

## Diel activity patterns of river otters (*Lontra canadensis*) in southeastern Minnesota

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An understanding of activity patterns of wildlife in relation to abiotic and biotic factors enables biologists to better understand the ecology of species, manage resources, standardize survey methods, and serve as an index of the relative density of a species. River otters (*Lontra canadensis*) were radiotracked between June 2002 and October 2003. Using radiotracking data, we conducted exploratory analyses to determine relative influence of abiotic and biotic factors on 2 measures of activity of otters. Abiotic factors included air temperature, barometric pressure, lunar phase, biological season, and time of day; the biotic factor was sex. Activity was measured indirectly via movement rates and directly as the proportion of location attempts recorded as active (PLA). Movement rate was defined as the distance traveled by an otter between consecutive location estimates. Generalized linear mixed models were used to explore the influence of covariates on both measures of otter activity. The model best explaining variation in movement rate included biological season, sex, a season\*sex interaction, and time of day. Males moved at greater rates than females during breeding and winter seasons but moved at similar rates to females during summer. Covariates found to account for most variation in the PLA of otters included time of day, season, and temperature. Otters were active throughout the day but with bimodal peaks in the PLA during late evening and early morning hours. The PLA of otters was highest during breeding season, lowest during winter, and intermediate in summer months. In addition, the PLA of otters decreased slightly with increasing temperature. Overall, the PLA of otters in our study area was influenced by abiotic factors, and movement rates of otters were influenced by abiotic and biotic factors. DOI: 10.1644/09-MAMM-A-083.1.

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Circadian activity patterns of many species of wildlife follow endogenous biological rhythms that are influenced by exogenous factors. An understanding of abiotic and biotic influences on activity patterns of wildlife enables identification of factors limiting population growth and is useful in determining population status of some species (Estes et al. 1982).

Abiotic factors such as photoperiod (Kolowski et al. 2007) and temperature (Alderman et al. 1989) vary widely in their influence on activity of wildlife. For example, activity of the red fox (*Vulpes vulpes*) was related inversely to temperature (Ables 1969), but percent of time that desert bighorn sheep

(*Ovis canadensis mexicana*) are active during the day was related positively to temperature (Alderman et al. 1989). However, weather conditions had no detectable influence on Blanford's foxes (*Vulpes cana*—Geffen and Macdonald 1993) or white-tailed jackrabbits (*Lepus townsendii*—Rogowitz 1997) and little effect on activity of wolves (*Canis lupus*—Theuerkauf et al. 2003). Temperature also can influence selection of habitats for microclimate, as was documented for



pine martens (*Martes martes*) in their selection of resting sites (Zalewski 1997), and thus may relate to activity associated with searching for and remaining near specific sites. Barometric pressure is another abiotic factor reported to affect activity of wildlife. For example, activity of the red fox was inversely related to barometric pressure during winter months (Ables 1969). However, effects of barometric pressure on activity of most mammalian species remain unknown. These abiotic factors may have a direct influence on animal activity, such as for thermoregulation and availability of prey, or an indirect influence, such as increasing risk of predation.

In addition to abiotic factors, biotic characteristics including sex, reproductive status, age-class, risk of predation (Drew and Bissonette 1997; Geffen and Macdonald 1993), and availability of prey (Geffen and Macdonald 1993; Sanderson 1966) can influence patterns of activity (Aschoff 1966; Gelatt et al. 2002; Ralls and Siniff 1990). A difference in activity between sexes appears particularly pronounced in species exhibiting sexual dimorphism (Moors 1980). For example, male honey badgers (*Mellivora capensis*) move at greater rates and distances than females (Begg et al. 2005), and hourly movement rates of male long-tailed weasels (*Mustela frenata*) are much greater than those of females (Gehring and Swihart 2004). Patterns of activity may be influenced proximately by an abiotic factor but ultimately driven by biotic factors such as minimizing risk of predation or improving capture efficacy of prey. For example, activity of snowshoe hares (*Lepus americanus*) decreases during full moon, presumably to avoid increased risk of predation (Griffin et al. 2005). Conversely, yellow-throated martens (*Martes flavivula*) increase nocturnal activity during full moon (Grassman et al. 2005), presumably because prey are easier to see.

In addition to gaining insight into factors influencing activity of wildlife, a good understanding of activity patterns enables biologists to improve design of surveys used for monitoring populations; for example, by enabling biologists to control for variation in detection probability (MacKenzie and Royle 2005; Sanderson 1966). Some have suggested using documented changes in activity patterns as an index to relative density (Estes 1990; Estes et al. 1982, 1986; but see Garshelis et al. 1990). Jenkins (1980) concluded that Eurasian otters (*Lutra lutra*) were primarily nocturnal when population density was low and more diurnal when population density was high. Thus, we suggest that it may be particularly important to understand variability in daily activity patterns to better detect fluctuations in populations of wildlife.

Although few studies have documented the activity patterns of members of the family Mustelidae, the literature demonstrates a variety of activity patterns for these species. Sea otters (*Enhydra lutris*—Estes et al. 1986) and fishers (*Martes pennanti*—Arthur and Krohn 1991) are most active during morning and evening hours, and American martens (*Martes americana*) and yellow-throated martens exhibited nocturnal peaks in activity (Drew and Bissonette 1997; Grassman et al. 2005; Thompson and Colgan 1994). Nearctic river otters (*Lontra canadensis*) in coastal areas were more diurnal than in

