.01$, $P = 0.0004$); core areas ($U = 17.00$, $P = 0.002$); kilometers of waterways within home ranges ($U = 17.00$, $P = 0.002$); kilometers of waterways within core areas ($U = 9.00$, $P = 0.0002$); MCP home ranges ($U = 33.00$, $P = 0.03$); and JT home ranges ($U = 26.00$, $P = 0.01$). To confirm observed results, I randomly selected six males and compared their home ranges and core areas with those calculated for all six pooled females. While medians of females home ranges differed significantly from those of the randomly selected males ($U = 5.00$, $P = 0.04$), the results obtained for core area comparisons fell just short of statistical significance ($U = 6.00$, $P = 0.06$).

Site comparisons (TS vs. GR) for males indicated no significant differences in home range sizes ($U = 52.00$, $P = 0.15$), core area sizes ($U = 55.00$, $P = 0.20$), or for kilometers of waterways within home ranges, ($U = 63.50$, $P = 0.40$). However, analyses of kilometers of waterways within core areas, MCP home ranges and JT home ranges did reveal statistically significant medians between these two male populations ($U = 41.00$, $P = 0.04$; $U = 32.00$, $P = 0.01$; $U = 37.00$, $P = 0.02$, respectively; Fig. 2.5 a, b).

No significant differences were found between age classes (non-breeders vs. breeders) for sizes of home ranges or core areas, or for proportion of core area size relative to home range size. Once separated by season or site, age class sample sizes were too small to be included in further analyses.

The percent of the total home range area occupied by an individual's core use area only revealed significant sex differences for total (aseasonal) pooled females versus pooled males (*U* = 37.00, *P* = 0.04). Males more extensively used a greater proportion of their home range (core area:home range area) than did females. When analyzed across sites with sexes pooled, when using only males, or when analyzed by reproductive class with sites pooled, no significant differences were found.

Spatiotemporal Patterns of Range Use

Breeding season.—No significant differences were found for the median number of radio locations and estimated kernels found for each otter between the sexes or between the males at the two sites. Overall range analyses for the breeding season revealed size differences between females (n = 4) and males (n = 22). Males occupied significantly larger areas for both their home ranges (*U* = 11.00, *P* = 0.01), and their core areas of use (*U* = 11.00, *P* = 0.01). However, the length of waterways within either home ranges or core areas indicated no differences between males and females.

No spatiotemporal differences in home range or core area size were found during the breeding season for males at TS versus males at GR. Likewise, the kilometers of waterways within both the home ranges and the core areas were also not significantly different between males at the two sites. To be certain this was not due to differences in radio-tracking effort, the number of radio fixes and the number of estimated kernels for each male at the two sites were compared, but no significant differences were found.

Non-breeding season.—When they were pooled across sites, significant differences were found between the sexes in their overall non-breeding season core area sizes and kilometers of waterways contained within these core areas ($U = 35.00$, $P = 0.03$; $U = 30.00$, $P = 0.02$, respectively). Differences observed between males and females in their total home range sizes and kilometers of waterways contained within home range kernels fell just short of significance ($U = 40.00$, $P = 0.057$; $U = 41.00$, $P = 0.064$).

Differences in spatiotemporal use of space were observed during the non-breeding season between males at the two sites. During the non-breeding season, male overall home range ($U = 40.00$, $P = 0.02$) and core area ($U = 41.00$, $P = 0.03$) sizes were significantly different. Males at the TS site maintained smaller home ranges and core areas than did males at the GR site. Kilometers of waterways contained within the home ranges and core areas used during the non-breeding season by males at the two sites were not statistically different.

Breeding season versus Non-breeding season.—Overall, no differences were found (for any of the range estimators employed: home range size; kilometers of waterways within home ranges; core area size; kilometers of waterways within core areas) between all females and all males (sites pooled) when comparing the reproductive seasons. Similarly, no range size differences were found among TS males or among GR males between the breeding season and the non-breeding season.

Spatial overlap.—At no time or at either site in this study did females overlap with other females in either home range or core areas. During the breeding season, only one male at the GR site overlapped the home range of a radio-tagged female. Consequently, no site comparisons could be made between the sexes for breeding season home range or core area overlap. On the other hand, at TS all males had home ranges that overlapped the home range of at least one female (mean overlap = 80.00% ± 25.82%, n = 10). In other words, there was extensive overlap with only approximately 20% of a home range being used exclusively by each male. With one exception, every male at both sites had home ranges that overlapped either or both sexes (n = 22**).** At the TS site, the amount of spatial overlap (i.e. log % overlap) by same versus opposite sex individuals was statistically different, with males overlapping a greater percentage of females' home ranges than they did those of other males' ($U = 60.00$, $P = 0.02$). The difference in the amount of male-male home range overlap between the two sites was extremely significant ($U = 6.00$, $P < 0.0001$), with males at TS overlapping significantly greater proportions of other males' home ranges than did males at the GR site. However, the core area overlaps for males at the two sites were not statistically different. Likewise, the percentage of intersexual versus intrasexual core area overlap by males did not differ. During the breeding season, male total home range and total core area overlap (of other males *and* females) was not significantly different.

During the non-breeding season, 20 out of 27 male home ranges were overlapped by at least one female (74.07%). Although a greater percent of male home range area was overlapped by females at the TS site (80%) versus the GR site (70.59%) this difference was not significant. When the sites were pooled, female-male overlap of home ranges was greater than male-male overlap (U = 176.00, $P = 0.04$), and male-female overlap was greater than male-male overlap ($U = 37.00$, $P = 0.04$). However, males and females did not differ in their total home range or core area overlaps. Similarly, total home range and core area overlap measurements were not different between males at the two sites. Females could not be compared between the two sites because number of females radio-tracked during the non-breeding season at each site was only three.

Overall, home range overlap by males over females was significantly greater during the breeding season versus the non-breeding season (U = 27.00, P = 0.001), a trend not typically found in carnivores. No other breeding season versus non-breeding season overlap analyses were statistically significant.

DISCUSSION

Anatomical measurements of northern river otters captured for this study were comparable to those reported elsewhere (Route and Peterson 1988; Reed-Smith 1995; Serfass1994; Baitchman and Kollias 2000), and as expected, non-reproductives (≤ 1 year old) were significantly smaller than breeding adults for all morphological measurements (Hamilton 1998). Size differences for otters from the two sites were not pronounced, but comparisons by sex revealed highly significant differences with males being larger than females for almost all measurements. In addition, no significant correlations of gross morphological measurements and home range or core area sizes were found, thus lending no support to H_1, that home range and core area size are positively correlated with body size. This is consistent with findings from other studies on mustelid morphology and space use (Kruuk 1995; Stevens et al. 1997; Gorman et al. 1998; Palazón and Ruiz-Olmo 1998).

For H_2, that male otters have larger home ranges and core use areas than females was supported in all cases, regardless of the predictive estimated analysis method employed (MCP, JT, fxK). In addition, kilometers of waterways contained within both home ranges and core areas were also significantly smaller for females than males. Although the sample size for pooled females was small (n = 6), a comparison of the home range and core area sizes for six randomly selected males produced similar results. The estimation of home range size using traditional techniques (e.g., MCP, JT, fixed or adaptive kernels) tends to overestimate home range size of individuals because unused tracts of land and water are often incorporated into their estimations (Worton 1989; White and Garrott 1991; Seamen and Powell 1996; Sauer et al. 1999). Although seemingly applicable for riparian species, the linear estimation method for calculating the total amount of waterway kilometers within kernels did not produce results different from those obtained using the other estimators (Sauer et al. 1999; Blundell et al. 2000, 2002a). Overall, males had larger home ranges and core areas than females, and they encompassed significantly greater distances of waterways than did females.

Furthermore, when divided into seasons, home range and core areas size comparisons during the breeding season (Feb 1 – April 30) also corroborated H_2, with males again occupying significantly larger areas of space. The length of waterways used within each of these areas during the breeding season, however, suggested no differences between males and females. During the non-breeding season, differences in use of space again existed for males and females, but in this case only their core area sizes and total kilometers of waterways were significantly different. Sexual differences in total home range sizes and kilometers of waterways in home range kernels were not quite significant. In this case, the linear estimation of kilometers contained within kernels provided results contradictory to those found with the fixed kernel area estimations, although there was a strong trend for males to use greater length of waterways than females.

While support for H_2 varied depending upon the range estimator used and seasonality, overall a significant trend was exhibited with males having larger home ranges and core areas than females. Spacing patterns are typically the result of those tactics employed by members of a population in their attempts to survive (attain food and shelter) and maximize their reproductive success (gain mating opportunities; Erlinge and Sandell 1986; Sandell 1989). The results of this study were consistent with the general patterns observed for most solitary carnivores where males' ranges are typically much larger than those of females', often encompassing a significant portion of several females' ranges, particularly during the mating season (Green et al. 1984; Dunstone and Birks 1985; Erlinge and Sandell 1986; Sandell 1989; Estes 1989).

In contrast, evidence from this study refuted H_3. Home range and core area size and degree of overlap were not larger during the breeding season. These findings probably warrant additional examination. In particular, a more equitable ratio of females to males should be concurrently tracked within a population in order to make robust statements about spacing and/or other behavioral tactics potentially employed by individuals in their attempts to maximize reproductive opportunities.

An accurate determination of an animal's use of space can be confounded by infrequent subsampling of the true space used by the individual, the statistical means by which we attempt to describe that space used, and the different statistical properties inherent to each type of analytical method (Swihart and Slade 1986; Harris et al. 1990; Seaman and Powell 1996; Blundell et al. 2001). In addition, the techniques available to determine the spaces encompassed by a given set of distributional locations are not equally appropriate, nor should one method necessarily be used to answer all questions in a given research project (Swihart and Slade 1986; Boulanger and White 1990; Harris et al. 1990; Worton 1995; Powell et al. 1997; Powell 2000; Blundell et al. 2001).

Many researchers have used the minimum convex polygon method for predicting home range and core area sizes (Bekoff and Mech 1984; Worton 1987). However, in general, animals tend not to move randomly through their home ranges (Swihart and Slade 1985; Legendre 1993; Powell 2000). Some species, such as many turtles (Morales-Verdeja and Vogt 1997), shorebirds (Warnock and Tekekawa 1995), beavers (*Castor canadensis*; Wheatley 1997), mink (*Mustela vison*; Stevens et al. 1997), and river otters (Bowyer et al. 1995; Sauer et al. 1999; Blundell et al. 2000, 2001, 2002a) restrict their movements to relatively linear, narrow paths, such as those that confine their movements to the aquatic-terrestrial interface along water drainages and/or shorelines. In these instances, some behavioral ecologists have recently determined the total length of shoreline/riverbank and used it to approximate the linear movement pathways traversed by individuals within their kernel home ranges (Sauer et al. 1999; Blundell et al. 2000, 2001).

As seen in Figure 2.3 a-c, and as revealed in post-hoc comparisons, the MCP and JT estimators were the primary contributors to the differences in home range sizes calculated for males in all cases. Given these findings, as well as those described above for linear pathways and by others (Worton 1987, 1989, 1995; Kie et al. 1996; Seaman and Powell 1996; Powell et al. 1997; Swihart and Slade 1997; Sauer et al. 1999; Seaman et al. 1999; Blundell et al. 2001), the fixed kernel, and the length of waterways within the areas determined by the fixed kernel method, appear to be the most appropriate methods to use in calculating and describing the ranges of river otters traveling in riparian systems along primarily linear pathways. In this study, kilometers of "waterways" (i.e. riverbanks, shorelines of lakes, ponds, backwater and wetland bodies of water such as oxbow lakes, sloughs, borrow ditches, etc.) seem most appropriate for defining home range and core area sizes for males and females and between two sites varying in their stream order and associated watershed/wetland habitats. However, polygon areas defined by fixed kernels should be used for discerning patterns in spatiotemporal gender overlap.

Some researchers assert that it is more accurate to define an animal's use of space as the proportion of the core area that encompasses the home range area. In this study females had significantly smaller core areas relative to their total (aseasonal) home range sizes than did males. These findings refute H_1, and contradict the findings for solitary carnivores that females have a greater percentage of their home range comprised of core areas of use (Sandell 1989;

Johnson and Berkley 1999; Blundell et al. 2000; 2002a; Ben-David et al. 2005). However, I did find support for the notion that females have smaller, resource-dependent ranges that seldom overlap those of other females' ranges. It is possible, however, that the females in this study were using a fewer number of denning/resting and feeding locations more intensely than that found in previous studies. Radio-tracking of females was rather predictable, and females were often found in one of a few regularly used sites. It is likely that females were moving over the majority of their home ranges on a regular basis in order to acquire necessary food resources, but when resting or denning, they returned to one of a limited number of sites (Melquist and Hornocker 1983; Newman and Griffin 1994; Johnson and Berkley 1999; Blundell et al. 2000, 2002a).

The findings of this study were consistent with those reported previously for otters elsewhere in the Midwestern portion of the United States (Lauhachinda 1978; Karnes and Tumlison 1984; Anderson and Woolf 1987; Erickson and McCullough 1987; Erickson and Hamilton 1988; Johnson and Berkley 1999). In a study of reintroduced otters in Indiana (Johnson and Berkley 1999), home range areas were similarly calculated using the kernel estimator (adaptive, not fixed), but were slightly larger than those reported here. Earlier studies in Missouri (Erickson et al. 1984), conducted at a site different from those reported here, used the minimum convex polygon estimator, and found smaller overall home range sizes than those revealed in the current study. In mountainous regions, whether in Tennessee, Idaho, or Alberta, Canada, home ranges tended to be much larger (from approximately 40 to over 200 km^2; Griess 1987; Melquist and Hornocker

1983; Reid et al. 1994, respectively). Clearly home range sizes in otters can vary widely depending on geography and habitat characteristics.

No evidence was found in support of H_3 as neither males nor females had larger home range or core area sizes during the breeding when compared to the non-breeding season. No seasonal differences were detected in space use among males, among females or between males at the two sites, regardless of range estimator used. Similarly, no range size differences were found among TS males or among GR males between the breeding and non-breeding seasons. These findings were surprising because, while the distribution of denning and resting sites, and perhaps even prey resources, can be concentrated and somewhat predictable within a given otter's range (especially in their core areas), the seasonal search for potential mates, especially in a wide-ranging species such as the river otter, would suggest that ranges for both sexes during the reproductive season should increase in overall home range size. This pattern has been documented in a variety of carnivore species (brown hyena, *Hyaena brunnea*, Mills 1982; brown bear, *Ursus arctos*, Servheen 1983; Canadian lynx, *Lynx canadensis*, Bailey et al. 1986; stoat, *Mustela erminea*, Erlinge 1977, Erlinge and Sandell 1986, Sandell 1986), but was not observed in this study.

