

Survival and Cause-specific Mortality of a Protected Population of River Otters in Minnesota

THOMAS A. GORMAN¹

Department of Biological Sciences, Minnesota State University, Mankato, 242 Trafton Science Center South, Mankato 56001

BROCK R. McMILLAN

Department of Biological Sciences, Minnesota State University, Mankato, 242 Trafton Science Center South, Mankato 56001

JOHN D. ERB

Minnesota Department of Natural Resources, 1201 East Highway 2, Grand Rapids 55744

CHRISTOPHER S. DEPERNO²

Minnesota Department of Natural Resources, 35365 800th Avenue, Madelia 56062

AND

DANIEL J. MARTIN³

Department of Biological Sciences, Minnesota State University, Mankato, 242 Trafton Science Center South, Mankato 56001

ABSTRACT.—Determining causes of mortality and estimating survival rates can provide insight into the status of species for which population trends are not well understood. From Apr. 2002–May 2004 we radio-marked and monitored 39 (13 adult males; 6 subadult males; 8 adult females; 12 subadult females) river otters (*Lontra canadensis*) in the upper Mississippi River watershed to document causes of mortality, and to evaluate the effects of season, age and sex on survival of river otters in southeastern Minnesota. Further, we assessed the relative importance of demographic parameters to population growth using a projection matrix, which incorporated reproductive data with our observed survival estimates. Human induced mortalities, including accidental captures by fur-harvesters targeting other species ($n = 6$) and vehicle collisions ($n = 1$), accounted for the majority of deaths while natural mortality was low ($n = 1$). Annual survival of females was 0.680 (SE = 0.099) and was 0.946 (SE = 0.052) for adult males. Elasticity of adult female survival was 3.1 times higher than subadult survival, 2.7 times higher than juvenile survival and 2.7 times higher than the sum of elasticity for subadult and adult female reproduction. River otters and other furbearers need to be monitored to assess population status, and management should be responsive to ensure persistence of populations experiencing intentional and/or accidental harvest.

¹Corresponding author present address: Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, 100 Cheatham Hall, Blacksburg 24061; e-mail: gormant@vt.edu

²Present address: Department of Forestry and Environmental Resources, North Carolina State University, Turner House, Box 7646, Raleigh 27695

³Present address: Colorado Division of Wildlife, Wildlife Research Center, 317 West Prospect Road, Fort Collins 80526

INTRODUCTION

River otters (*Lontra canadensis*) are a top predator of aquatic ecosystems (Ben-David *et al.*, 2001) and an economically and ecologically valuable furbearer (Melquist and Hornocker, 1983; Bowyer *et al.*, 2003; Melquist *et al.*, 2003). Populations of river otters in many regions of North America declined after the 19th century, which was likely a result of anthropogenic factors such as land use changes, unregulated harvest and water pollution (Nilsson, 1980; Toweill and Tabor, 1982; Melquist and Dronkert, 1987; Raesly, 2001). Despite a relatively low reproductive rate (Berg, 1984; Rolley and Roth, 2004), improvements in water quality, habitat and harvest management, population monitoring and successful reintroduction programs have contributed to recovery of river otters across much of their historical range (Raesly, 2001). The successful recovery of otters may have important implications for proper ecosystem function in terrestrial and aquatic systems because otters are a connection between these two systems (Bowyer *et al.*, 2003; Ben-David *et al.*, 2005).

River otters are indigenous to Minnesota and were historically distributed statewide (Swanson *et al.*, 1945). River otters were unprotected in Minnesota prior to 1917 and received complete protection from 1917 through 1942. After 1942 limited harvest seasons were established and a 10-wk trapping season is currently in place in northern Minnesota, with a season bag limit of 4 otters/trapper. In southern Minnesota the trapping seasons have remained closed for the past 87 y.

River otters have few natural predators and mortality is often associated with anthropogenic factors such as vehicle collisions and trapping (Melquist *et al.*, 2003). Although river otters are not legally harvested in southern Minnesota, they are occasionally captured incidentally through trapping of other furbearers (Erb and DePerno, 2000). In fact, increased sightings, accidental captures (Minnesota Department of Natural Resources, in litt.) and vehicle-kills may suggest the population in this region has been increasing, although demographics are not well understood. In addition, river otters may be at risk of elevated mortality in areas where waters are polluted (Ben-David *et al.*, 2001). Also, diseases may contribute to mortality, but are not considered a major factor (Melquist and Dronkert, 1987; Melquist *et al.*, 2003). Therefore, an estimate of survival and cause-specific mortality is essential to determine factors that may influence population growth (White and Burnham, 1999) and to improve management of populations (White and Garrott, 1990).