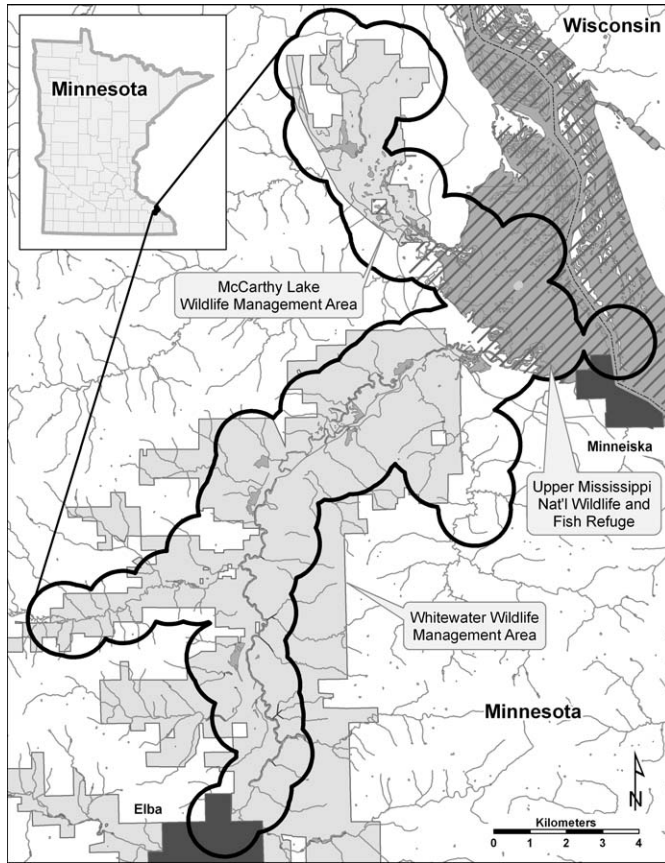
other areas (Foy 1984; Larsen 1983; Woolington 1984). Marine otters (*Lontra felina*) appeared to be active arrhythmically with peaks of activity occurring during times of low human activity (Medina-Vogel et al. 2007).

Activity patterns of the Nearctic river otter (hereafter otter) have been described in several environments throughout North America, including southern coastal (Foy 1984), eastern deciduous forest (McDonald 1989), and in northern climes (Larsen 1983; Melquist and Hornocker 1983; Reid et al. 1994b; Route and Peterson 1988). However, few attempts have been made to examine the influence of abiotic and biotic factors on patterns of activity of otters. Several studies have reported differences in home-range size and movement patterns between sexes of otters and among seasons (Gorman et al. 2006a; Melquist and Hornocker 1983; Reid et al. 1994b; Route and Peterson 1988), but few others have attempted to quantify potential influences on activity at a relatively fine scale (e.g., <1 day).

Our objective was to determine the relative importance of select biotic and abiotic factors in influencing patterns of activity of a legally protected population of otters in southeastern Minnesota. Biotic (e.g., sex) and abiotic (e.g., hour of day, biological season, temperature, lunar phase, and barometric pressure) factors that we investigated were based on activity theory, previous studies of otter life history, and those measurable factors thought to most likely influence patterns of activity (Melquist and Hornocker 1983; Reid et al. 1994a; Route and Peterson 1988). Based on the evidence presented above, we expected males to be more active than female otters, and bimodal peaks in diel activity during morning and evening hours. We also expected increased activity during breeding season relative to other seasons and increasing activity with increased air temperature. Although barometric pressure may influence activity of prey species, we did not expect this factor to influence activity patterns of otters relative to others due to the lack of evidence of influences of barometric pressure on activity of other species of Mustelidae. Finally, we predicted that otters do not alter activity based on lunar phase because otters are capable of foraging using tactile senses in low light or murky water conditions (Carss 1995; Noordhuis 2002).

## MATERIALS AND METHODS

*Study area and conditions.*—The study area was located in the Paleozoic Plateau of southeastern Minnesota, a subunit of the Eastern Broadleaf Forest (Fig. 1). The majority of the study site is within the blufflands subsection including the Mississippi River basin, consisting of a loess-capped plateau furrowed with river valleys. Bedrock in the area is composed of Ordovician dolomite, limestone, and sandstone. Mean annual precipitation is 81 cm (Minnesota Department of Natural Resources, Climatology Working Group 2004) and mean annual temperature 8.2°C (National Climatic Data Center, United States Department of Commerce 2004). Approximately 30% of this area is cultivated, 20% is



**FIG. 1.**—Area of study for activity of 10 river otters in southeastern Minnesota, 27 June 2002–27 October 2003. Study boundaries displayed represent 1-km buffers around all locations estimated using triangulation of data obtained during radiotracking efforts. Wildlife Management Areas are displayed in solid light gray. The Upper Mississippi National Wildlife and Fish Refuge is the hatched area.

rangeland, and 50% is woodland (Minnesota Department of Natural Resources 2004). Red oak (*Quercus rubra*), white oak (*Quercus alba*), shagbark hickory (*Carya ovata*), basswood (*Tilia americana*), and black walnut (*Juglans nigra*) histori-

cally dominated the slopes along riparian areas; tallgrass prairie and bur oak (*Quercus macrocarpa*) savanna dominated ridge tops (Minnesota Department of Natural Resources 2004).

Primary bodies of water in the study area are the main branch of the Whitewater River and associated wetlands, and McCarthy Lake, a wetland formed at the confluence of Snake Creek and the Mississippi River. The study area is almost entirely within the Whitewater and McCarthy Lake Wildlife Management Areas and the Upper Mississippi National Wildlife and Fish Refuge (Fig. 1), and many oxbows and man-made wetlands exist within the study area.

**Otter capture and handling.**—We captured 39 otters for several research objectives (Gorman et al. 2006a, 2006b, 2008; Martin 2007), but 10 otters (5 males and 5 females; Table 1) resided in the area of interest for this study of activity. All capture and handling methods were approved by the Institutional Animal Care and Use Committee at Minnesota State University, Mankato (Project 01-3), and followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). We captured otters to implant radiotransmitters primarily during spring and fall 2002–2003. Otters were captured using Sleepy Creek No. 11 double-jaw foothold traps (Sleepy Creek Manufacturing, Berkley Springs, West Virginia—Blundell et al. 1999; Shirley et al. 1983) modified with an in-line shock-spring and ≥3 swivels; total chain length was <66 cm. Traps were checked each morning, and a Fischer Capture Tube (M. Fischer, Lonsdale, Arkansas, pers. comm.) or capture net–tube combination was used to remove otters from traps and for transporting otters from and to the capture site. Fischer Capture Tubes are 60.6-liter white plastic barrels modified with drain holes and a sliding door, designed to minimize internal hardware that potentially could injure otters. If otters needed to be held overnight, they were transferred to and held individually in a 46 × 48 × 91-cm cage made of plastic-coated 2.5 × 2.5-cm wire mesh (C. E. Shepherd Company, Houston, Texas) with carpet or other cloth covering the bottom panel.