One might expect, given the previous findings, that the ranges of males likely overlap those of several females with whom he has the potential to acquire mating opportunities (Mills 1982; Sandell 1986, 1989). When densities of females are low, it benefits males to move around more over a larger area in search of receptive females than to stay in a smaller range and secure matings from only a few females (Sandell 1989). Although female densities in this study were low, the amount of observed home range overlap by males over females was significantly greater during the non-breeding season than during the breeding season, a trend not typically found in carnivores and contrary to most predictions (Sandell 1989; Gittleman 1989; Blundell et al. 2002a; Ben-David et al. 2005) in Thus, these findings refute the second half of my third hypothesis, and perhaps suggest that females with whom males normally overlap during the non-breeding season were avoided during the breeding season (e.g., possibly inbreeding avoidance; Gompper et al. 1998; Blundell et al. 2002b; Field and Guatelli-Steinberg 2003). Erickson and McCullough (1987) and Johnson and Berkley (1999) found dispersal distances to be less (with, therefore, greater potential for kin clustering) for otters released in wetlands diverse in their composition of aquatic habitats as compared to smaller riverine sites; others have found far greater dispersal distances (therefore, less potential for kin clustering) in mountainous, riverine habitats in Tennessee (Griess 1987) and Idaho (Melquist and Hornocker 1983). However, since data on dispersal and genetic relatedness were not collected in this study, I can only speculate, but not conclude with any certainty, that the pattern of decreased overlap during the non-breeding season could be due to inbreeding avoidance. Two recent molecular genetic studies did not find evidence of kin clustering, but additional studies should be conducted on other populations (Serfass et al. 1998; Blundell et al. 2002b).

Evidence generated by this study supported H_4 in that total annual percent home range and core area overlap was greater for males than for females. At no time or at either site in this study did the home ranges or core areas of females overlap those of other females. Some degree of home range overlap was observed for every male at both sites except for one case. Moreover, during the breeding season, home range overlap by all males of at least one female's home range was found, but the degree of overlap was surprisingly more pronounced during the non-breeding season.

These results, however, may have been affected by the small sample size obtained in live-trapping and tagging of females at both sites. Johnson and Berkley (1999) found that 14 reintroduced otters in Indiana displayed both intersexual (mean = 59% for males; mean = 36% for females) and intrasexual overlap (mean = 48%). None the less, their findings might be attributable to the fact that the range data reported came from individuals that had just been released following a reintroduction effort (i.e. individuals were likely still in the process of establishing their home ranges and core use areas; Johnson and Berkley 1999).

Given the findings of this study that home range overlap by males over females was significantly greater during the non-breeding season, it perhaps follows that the extent of range overlap between individuals was less influenced by maximizing mating opportunities than by resource abundance and distribution. Overlapping ranges are likely to be found in systems where the timing and spacing of available key resources (food and shelter) vary (Ward and Krebs 1985; Litvaitis et al. 1986; Sandell 1989). A larger area containing a surplus of food for most of the year is likely to support several animals, thus developing a system of overlapping ranges. Similarly, when ranges are non-overlapping they likely include only enough resources for one animal, and hence the prediction is that exclusive ranges are relatively smaller than overlapping ranges. This may be the governing factor in these Missouri watersheds, with shelter (and perhaps to some degree food) limiting the range overlap in females who need exclusive denning and resting space more so than males due to their solitary rearing of young. River otters tend to be opportunistic denners and no significant evidence of territoriality has been found in this or related species (Green et al. 1984; Melquist and Hornocker 1983; Kruuk 1995; Dunstone and Gorman 1998; Blundell et al. 2000). It therefore follows that males may not be as dependent upon shelter as females, and therefore can range further to acquire adequate food resources. Unfortunately, until there are sufficient methods to adequately measure all aspects of resource distribution and prey density, the prediction that ranges will overlap when resources (food and shelter) are spatially and temporally variable cannot be satisfactorily tested (Van Orsdol et al. 1985; Sandell 1989; Blundell et al. 2002a; Ben-David et al. 2005).

Site comparisons (TS and GR) for total (annual) use of space by males indicated no significant differences in home range sizes, core area sizes, or kilometers of waterways within home ranges, however the length of waterways within core areas were significantly different between these two male populations (Fig. 2.6 a, b). Males at the Grand River site traveled along more kilometers of waterways within their core areas than did males at the Ted Shanks site. This could in part be explained by differences in ecogeomorphology. The GR site contains more streams and tributaries, but expanses of land often separate riparian habitats. The TS site encompasses a portion of the Mississippi River which floods periodically creating an abundance of connected backwater and wetland habitats (Thom and Wilson 1980). However, when these data are examined as a proportion of core area size within the corresponding home range area, no significant differences were detected between the two sites.

Seasonally, no differential use of space was found during the breeding season for males at the two sites (regardless of range estimator used). Differential use of space was observed, however, during the non-breeding season with males at the TS site maintaining smaller home ranges and core use areas than males at the GR site. It is interesting to note, however, that kilometers of waterways contained within each of these use polygons during the non-breeding season by males at the two sites was not statistically different. It is likely that otters at the TS site, an area composed primarily of an 11th order and an 8th order stream and their associated backwater, wetland ecosystem, were provided with such a locally rich, concentrated habitat that a wide area over which to range for resources was not required. This area is a floodplain of the Mississippi River, which is inundated with water on a regular basis (both naturally and by anthropogenic forces) thereby resulting in an abundance of backwater sloughs, oxbow lakes, and ditches (Thom and Wilson 1980). Because of this, otters at the Ted Shanks site did not necessarily have to range over as great a linear riparian distance (traveling up and/or down river), but their ranges did cover an area with about the same lengths of waterways as found at the GR site.

In comparing range overlap between the two sites, during the breeding season the total home range overlap for males was greater at the TS site. In this big river system, males overlapped a greater percentage of females' home ranges than they did those of other males', and more males overlapped each other at TS than they did at GR. During the non-breeding season, the home ranges of TS males likewise showed significantly more overlap than found for the GR males. When comparing total core area overlap, however, the differences for males at the two sites were not significant. This could in part be explained by differences associated with stream order. A positive correlation often exists between stream order and indices of biotic integrity for macroinvertebrate and fish communities (Wright and Li 2002; Fayram et al. 2005). These groups comprise the major prey sources for otters and other mustelids (Knudsen and Hale 1968; Lauhachinda 1978; Gilbert and Nancekivell 1982; Serfass and Rymon 1985; Anderson and Woolf 1987; Tumlison and Karnes 1987; Serfass 1994; Roberts 2003). In addition, Fayram et al. (2005) found that the variability in the indices of biotic integrity tended to be greater in smaller streams. It is possible, therefore, that differences in prey abundance, variability and distribution in the two stream order systems examined here are at least in part responsible for the differences in space use by otters.

Support was similarly found for H_5 as home range and core area size, as well as percent overlap differed by site. Use of space by otters in the big river system (stream orders > 8, with its associated backwater, wetland ecosystem) revealed smaller home range and core area sizes, particularly during the non-breeding season, than those observed in a smaller river system (stream orders 3-7). It would be interesting to determine if the characteristics defining the portions of the habitat intensively used by otters within these two river systems differ significantly. Since we were unable to assess the ranging patterns among females at the two sites, it is not possible to determine if females were the resource that influenced the observed spacing patterns in males (often reported for solitary carnivores; Sandell 1989), or if the abundance of food and shelter dictated the spacing patterns I observed. The ranging patterns of males at the two sites were not significantly different during the breeding season. Perhaps this is because, regardless of location, males needed to cover more ground in search of potential mates.

Finally, on three occasions, radio equipped otters were observed in groups ranging from 4-9 individuals. Group living in otter species was thought to be quite rare, with the exception of the sea otter and neotropical giant otters, *Pteronura brasiliensis*; most otter species are solitary, or sometimes occur in pairs; the only exception to this are females with young that occasionally coalesce into larger groups (Erlinge 1967b, Melquist and Hornocker 1983; Chanin 1985; Mason and Macdonald 1986; Estes 1989). Recent studies (Blundell et al. 2000, 2002a; Ben-David et al. 2005), however, have suggested that coastal river otters, especially males, may spend significant amounts of time foraging in social groups. Although group living across the entire Carnivora is relatively rare (10-15% of all species), hypotheses for its evolution include primarily the benefits of anti-predator defense and the exploitation of food, with group defense found primarily in smaller species, especially those living in open habitats (Hamilton 1971; Kleiman and Eisenberg 1973; Kruuk 1975; Gittleman and Harvey 1982; Macdonald 1983; Rood 1986; Gittleman 1989). In Missouri, river otters do not have any predators other than humans, and are typically not found in open areas (Schwartz and Schwartz 1981; Hamilton et al. 1994). Studies on coastal river otters indicate that the ranging patterns of individuals found in social groups tend to be smaller in overall home range and core area sizes compared to solitary individuals foraging on inland, riverine prey and solitary females with young foraging on inter- and sub-tidal fishes (Blundell et al. 2000, 2002a; Ben-David et al. 2005).

In a similar fashion, it appears quite likely that features associated with stream order and wetland ecosystems, upon which individuals ultimately depend for their food and shelter, could have pronounced effects on the habitat use, and thus spacing patterns and social structure of river otters studied in two different riparian watersheds (Cowardin et al. 1979; McNab 1980; Frayer et al. 1982; Gittleman and Harvey 1982; Murphy and Willis 1996; Fayram et al. 2005). It is worth reiterating that the vast majority of all individuals trapped at both field sites were males of reproductive condition. Since traps were placed primarily at cross-overs with evidence of current otter use (i.e. spraints, latrines, slides), it is possible that these portions of otters' ranges are disproportionably used by males in these locations. Although the typical spatial organization of solitary carnivores is considered resource-dependent (Sandell 1989), apparently other forces may be playing a significant role in determining the use of space in reintroduced populations of river otters in Missouri. In group living carnivores, quantitative analyses of ecological factors indicate that both the exploitation of food resources and habitat are influential in determining the ranging patterns and mating systems of these species (Gittleman 1989). Quantitative examinations of habitat predictors aimed at determining the use of space and social structures in solitary carnivores are lacking. Spatial studies of semi-aquatic carnivores should be certain to address their dual, connective habitat usages, because while prey resources are almost entirely aquatic, shelter, resting and reproduction requirements are most often met on land (Melquist and Dronkert 1987; Reid et al. 1994). Research is particularly essential to document the success of reintroduction projects, such as those that have been conducted in the past 25 years for the northern river otter throughout much of historic range. Assurance of habitat quality, adequate prey base and suitable denning locations are essential to the perseverance of this species.

From a conservation view, the Missouri Department of Conservation's river otter reintroduction program was certainly a success in reestablishing a threatened species to portions of its former range. However, the impact of these top carnivores on many ecosystem-level properties (e.g., on their prey populations) is not yet understood. In Missouri, reintroduced populations of river otters have quickly spread across much of the state. Perhaps this rapid expansion was in part due to effects similar to those found in the variable spacing patterns observed in this study. The effects of these carnivores on local fish communities have recently received much attention in Missouri, especially with regard to game species. However, little experimental field work on predator-prey relationships of reintroduced carnivores has been conducted in Missouri or elsewhere. In fact, most reintroduction projects do not adequately examine the potential trophic effects, that either the prior absence or reestablished presence of such wide-ranging predators, have on community structure. Such research efforts, conducted both prior to and following carnivore reintroductions, would not only provide fundamental scientific data, but would also help resolve management problems should they arise following population establishment.

Extensive reintroductions of carnivores can quickly impact not only prey populations, but also those species, including humans, with which competition for food and shelter resources is inevitable. Whenever possible, the implications for natural recolonization of extirpated populations via habitat remediation should be considered in lieu of, or in conjunction with, reduced reintroduction effort. Although the benefits may not be as immediate or dramatic, the impacts on community-level interactions may be less severe. More specifically, impacts relevant to a species such as the northern river otter may include potential human conflicts, disruptions to population genetic structure, and environmental ramifications from the reestablishment of carnivore species.

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Table 2.1.— Morphological data expressed as means (± SE) or medians, *t*- or *U*-values, and significance levels (*P*-values), for all otters live-trapped and measured at two sites (Ted Shanks Conservation Area and north-central Grand River region) in Missouri. Data are compared in the following pair-wise categories: reproductive class [non-reproductives (**NR**) versus reproductives (**R**)], gender (males versus females), and site (TS versus GR). For all tests, mass is reported in kg, length in cm, and $P \leq 0.05$ is the level of significance.

Morphological Variables	**NR-All** mean ± SE	**R-All** mean ± SE	df	*t*	*P*
Mass	5.70 ± 0.34	8.77 ± 0.18	35	8.59	<0.0001
Total Length	106.40 ± 1.78	118.40 ± 1.04	35	6.20	<0.0001
Tail Length	39.07 ± 1.08	42.08 ± 0.64	35	2.56	0.02
Hind Foot Length	11.95 ± 0.15	12.72 ± 0.17	35	3.11	0.004
Girth	33.09 ± 0.84	39.94 ± 0.45	35	7.78	<0.0001

Morphological Variables	**NR-TS** mean ± SE	**R-GR** mean ± SE	df	*t*	*P*
Mass	6.35 (15)*	5.72 (15)*		18.00*	0.44
Total Length	107.50 ± 1.58	105.85 ± 2.60	13	0.42	0.68
Tail Length	39.30 ± 1.56	38.95 ± 1.47	13	0.15	0.88

Table 2.1 continued

Hind Foot Length	12.03 ± 0.28	11.91 ± 0.19	13	0.35	0.73
Girth	34.50 (15)*	32.00 (15)*		19.00*	0.50

Morphological Variables	**R-TS** mean ± SE	**R-GR** mean ± SE	df	*t*	*P*
Mass	9.15 ± 0.30	8.45 ± 0.18	20	2.08	0.05
Total Length	117.05 ± 1.58	119.52 ± 1.36	20	1.19	0.25
Tail Length	40.4 ± 0.84	43.48 ± 0.75	20	2.74	0.01
Hind Foot Length	12.67 ± 0.29	12.75 ± 0.22	20	0.22	0.82
Girth	39.92 ± 0.76	39.96 ± 0.57	20	0.04	0.97

Morphological Variables	**Females-All** mean ± SE	**Males-All** mean ± SE	df	*t*	*P*
Mass	5.73 ± 0.52	8.10 ± 0.29	35	3.98	0.0003
Total Length	105.72 ± 1.58	116.04 ± 1.43	35	3.83	0.0005
Tail Length	38.00 ± 1.15	41.78 ± 0.65	35	2.85	0.007
Hind Foot Length	11.60 ± 0.18	12.67 ± 0.14	35	4.06	0.0003
Girth	33.21 ± 0.94	38.44 ± 0.74	35	3.71	0.0007