Sex-specific survival rates and cause-specific mortality of native protected populations of river otters are not well documented. Causes of mortality have been examined (Melquist and Hornocker, 1983; Reid *et al.*, 1994), but few studies have formally estimated survival rates of river otters. Ben-David *et al.* (2001) reported a survival estimate for river otters in coastal Alaska and Tabor and Wight (1977) reported female survival estimates based on harvest data in Oregon. In many furbearer species, annual survival often varies as a function of sex, age, season, and/or harvest pressure (*e.g.*, Clark and Fritzell, 1992; Gehrt and Fritzell, 1999; Kamler and Gipson, 2004). However, there is a paucity of information in the literature regarding sex-specific survival rates of river otters, particularly for native populations closed to legal harvest.

We conducted a study from Apr. 2002–May 2004 to document causes of mortality, and to evaluate the effects of season, age and sex on survival of river otters in southeastern Minnesota. Further, we incorporated survival estimates of female otters with previously reported estimates of reproductive rates in the region to evaluate the sensitivity and elasticity of population growth to changes in survival and reproduction. Combined, this information will help parameterize population models, prioritize research needs and ultimately improve future decisions regarding population management of river otters. In addition, it will

provide important comparative data for examining the extent of regional or range-wide variability in demography of otters.

STUDY AREA

This study was conducted along the Mississippi River watershed in Winona and Wabasha Counties of southeastern Minnesota (Fig. 1). The area was closed to the legal harvest of river otters but was open to trapping of beaver (*Castor canadensis*), raccoon (*Procyon lotor*), American mink (*Mustela vison*) and muskrat (*Ondatra zibethicus*). The study area included the backwaters of the Mississippi River and the major tributaries of the region (primarily the Zumbro and Whitewater Rivers) that flow into the Mississippi River from the west. The entire Zumbro River watershed was 4296 km², composed of 89% cropland, 6% grassland and pasture, 3% forest and <1% wetlands. The Whitewater River watershed is 829 km², composed of 58% cropland, 8% grassland and pasture, 13% forest, 14% wetlands and 7% other. The region was devoid of natural lakes, but some small human-made ponds were present. Conversely, the Mississippi River was an expansive aquatic system with vast emergent and submergent marshes, and a variety of channels ranging from slow to fast flows. This research was conducted in or near the McCarthy Lake Wildlife Management Area, Whitewater Wildlife Management Area, the Upper Mississippi River National Wildlife and Fish Refuge, and on private land.

The topography of the study area was predominantly blufflands with up to 183 m elevation. The blufflands are a bedrock plateau covered with a windblown layer of silt that was significantly eroded by rivers. Annually, southeastern Minnesota receives 87.8 cm of precipitation with an annual mean temperature of 8.0 C, and minimum and maximum annual temperatures of 2.8 C and 13.1 C, respectively (Garoogian, 2000).

METHODS

ANIMAL CAPTURE AND MONITORING

River otters were trapped from 3 Oct.–19 Oct. 2001, 21 Apr.–30 May 2002, 27 Aug.–22 Sept. 2002, 3 Apr.–14 Jun. 2003 and 21 Aug.–8 Oct. 2003. These time periods were selected because daily temperatures were moderate, reducing the likelihood of thermal stress on captured animals. A random trapping design was not appropriate for river otters as they are difficult to capture. Therefore, we used a systematic approach, which involved extensive searching of river banks, backwater sloughs, and wetland levees for areas with river otter sign (e.g., scat, tracks, trails, etc.). At trap sites, we set Sleepy Creek® No. 11 double-jawed foothold traps (Sleepy Creek Manufacturing, Berkley Springs, WV) to capture river otters (Shirley *et al.*, 1983; Blundell *et al.*, 1999). Traps were equipped with a shock spring and multiple swivels to decrease the chance of trap-related injury. Traps were checked each morning, and when captured, otters were transferred from the trap to a transport tube without anesthesia. Otters were taken to Plainview Veterinary Clinic (Plainview, MN) for surgical implantation of a radio transmitter (Models: 1245 2-stage, 1250 2-stage or 3-stage; Advanced Telemetry Systems, Inc., Isanti, MN; or Model FH-3, Global Tracking Systems, Coleman, AB). All transmitters were equipped with mortality sensors that were activated after 8 h of complete inactivity.

Prior to surgery for transmitter implantation, otters were chemically immobilized with an intramuscular injection of ketamine (\bar{X} = 16.7 mg/kg) and xylazine (\bar{X} = 10.2 mg/kg). A radio transmitter was surgically implanted into the peritoneal cavity of each otter through a paralumbar incision. While under anesthesia, otters were sexed and an upper premolar