**TABLE 1.**—First and last dates that river otters were tracked in southeastern Minnesota, 27 June 2002–27 October 2003, by individual and season, with number of movement paths (MVMT) and activity of otters for recorded bearings (ACT). Data from summers 2002 and 2003 are pooled. Seasons were defined as summer = 1 June–31 October, winter = 1 November–28 February, and breeding = 1 March–31 May.

Otter ID	Dates tracked		No. tracking sessions/season			No. bearings recorded	% bearings used <sup>a</sup>	
	First	Last	Breeding	Summer	Winter		ACT	MVMT
161 ♂	27 June 2002	30 March 2003	5	14	44	1,144	98.3	75.1
347 ♀	3 September 2002	31 March 2003	7	9	43	1,020	98.5	71.3
505 ♀	27 June 2002	5 June 2003	13	19	44	1,322 <sup>b</sup>	97.8	71.2
680 <sup>c</sup> ♀	4 June 2003	17 June 2003	2	4	0	82	98.8	74.4
757 ♀	27 June 2002	27 October 2003	16	44	43	1,848	99.1	74.0
827 ♂	27 June 2002	22 April 2003	14	13	43	1,224	98.9	74.7
851 ♂	7 July 2003	27 October 2003	0	16	0	227	93.8	73.1
867 ♀	27 June 2002	27 October 2003	16	45	44	1,846	99.3	74.1
942 ♂	27 June 2002	27 October 2003	13	36	44	1,507	99.1	75.8
962 ♂	7 July 2003	27 October 2003	0	17	0	242	95.0	69.0
Total			86	217	305	10,462	98.6	73.7

<sup>a</sup> Percent of bearings used from total in estimating locations (movement) or estimating the proportion of bearings active (activity).

<sup>b</sup> There were 1,320 recorded bearings and 1,322 recorded activity points associated with location attempts. Percent bearings used takes this discrepancy into account.

<sup>c</sup> Excluded from analyses because of low number of samples.

Upon capture, each otter was transported to a licensed veterinarian, where it was administered an intramuscular injection of ketamine at approximately 11 mg/kg and xylazine at approximately 1.65 mg/kg. Depending on the size and weight of the individual, 1 of the following radiotransmitters was implanted in the peritoneal cavity of each otter: ATS 1245 2-stage, 1250 2-stage, or 1250 3-stage (Advanced Telemetry Systems, Isanti, Minnesota), or GTS FH-3 (Global Tracking Systems, Sylvan Lake, Alberta, Canada). Implant transmitters were used because they have been demonstrated to have no negative effect on reproduction in otters (Reid et al. 1986), and no adverse effects were reported on the behavior of sea otters (Garshelis and Siniff 1983). Water was provided to otters ad libitum before and after surgery, and food (trout) was provided to individuals held for more than a few hours.

Sex was determined via examination of external anatomy, and age-class was estimated based on total body length, mass, and hind-foot length (Stephenson 1977). Each otter received an injection of penicillin, clostridium (2 ml each), and enrofloxacin (1 ml) to reduce risk of capture myopathy (Hartup et al. 1999). All otters were released at or near their capture site. Six otters were released within 13 h of capture and after recovery from anesthetics (i.e., when motor control appeared normal); 4 individuals were held for 31–74 h prior to release.

*Radiotracking.*—We established 283 telemetry stations throughout the study area from which we attempted to obtain bearings on otters. Station locations were selected to maximize area in line-of-sight, decrease error associated with bounce, and reduce electromagnetic interference (Garrott et al. 1986). The location coordinates of each telemetry station were recorded with a Garmin Map76S global positioning system (Garmin International, Inc., Olathe, Kansas), using the average location function until estimated error was <7.0 m.

We conducted radiotracking of test beacons and otters using an ATS Challenger Model R4000 radiotelemetry receiver with a handheld 3-element yagi antenna (AF Antronics, Urbana, Illinois). Compass bearings (i.e., azimuths) were determined using the loudest-signal method to reduce bias (Springer 1979) and recorded to the nearest 1° using a Silva Trekker 420 compass (Silva Sweden AB, Sollentuna, Sweden). The magnetic declination for the study site was <0.5°; therefore, no adjustment was made to bearings.

We assessed accuracy and precision of the radiotracking system by locating 2 test beacon transmitters placed at known locations throughout the study area. Test beacon transmitters were placed on a natural substrate on the river valley floor at locations thought to be similar to terrestrial areas used by otters. The Maximum Likelihood Estimator in program LOCATE II (Nams 2000) was used to estimate locations of test beacons and otters (Withey et al. 2001). To assess error of the telemetry system, subsamples of beacon location estimates, with replacement, were taken by using various combinations of  $\geq 2$  bearings. For each location estimate we recorded or computed the following data: estimated location, *SD* of bearing error, sum of squares of bearing error, number

of bearings used to derive the location estimate, and whether the true location was within the area of the 95% confidence ellipse (*CE*). To give values of error from each beacon equal weight, overall means for measures of error were calculated by averaging the mean values for each beacon.

We computed 3 measures of accuracy of the telemetry system: coverage (percent of estimates in which the 95% *CE* covered the true location), bias (difference between the observed bearing and true bearing), and linear error (mean distance between estimated and true locations—Garrott et al. 1986; Saltz and White 1990; Withey et al. 2001). Coverage was recorded for each location estimated with  $\geq 3$  bearings. We assessed precision of the telemetry system using the *SD* of bearing error for each location estimate obtained using 3–6 bearings (Garrott et al. 1986; Springer 1979; Withey et al. 2001). Locations estimated using 2 or >6 bearings were excluded from calculation of bias due to their limited occurrence.