Table 2.1 continued

Morphological Variables	**Females-TS** mean ± SE	**Males-TS** mean ± SE	df	*t*	*P*
Mass	6.70 ± 0.47	8.71 ± 0.46	13	2.43	0.03
Total Length	107.88 ± 1.39	116.04 ± 1.81	13	2.57	0.02
Tail Length	38.62 ± 1.40	40.54 ± 0.86	13	1.16	0.27
Hind Foot Length	11.76 ± 0.41	12.71 ± 0.23	13	2.08	0.06
Girth	34.98 ± 1.29	39.11 ± 0.94	13	2.37	0.03

Morphological Variables	**Females-GR** mean ± SE	**Males-GR** mean ± SE	df	*t*	*P*
Mass	4.95 ± 0.70	7.71 ± 0.36	20	3.61	0.002
Total Length	104.00 ± 2.48	116.04 ± 2.09	20	2.92	0.008
Tail Length	37.50 ± 1.86	42.57 ± 0.88	20	2.66	0.02
Hind Foot Length	11.47 ± 0.09	12.64 ± 0.17	20	3.57	0.002
Girth	31.80 ± 1.03	38.00 ± 1.06	20	3.01	0.007

Morphological Variables	**TS-All** mean ± SE	**GR-All** mean ± SE	df	*t*	*P*
Mass	8.18 ± 0.42	7.08 ± 0.40	35	1.82	0.08
Total Length	113.87 ± 1.66	113.31 ± 2.01	35	0.20	0.84

Table 2.1 continued

Tail Length	40.03 ± 0.74	41.42 ± 0.91	35	1.10	0.28
Hind Foot Length	12.46 ± 0.22	12.37 ± 0.17	35	0.32	0.75
Girth	38.01 ± 0.89	36.59 ± 1.02	35	0.99	0.33

Morphological Variables	**TS-Males** mean ± SE	**GR-Males** mean ± SE	df	*t*	*P*
Mass	8.71 ± 0.46	7.71 ± 0.36	26	1.72	0.10
Total Length	116.04 ± 1.81	116.04 ± 2.09	26	0.00	1.00
Tail Length	40.54 ± 0.86	42.57 ± 0.88	26	1.56	0.13
Hind Foot Length	12.71 ± 0.23	12.64 ± 0.17	26	0.27	0.79
Girth	39.11 ± 0.94	38.00 ± 1.06	26	0.73	0.47

Morphological Variables	**TS-Females** mean ± SE	**GR-Females** mean ± SE	df	*t*	*P*
Mass	6.70 ± 0.47	4.95 ± 0.70	7	1.96	0.09
Total Length	107.88 ± 1.39	104.00 ± 2.48	7	1.27	0.24
Tail Length	38.62 ± 1.40	37.50 ± 1.86	7	0.46	0.66
Hind Foot Length	11.62 (9)*	11.43 (9)*		10.00*	>1.00
Girth	34.98 ± 1.29	31.80 ± 1.03	7	1.95	0.09

* Non-parametric Mann-Whitney *U*-test results: median (n), *U*-statistic

Figure 2.1. —Land use/land cover maps of the two field sites in Missouri: Grand River site shown on lower left, and Ted Shanks/Mississippi River site on lower right. Points on expanded maps indicate waypoints of radio-tracked otters.

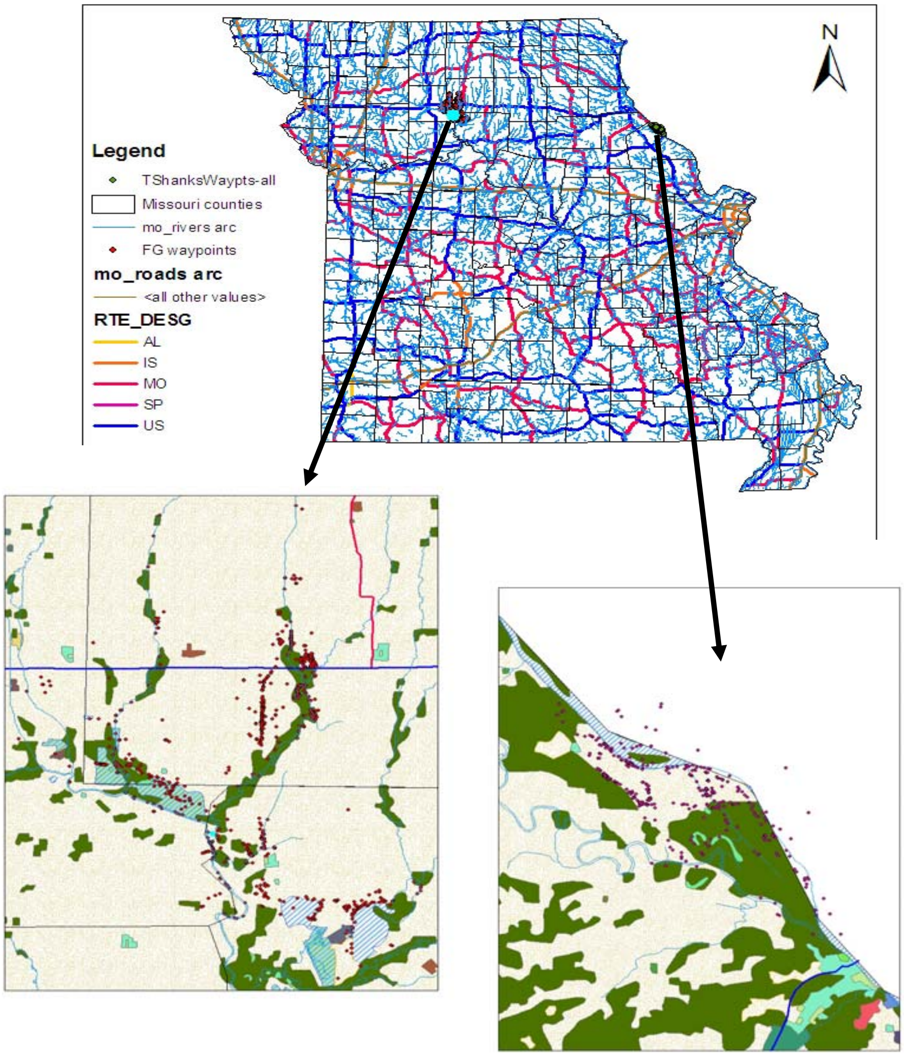


Figure 2.2. — Map of Grand River field site illustrating the home range and core areas estimated for one male otter using three different home range estimators: minimum convex polygon in red, Jennrich-Turner in blue, and fixed Kernel in purple.

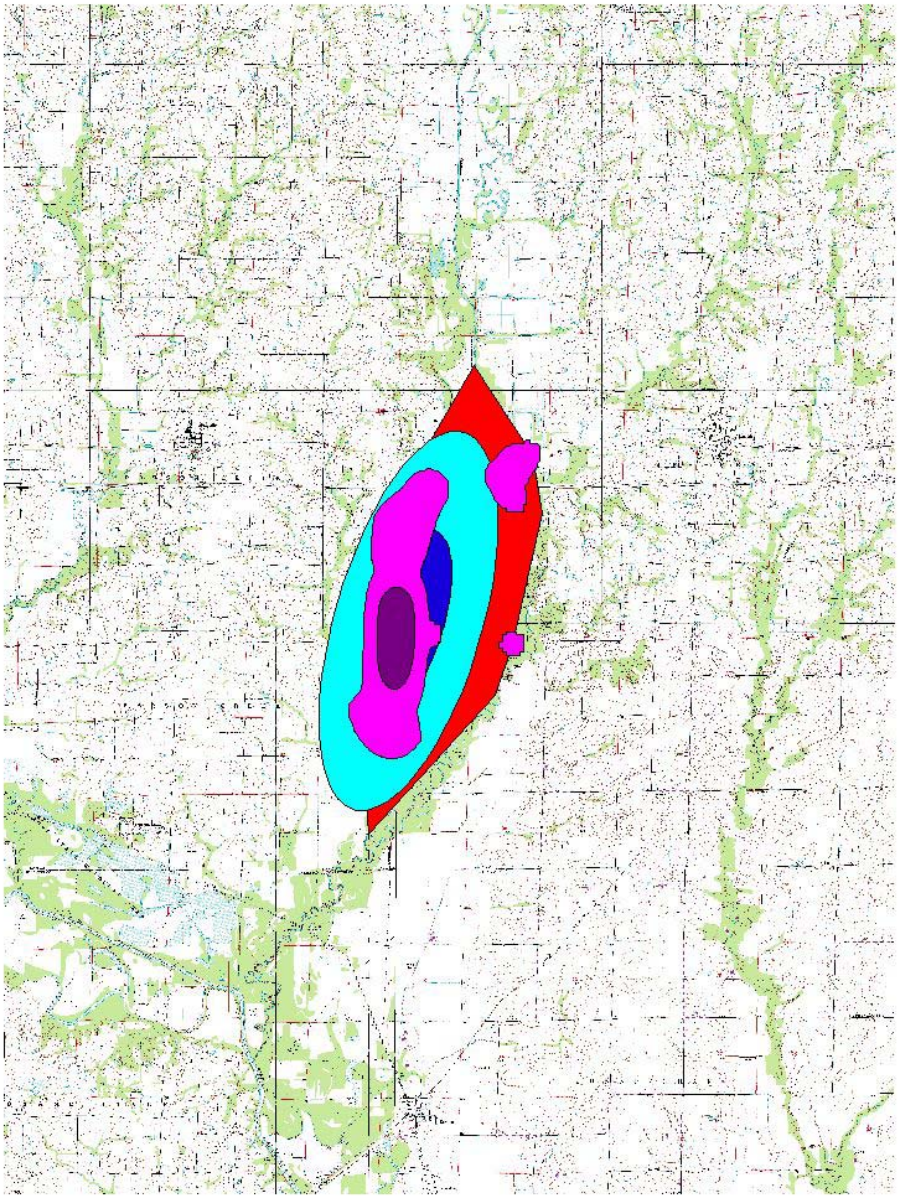
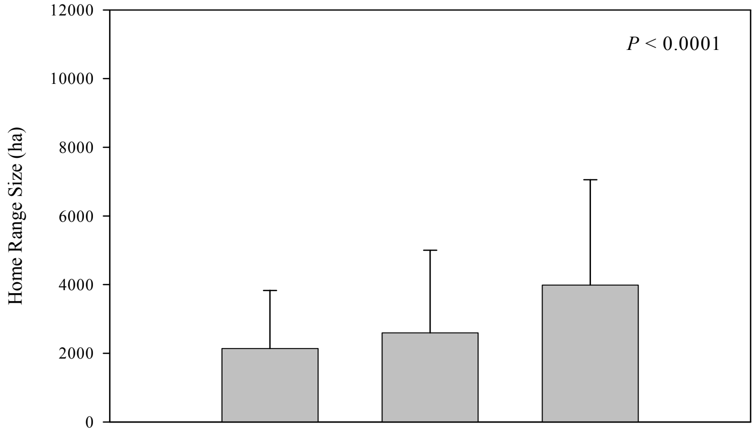
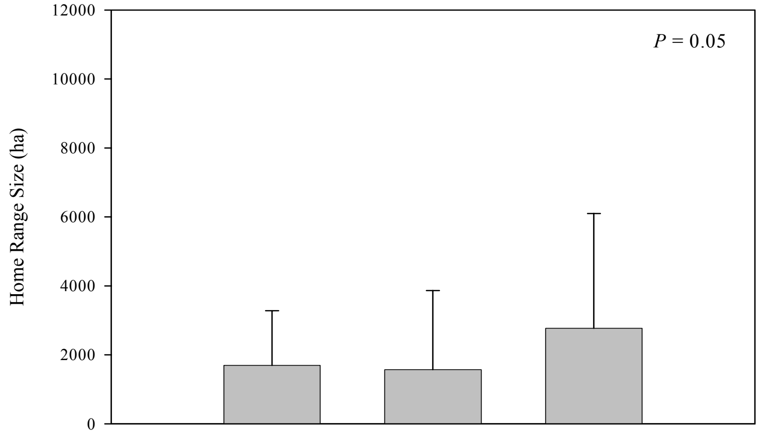


Fig. 2.3.-ANOVA comparisons of home range size estimations determined by three different analysis techniques ixed kernel, minimum convex polygon and Jennrich-Turner) for (a) all males combined, (b) males from Ted Shank te, and (c) males from Grand River site.

(a) All Males-Sites Pooled



(b) TS Males



(c) GR Males

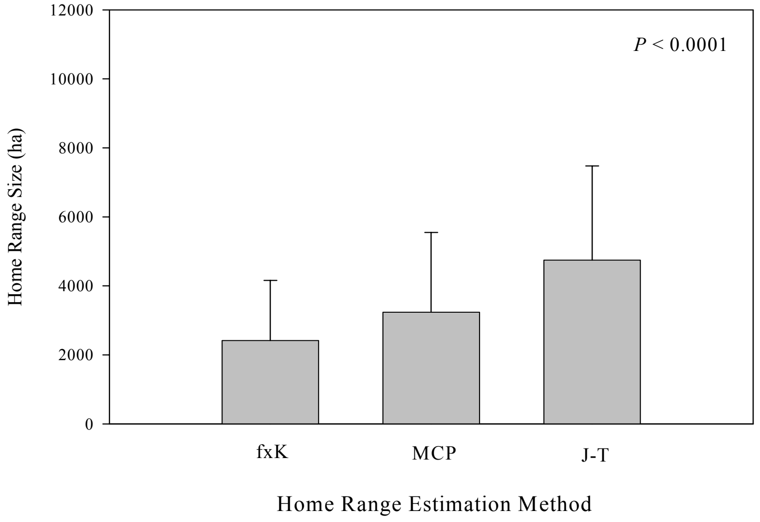


Figure 2.4.- (a) Home range (95% fixed kernel) and (b) core area (50% fixed kernel) estimated size
r males and females from two pooled sites in Missouri, (c) with km of waterways within home range
nd core areas, and (d) calculated using minimum convex (MCP) and Jennrich-Turner (J-T) methods.