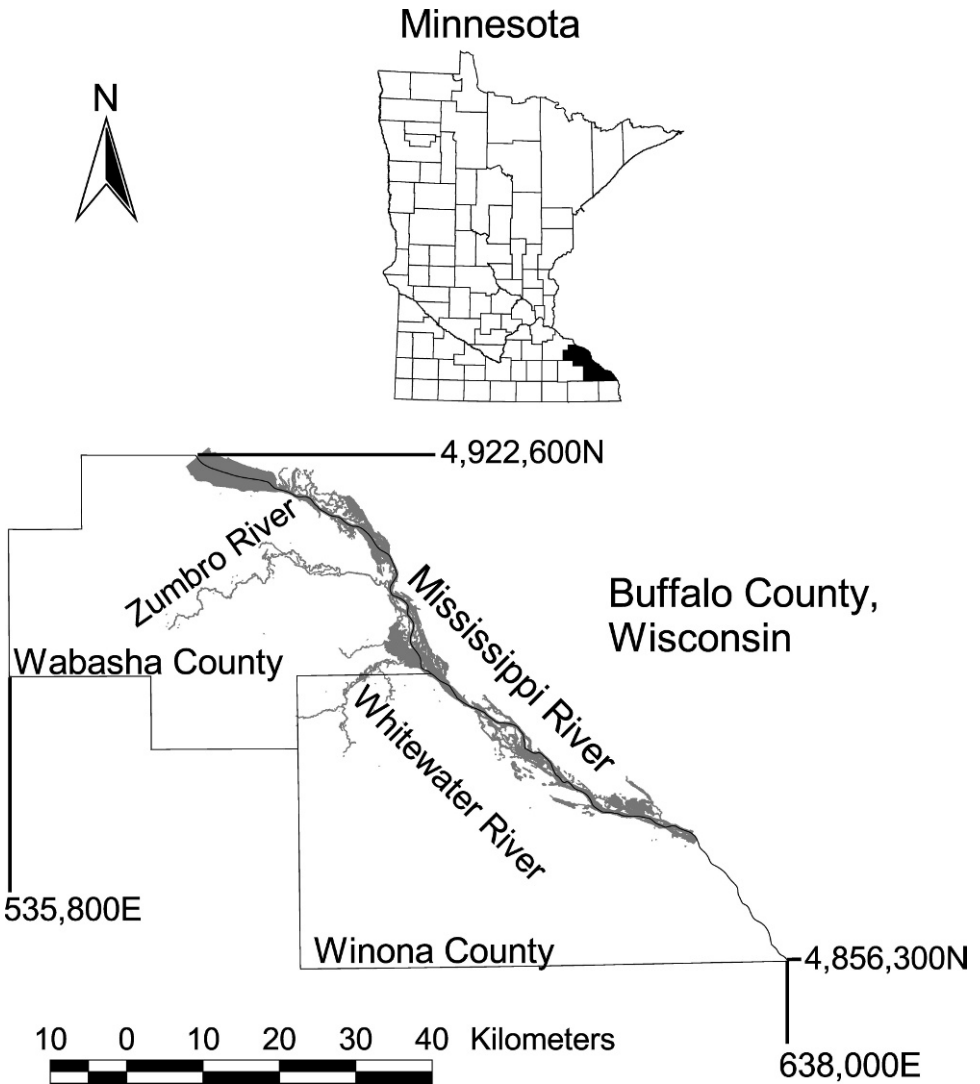


FIG. 1.—Study area in southeastern Minnesota where cause-specific mortality and survival of river otters (*Lontra canadensis*) was examined, 2002–2004

was extracted for aging by cementum annuli (Kuehn and Berg, 1984). Sex, body condition and other morphological measurements were recorded. Otters were tagged with no. 1 Monel ear tags and no. 3 Monel web tags (National Band and Tag Company, Newport, KY). To minimize the likelihood of infection, each otter received 2cc of long-acting penicillin, 1cc of enrofloxacin, and 2cc of clostridium anti-toxin. Otters were allowed to recover naturally from anesthesia and were released at the site of capture within 6–74 h. All capture and handling procedures were approved by the Minnesota State University, Mankato, Institutional Animal Care and Use Committee (Project # 01-3).

River otters were monitored an average of 2 d/wk. We monitored their status (dead/alive) from the ground using an ATS R4000 scanning receiver and a 3-element Yagi antenna. In addition to ground-based mortality checks, aerial monitoring was conducted at 7–10 d intervals via a Cessna Skylane 182 fixed-wing aircraft equipped with a 4-element Yagi antenna on each wing. If we could not locate animals, we continued to search for them during both ground and aerial searches throughout the duration of the study.

MORTALITY

Cause-specific mortality was determined for all animals within 48 h of the death, except for one juvenile female that was located nearly 3-mo after disappearing from the study site. This animal had moved >20 km from the study area and was not located for several flights. In this situation the midpoint between the last known date alive and the date of relocation was used as the date of death (Heisey and Fuller, 1985). When the cause of death of the otter was not apparent from field observations (*e.g.*, not caught in a trap or struck by a vehicle), a necropsy was performed by a licensed veterinarian.

SURVIVAL ESTIMATION

We estimated monthly survival separately for male and female river otters during two different seasons. We differentiated between the trapping season for other furbearers (Nov.–Mar.) when otters may be accidentally captured, and the non-trapping season (Apr.–Oct.). We estimated survival separately for males and females and between seasons because sex and season are common factors that influence survival in mustelids (Tabor and Wight, 1977; Melquist and Hornocker, 1983; Reid *et al.*, 1994; Hodgman *et al.*, 1994), and these factors identified key differences in survival observed in this study. We used a known fate model in Program MARK (White and Burnham, 1999) to estimate monthly survival of otters in the study area. We allowed survival to vary among each sex*season group, but assumed constant monthly survival within each sex*season combination. We then used the product of monthly survival (months pooled across years) to calculate seasonal and annual survival, with variances calculated using the delta method (Seber, 1982).