From June 2002 to October 2003 radiotracking was conducted using a 6-h stratified-block sampling scheme with consecutive tracking sessions separated by  $\geq 6$  h. For example, if we tracked from 0401 to 1000 h, we did not begin to collect additional data until at least 1601 h. The relatively continuous sampling scheme we used should have negated the chance of observations corresponding to the period length of temporal cycles in otter activity (Swihart and Slade 1985). We quantified activity of otters using 2 simultaneous measures: a direct method, the hourly proportion of radiotracking location attempts of otters recorded as active based on fluctuation in radiosignal strength (hereafter, PLA for proportion of location attempts active—Garshelis et al. 1982; Jefferies et al. 1986; Ralls and Siniff 1990; Ribic 1982); and an indirect method, the hourly movement rates estimated from sequential radiolocations (hereafter, movement—Palomares and Delibes 1991).

Location data collected within 2 weeks postrelease were excluded from analysis to avoid potential bias caused by any abnormal behavior due to capture and handling. Homing, which could disturb animals, was used only on occasions in which otters were known to be inactive, thought to be in bank dens, and in relative close proximity to a road. These locations were recorded with the global positioning system and used in the movement analysis along with locations estimated via triangulation.

We obtained hourly data for temperature and barometric pressure from the National Oceanic and Atmospheric Administration's National Climatic Data Center (National Climatic Data Center, United States Department of Commerce 2004). Data were obtained for Rochester International Airport for June–August 2002 and Winona Municipal Airport for September–December 2002 and January–October 2003. Solar and lunar phase data were obtained for Elba, Minnesota, from the Astronomical Applications Department of the United States Naval Observatory (<http://aa.usno.navy.mil>). Biological seasons were defined as breeding (1 March–31 May), summer (1 June–31 October), or winter (1 November–28 February).

Breeding season dates were broadly designated to include behaviors such as searching for birthing dens and mates (Gorman et al. 2006b; Hamilton and Eadie 1964; Liers 1951), and summer and winter seasons included behaviors primarily associated with maintaining individual health during relatively warm, ice-free months and colder months, respectively. Data from both summers were pooled to determine variation among seasons; Gorman et al. (2006b) found no year effect on home ranges of otters in the study area.

*Movement analyses.*—Location estimates were triangulated using  $\geq 2$  bearings within a 20-min time period, when possible (White and Garrott 1990). The overall mean *SD* of bearing error from precision testing using the 2 test beacons was used as the *SD* for all location estimates of otters. No restrictions were placed on the angle of bearing intersections due to the existence of only 1 road along 1 side of most of the study site.

We designated a move as a line connecting 2 estimated locations for an otter within 1 tracking block; a path was composed of sequential moves for each tracking session. Distances of each move and path were calculated in the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997). Because we were not able to acquire locations at consistent time intervals, all move distances were standardized by calculating the rate of movement (i.e., m/h) for each path. To assign each movement rate a time value, we calculated the mean of the mean times for the beginning and end location estimates used. For example, a single location estimate that used bearings recorded between 0800 h and 0810 h would be represented by the mean time of 0805 h. Thus, if the move was represented by estimates with mean times of 0805 h and 0905 h, we used the mean of those times (0835 h) as the time value for the movement rate. All times were rounded to the nearest hour for analyses. Climatologic data were treated similarly.

To explore influences of abiotic and biotic factors on movement rates of otters we used linear models accounting for our repeated-measures design (Littell et al. 1998). We used a natural log transformation on the response variable (movement rate) to provide greater assurance that the assumption of normality was met. We also examined several different functions of the time variable to determine the simplest model of time as it relates to otter movement. Specifically, we examined linear, quadratic, cubic, quartic, and cosine function models of time. In these models we used a restriction such that if a higher-order term was included in the model, all lower-order terms also were included. We also included the following dependent variables: temperature, barometric pressure, lunar phase, biological season, and sex of otter. In addition to these dependent variables, we included interaction terms for both season and sex and season and temperature. These interaction terms were the only interaction terms we believed to be biologically relevant. We placed the modeling restriction on the model set such that if an interaction term was included, its component terms also must be included in the model.

We used an iterative hierarchical approach to modeling the mixed-effects model. First, we used the global model containing all the fixed effects, and varied the R-sided covariance structure on the residuals. We assumed that only measurements taken within a day on an individual otter were autocorrelated. Thus, the R-sided covariance structures included in the suite of candidate models were block diagonal, and blocking was based on otter\*date. We examined the following models: CS, ARMA(1,1), AR(1), TOEP, TOEP(1–9), and the null model (i.e., only a constant residual structure; SAS Proc MIXED [SAS Institute Inc. 2008]). A random intercept model was used for the G-sided covariance matrix to account for the random otter effect. We used an information-theoretic approach to model selection to determine the most parsimonious models supported by the evidence in the data by determining the covariance structure with the minimum Akaike information criterion corrected for small sample size ( $AIC_c$ ) value (Burnham and Anderson 2002). We considered  $\Delta AIC_c$  values  $< 2$  competitive. We then set the covariance structure to this “best” covariance model and examined all possible subsets of the fixed effects using the same model selection procedure. Once a top model was selected, we used this model to examine each of the covariance structures once again to determine if the top covariance structure still carried the weight of evidence. Lastly, we calculated fixed and random parameter estimates from the top model for both the covariance structure and fixed effects. All analyses were conducted in SAS Proc MIXED (SAS Institute Inc. 2008). In matrix notation, the model used was:

$$Y = X\beta + Zu + \varepsilon,$$

where *Y* is log movement rate as the response variable, *X* and *Z* are known matrices that relate elements of  $\beta$  and *u* to *Y*,  $\beta$  is a vector of parameters for the fixed effects, *u* is a vector of unknown effects of random variables and is distributed as  $N(0, G)$  with *G* being a covariance model for the random effects, and  $\varepsilon$  is a vector of unknown residual effects and is distributed as  $N(0, R)$  with *R* being a covariance model for the residuals. In this analysis the fixed effects composing the *X* matrix were 2 class variables, SEASON and SEX. The continuous variables included were TIME, TEMP, BP (barometric pressure), and LUNAR phase.