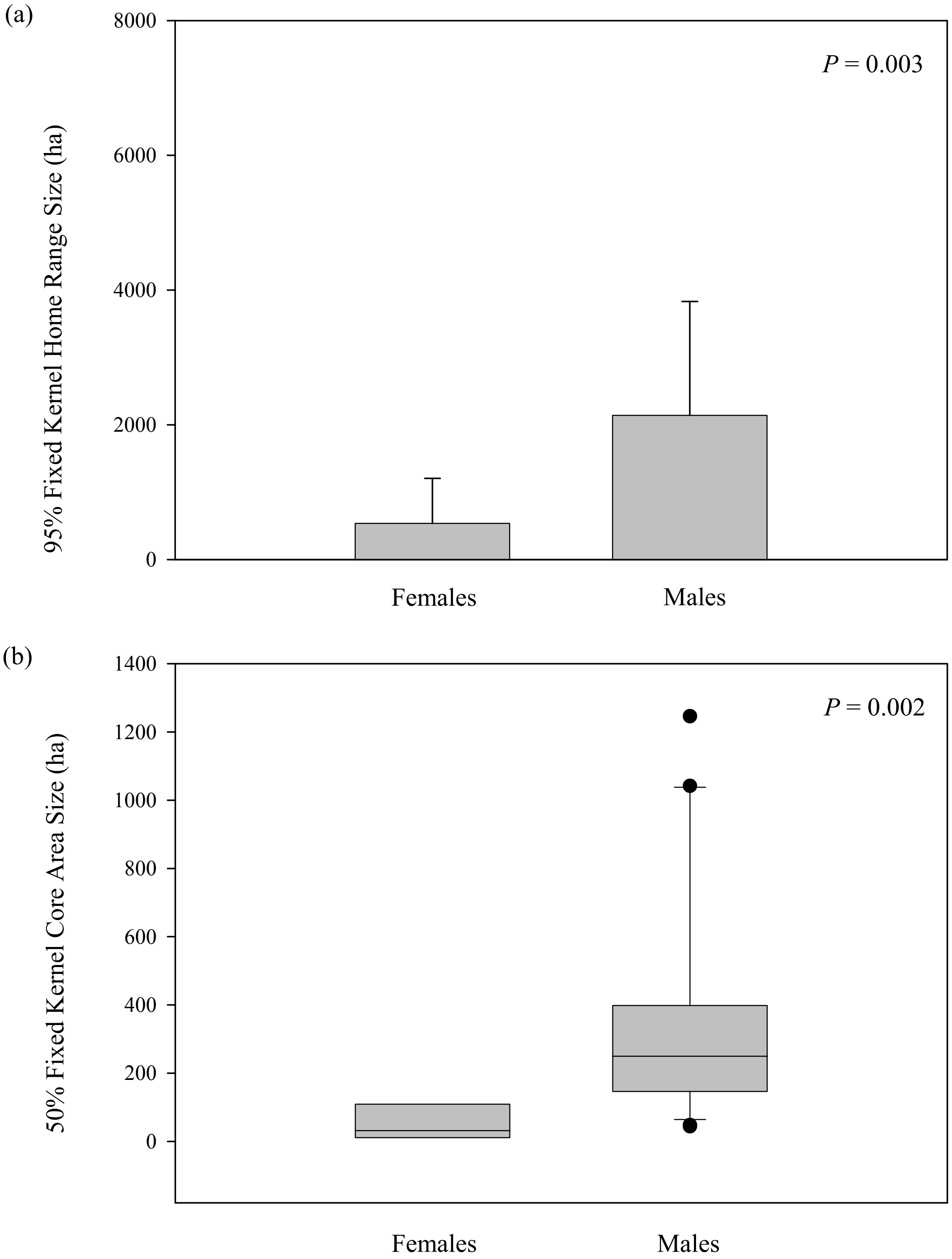


Figure 2.4-continued

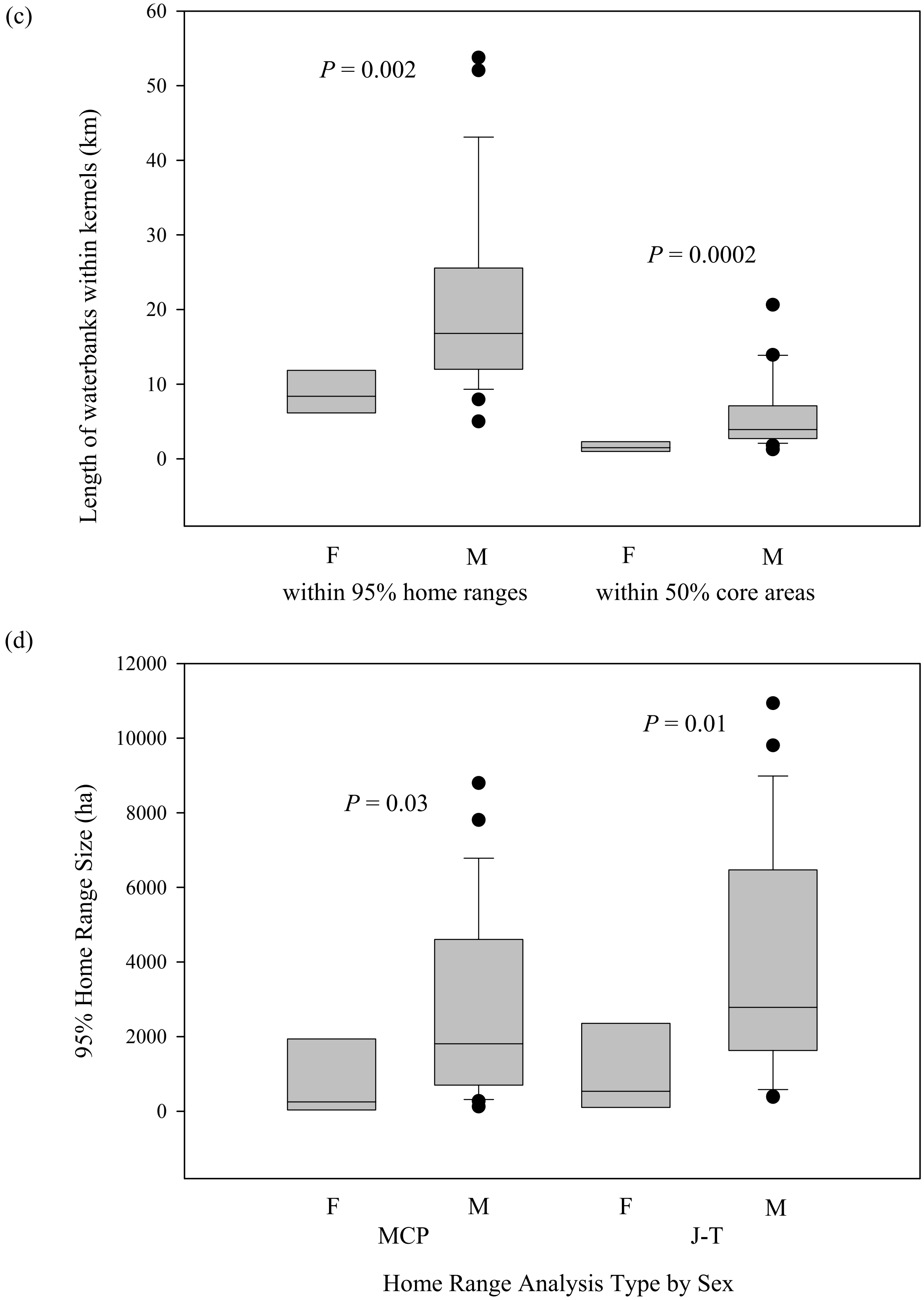
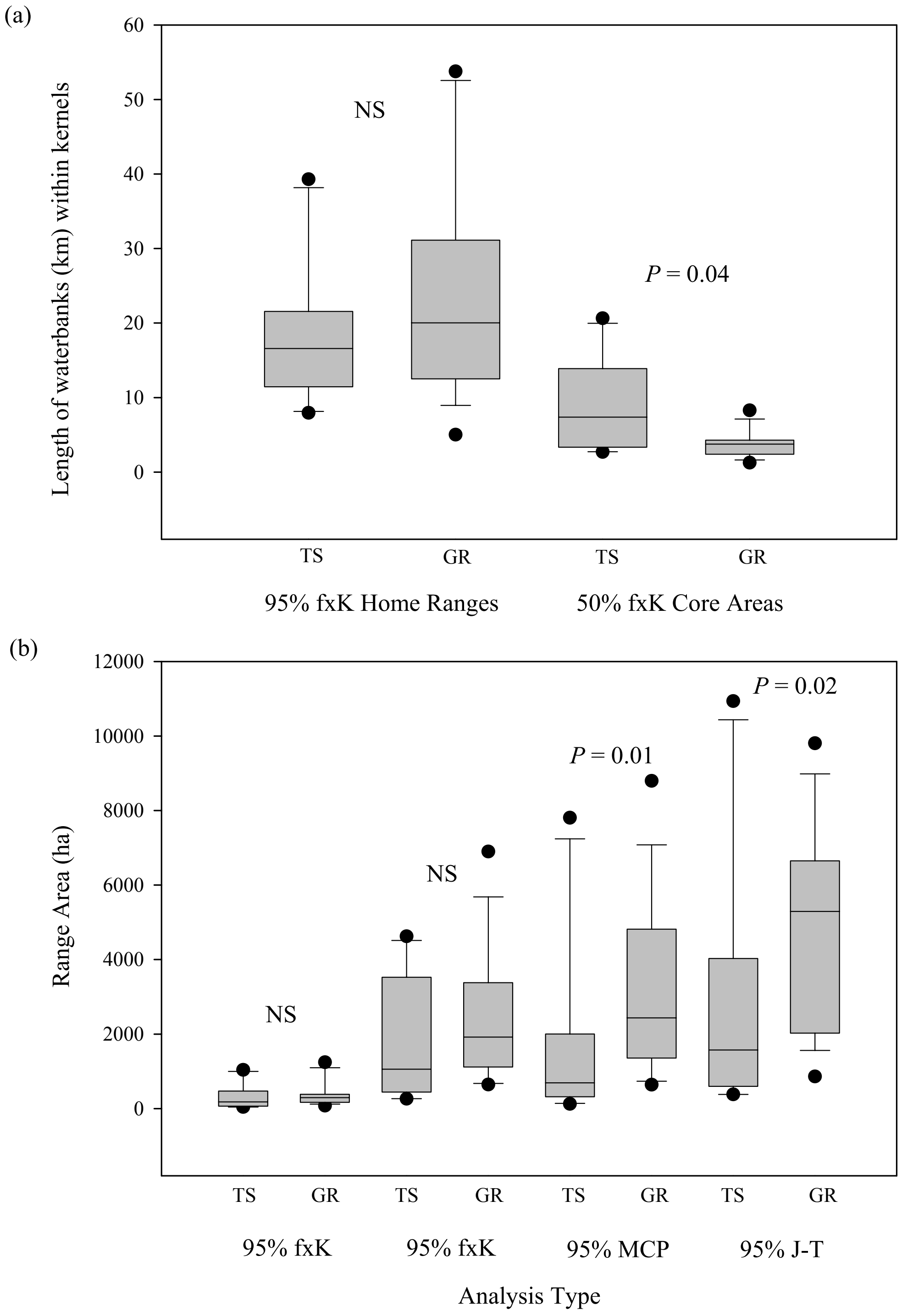


Figure 2.5.- Range comparisons for males at two sites (TS versus GR) in Missouri expresseed as (a) km f waterways within 95% fixed kernel home ranges and 50% core areas, and (b) range size for 50% core eas, and 95% home ranges calculated using kernel, minimum convex polygon and Jennrich-Turner method



Chapter 3

Northern River Otter, *Lontra canadensis*, Utilization of Two Distinct River Systems in Missouri

ABSTRACT

Two sites in Missouri, both with reintroduced but flourishing northern river otter populations (*Lontra canadensis*) were compared to determine whether there were differences in use of core areas in contrasting riparian habitats by radio-fitted otters. Stream-order and quantitative habitat descriptors found at the aquatic-terrestrial interface were measured at intensely used latrine sites. One study location had extensive backwater and wetland habitat associated with a portion of the Mississippi River near its confluence with another high-order stream. The second location encompassed a portion of the Grand River watershed, a prairie river relatively unaffected by impoundments or channelization, and associated low-order, meandering tributaries and marsh areas. I therefore tested six hypotheses, and evidence in support of these included: H_1 significantly greater consumption of crayfish (Cambaridae) occurred in the spring/summer than during fall/winter seasons, whereas avian prey types were significantly more evident in fall/winter scat; H_2 significantly greater consumption of crayfish occurred at the Mississippi River site than at the Grand River site; H_3 habitat variables characterizing latrine and non-latrine sites varied significantly. The three factors that contributed most to latrine versus non-latrine site discriminations were: (i) presence of high ground upon which otters deposit spraints, (ii) presence of

beaver (*Castor canadenesis*) activity within 10 m radius from sample site, and (iii) presence of “point of land” (i.e. projections within sample sites that extend ≥ 1.0 m into the water from the bank); H_4 habitat variables characterizing latrine sites differed between the two sites were total water hardness ($CaCO_3$ concentrations) and presence of backwater/sloughs within 50 m up- or down-stream from sample sites being significantly greater at the Mississippi River site than at the GR site. Hypothesis H_5 was corroborated with core areas (as indicated by latrines) of otters at the Mississippi River site being significantly greater (i.e. further) from roads than those at the Grand River site. However, H_6 was not corroborated; proximities to the nearest city were significantly less (i.e. closer) at the Mississippi River site than at the Grand River site. Differences in the spatial distribution of resources seemed to have significant impacts on the use of habitats by northern river otters. Spatiotemporal changes in the movements and behavior of species such as the river otter, an influential specialist in many drainage systems, can in turn have profound effects on landscape heterogeneity and local ecosystem processes.

INTRODUCTION

Northern river otters (*Lontra canadensis*) were extirpated by the early 1900s from most states with interior riverine habitats (Nilsson, 1980). These losses were primarily due to unregulated trapping of fur-bearers during the European settlement era, and landscape changes, including wetland drainage, pollution, and increased human population densities (Toweill and Tabor 1982; Melquist and Dronkert 1987). Restricted trapping regulations and wetland preservation were adopted as conservation measures in some parts of the otters' former range by the 1920s. But it was not until the 1970s that concerns about otter population declines and extirpations became increasingly evident (Endangered Species Scientific Authority, 1978). At the same time, wetlands across the continental United States decreased markedly in area, changed in overall biotic composition, and/or were destroyed by human development (Frayer et al. 1982; Paulsen et al. 1998; Lammert and Allan 1999). Likewise, rivers across much of the Midwestern United States have been altered, primarily through impoundments and channelization (Pitchford and Kerns 1999). Riparian and wetland loss, and the corresponding changes in habitats found at this aquatic-terrestrial interface have likely had profound effects on river otter populations in these regions. Until relatively recently, following many reintroduction projects, river otters were still almost completely absent from the Midwest and southwest states of the USA (Jenkins 1983). Little, however, is known about the effects of wetland dynamics on river otter populations (Newman and Griffin 1994).