In addition, we calculated a Cox's Proportional Hazards Model (Riggs and Pollock, 1992) to evaluate the relative risk of river otters as a function of age and sex. The risk ratio is a measure of the difference in the instantaneous risk of mortality for individuals within different classes of the same covariate group (*e.g.*, sex: males vs. females). We used 95% confidence intervals to determine whether risk ratios differed from 1 (*i.e.*, equal risk). We fit Cox's Proportional Hazards Model using Program R (R Development Core Team, 2004).

POPULATION DEMOGRAPHY

We used an age-structured, female-specific, post-breeding projection matrix (Caswell, 2001) to evaluate the relative 'demographic importance' (*i.e.*, sensitivity and elasticity) of population parameters, and secondarily to estimate population growth (λ) of river otters in the study site. Sensitivity analysis is useful for estimating how much λ will change following an absolute change in a parameter value, assuming other parameters are held constant. For example, if sensitivity is 0.5 for adult survival, and survival were to decrease from 0.9 to 0.8, λ will change by *approximately* -0.05 [*i.e.*, $0.5 \cdot (0.8 - 0.9)$]. A more detailed formula for computing such changes was provided by Caswell (2001). Because variables (in this case survival and reproduction) are measured on different scales, sensitivity analysis cannot provide a relative comparison of the proportional influence of all parameters on λ . Elasticities, which sum = 1, estimate the proportional response of λ to a proportional change in all parameters. For example, if elasticity for adult survival was 0.7, and all

parameters were adjusted by 10% of their value, we know that 70% (elasticity*100) of the change in λ would stem from the change in adult survival, with the remaining 30% being attributable to the other parameters according to their elasticities. Sensitivity/elasticity analysis provides an assessment of the relative contributions of survival and reproduction to population growth, which can be useful information for making management decisions and prioritizing future research needs.

The matrix was constructed based on three age-classes [*i.e.*, juvenile (<1 y old), subadult (>1 and <2 y old) and adult (>2 y old)]. For this analysis we incorporated age-specificity to estimate survival of subadult and adult females because we believed the mortality data for females was adequate to support separate estimation. We assumed that juvenile female survival was similar to subadults, because data we had for animals from 5–12 mo of age did not indicate differences from subadults and we had no evidence of complete reproductive failure (*e.g.*, den abandonment; Gorman *et al.*, 2006a). Therefore, we constructed a three (rather than two) age-class matrix to more explicitly account for reproductive differences.

We obtained natality estimates from female otter carcasses previously collected in northern Minnesota ($n = 267$) and Wisconsin ($n = 747$; Rolley and Roth, 2004). The mean pregnancy rates for the combined Minnesota and Wisconsin data were 0.77 ($n = 629$), 0.32 ($n = 385$), and 0, for adults, subadults and juveniles, respectively. The mean corpora lutea counts for parous females were 2.22, 1.77, and 0, for adults, subadults and juveniles, respectively, and we assumed a 50:50 sex ratio for offspring. We attempted to collect otter carcasses specifically from southeastern Minnesota during the duration of our study, but the age-specific sample sizes were too small to separately estimate reproductive parameters ($n = 27$ total females). However, those limited data produced natality results (pregnancy rate \times mean # offspring) essentially identical to the larger regional sample for all three age-classes, suggesting our regional data were representative of our specific study area. The 'recruitment row' of the matrix was based on the product of age-specific survival and natality (# of females/female/year) for adult females, subadult females and juvenile females. Hence, 'natality' parameters in sensitivity/elasticity graphs should be interpreted as age-specific recruitment contributions to population growth. All matrix calculations were performed with PopTools (Version 2.5, CSIRO Sustainable Ecosystems) add-in for Microsoft Excel (Version 10.0, Microsoft Corporation).

RESULTS

We captured 39 river otters 42 times (13 adult males; 6 subadult males; 8 adult females; 12 subadult females). We monitored survival of river otters from Apr. 2002–May 2004, for a total of 439 river otter-months.

The main causes of mortality of river otters in the study area were from human-related activities. There were nine known mortalities during the study (8 females, 1 male). Accidental captures by fur-harvesters resulted in 6 deaths (3 subadult females; 3 adult females). One adult male was killed after it was struck by an automobile, one adult female died from an infection which was attributed to natural causes and one subadult female died from unknown causes.