*Proportion of location attempts active analyses.*—To model PLA data generalized linear mixed models were used to account for the random effects of otter and to model the serial correlation of observations. Serial correlation arose from the study design, which took multiple measures of otter activities within relatively short time periods. We used the same matrix as defined for the movement rate analysis, except where *Y* in the PLA analysis included logit link function of activity as a binary variable of active (1) or inactive (0).

We used an iterative hierarchical modeling approach to determine the model structure upon which to base inference. This approach involved using the global model including all the fixed effects of interest and the random otter effect, while varying the R-sided covariance structure in SAS Proc

GLIMMIX (SAS Institute Inc. 2008). All covariance structures were blocked on otter\*date, and it was assumed that PLA was independent between otters and for each otter within a day (but see Gorman et al. 2006a). Because the fixed effects and G-sided effects did not vary, AIC values were used to determine the best model to account for the serial correlation (i.e.,  $\Delta AIC_c$  values  $< 2$  were considered competitive). A random intercept model was used for the G-sided covariance matrix to account for the random otter effect. Once a covariance structure was selected, we performed forward, backward, and stepwise model selection using Type III tests of the fixed effects and  $\alpha = 0.05$  (Ott and Longnecker 2001; SAS Institute Inc. 2008). Information-theoretic model selection techniques such as AIC are not available for generalized linear mixed models; thus we used Type III tests of the fixed effects provided in GLIMMIX in the model selection procedures. These tests are likelihood ratio tests of the fixed effects, and documentation for Proc GLIMMIX provides details (SAS Institute Inc. 2008). We used all 3 types of model selection procedures to compare the top model from each, because differences can arise in the best model selected between techniques.

Once a top model for the fixed effects was selected, we repeated the covariance analysis to determine if the top model previously selected for the R-sided covariance structure was still selected as such (i.e., when using the model of the fixed effects). We then conducted likelihood ratio tests for the G-sided effects to determine if they should be included in the model using the COVTEST statement (SAS Institute Inc. 2008). We also tested whether the off-diagonal terms of the R-sided covariance matrix should be 0. Based on these results, we repeated the entire covariance and fixed effects model selection processes again. All inference was made from this final model.

The fixed effects and continuous variables investigated here were the same as in the movement rate analysis, including the season\*sex and season\*temperature interaction terms. The time variable was transformed using a cosine function to account for the circular nature of the variable.

## RESULTS

*Otter capture and handling.*—Of the 10 otters used in this study, 5 appeared uninjured upon examination and 5 had minor injuries, including shallow cuts or slight edema of the capture foot, that were attributed to capture (D. Martin, pers. obs.). One otter was included in descriptive statistics but excluded from formal analyses due to the limited data collected (female 680; Table 1); we suspect that the transmitter failed shortly after deployment. It is possible that other unmarked otters inhabited the study area, but we suspect that the majority of otters residing in the study area were marked during this study.

*Radiotracking.*—Test beacons were located between 0900 and 1700 h on 11 days from 14 October 2002 to 12 January 2003. All beacon locations were recorded with a global

positioning system (mean accuracy = 5.2 m, range = 4.0–7.3 m). Forty-seven telemetry stations (28% of those established for radiotracking otters) were used for beacon triangulation. Estimates of error were: 58% coverage ( $n = 51$  and 71 location estimates, beacons 1 and 2, respectively),  $\pm 2.9^\circ$  bias ( $n = 61$  and 100 bearings, beacons 1 and 2, respectively), 125-m linear error ( $n = 64$  and 83 bearings, beacons 1 and 2, respectively), and *SD* of bearing error of  $5.65^\circ$  ( $n = 45$  and 55, beacons 1 and 2, respectively).

Ten otters were radiotracked for a total of  $\sim 660$  h between 5 June 2002 and 27 October 2003 ( $n = 106$  days). Transmitters from 5 otters failed before the end of this study, and thus those otters were not tracked through October 2003 (Table 1). Overall, we located otters in 89% of our attempts, resulting in 10,462 total bearings (Table 1). Of those bearings, 10,316 (99%) were used for PLA calculations (Table 1). We collected PLA data from females and males on 349 and 259 tracking sessions, respectively (counting individuals independently for each tracking session; Table 1). A total of 2,571 location estimates and 1,964 movement rates were calculated, with a mean of 90 min between location estimates (Table 2). Location estimates incorporated bearings taken within 1–37 min of each other ( $\bar{X} = 11$  min; Table 2).

*Movement rates.*—The radiotracking scheme typically resulted in 4–6 location estimates per 6-h tracking block for each otter. We pooled data among otters and seasons to view trends in movement rates more easily (Fig. 2); diel movement rates appear bimodal with peaks around 0400 h and from 2200 to 2300 h. Several smaller peaks in movement rate were documented at 0900 h, 1200 h, and between 1500 and 1800 h. The range of movement rates recorded was 0–6,435 m/h (Table 2).

During analysis, the random intercept term was set to 0 because the mean-squared error was higher within than between subjects. Thus, we removed this term from further modeling. Based on results of model selection, the 1st-order autoregressive moving average model (ARMA(1,1):  $\sigma^2[\gamma\rho^{|i-j|-1}1(i \neq j) + 1(i = j)]$ ) was determined to be the best covariance structure using the global model and the best fixed-effects model (Table 3). All other covariance structures were  $> 2 \Delta AIC_c$  from the best model, so little evidence existed for a competing model within the suite of structures we examined. The fixed-effects model with the lowest  $AIC_c$  value contained the sex, season, season\*sex interaction, and the time variable modeled by a cosine function (see Tables 3 and 4 for parameter estimates, and Fig. 3 for plot of interaction). Time modeled by a cosine function was shown to be an important predictor of movement rates. The cosine function was included in the candidate model set because it parsimoniously models the cyclic pattern of activity; this model was chosen over the more complicated models that included multiple higher-order terms.