These aforementioned concerns, along with nation-wide attention to improving water quality, and terrestrial habitats and general ecology, and ethical furbearer management techniques, prompted many wildlife agencies to restore or enhance their river otter populations (Ralls 1990). By 1998, 4,018 otters were reintroduced in 21 states, including Missouri, the Canadian province of Alberta and one National Park (Reed-Smith 1995; Raesly 2001). At present, otter populations are thriving in many parts of the USA, including Alaska, the Pacific Northwest, the Great Lakes, and most of the Gulf and Atlantic coast states, and most of Canada (Hall 1981).

In response to diminished numbers of river otters, and concerns that they might, in the near future, become extirpated in the state, the Missouri Department of Conservation (MDC) began a river otter restoration program to supplement the extant, but significantly reduced population. From 1982 until April 1992, the MDC released 845 otters into 43 locations throughout the state of Missouri; these otters were primarily taken from large populations in coastal Louisiana (Erickson and Hamilton 1988; Hamilton et al. 1994; Hamilton 1998). However, aside from a few post-release survival and movement studies of reintroduced otters (Serfass and Rymon 1985; Erickson and McCullough 1987; Serfass et al. 1993; Johnson and Berkeley 1999), few publications based on long-term studies exist on the success, persistence and status of river otters following reintroduction efforts. In addition, it is difficult to tease apart potential reintroduction success from that due to environmental improvements and habitat remediation, particularly along corridors (Ben-David et al. 1998, 2005; Blundell et al. 2002b). It was not until recently that the implications for natural recolonization of extirpated populations of river otters have been evaluated, shedding light on the importance of genetic implications and environmental factors (Blundell et al. 2002b).

In order to manage riverine habitats and assess river otter reintroductions, it is necessary to understand how environmental variables affect otter habitat utilization. Unfortunately, little information exists on the relationship between habitat structure and its use by northern river otters. In assessing suitable habitat for any given species, many factors must be taken into account. Possible human-induced effects, such as pollution, roadways and incidental deaths due to fishing and/or trapping gear, can all have strong negative consequences for animal populations, especially those recently reintroduced into a new area, and thus unfamiliar with the potential dangers. For example, 29 of 346 otters reintroduced from Louisiana into three river basins in Illinois died, probably due to human factors such as hoop nets, vehicles, traps, stress and domestic dogs (Bluett et al. 1999). Similarly, the continued demise and fragmentation of Eurasian otter (*L. lutra*) distributions in Spain have been attributed to several negative anthropogenic factors (i.e. pollution, human disturbance, habitat destruction, hunting), variations in water quality, and high human population densities (Cortes et al. 1998).

Habitat suitability models have been developed for a wide variety of carnivore species (Brooks 1997; Larson et al. 2004). Recent technological advancements, such as remote sensing, geographic information system analyses, and satellite imagery, make the identification of suitable habitat for a given species much more direct, which allows for survey effort to be maximized (Gese 2001). At the same time these methodologies have their limitations. Range estimates, particularly for a wide-ranging species such as the river otter, often underestimate the true use of habitats by individuals (Blundell et al. 2002a; Ben-David et al. 2005). In addition, one can never know with absolute certainty where individuals might not be spending time. Maps can often be the limiting factor when choosing the types of environmental variables that can be used to model habitats that might be suitable for a given species. For example, I am not aware of any GIS map layers that indicate locations of beaver presence/activity in my study sites. However, this factor was found to be an important correlate of habitat used by otters for latrines. In addition, which aspects of a habitat are determined to be suitable and/or available may not be what the animal perceives as suitable or available (White and Garrott 1990). For these reasons, I have not attempted to predict which areas may or may not be used by otters outside the field sites studied herein, but simply present data reflecting which habitat variables were associated with otter habitat utilization.

The total number of river otter inhabiting an area is influenced by prey abundance and distribution, suitable den site availability, local climate conditions and topography, competitive interactions, and human activities (Melquist and Hornocker 1979; Serfass 1984, 1994; Blundell et al. 2000, 2002a; Ben-David et al. 2005). White et al. (2003) in a study monitoring the success of translocations of Eurasian otters (*L. lutra*) in northeast England found that sprainting activity increased significantly with stream order, trout density, and surrounding riparian cover by woodland and semi-natural grassland vegetation. Similarly, Medina (1998) found diet to play a critical role in determining habitat use by southern river otters (*Lutra provocax*) in southern Chile; while crustacean remains were most commonly found in scat collected from lakes, fish were the primary prey found in scat collected at river sites. This crustacean-dependent diet, with a foraging shift in riverine systems, is similar to that previously described in South Africa for the African clawless otter (*Aonyx capensis*) and the spotted-necked otter (*Lutra maculicollis*) (Perrin & Carranza, 2000; Perrin & Carugati, 2000).

In this study I compared the utilization of habitats contained within the core areas of ranges of northern river otters at two differing aquatic sites in Missouri. Both sites were comprised of reintroduced and now flourishing otter populations. Aspects of Strahler’s (1964) stream-order and the habitat characteristics found at the aquatic-terrestrial interface were assessed at sites intensely used by otters (e.g., latrines). One site consisted of the extensive backwater, wetland habitat associated with a portion of the Mississippi River near its confluence with another high-order stream. The second site contained a portion of the Grand River watershed, a prairie river relatively unaffected by impoundments or channelization, along with its associated low-order, meandering tributaries and marsh areas. Prey preferences were discerned by scat analysis, and results were examined by site and season. I also determined whether habitat selection varied by season or wetland type by comparing 21 habitat variables at 56 latrine sites within known core areas of otters. Additionally, habitat features, identified in this and previous studies as potentially important to otter ecology, were compared at latrine versus 56 neighboring (> 50 m away) non-latrine sites.

My goal was to determine which habitat characteristics define those portions of known (i.e. radio-tracked) otter core areas that are extensively utilized for latrine activities. Accordingly, six hypotheses were tested: H_1 prey selection by otters (as indicated by presence of prey types in scat) varies seasonally as the abundance and distribution of prey shifts; H_2 prey selection differs between otter populations in two distinct riparian sites of Missouri; H_3 core area habitat use is defined by variables present at latrine and not at non-latrine sites; H_4 habitat variables found to be indicators of intensely used portions of otters' home ranges (i.e. latrines) differ between two sites in Missouri that are characterized by differing stream-order systems and associated ecoregions; and given previous findings in this system that otters at the Grand River site had larger home ranges than otters at the Mississippi river site; H_5 proximity from latrine sites to the nearest state road; and H_6 proximity from latrine sites to the nearest city, will be significantly greater (i.e. further away) for the Mississippi River site (i.e. Ted Shanks) versus the Grand River site.

These last two hypotheses would be expected if a positive correlation exists between stream-order and indices of biotic integrity for macroinvertebrate and fish communities (Wright and Li 2002; Fayram et al. 2005). These taxa comprise the major prey sources for otters and other mustelids (Knudsen and Hale 1968; Lauhachinda 1978; Gilbert and Nancekivell 1982; Serfass and Rymon 1985; Anderson and Woolf 1987; Tumlison and Karnes 1987; Serfass 1994; Roberts 2003). Therefore, it is likely that otters at the Ted Shanks site, an area composed primarily of 11th order and 8th order rivers and their associated backwater and wetland elements (Brooks 1980; Thom and Wilson 1980; Brooks and Dodge 1981, 1986), were provided with such a locally rich, concentrated habitat that a wide area over which to range for resources was not required to maintain several individual otters. Consequently, distances to towns and roads would be expected to be greater for the otter population at Ted Shanks that does not range as far. In addition, Fayram et al. (2005) found that the variability in the indices of biotic integrity tended to be greater in smaller streams. It is possible, therefore, that differences in prey abundance, variability and distribution in the two stream order systems examined here are at least in part responsible for the differences in space use by otters.

MATERIALS AND METHODS

Study Species.—Details regarding many aspects of northern river otter (*Lontra canadensis*) natural history, specifically as it pertains to this study system, can be found in Chapter 2. In addition, otters are known to create and revisit latrines (Greer 1955), places where they exit the water to deposit sprints (i.e. feces or scat, urine, and anal gland secretions at specific locations throughout their home ranges; Durbin 1989; Kruuk 1992, 1995; Testa et al. 1994; Bowyer et al. 1995; Ben-David et al. 1996, 1998, 2005; Swimley et al. 1998; Rostain et al. 2004). These scent-marking stations are typically along river banks or shorelines, and are often associated with activity centers, such as denning locations, foraging areas, and haul-outs where they eat, roll and rest (Mowbray et al. 1976; Melquist and Hornocker 1983; Durbin 1989; Newman and Griffin 1994; Swimley et al. 1998; but see Bowyer et al. 1995). Latrine sites are quite obvious evidence of otter activity (Mowbray et al. 1976; Melquist and Hornocker 1979), typically containing many piles of “jellies” (Rostain et al. 2004) mixed with fresh and dried excrement. Latrines are typically found within several meters of the aquatic-terrestrial interface on high ground (Poole 1954; Melquist and Hornocker 1983, Chanin 1985; Durbin 1998; Swimley et al. 1998). Latrines are posited to function in the advertisement of individual chemical identities, health status, reproductive status, intra-group communication, and/or territoriality, depending upon the social organization of the population in question (Gosling 1982; Hornocker et al. 1983; Durbin 1989; Gorman and Trowbridge 1989; Kruuk 1992, 1995; Blundell et al. 2002a, 2004; Ben-David et al. 2005). Otter marking intensity fluctuates seasonally, with peaks in spring and fall (Foy 1984; Robson and Humphrey 1985;

Serfass and Rymon 1985; Serfass 1994; Swimley 1998; Ben-David et al. 2005). Furthermore, northern river otter scat most often consists of fish scales and crayfish (*Cambarus* spp., *Procambarus* spp., *Astacus* spp.) exoskeletons, thus producing an overall fishy odor at the site that aids in locating latrines.

Study Sites.—Detailed descriptions of field sites can be found in Chapter 2. River otters at two distinct sites in Missouri, USA were evaluated in this study at Ted Shanks Conservation Area (TS) which is located along the Mississippi River; it is an 11th-order river, north of and including its confluence with the Salt River, an 8th-order river (Strahler 1964). Most of the backwater, wetland habitats found in this system have arisen due to the primary or secondary effects of human activities on the Mississippi River (channelization), and from management practices on parts of the associated floodplain using human impoundments (Thom and Wilson 1980). The second location was the Grand River site (GR) which encompasses the Grand River (GRB), an 8th-order river, and numerous 3rd-order streams. This site is unusual in that it contains much of the remaining bottomland hardwood forest in Missouri, and it is not affected by impoundments or channelization, and includes rich, winding river systems, such as Locust Creek, which are rare habitats of the Western Glaciated Plains. It merits mention that on both sites, but in particular at Swan Lake National Wildlife Refuge within the GR site, fall migration of birds exceeds 150,000 ducks, geese, bald eagles and other species.

Scat analysis.—Fifty-two fresh river otter scats were collected during the fall/winter (September-January) and spring/summer (February-August) seasons of 1999, 2000 and 2001 from known, radio-located otters found along the river systems at both the TS and GR field sites. Scats were stored frozen in plastic freezer bags, and were later thawed and oven dried at 60° C for 48 h before analysis (Erlinge 1968; Roberts 2003). Erlinge (1968) found that the relative importance of prey types could be accurately discerned in the diets of captive European otters (*L. lutra*) by identifying the frequency of occurrence of each prey type in collected scat samples. Therefore, samples were subsequently hand-sorted to determine frequency (%) of occurrence of five prey types contained in scats, crayfish, fish, birds, mammals, and other vertebrates (amphibians, reptiles and other unidentifiable vertebrate structures). Materials of diagnostic value included fish scales, crayfish exoskeleton parts, feathers, hair and bones. Calculating percent of each prey type by volume was not possible because some food types digest at different rates, and thus would bias the results, for example, crayfish exoskeletons would comprise a higher proportion of scat by volume compared to a fish or frog of the same mass (Reynolds and Aebischer 1991).

Latrine site selection.—Thirty three otters were surgically implanted intraperitoneally with radio-transmitters (Melquist and Hornocker 1983; Serfass 1994; Kollias 1999; Blundell et al. 2000; Chapter II). Radio-tracking occurred from 23 November 1999 until 24 May 2003 year-round (mean = 3 d/wk during each spring and autumn trapping season; mean = 4 d/mo during the remaining parts of each year) by myself and the Missouri Department of Conservation (MDC) for a concurrent study (Chapter II). Home range (95%) and core area (50%) sizes were estimated using fixed kernel methodologies. Latrine sites evaluated in this study were located within known core areas of radioed otters, and were identified by visually searching all shorelines of waterways ≤ 10 m inland (Mowbray et al. 1976) contained within these areas for evidence of river otter latrines (≥ 2 scats; Swimley et al. 1998). Eventually, repetitive tracking of individuals to predictable locations (i.e. dens, haul-outs, latrine sites) indicated which latrines were used on a regular basis by radioed (and presumably other) otters.

Identified sites were subsequently measured in a variety of ways. The distance of the streamward side of the latrine to the aquatic-terrestrial interface (i.e. shoreline, river bank) was measured to the nearest 0.01 m. The height of each latrine above the current water level was measured by using a graduated stick, string and level. Non-latrine sites were randomly selected locations ≥ 50 m either up- or down-river from a known latrine site (Newman and Griffin 1994; Swimley et al. 1998). All variables scored or measured were made at the same distance from the shoreline as was the corresponding latrine location. Both latrine and non-latrine locations were recorded using Global Positioning System (GPS; software version 4.02; MapSource® software version 6.5; Garmin International Inc., Olathe, KS, 66062, USA) and data were recorded as Universal Transverse Mercator (UTM) coordinates.

Habitat variables.— Twenty-one habitat variables, based on previous tracking experience, especially from the MDC personnel, and published research in different parts of the northern river otter's range (Greer 1955; Mowbray et al. 1976; Karnes and Tumlison 1984; Serfass 1984; Newman and Griffin 1994; Reid et al. 1994; Swimley et al. 1998; Kiesow and Dieter 2005) were evaluated at latrine and non-latrine sites at both field locations. Of the 21 variables measured, six were continuous, 15 variables were ordinal, evaluated as either present (rank =

1) or absent (rank = 0) within a prescribed area (typically within 5 m radius). The potential impact of human land use was evaluated as low (rank = 1) or high (rank = 0) based on land use/land cover map layers for these regions (Fig. 3.1). These data are presented in Table 3.1 where definitions of each habitat variable are provided.