Monthly survival of females during the non-trapping season was 0.983 (SE = 0.012) and 0.948 (SE = 0.022) during the trapping season. Monthly survival of males was 1.0 (SE = 0.0) during the non-trapping season and 0.989 (SE = 0.011) during the trapping season. During the 7-mo non-trapping season female survival was 0.886 (SE = 0.075) and during the 5-mo trapping season female survival was 0.768 (SE = 0.090). Male survival was 1.0 (SE = 0.0) during the non-trapping season and was 0.946 (SE = 0.052) during the 5-mo trapping

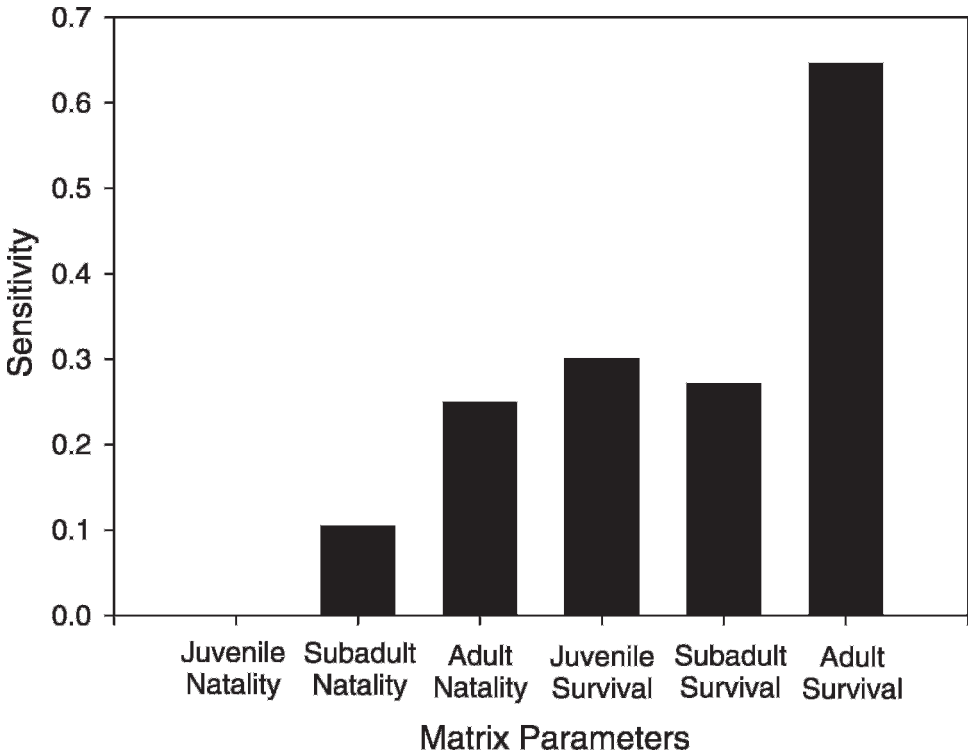


FIG. 2.—Sensitivity estimates for demographic parameters of female river otters (*Lontra canadensis*) from southeastern Minnesota, Apr. 2002–May 2004. Sensitivity reflects the response of lambda to an absolute change in one of the matrix parameters

season. Annual survival of females was 0.680 (SE = 0.099) and for adult males was 0.946 (SE = 0.052).

The estimated risk ratio indicated that the instantaneous risk of mortality for females was 11 times higher than for males (11.39:1.0; 95% CI = (1.4, 95.4)). Sub-adults and adults were equally at risk (0.53:1.0; 95% CI = (0.13, 2.2)), based on a 95% confidence interval that overlapped one.

The 'recruitment row' of the age-structured, female-specific, post-breeding projection matrix was 0, 0.17, and 0.65 for juvenile females, subadult females and adult females, respectively. Annual survival estimates used in the 'survival rows' of the post-breeding projection matrix for adult females, sub-adult females and juveniles were 0.765 (SE = 0.127), 0.598 (SE = 0.155), and 0.598 (SE = 0.155), respectively. Based on sensitivity (Fig. 2) and elasticity (Fig. 3) analyses, survival of adult females had the greatest influence on λ . Elasticity of λ to adult female survival was approximately 3.1 times higher than that for sub-adult survival, 2.7 times higher than juvenile survival and 3.1 times higher than adult natality. Perturbations in sub-adult and juvenile natality had minimal influence on λ . Based on the analyses, the population of river otters in the study site was estimated to be increasing at an annual rate of 1.6% ($\lambda = 1.016$).