Based on the results of modeling, we found sex-specific seasonal variation in movement rates. Male otters move at highest rates during the breeding season and lowest rates during the summer, and females move at highest rates during

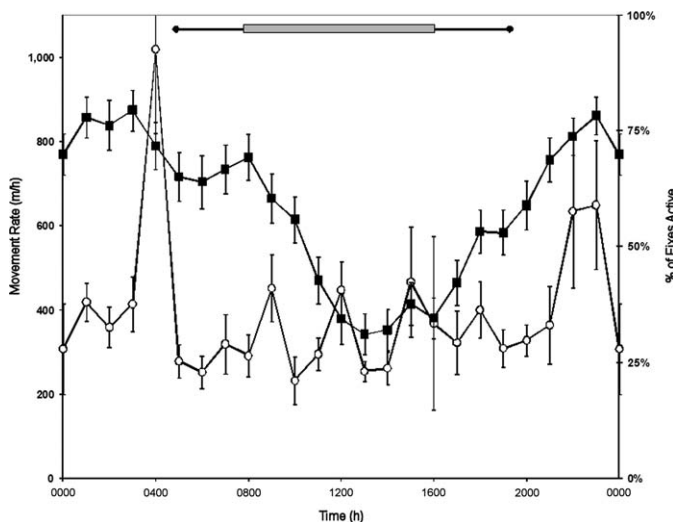
**TABLE 2.**—Values for movement paths derived from location estimates of 10 river otters radiotracked in southeastern Minnesota, 27 June 2002–27 October 2003. All values are means unless otherwise indicated. Standard error (*SE*), correlation (*P*), *SD* of bearings, and sum of squares of errors of bearings were all estimated using the Maximum Likelihood Estimator in program LOCATE II (Nams 2000).

Otter ID	No. moves used	Time within location estimates <sup>a</sup> (min)	<i>SE</i> <sub>X</sub> <sup>b</sup> (m)	<i>SE</i> <sub>Y</sub> <sup>b</sup> (m)	<i>P</i> <sup>c</sup>	<i>SD</i> bearings <sup>d</sup> (±°)	SS bearing error <sup>e</sup>	Total no. locations used	Time between location estimates <sup>f</sup> (min)	Move rate (m/h)	Range move rate (m/h)
161 ♂	218	14.3	64.7	64.9	-0.32	5.61	110.8	281	75	385	3–6,509
347 ♀	193	11.0	56.9	45.4	-0.18	6.36	128.8	252	88	299	0–2,855
505 ♀	256	11.1	90.8	61.7	-0.19	5.71	122.7	332	76	432	0–6,435
680 <sup>g</sup> ♀	15	5.0	30.5	31.4	0.00	3.56	53.2	21	114	107	7–334
757 ♀	344	12.3	55.1	56.3	-0.34	5.73	97.4	447	87	291	3–2,859
827 ♂	235	13.1	84.1	70.0	-0.33	5.36	102.5	305	88	385	5–4,534
851 ♂	36	10.4	121.3	73.3	0.03	6.96	132.9	52	101	391	17–2,633
867 ♀	348	12.1	53.6	53.4	-0.33	5.23	100.2	453	82	294	3–5,857
942 ♂	281	12.4	67.1	59.2	-0.21	6.42	130.7	373	81	364	0–2,891
962 ♂	38	9.7	86.2	61.3	-0.17	4.13	44.1	55	104	261	40–933
Total	1,964	—	—	—	—	—	—	2,571	—	—	—
$\bar{X}$	196	11.1	71.0	57.7	-0.20	5.51	102.3	257	90	321	—

<sup>a</sup> Mean time span between 1st and last bearings used for each location estimate.  
<sup>b</sup> *SE* of estimate (X or Y).  
<sup>c</sup> *P* = correlation between X and Y estimates.  
<sup>d</sup> *SD* of bearing error.  
<sup>e</sup> Sum of squares of errors of bearings.  
<sup>f</sup> Mean time span between consecutive location estimates.  
<sup>g</sup> Excluded from formal analyses because of low number of samples.

the summer and lowest rates during the winter (Fig. 3). Overall, male otters move at greater rates than do females.

**Proportion of location attempts active.**—Diel activity of otters, measured by percent of location attempts active (PLA), peaked at ~2300 h, then declined to lowest daily levels between 1200 and 1600 h (31–38% bearings active; Fig. 2). Although the mean PLA was lowest near 1300 h (31% of



**FIG. 2.**—Estimated hourly activity of river otters based on 10,317 binomial records of activity used to calculate the proportion of location attempts active (i.e., PLA, closed squares; *n* = 3,199), and movement rates (open circles; *n* = 1,941). All measures were pooled across all otters by averaging estimates for each rounded hour. Data were collected for 10 otters radiotracked in southeastern Minnesota, 27 June 2002–27 October 2003. Daylight is represented by the gray bar (shortest day) and extending black bars (longest day). Error bars represent 1 *SE*.

bearings active; Fig. 2), cessation of activity never was observed. Otters were most active at night, with greatest PLA between 2200 and 2300 h and 0100 and 0200 h. During these periods animals were active 74–79% of the time.

Based on AIC values, the best model for the covariance structure consisted of ARMA(1,1) structure for the R-sided covariance parameters (Tables 5 and 6). Likelihood ratio tests indicated no evidence for a random otter effect ( $\chi^2_1 = 0.00$ , *P* = 0.49). We found evidence that the R-sided covariance matrix was not diagonal, that is, evidence existed for temporal autocorrelation of PLA observations of otters ( $\chi^2_2 = 3269.77$ , *P* < 0.0001). Covariance parameter estimates from this best

**TABLE 3.**—Parameter estimates and *SE* from the best model (TIMECOS + SEASON + SEX + SEASON\*SEX) for factors influencing the daily movement rates of 9 river otters from southeastern Minnesota, 2002–2003. Time was a cosine (TIMECOS) function in the best model. SEASON was defined as summer (S: 1 June–31 October), winter (W: 1 November–28 February), and breeding (B: 1 March–31 May). F: female, M: male.