Proximity calculations.— Location data for latrine and non-latrine sites were entered into a geographical information system (GIS) for analysis. GPS data entered in the Universal Transverse Mercator (UTM) Nad 1983 Zone 15N projection were converted into point shape files using DNRGarmin® v5.0.4software (Minnesota Department of Natural Resources 2001) which were then saved directly into the ESRI® ArcMap™ 8.3 (Redlands, CA, USA). All core area estimates were calculated using fixed kernel range estimators within the ArcView™ Animal Movement Analysis Extension® 2.0 (see Chapter 2 for additional details; Hooge and Eichenlaub 2000) for ArcView® 3.2 in kilometer map units. Map layer sources included ESRI® Data and Maps 2003 county data layers, and MSDIS river, county, state, and land use/land cover layers. Proximity to roads and human population centers were evaluated using ESRI® ArcMap™ 8.3 Analysis Tools; the "near function" was used to compute the distance (in meters) from each point (i.e. latrine and non-latrine sites) to the nearest road and to the nearest human populated area (ESRI® 1996; Loiselle 2004).

Statistical Analyses

Statistical tests were performed using JMP (v.5.1.2, SAS Institute Inc., Cary, NC) and GraphPad InStat (v.3.06, GraphPad Software, San Diego, CA) software packages. Whenever possible, parametric tests were used and unless otherwise noted, numerical results are presented as mean ± 1 SD.

Scat analysis.— Relative frequencies of prey types found in river otter scat were analyzed to elucidate possible differences due to site (TS vs. GR) or season (Spring/Summer vs. Fall/Winter). Chi-squared tests for independence 2 × 4 contingency table analyses with likelihood post tests were used to test the following hypotheses: (1) H_0: prey type relative frequencies found in river otter scat are the same for both sites, i.e. are independent of site differences, and (2) H_0: prey type relative frequencies found in river otter scat are the same for both seasonal groups, i.e. are independent of season.

Because chi-square calculations are only valid when all expected values are greater than one and at least 80% of the expected values are greater than five (Motulsky, 2000), two non-significant prey type columns ("mammal" and "other vertebrates") were combined (Zar, 1996). Likelihood post tests were used to reveal which prey type(s) contributed significantly to any non-independent results obtained. Mosaic tile displays were created of the 2 × 4 contingency tables for testing of independence of prey type relative frequencies by site and by season.

Habitat variables.— Each habitat variable (Table 3.1) was compared between latrine vs. non-latrine sites, and latrine habitat variables were compared between the TS and GR sites using either *t*-tests or, when necessary, the Mann-Whitney U statistic for non-parametric data (Thomas and Taylor 1990; Newman 1990; Newman and Griffin 1994; Swimley et al. 1998).

Forward stepwise regression analyses (Agresti 1984; Cox and Snell 1989; Hosmer and Lemeshow 1989; Newman and Griffin 1994; Swimley et al. 1998) and discriminant analyses (Swimley et al. 1998; Anderson and Robinson 2003; Anderson and Willis 2003) were performed to estimate the influence of the habitat variables (independent variables) simultaneously on latrine versus non-latrine sites and between latrines at the two field locations (dependent, or response, variables). These steps were taken to be certain that variables were independent, and to identify which variables contributed most to group (latrine versus non-latrine; latrines at TS versus latrines at GR) separation (Newman and Griffin 1994; Swimley et al. 1998). Variables were entered in stepwise manner until no significant variables remained, based on the likelihood ratio Chi-square test (Hosmer and Lemeshow 1989) on all variables for latrine vs. non-latrine sites and latrines at the two disparate field sites. Variables were subsequently identified as potential contributors to the differences in microhabitat community structures observed at the two sites.

Proximity of latrine sites at the TS location versus the GR location were calculated to roads and to human population centers (i.e. towns), and were statistically compared using Mann-Whitney U-tests. The significance level of all tests was fixed at $\alpha = 0.05$.

RESULTS

Scat composition.—A chi-squared test for independence with likelihood post tests revealed that prey type relative frequencies found in river otter scat are not independent of site ($\chi^2 = 9.74$, $d.f. = 3$, $P = 0.02$), with significance being contributed primarily by crayfish ($\chi^2 = 18.30$, $d.f. = 3$, $P < 0.0001$) and marginally by bird ($\chi^2 = 3.42$, $d.f. = 3$, $P = 0.06$) prey categories (Fig. 3.2a). Prey type relative frequencies were also significantly different by season ($\chi^2 = 23.40$, *d.f.* = 3, $P < 0.0001$) with post hoc likelihood ratios revealing significance being contributed by fish, crayfish and bird prey types ($\chi^2 = 6.64$, *d.f.* = 3, $P = 0.01$; $\chi^2 = 32.65$, *d.f.* = 3, $P < 0.0001$; $\chi^2 = 18.85$, *d.f.* = 3, $P < 0.0001$, respectively; Fig.3.2b).

Habitat variables.—Significant differences were found for latrines and randomly selected non-latrine sites (n = 56 for both) for several habitat variables, and these results are listed in Table 3.2. In addition, significant differences for comparisons of latrines at the two field sites (TS, n = 33; GR, n =23) included phosphates ($U = 48.00$, $P = 0.04$), turbidity ($t_{26} = 2.24$, $P = 0.03$), total hardenss ($U = 10.00$, $P < 0.0001$), log percent cover ($U = 26.50$, $P = 0.002$), and backwater/sloughs ($U = 184.50$, $P = 0.001$). Stepwise regression analyses indicated six environmental variables as being significant differences between latrine versus non-latrine sites (log-likelihood, R-Square): (1) high ground (77.63, 0.0); (2) beaver activity (39.55, 0.49); (3) point of land (27.88, 0.64); (4) low access to humans (11.11, 0.86); (5) total hardness (8.16, 0.90); and (6) trees > 30 cm diameter (5.99, 0.92). Only three differences were found when comparing latrine sites between the two field sites: . Discriminant analyses were significant for the same environmental factors (Fig. 3.3 and Fig. 3.4).

Proximity to man-made structures.—Distances from latrine sites to the nearest town were significantly less at the Ted Shanks than at the Grand River site (U = 0.00, P < 0.0001). However, distances from latrine sites to the nearest road where significantly greater at the Ted Shanks site than at the Grand River site (U

= 88.00, $P < 0.0001$). Latrine and non-latrine comparisons could not be made because “non-latrine” sites were at a predefined distance of 50 m from latrines.

DISCUSSION

This study found seasonal shifts in diet with support for H_1 such that more crayfish remains were found in scat deposited during the spring/summer seasons than during the fall/winter season. In addition, significantly more fish and bird prey remnants were present in fall/winter scat. These results were important for predicting the composition of potential diets of otters at different times of the year. The abundance and at times exclusivity, of crayfish remains clearly observed in scat collected during the spring and summer from both field sites must provide an ample food resource for otters during these seasons because at times otters did not appear to include any other prey items in their diets (Hobbs 1988; Roberts 2003; D. D. Tobin pers. observ.). Roberts (2003) similarly found summer diets of otters in the Missouri Ozarks to be composed primarily, and sometimes exclusively, of crayfish, whereas winter diets included primarily fish prey. This seasonal tendency of otters to shift the primary component of their diet was also observed in river otters in Illinois (Anderson and Woolf 1987). Similarly, studies of Eurasian otters in Finland indicated that otters shifted their foraging activities seasonally, choosing predictable prey in particular habitats (i.e. stocked salmonid-rich habitats in winter) when the availability of other prey types was low due to seasonal variation (Ludwig et al. 2002).

Such seasonal shifts could be explained by the temporal behavioral variation of the fish and crayfish (Hobbs 1988), or by the opportunistic foraging strategy used by most northern river otters (Toweill 1974; Lauhachinda 1978; Melquist and Hornocker 1983; Reid et al. 1994; Ben-David et al. 1998, 2005; Blundell et al. 2000, 2002a, 2004). Similary, in several studies throughout Europe on the diet of *L. lutra*, scat composition revealed that otters preyed upon frogs and other non-fish items primarily in the spring and summer, whereas perch and large cyprinid fish remains were found much more frequently in spraints collected during winter. And earlier studies revealed that in regions with very abundant crayfish populations, otters preyed more so on crayfish even when abundant fish prey items were present, especially in the spring and summer (Erlinge 1967; Gerell 1967; Kyne et al. 1989; Adrian and Delibes 1987). Unfortunately, during recent decades the native crayfish (*Astacus astacus*) and the introduced crayfish (*Astacus leptodactylus*), both of which had been extremely abundant in small rivers and lakes throughout Europe, have undergone severe declines or exterpations (Duris and Smutny 1998; Umapathy 2000; Jędrzejewska et al. 2001). Shortly thereafter, amphibians have been reported in several studies to have become increasingly important in the diets of otters found on smaller, inland water sources, often accompanied by a high degree of forest or vegetation cover (Erlinge 1967; Sulkava 1996; Sidorovich 1997; Jędrzejewska et al. 2001).

Overall, otters appear to be highly opportunistic predators, hunting much more so on the bottom of rivers and along river banks than in the open water (Libois1997; Kosco and Kornan 1999; Taastrom and Jacobsen 1999). When prey fish populations in these regions were estimated, for example using electrofishing techniques, in general the fish species composition in the otter diet reflected that of the foraging area (Taastrom and Jacobsen 1999). In this study system, the availability of crayfish decreases during the winter seasons (Muck et al. 2002), and this factor combined with the tendency of fish to be slower, more clumped, and less active (Wardle 19880), falling more easily to prey by otters, perhaps explains why an increase in fish remains are observed in scats collected during the fall/winter seasons.

Support was also found for the second hypothesis that otters prey utilization will differ spatially. When examined by site, crayfish were found to be more abundant in the scat of otters at the Ted Shanks (Mississippi River), whereas bird prey was more evident in the scat at Grand River, although this last trend fell short of significance (Fig. 3.2). The presence of fish prey varied spatially with smaller fishes (Fundulidae and Percidae) found more frequently in the scat of otters ranging in smaller tributaries (Roberts 2003). These reports are in accordance with Wright and Li's (2002) findings that variance in macroinvertebrate and fish communities are greater in smaller stream-order systems.

Throughout the literature references can be found documenting the shift in Eurasian otter diets based not on changes in latitude (as one might expect due to degree of climatic temperature severity, and thus degree and duration of freezing), but rather on changes in type of habitat use. Water capacity, and thus density and diversity of fish communities, is typically higher in large rivers and lakes, as well as in coastal habitats. When ranging in smaller, inland rivers and streams, otters often compensate for the lower abundance of fish by preying more heavily on amphibians or crustaceans (Pikulik et al. 2000; Jędrzejewska et al. 2001; but see Adrian and Delibes 1987). Similar to that described herein, Medina (1998) found crustacean remains to be the most common item overall in southern river otter (*Lutra provocax*) scat collected along lakes and sloughs in southern Chile, whereas scat collected at meandering river sites contained remains indicating a more diverse diet. This crustacean-dependent diet, with a foraging shift in riverine systems, is also found in South Africa for the African clawless otter (*Aonyx capensis*) and the spotted-necked otter (*Lutra maculicollis*) (Perrin & Carranza, 2000; Perrin & Carugati, 2000).

Addition evidence of the spatial influence on prey utilization can be seen in Clavero et al. (2003), wherein *L. lutra* spraints were analyzed in terms of relative frequency of occurrence of seven main prey categories throughout European temperate and Mediterranean freshwater habitats. They found a clear latitudinal gradient in diet composition. In the northern, temperate localities, otters were more piscivorous, while in the southern, Mediterranean localities, otter diets were more diverse, featuring more prey classes. In general, their studies indicate that, in Mediterranean areas, strong spatial and temporal water shortages have produced more diversified diets in otters, causing populations in this region to behave more as generalist predators. In these regions, otters relied less on fish and fed more on aquatic invertebrates and reptiles. Conversely, otters found in inland, temperate, freshwater ecosystems were able to behave as highly specialized piscivorous predators due to the comparatively stable water regime, and thus reliable abundance of fish prey items (Clavero et al., 2003).

It should be noted, however, that in this study, scat composition was scored by presence or absence of prey types. Although this method has been employed in other river otter diet analyses (Melquist and Hornocker 1983; Serfass

1984; Reid et al. 1994; Roberts 2004), it may not be sufficient in accurately describing the prey base of river otters (Kloskowski 2000). Ideally, scat ratios (% mass for each prey type of total) should be positively correlated with the ratios of habitat-specific prey that is available in a system and these values should instead be expressed in terms of weight and relative frequency of occurrence (Kloskowski 2000). For example, in central France, when examined by percent occurrence, small sized fish species comprise more than 50% of the Eurasian otter's diet, however, when expressed as relative biomass, this same group only accounts for 8% of the diet, with the bulk coming from brown trout, large cyprinid fish, birds and mammals (Libois, 1997).

Furthermore, my results also support H_3 with three factors contributing most to the discriminations of latrine versus non-latrine sites. The first of these factors, presence of high ground upon which otters deposit spraints, has been found in several other studies on river otter habitat utilization and scent-communication (Melquist and Hornocker 1983; Newman and Griffin 1994; Ben-David et al. 1998, 2005; Swimley et al. 1998; Rostain et al. 2004). Otters may deposit spraints at al latrines encountered, but areas receiving extensive deposition of spraints appear to be within activity centers, such as near dens and/or foraging places (Melquist and Hornocker 1983; Swimley et al. 1998; Rostain et al. 2004). In this study, otter latrines were typically associated with elevated structures, natural or anthropogenic in source, upon which otters sometimes had to climb in order to partake in marking activities at a latrine.

For example, at the Mississippi site, many cement and steel water control structures exist whereby water is allowed to flood the wetland according to human determination. These structures rise approximately 5-10 m out of the water. Given their construction and the fact that they are located in more open areas, they are typically not associated with much vegetative cover. However, if a latrine is present anywhere in the area, it is almost always found either atop or at the base (which is also elevated as these water control structures are located on levees) of such structures, and are typically associated with a cross-over pathway from a body of water on one side of a levee to the other (pers. observ.). Additional elevated structures included riverine flood debris, extensive root systems of riparian trees (e.g., cottonwoods), and beaver or muskrat (*Ondatra zibethicus*) lodges or dams. Other studies have found sources of elevation along river or lakes to be associated with latrine activity although in most cases these structures were natural (e.g., rock formations, boulders, isthmuses; Serfass et al. 1986; Newman 1990; Newman and Griffin 1994; Reid et al. 1994; Ben-David et al. 1998, 2005; Swimley et al. 1998).

The second environmental factor that contributed to discriminating between latrine and non-latrine sites was presence of beaver activity within a 10 m radius. Many previous studies have reported the importance of beaver activity to otter habitat utilization (Greer 1955; Melquist and Hornocker 1983; Debuc et al. 1990, 1991; Malville 1990; Newman 1990; Waller 1992; Newman and Griffin 1994; Reid et al. 1994; Swimley et al. 1998, 1999; Kiesow and Dieter 2005). Swimley et al. (1999) found that 95% of otter latrines were associated with areas currently or previously occupied by beavers. They also found that 34% of otter latrines were located within 50 m of beaver lodges, with 85% overall were found in lake-or pond-dominated and low-gradient stream habitats. In addition, interactions of beaver and otter in Delaware found a highly significant positive relationship between presence of beaver activity (active or inactive) and otter use of the same surveyed riparian habitat reaches (Swimley et al. 1998, 1999).