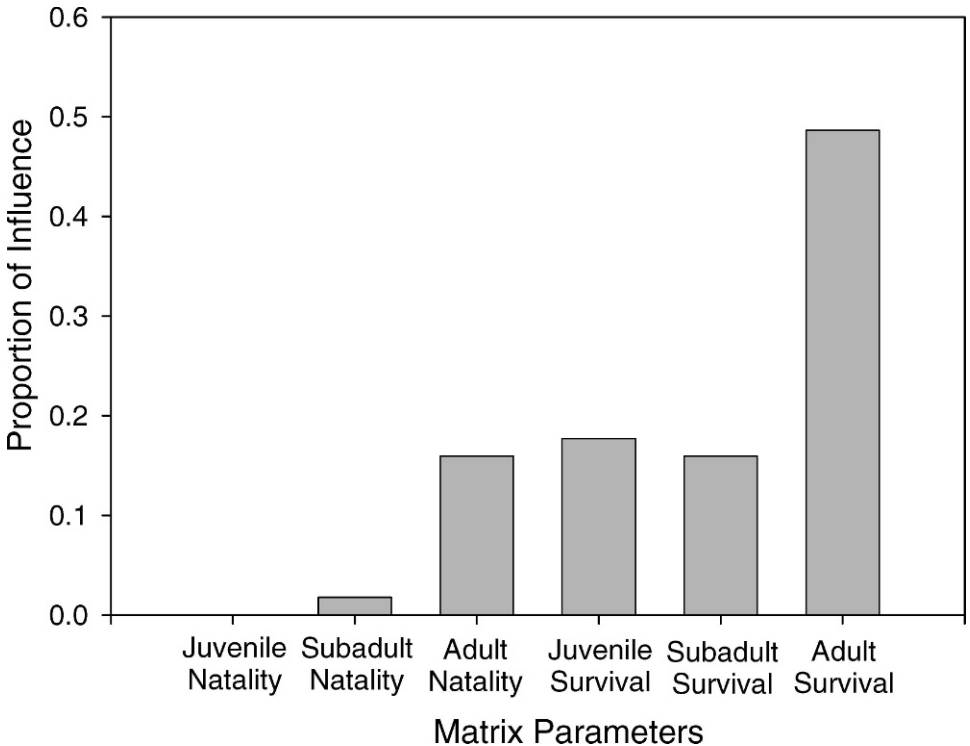


FIG. 3.—Elasticity estimates for demographic parameters of female river otters (*Lontra canadensis*) from southeastern Minnesota, Apr. 2002–May 2004. Elasticity reflects the proportional response of lambda to a proportional change in the matrix parameters

DISCUSSION

Over the course of this study, accidental trapping was the main cause of mortality for river otters in southeastern Minnesota. All accidental trapping mortalities were females ($n = 6$). No males marked during this study were known to have been killed by trapping and only a single marked male died over the duration of the study. The study area and the surrounding region have been closed to legal harvest of river otters since 1917, but legal trapping of other furbearers has resulted in the accidental capture of otters by avocational trappers.

We collected otters accidentally trapped in a broader area surrounding and including the study area and we collected carcasses during 3 trapping seasons (2001–2004) to examine the overall prevalence of accidental captures of river otters by trapping activities directed towards other species. Of the animals turned in from accidental captures, 62% ($n = 21$) were females and 38% were males ($n = 13$), supporting our results that females were more susceptible than males to accidental trapping (Gorman, unpubl. data). Typically, trapping pressure in a legally harvested population of furbearers affects males disproportionately to females (Hamilton and Eadie, 1964; Stephenson, 1977; Melquist and Hornocker, 1983). Buskirk and Lindstedt (1989) suggested males might be at greater risk to trapping, because in general they have larger home ranges than females.

Home range data from this study site indicated that home ranges of males on average are twice as large as those of females (Gorman *et al.*, 2006b). Therefore, home range size does not explain the greater number of females captured by trappers. It is possible that males in a protected non-target population actually benefit from larger home ranges. For example, if habitat of otters were distributed patchily, male otters may spend less time in close contact with traps set for other species as a result of more time spent traveling in 'trap-free' areas between patches. In harvested otter populations, these travel corridors are frequently targeted by other trappers, and may produce balanced or male-biased harvest. Alternatively, habitats targeted by trappers pursuing other species may be used disproportionately by female otters in our study area (*e.g.*, beaver habitat). We previously documented that female otters used natal dens in upland areas with steep relief, perhaps to avoid flooding (Gorman *et al.*, 2006a). In our study area, these areas were generally where human access (and hence trapping activity) appeared more common, and it may be that females maintain a closer affinity to these higher-risk areas throughout the year.

Even though the majority of the mortalities were female, survival of females was similar to other populations of river otters. Annual survival of female river otters in Oregon was 0.73 (Tabor and Wight, 1977). This population was legally harvested and the survival estimate was based on a life table analysis and parameterized by carcass collections. In coastal Alaska, Ben-David *et al.* (2001) estimated 20-mo survival of otters (sexes combined) to be 0.80. On an annual basis this would result in an overall survival estimate of 0.87. Their study area was closed to all trapping and represents a non-harvested population. However, the authors did not report separate estimates by age or sex. For comparison, pooling sexes, and assuming our 2-season model (constant survival within season), overall annual survival on our study area was 0.80. It is interesting to note that our study yielded a survival estimate closer to an unharvested population in Alaska for males (Ben-David *et al.*, 2001), and closer to a harvested population in Oregon for females (Tabor and Wight, 1977). This suggests that legalized harvest may disproportionately increase risk of trapping mortality for males, which may serve to balance overall (unintentional and intentional) harvest sex ratios. In northern Minnesota, where otters are legally harvested, the 28-y weighted average for harvest sex ratios is 53M:47F. It remains unclear whether our observed female-bias in mortality is a local phenomenon and/or a temporal anomaly on our study area. If such a pattern persisted indefinitely, population sex ratios would become significantly male-biased unless offspring sex ratios (or sex-specific neonate mortality) were not balanced or unless mortality of legally harvested otters in adjacent Mississippi River counties in Wisconsin were male-biased and population mixing was occurring. The sex ratio of our radio-marked sample was not male biased (19M:20F). No other studies have formally presented survival estimates for sex and age classes of otters, so our results provide useful information for future monitoring and comparison of river otter survival.