	Estimate	<i>SE</i>
(Intercept)	5.414	0.078
SEASON B	0.107	0.196
SEASON S	-0.057	0.119
SEASON W	0	—
SEX F	-0.395	0.102
SEX M	0	—
TIMECOS	0.188	0.041
SEASON B*SEX F	0.192	0.249
SEASON B*SEX M	0	—
SEASON S*SEX F	0.413	0.158
SEASON S*SEX M	0	—
SEASON W*SEX F	0	—
SEASON W*SEX M	0	—

**TABLE 4.**—Covariance parameter estimates from the best covariance model with a 1st-order autoregressive moving average structure (ARMA(1,1)) for estimating the movement rates of 9 radiocollared otters in Minnesota, 2002–2003. Rho and gamma are parameters of the ARMA(1,1) model.

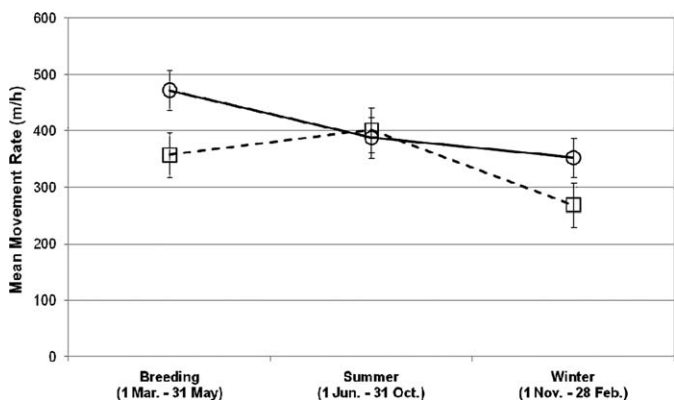
Covariance parameter	Subject	Estimate	SE
Rho	Otter*date	0.722	0.076
Gamma	Otter*date	0.355	0.027
Residual		1.415	0.051

model indicate evidence for serial correlation between observations on the same otter on the same day (Table 6). Overdispersion did not appear problematic based on generalized chi-square statistic divided by the degrees of freedom for the top model, which equaled 0.99.

For all 3 model selection techniques the best model for the fixed effects, given the above covariance parameter estimates, contained the time of day (cosine transformed) and season and temperature effects (Table 5). Based on these parameter estimates of PLA, otter activity was cyclic, with the probability of activity greatest in the evening and night hours and lowest during midday. For a given time of day and temperature, the PLA for otters was lowest in winter, greatest during breeding season, and intermediate in summer (Table 5). Last, as air temperature increased the PLA for otters declined.

**DISCUSSION**

We examined the influence of abiotic and biotic factors on the diel activity patterns of river otters using 2 methods, a direct measure of activity (i.e., the PLA) and an indirect measure of activity (i.e., the hourly rate of linear distance moved between consecutive locations, or movement rate). Because an otter can be active without moving a detectable distance between consecutive locations, different factors may be influencing the PLA and movement rates. For example, otters likely forage during every 24-h period, and therefore,



**FIG. 3.**—Estimated mean hourly movement rates of 5 male (circles) and 4 female (squares) river otters based on 1,941 measures, by biological season. Data were collected in southeastern Minnesota, 27 June 2002–27 October 2003. Error bars represent 1 SE.

**TABLE 5.**—Parameter estimates and SE from the best fixed-effects model (TIMECOS + SEASON + TEMP) for factors influencing the daily activity rates of 9 river otters from southeastern Minnesota, 2002–2003. SEASON was defined as summer (S: 1 June–31 October), winter (W: 1 November–28 February), and breeding (B: 1 March–31 May).

	Estimate	SE
(Intercept)	0.336	0.056
TIMECOS	0.338	0.044
SEASON B	0.357	0.144
SEASON S	0.240	0.132
SEASON W	0	—
TEMP	−0.020	0.005

the direct measure of activity might be related to vulnerability of prey species or to localized foraging behavior. In contrast, linear movements large enough to be measured via radio-tracking might be related more closely to social or reproductive behaviors (e.g., marking at latrines or searching for potential mates or denning sites), or movement between foraging sites, than to localized foraging. However, both measures of activity could be related simultaneously to the same underlying behaviors (e.g., longer movements between foraging or latrine sites influence both the PLA and movement).

Consistent with the idea that different factors may be influencing the PLA and rates of movement of otters, we found that only abiotic factors influenced the PLA, whereas both biotic and abiotic factors influenced movement. The PLA of otters was cyclic, with the peak extending from late evening to early morning hours and the lowest PLA during midday. In contrast, the pattern for rates of movement was bimodal, with relatively constant rates throughout the diel period except for peaks just after sunset (i.e., 2200–2300 h) and just before sunrise (i.e., 0400 h). Movement rates during these times were as much as 3 times greater than during the day and the rest of the night and are consistent with movements related to visitation of latrine sites (Stevens and Serfass 2008). The pattern of activity as measured by the PLA demonstrates that otters are primarily nocturnal, likely foraging throughout the night. Conversely, the bimodal pattern in rates of movement leads us to suggest that otters likely move between resting sites and foraging or latrine sites during peaks. This finding is not consistent with our prediction that both measures of activity would demonstrate bimodal and crepuscular activity.

**TABLE 6.**—Covariance parameter estimates from the best covariance model with a 1st-order autoregressive moving average structure (ARMA(1,1)) for estimating the probability of activity of 9 radiocollared otters in Minnesota, 2002–2003. Rho and gamma are parameters of the ARMA(1,1) model.