Otter utilization of space co-inhabited by beaver is primarily determined by the fact that otters are opportunistic denners (Liers 1951; Toweill and Tabor 1982; Melquist and Hornocker 1983). Otters do not typically construct their own dens, but rather modify previously constructed lodges and dens created by other semi-aquatic mammals, such as beavers, muskrats and, at times, coyote (*Canis latrans*), although they will also use natural cover created by extensive tree root systems and hollowed logs (Liers 1951; Toweill and Tabor 1982; Melquist and Hornocker 1983; Estes 1989; Kruuk 1995). Shoreline and riverbank burrows created above the flood-line provide ideal denning and resting locations and were frequently used by radio-tagged otters in this study.

Beaver activity alters habitats in a variety of ways, although unlike human-induced habitat alterations, most of those caused by beavers benefit otters, and other organisms such as muskrat, hares, deer, and birds considerably. This occurs primarily because beaver dam construction causes changes in habitat structure and landscape that normally increase species diversity and biomass, specifically of lentic species (Rosell and Parker 1996). Areas created by beaver damming produce still water habitats optimal for foraging, nesting and brooding by a variety of fish, insects, amphibians, birds and their predators, such as otters. Aside from at times destroying fish spawning areas and temporarily hindering their migration, the species that suffer the most from beaver alterations are humans (Newman and Griffin 1994; Rosell and Parker 1996).

Given that the preferred management tool for beaver throughout most of its range is fur trapping, substantial incidental captures of otters and other non-target species, can be substantial (Swimley et al. 1999). Thus, when selecting reintroduction sites or designing habitat refuges for otters, attention must be paid to other riparian species present in those areas that are actively managed using programs permitting non-releasable trapping methods. Management programs in such areas could instead utilize water level control devices and/or education and enforcement of non-lethal capturing techniques to minimize the impacts such practices have on otters (Swimley et al. 1999).

The third primary environmental predictor of latrine site selection within core areas in this study was the presence of “point of land.” This variable was defined similar to previous studies (Newman 1990; Newman and Griffin 1994; Swimley et al. 1998, 1999) as any projection within the sample site that extended ≥ 1.0 m from the bank into or suspended above the body of water. Other studies have similarly found points of land to be significantly present at and predict the occurrence of river otter latrine sites (Mowbray et al. 1976, Serfass 1984; Newman 1990; Newman and Griffin 1994; Swimley et al. 1998). Such structures may increase scent dissemination to other otters as they pass by, and thus play a role in olfactory communication within this species (Durbin 1989; Estes 1989; Kruuk 1992, 1995; Bowyer et al. 1995; Ben-David et al. 1996).

When comparing the environmental variables that discriminated latrine sites at the two field sites, limited support for the fourth hypothesis was found. The habitat variables that characterized latrine sites between the two riparian locations in Missouri were total water hardness ($CaCO_3$ concentrations) and presence of backwater/sloughs within 50 m up- or down-stream from sample sites, both of which were significantly greater at the Mississippi site than at the Grand River site.

Measurements taken at latrines found in the core areas of radio-tagged otters on the Mississippi River site contained higher levels of total water hardness than did those at the Grand River site. Total water hardness negatively affects the uptake of metals, many of which are toxic in nature once they have accumulated in typically the kidney or gills (Gordon et al. 1992). Studies in striped bass (*Morone saxatilis*) and rainbow trout (*Oncorhynchus mykiss*), common prey species of northern river otters, have found that the presence of hard water ($CaCO_3$-rich) acts as a regulator of gill permeability to the toxic action of some metals, such as cadmium (Calamari et al. 1980; Hollis et al. 2000). The presence of heavy metals in aquatic systems, which when present in significant concentration can cause tissues to become toxic, is important for a riparian species such as the river otter that feeds almost exclusively on fish and crayfish. Given the nature of trophic food chains, a higher level of total hardness in water would indicate potentially less toxicity in the tissues of prey species, which in turn would mean less accumulation of toxic metals in the tissues of otters (Calamari et al. 1980; Gordon et al. 1992; Hollis et al. 2000). Although fat and muscle tissue samples were collected from otters during surgical implantation procedures, they have not yet been analyzed.

Hydrological and chemical environmental gradients can significantly influence the aquatic communities represented by, for example, fish species with both widespread and restricted distributions, across major drainage systems

(Wright and Li 2002; Fayram et al. 2005). Rivers of medium to high stream-order are typically less affected by such hydrological and chemical factors, in many cases due to simple dilution (Strahler 1964; Pitchford and Kerns 1999). Reports of such systems have reported less variability and greater abundance of fish and aquatic macroinvertebrate species in larger-order streams (Wright and Li 2002; Fayram et al. 2005). For example, Koel & Peterka (2003) found that total hardness of waters was one of the most important factors correlated with fish community composition in the Red River drainage of Minnesota and North Dakota. In this region, many sucker fish (catostomids), catfish (ictalurids), shiners (cyprinids) and darters (percids) were also correlated with habitats characterized by low-flow variability, high discharges, low residue, conductivity and total hardness. Regional environmental conditions are important in structuring the fish communities in streams, and as such models could be used in the future, as conditions continue to be altered by anthropogenic factors, at the landscape scale to predict fish community response and support conservation efforts aimed at preserving or restoring riparian species (Koel & Peterka, 2003). Griess (1987) found that river otters do not use highly polluted waterways. Although several indicators of potential pollution (nitrates and phosphates) were investigated in this study, none showed any significance for latrine versus non-latrine, nor TS versus GR sites. Of course, no definitive conclusions can be drawn from this study with regard to heavy metal contamination or other sources of pollution in either field study system. However, the presence of greater levels of total water hardness in an 11th-order river, such as the Mississippi, as compared to a system containing primarily 3rd to 7th-order streams may indicate the potential for greater detoxification schemes within the gills of those species preyed upon most heavily by river otters in this area, thus creating a healthy prey base, as well as less potential accumulation of toxic metals in the tissues of the otters themselves (Wright and Li 2002; Blevins 2004; Fayram et al. 2005).

Furthermore, the presence of backwater (sloughs, oxbow lakes, drainage channels, ditches) in the vicinity (50 m up-or down-stream) of latrines was greater in the 11th-order Mississippi river system than in the lower-order Grand River system. Backwater areas are especially critical during summer when females with pups increase their activities and den in these habitats (Melquist and Hornocker 1983; Route and Peterson 1988; Newman and Griffin 1994). Studies on habitat use by muskrats have also found a reliance on backwater areas for populations that inhabit rivers, with high quality habitat along rivers being defined as having an abundance of backwaters, among other things (Brooks and Dodge 1981; Allen and Hoffman 1984). Rivers that provide additional water sources, such as backwater sloughs and wetlands, that serve as additional permanent water supplies (i.e. do not typically freeze in winter), and therefore sources for transportation and foraging, have been found to be strong indicators of habitats used by otters (Melquist and Hornocker 1983, Route and Peterson 1988; Debuc et al. 1990; Newman and Griffin 1994). While the Grand River system also has numerous lakes and some backwater/wetland associated watercourses, most are quite shallow and freeze during typical winters (Pitchford and Kerns 1999).

Although discussed previously, it bears mention that presence of high ground was elucidated in stepwise regression, but not in discriminant analyses as being significantly greater at the Mississippi River site than at the GR site. A wide, relatively deep, channelized river such as the Mississippi has not only steeper banks associated with its shoreline, but also the water control structures mentioned above upon which otters often create latrines. Neither the Grand River nor Locust Creek, the two primary waterways in the second field site, are affected by impoundments or channelization, but rather include rich, winding river systems, which are rare habitats of the Western Glaciated Plains (Thom and Wilson 1980).

In my evaluation of hypotheses 5 and 6, point locations and core are polygons of radio-tracked otters were evaluated using GIS with regard to proximity to roads and human populations (i.e. towns). As reported in Chapter 2, home ranges of otters at the Grand River site were significantly larger than those of otters at the Ted Shanks site. I predicted that if otters are moving over greater expanses of land, their core areas (i.e. centers of activity), and the latrines contained within these spaces, would likely be nearer to, and therefore encounter more, roads and towns. This prediction was supported with respect to roads; core areas (indicated by latrine presence) of otters at the Mississippi River site were significantly further from roads than those at the Grand River site. However, H_6 was not corroborated in this same regard; proximities to the nearest city (Ashburn or Louisiana, MO) were significantly less (i.e. closer) at the Mississippi River site than at the Grand River site. These discrepancies can be explained by examining the local geography and land use coverages for each site (Figure 3.1).

The Ted Shanks site is bordered to the east by the Mississippi River and to the west by a series of associated riverine bluffs. The nearest road of the same magnitude as those examined at the GR site lies on the opposite side of the bluff system (Thom and Wilson 1980; Dames and Todd 2002). Although access to the western side of the bluffs can be achieved via borrow ditches, minor tributaries and agricultural drainages, the pathways are not direct and are primarily completely exposed (i.e. very little shoreline vegetative cover exists). Conversely, small, established riverine towns have dotted the course of the Mississippi for more than 200 years (Dames and Todd 2002). Although the human population density is in most cases very low, human presence is definitely detected on the Ted Shanks/Mississippi field site.

In contrast, the Grand River site consists primarily of flat, agricultural land with many county roads connecting the homesteads, expanses of rivers and interspersed, remnant bottomland wet forest (Thom and Wilson 1980). While towns (or rather cities) exist in this region, human populations are more concentrated, but further dispersed from neighboring towns. Fortunately, although many roads and much highway traffic exist in this north-central region of Missouri, most watercourses proceed under roads via viaducts, thus minimizing the potential impact on river otters traversing these paths.

Differences in the spatial distribution of resources seemed to have significant impacts on the use of habitats by northern river otters. Spatiotemporal changes in the movements and behavior of species such as the river otter, an influential specialist in many drainage systems, can in turn have profound effects on landscape heterogeneity and local ecosystem processes.

Therefore, it is likely that otters at the Ted Shanks site, an area composed primarily of 11th-order and 8th-order rivers and their associated backwater, wetland ecosystem (Brooks 1980; Thom and Wilson 1980; Brooks and Dodge

1981, 1986; Frayer et al. 1982), were provided with such a locally rich, concentrated habitat that a wide area over which to range for resources was not required (Wright and Li 2002). Although the effects of human activities are apparent in other populations, they do not appear to play a significant role in determining the utilization of habitat by otters in the two sites examined in Missouri. In addition, Fayram et al. (2005) found that the variability in the indices of biotic integrity tended to be greater in smaller streams. Overall, large rivers, such as the Mississippi, appear to have more backwater and associated wetland habitats, thus providing, regardless of season, more habitat for prey and more suitable sites for foraging, denning and resting; therefore, smaller otter home range and core area sizes are maintained. White et al. (2003) in a study monitoring the success of translocations of Eurasian otters (*L. lutra*) in northeast England found that sprainting activity increased significantly with stream order, trout density, and surrounding riparian cover by woodland and semi-natural grassland vegetation. It is possible that similar differences in prey abundance, variability and distribution, as well as environmental predictors of suitable core areas (i.e. latrine sites), exist in the two different stream-order systems examined here, and are at least in part responsible for the differences in the utilization of habitat by northern river otters in this region.

Reintroduced carnivores such as northern river otters can considerably alter an ecosystem. The success of the Missouri river otter reintroduction project has been widespread across the state, to the extent that in some locations they are considered a nuisance species by many fishermen. The findings of this and other studies, however, indicate that the main prey source of otters are both fish and crayfish, and that game fish species do not comprise the majority of prey in river otter scats. In addition, otters' prey consumption varied both seasonally and among two different habitat types. The impact of predators on their prey populations are generally not very well understood prior to reintroduction efforts, nor are they well documented after. While, in fact, prime opportunities exist in the context of reintroduction projects to study predator-prey and other community-level relationships, few such studies, if any, are ever conducted. Typically, the impacts of reintroduced carnivores on prey populations are not addressed until they noticeably affect another population which, in turn, affects some portion of the local human population (e.g., hunters, fishermen); nonetheless, studies such as those described herein show that core areas intensely used by carnivores are often far from human roads and towns.

In addition, reintroduction programs are most often conducted by state or national management or conservation organizations without the involvement of members of the scientific community. A cohesive and unified approach to species restoration projects involving governmental and conservation organizations, scientific authorities, and local townspeople, may ameliorate many post-reintroduction problems and controversies, thus benefiting all members of the community. For example, several studies of habitat selection in northern river otters have found that populations thrive in the presence of high denning/sprainting ground (particularly along shoreline points of land) and beaver activity. By reintroducing individuals or, better still, by concentrating efforts on habitat restoration, populations would perhaps not expand as rapidly as when animals are released into just a few disjointed areas. Specifically, the reintroduction of otters into large areas that are interconnected by backwater sloughs could result in a more dispersed distribution, thereby reducing negative effects due to overcrowding.

In summary, differences in the spatial distribution of resources appear to have significant impacts on the use of habitats by northern river otters. Spatiotemporal changes in the movements and behaviors of wide-ranging riparian carnivores, such as the river otter, can in turn have profound effects on landscape heterogeneity and local ecosystem processes. Consequently, all relevant ecosystem dynamics should be taken into account when considering which conservation strategies best suite the needs of any threatened or endangered species.

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Table 3.1.—Environmental variables measured at 56 river otter latrine and 56 random (non-latrine) sites within Ted Shanks and Grand River sites.