Using a projection matrix, we estimated the population of river otters on our study site to be increasing slightly ($\lambda = 1.016$). While there is undoubtedly uncertainty in this estimate, the result is consistent with field observations that suggest otter distribution and abundance have been slowly, but steadily, increasing in southeastern Minnesota. Hence, there is no indication the magnitude or female-biased nature of mortality is causing population declines. Given the high elasticity of λ to adult female survival (Fig. 3), obtaining such estimates will likely be important for monitoring population status, particularly if reliable population trend indicators are not available or used. However, obtaining reliable estimates of the recruitment contributions from adult females may be important as well, particularly if the separate components of recruitment (adult natality and juvenile survival) can be

extracted from recruitment measures (e.g., the summed elasticity of λ to adult natality and juvenile survival was 0.34).

CONCLUSIONS

We documented that female river otters were more susceptible than males to accidental trapping-caused mortality in an area that was not open to legal harvest. Therefore, female river otters in the study area were at greater risk of death and had lower annual survival than males. Nevertheless, accidental mortality from trapping (combined with other observed causes of mortality) does not appear to be reducing populations in this area. Our results not only provide useful information that will improve our ability to understand and potentially reduce accidental harvest of otters, but will improve our ability to make sound management decisions regarding future harvest management. Given that survival of adult females had the greatest influence on population growth and given the relative scarcity of such information, we believe similar research in other geographic areas is needed to assess the generality of our results and improve decisions regarding otter populations and harvest management. Further, our results demonstrate the need for understanding how space use of otters corresponds with the effort of trappers, particularly for protected populations.

Acknowledgments.—We thank Minnesota State University, Mankato, the Minnesota Department of Natural Resources (MN DNR) and the United States Fish and Wildlife Service for their financial and logistical support. We thank J. Krenz for assistance with this research and M. Fischer, J. McIntire, S. Gappa and J. Homyack for assistance with trapping and fieldwork. Also, we thank the experienced MN DNR pilots, D. Carpenter, B. Maas, J. Heineman and M. Trenholm. Valuable statistical assistance was provided by J. Homyack, J. Fieberg and J. Giudice. Finally, we thank the editor and two anonymous reviewers that have improved this manuscript.

LITERATURE CITED

- BEN-DAVID, M., L. K. DUFFY, G. M. BLUNDELL AND R. T. BOWYER. 2001. Exposure of coastal river otters to mercury: relation to age, diet, and survival. *Environ. Toxicol. Chem.*, **20**:1986–1992.
- , G. M. BLUNDELL, J. W. KERN, J. A. K. MAIER, E. D. BROWN AND S. C. JEWETT. 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. *Ecology*, **86**:1331–1345.
- BERG, W. E. 1984. Otter Status Report, 1983–1984. Minnesota Department of Natural Resources, Grand Rapids, MN, USA.
- BLUNDELL, G. M., J. W. KERN, R. T. BOWYER AND L. K. DUFFY. 1999. Capturing river otter: a comparison of Hancock and leg-hold traps. *Wildl. Soc. Bull.*, **27**:184–192.
- BOWYER, R. T., G. M. BLUNDELL, M. BEN-DAVID, S. C. JEWETT, T. A. DEAN AND L. K. DUFFY. 2003. Effects of the Exxon Valdez oil spill on river otters: injury and recovery of a sentinel species. *Wildl. Monog.*, **153**:1–53.
- BUSKIRK, S. W. AND S. L. LINDSTEDT. 1989. Sex biases in trapped samples of Mustelidae. *J. Mamm.*, **70**:191–193.
- CASWELL, H. 2001. Matrix Population Models: construction, analysis, and interpretation, Second edition. Sinauer Associates, Inc., Sunderland, MA, USA.
- CLARK, W. R. AND E. K. FRITZELL. 1992. A review of population dynamics of furbearers, p. 899–910. In: D. R. McCullough and R. H. Barrett (eds.). *Wildlife 2001: Populations*. Elsevier Applied Science, London, England.
- ERB, J. D. AND C. S. DEPERNO. 2000. Distribution and relative abundance of river otter in southern Minnesota, p. 19–26. In: B. Joselyn (ed.). *Summaries of Wildlife Research Findings*. Section of Wildlife, Minnesota Department of Natural Resources, St. Paul, MN, USA.
- Garoogian, D. (ed.). 2000. *Weather America: a thirty year summary of statistical weather data and rankings*. Grey House Publishing, Inc., Millertown, NY, USA.