Variable	**Description**
Dissolved Oxygen	Water quality measurement (ppm)
Nitrogen	Water quality measurement; Nitrate-Nitrogen (mg/l)
Phosphorus	Water quality measurement; orthophosphate (mg/l)
Turbidity	Water quality measure of clarity (JTU)
Total Hardness	Water quality measure of [$CaCO_3$] (ppm)
Percent Cover	Degree of canopy cover (i.e. amount of light that can penetrate through); (Fc); log transformed
High Ground	Presence or absence of an elevated structure (natural or man-made)
Variable Water Depth	Presence or absence of a variable water level 0.1 m from shore, in front of latrine
Vertical Bank	Presence or absence of vertical-undercut bank dominating the area defined as latrine
Point of Land	Presence or absence of 1+ projections of land feature extending ≥ m into the water from a transect parallel to the shoreline at the aquatic-terrestrial interface; in area defined as latrine
Shallow Foraging Habitat	Presence or absence of shallow water (≤ 3.0 m) 1.0 m from shore, in front of latrine

Water Permanence	Presence or absence of water maintaining a constant fluid-stae (flow) throughout entire year
Beaver Activity	Presence or absence of any beaver activity within 50 m upstream or downstream of center of latrine
Conifers	Presence or absence of 1+ conifers within 5.0 m upstream or downstream of center of latrine
Underlying Grass	Presence or absence of graminoid ground cover underlying area defined as latrine
Stream Mouth	Presence or absence of a stream mouth entering the main body of water within 50 m upstream or downstream from the center of latrine
Backwater	Presence or absence of a backwater area (see text for defining properties) within 50 m upstream or downstream of latrine
Fallen Logs	Presence or absence of fallen logs within the area defined as latrine
Access to Humans	Presence or absence of defined accessibility points (e.g., boat ramps, boardwalks) within 50 m upstream or downstream of latrine
Low Land Use	Presence or absence of land use/land cover defined as low impact within 50 m upstream or downstream of latrine
Trees	Presence or absence of 1+ trees ≥ 30 cm in diameter within area defined as latrine

Table 3.2.—Statistical comparisons of 21 environmental habitat variables evaluated between 56 river otter latrine sites versus 56 random, non-latrine sites; *U*- value, and *P*- values given.

Environmental Variable	*U*	*P*
Dissolved Oxygen	1443.5	0.47
Nitrates	1541.00	0.87
Phosphates	1530.00	0.82
Turbidity	990.50	0.0008
Total Hardness	1568.00	0.99
Log % Cover	937.00	0.0002
High Ground	420.00	0.0001
Variable Water Depth	1092.00	0.005
Vertical Bank	1512.00	0.74
Point of Land	532.00	<0.0001
Shallow Foraging Habitat	1596.00	0.86
Water Permanence	1428.00	0.41
Beaver Activity	448.00	<0.0001
Conifers	1176.00	0.02
Underlying Grass	1176.00	0.02
Stream Mouth	1456.00	0.50
Backwater	1316.00	0.14

Fallen Logs	980.00	0.0005
Stream Access to Humans	1568.00	1.0
Low Land Use Impact	1568.00	1.0
Trees > 30 cm diameter	1232.00	0.05

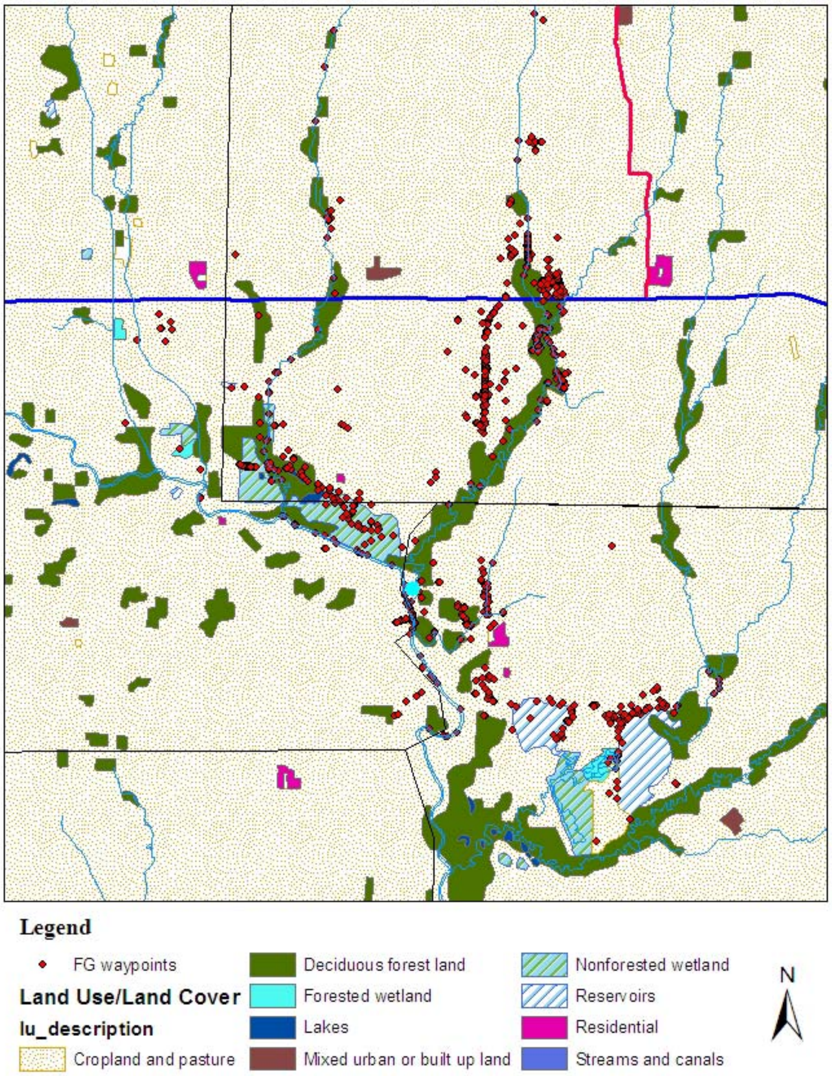
Table 3.3.—Forward stepwise regression analysis testing the effect of 21 environmental habitat variables on latrine (n = 56) and non-latrine sites (n = 56) at Ted Shanks and Grand River field locations in Missouri. Only those explanatory variables are shown that were added to the model until R^2 approached 1.0 ($P > 0.05$).

Response Variables	Explanatory Variables	Wald χ^2	R^2	*P*
Latrine Site	High Ground	2.81	0.40	<0.0001
Non-Latrine Site	Beaver Activity	2.75	0.64	<0.0001
	Point of Land	2.66	0.77	<0.0001
	Stream Access to Humans	2.47	0.86	0.0002
	Total Hardness ([$CaCO_3$])	2.37	0.90	0.015
	Trees > 30 cm diameter	2.24	0.92	0.038

Table 3.4.—Forward stepwise regression analysis testing the effect of 21 environmental habitat variables on latrine sites at Ted Shanks (TS; n = 33) and latrine sites at Grand River (GR; n = 23) field locations in Missouri. Only those explanatory variables are shown that were added to the model until R^2 approached 1.0 ($P > 0.05$).

Response Variables	Explanatory Variables	Wald χ^2	R^2	*P*
Latrines at TS	Total Hardness ([$CaCO_3$])	6.99	0.61	<0.0001
Latrines at GR	High Ground	0.01	0.73	0.002
	Backwater	4.55	0.82	0.009

Figure 3.1. - Land use/Land cover polygons for the Grand River site in north-central Missouri.



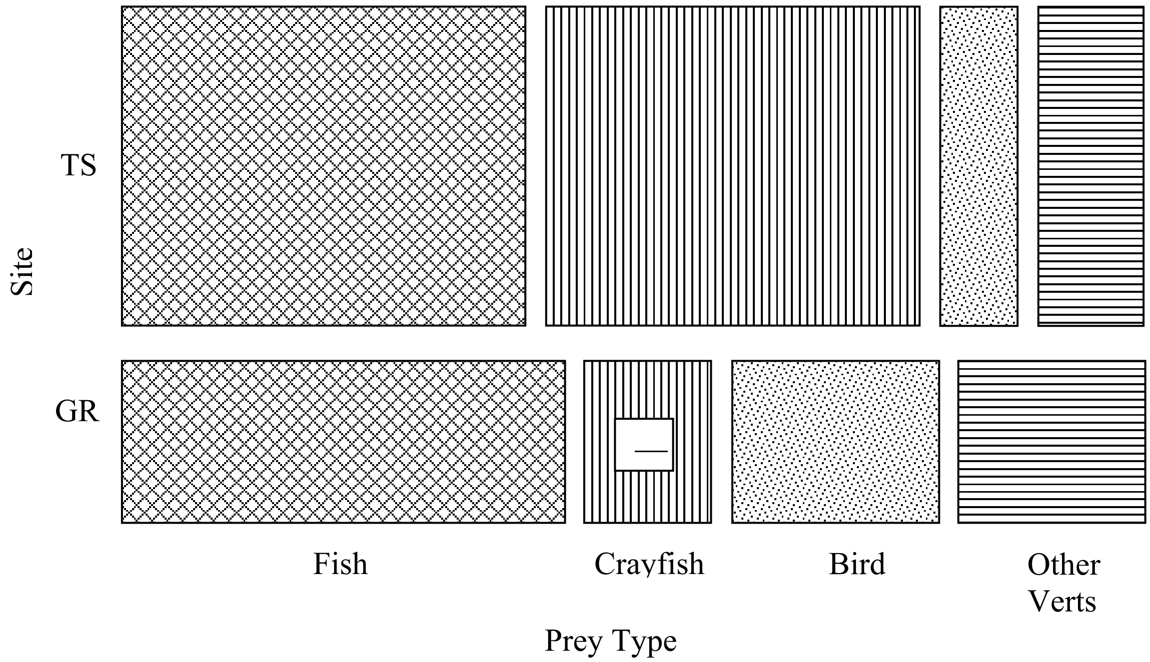


FIG. 3.2a.—Mosaic tile display of frequencies by site (TS = Ted Shanks; GR = Grand River) used in a 2 × 4 contingency χ^2 test of independence for prey types ingested by river otters (– crayfish were less than expected).

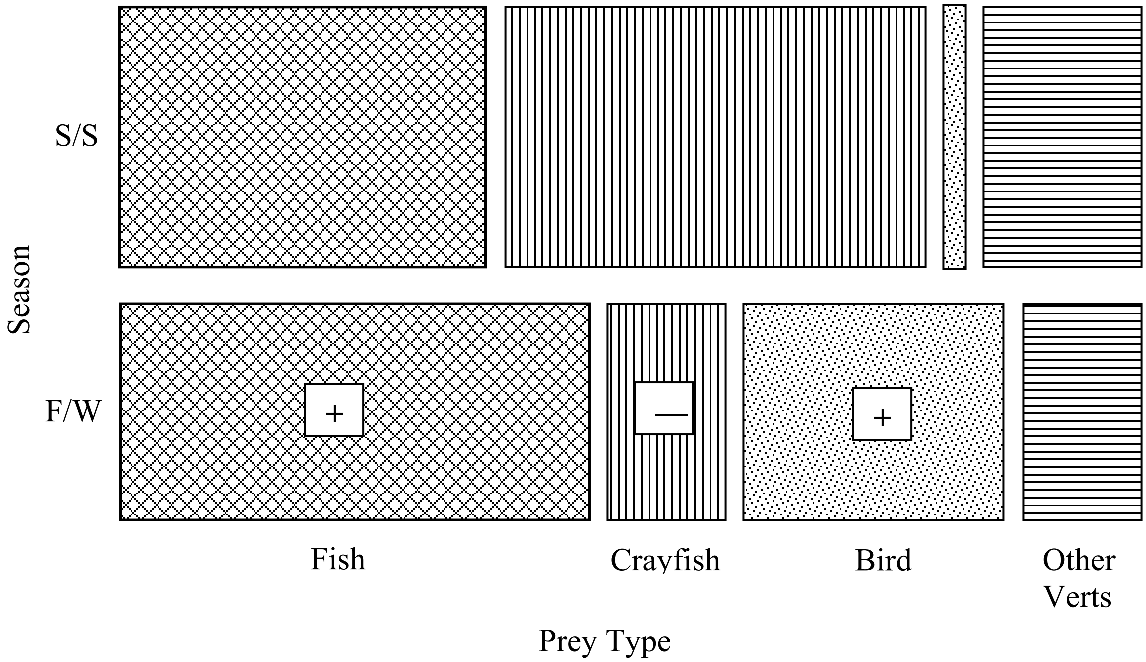


FIG. 3.2b.—Mosaic tile display of frequencies by season (S/S = spring/summer; F/W = fall/winter) used in a 2 × 4 contingency χ^2 test of independence for prey types ingested by river otters (+ fish and bird were more than expected; – crayfish were less than expected).

Figure 3.3. - Discriminate anaylsis of environmental variables for latrine vs. non-latrine sites at two field locations in Missouri.

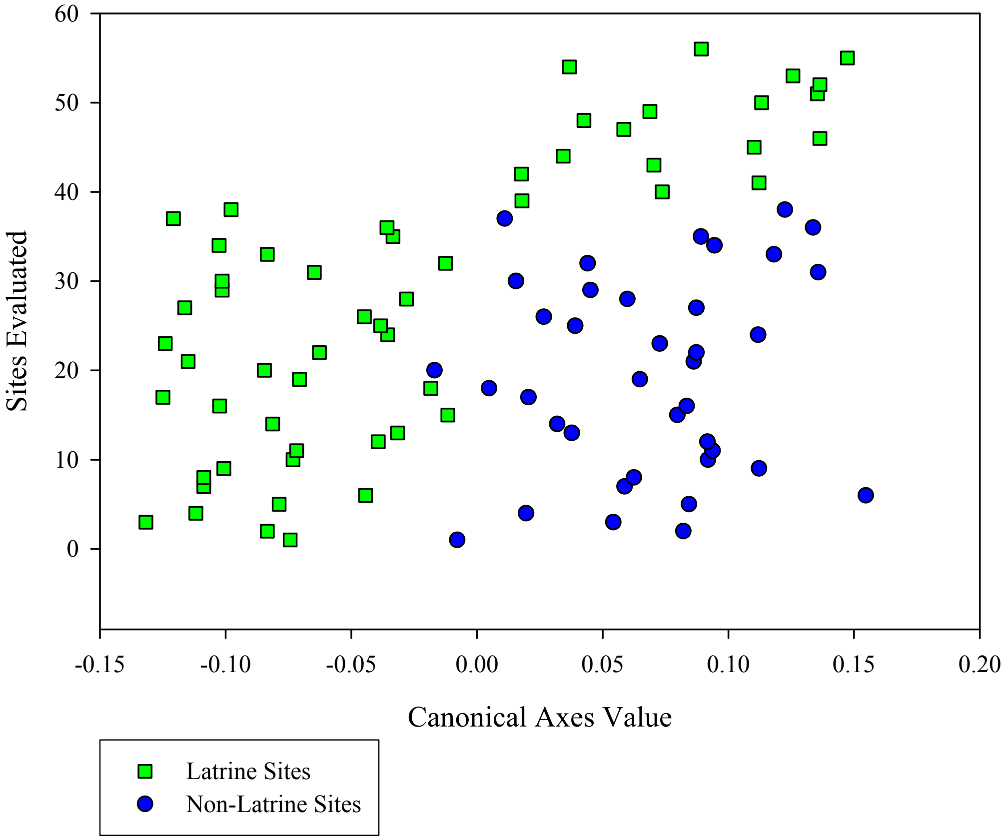


Figure 3.4. - Discriminate analysis of environmental variables at latrine sites; comparisons between Ted Shanks and Grand River field sites.