- GEHRT, S. D. AND E. K. FRITZELL. 1999. Survivorship of a nonharvested raccoon population in south Texas. *J. Wildl. Manage.*, **63**:889–894.
- GORMAN, T. A., J. D. ERB, B. R. McMILLAN, D. J. MARTIN AND J. A. HOMYACK. 2006a. Site characteristics of river otter natal dens (*Lontra canadensis*) in Minnesota. *Am. Mid. Nat.*, **156**:109–117.
- , ———, ——— AND ———. 2006b. Space use and sociality of river otters (*Lontra canadensis*) in Minnesota. *J. Mamm.*, **87**:740–747.
- HAMILTON, W. J., JR. AND W. R. EADIE. 1964. Reproduction in the otter, *Lutra canadensis*. *J. Mamm.*, **45**:242–252.
- HEISEY, D. M. AND T. K. FULLER. 2004. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.*, **49**:668–674.
- HODGMAN, T. P., D. J. HARRISON, D. D. KATNIK AND K. D. ELOWE. 1994. Survival in an intensively trapped marten population in Maine. *J. Wildl. Manage.*, **58**:593–600.
- KAMLER, J. F. AND P. S. GIPSON. 2004. Survival and cause-specific mortality among furbearers in a protected area. *Am. Mid. Nat.*, **151**:27–34.
- KUEHN, D. W. AND W. E. BERG. 1983. Use of radiographs to age otters. *Wildl. Soc. Bull.*, **11**:68–70.
- LANDWEHR, T. J., compiler. 1985. A summary of Minnesota game regulations, harvests, and population statistics, 1858–1983. Unpublished Report. Section of Wildlife. Minnesota Department of Natural Resources, St. Paul, MN, USA.
- MELQUIST, W. E. AND M. G. HORNOCKER. 1983. Ecology of river otters in west central Idaho. *Wildl. Monog.*, **83**:1–60.
- AND A. E. DRONKERT. 1987. River otter, p. 625–641. *In*: M. Novak, J. A. Baker, M. E. Obbard and B. Malloch (eds.). *Wild Furbearer Management and Conservation in North America*. Ontario Trappers Association, North Bay, ON, Canada.
- , P. J. POLECHLA, JR. AND D. TOWELL. 2003. River otter, p. 708–734. *In*: G. A. Feldhamer, B. C. Thompson and J. A. Chapman (eds.). *Wild Mammals of North America: Biology, Management, and Conservation*, Second edition. Johns Hopkins University Press, Baltimore, MD, USA.
- NAMS, V. O. 1990. LOCATE II user's guide (version 1.82). Pacer, Truro, Nova Scotia, Canada.
- NILSSON, G. 1980. River otter research workshop. Florida State Museum, Gainesville, FL, USA.
- R Development Core Team. 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- RAESLY, E. J. 2001. Progress and status of river otter reintroduction projects in the United States. *Wildl. Soc. Bull.*, **29**:856–862.
- REID, D. G., T. E. CODE, A. C. H. REID AND S. M. HERRERO. 1994. Spacing, movements, and habitat selection of the river otter in boreal Alberta. *Can. J. Zool.*, **72**:1314–1324.
- RIGGS, M. R. AND K. H. POLLOCK. 1992. A risk ratio approach to multivariate analysis of survival in longitudinal studies of wildlife populations, p. 74–89. *In*: D. R. McCullough and R. H. Barrett (eds.). *Wildlife 2001: populations*. Elsevier Applied Science, London, England.
- ROLLEY, R. E. AND A. M. ROTH. 2004. Otter population analyses, 2004, p. 625–641. *In*: *Wildlife Surveys*, Aug. 2004, Volume 14, Issue 5. Wisconsin Department of Natural Resources, Madison, WI, USA.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters, Second edition. Macmillan, New York, NY, USA.
- SHIRLEY, M. G., R. G. LINScombe AND L. R. SEVIN. 1983. A live trapping and handling technique for river otter. *Proc. Annu. Conf. Southeast. Assoc. of Fish and Wildl. Agencies*, **37**:182–189.
- STEPHENSON, A. B. 1977. Age determination and morphological variation of Ontario otters. *Can. J. Zool.*, **55**:1577–1583.
- SWANSON, G., T. SURBER AND T. S. ROBERTS. 1945. The Mammals of Minnesota. Minnesota Department of Conservation Technical Bulletin No. 2, St. Paul, MN, USA.
- TABOR, J. E. AND H. M. WIGHT. 1977. Population status of river otter in western Oregon. *J. Wildl. Manage.*, **41**:692–699.
- TOWELL, D. E. AND J. E. TABOR. 1982. The northern river otter *Lutra canadensis* (Schreber), p. 688–703. *In*: J. A. Chapman and G. A. Feldhamer (eds.). *Wild Mammals of North America: Biology, Management, and Conservation*. Johns Hopkins University Press, Baltimore, MD, USA.

- WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**:120–138.
- AND R. A. GARROTT. 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego, CA, USA.

SUBMITTED 29 JANUARY 2007

ACCEPTED 17 MAY 2007