Covariance parameter	Subject	Estimate	SE
Rho	Otter*date	0.806	0.011
Gamma	Otter*date	0.532	0.010
Residual		0.991	0.020

The PLA for otters was related inversely to ambient air temperature, but no relationship existed between rate of movement and ambient temperature. The relationship to temperature was consistent with activity patterns of otters in coastal Texas (Foy 1984) and with observations of male mink (*Neovison vison*—Gerrell 1969). However, air temperature had no apparent influence on the PLA of otters in Idaho (Melquist and Hornocker 1983). Water temperature is related inversely to metabolic rate of Eurasian otters (Kruuk et al. 1994). Therefore, it seems likely that otters increase foraging activity to meet the increased energy demands of thermoregulation. Ice cover may affect the amount and quality of available habitat and thus restrict the movement of otters (Anderson and Woolf 1987; Jenkins 1980; Melquist and Hornocker 1983; Reid et al. 1994b; Storrack et al. 2002; Zackheim 1982) and access to prey (Ruiz-Olmo 1998; Sheldon and Toll 1964). Accumulation of ice cover and snow was prevalent on our site, and although not directly measured, was no doubt related to ambient temperature. Because we found no effect of ambient temperature on movement rates, it does not appear that ice cover is restricting movements in our system, except possibly at a scale smaller than we were able to detect.

Other abiotic factors, including barometric pressure and lunar phase, were not related to movement rates or the PLA of otters. Given the paucity of evidence for influences of barometric pressure on activity of mammals, this result was expected. In contrast, considerable evidence exists for influences of nighttime illumination and lunar phase on the behavior of many mammals (Grassman et al. 2005; Griffin et al. 2005). However, otters can use tactile senses to capture fish in murky water when visibility is poor (Carss 1995; Noordhuis 2002); therefore, the lack of an influence of lunar phase on activity was not unexpected.

We predicted that males of this polygynous, sexually dimorphic species (Moors 1980) would have greater levels of activity than females (e.g., rates of movement and the associated PLA), particularly during breeding season (McDonald 1989; Reid et al. 1994b; Route and Peterson 1988). Consistent with our predictions, male otters moved at greater rates than females, and males moved at greater rates during the breeding season than during winter and summer. The greatest rates of movement by male otters were during breeding season when movement rates were approximately 24% greater than for females and were 18–25% greater than for males during other seasons. The pattern of increased movement rates exhibited by males during the breeding season likely was due to searching for mates. Conversely, females demonstrated the greatest rates of movement during both breeding season and summer. This increase in movement rates by females likely was due to increased demands on energy related to searching for dens that were distant from areas of normal activity (Gorman et al. 2006a), gestation, lactation (e.g., daily travel between distant dens and foraging areas), care for dependent young, and the increased energy requirements associated with these activities.

During winter, male otters moved at greater rates than did females. We suspect that the biological differences that exist between male and female otters reflect their relative requirements for use of space and might be a consequence of both social behavior (e.g., a polygynous mating system) and foraging behavior (e.g., increased energetic demands). Although it is difficult to assign relative importance to each of these factors without experimental study, we know that males on our study site have larger home ranges than females (Gorman et al. 2006b). In addition, diet of otters can differ between males and females (Blundell et al. 2002). Therefore, increased movements in winter may reflect a change in foraging location associated with seasonal variation in prey use, which has been well documented (Knudsen and Hale 1968; Larsen 1984; McDonald 1989; Reid et al. 1994a; Sheldon and Toll 1964; Tumilson and Karnes 1987). In contrast to our results, otters in other areas do not differ between sexes in their rates of movement in winter (Melquist and Hornocker 1983; Reid et al. 1994b; Route and Peterson 1988; Spínola et al. 2008). Different results could be due to variation in otter ecology relative to each study area. For example, movement rates of male and female otters can vary based on seasonal differences in intraspecific competition (e.g., between family groups and males) and diet (e.g., prey-switching by males). A concurrent study of otter activity and selection of prey species would allow researchers to uncover any potential influence of prey species on seasonal patterns of diel activity relative to energy demands and activity of prey (Zielinski et al. 1983).

We did not detect an influence of sex on changes in diel activity patterns as measured by the PLA. Although male and female otters did not differ in PLA, otters of both sexes demonstrated highest PLA during breeding season. This finding is contrary to that of other mustelids where differences in levels of activity between sexes and among seasons have been documented. The PLA of pine martens (*M. martes*) in Poland varied by sex and season; the differences in activity of females during spring were suggested to be related to care for young (Zalewski 2001). Male European polecats (*Mustela putorius*) were found to be primarily nocturnal, and although activity of females varied widely, they were primarily diurnal or crepuscular (Marcelli et al. 2003). Our contrary finding could be due to a lower risk of predation for otters versus martens or polecats. Otters are substantially larger than martens or polecats and may be able to escape more easily from potential predators. Furthermore, the differences in seasonal patterns of the PLA reported between sexes for smaller mustelids may be related to potential reproductive benefits of increased risk of predation for males (e.g., maintaining relatively large territories that exclude other males and include home ranges of multiple females). Female otters also may be able to feed young more efficiently than can smaller mustelids, and thus not need to alter activity (e.g., the PLA) seasonally.

The PLA of otters followed a pattern similar to that of movement rates of female otters. Activity was greatest during

breeding season, similar during summer, and lowest during winter. Similarly, differences between the 2 measures of activity movement patterns of female fishers did not change between denning and nondenning periods, but the PLA increased during the denning season (Arthur and Krohn 1991). This seasonal increase in PLA is likely associated with rearing of young, and movements of females may be restricted during this time to maintain close proximity for defense of young against predators. Furthermore, Paragi et al. (1994) suggested that the increased activity of female fishers during diurnal hours after their kits were weaned is related to biotic factors that include individual health and litter size; that is, kits become more efficient at thermoregulation as they grow.

Diel patterns of activity in otters could be influenced by biotic and abiotic factors in addition to those we examined. For example, we did not examine the effects of age on activity. Differences in activity exist among age classes in sea otters (Gelatt et al. 2002; Ralls and Siniff 1990). We expect that similar effects likely influence age classes of river otters because of differences in energy requirements associated with growth and increased exploratory movements associated with dispersal of subadults and mate-searching in adult males. In addition, degree of sociality likely affects activity of otters and has been shown to vary among populations of otters (Beckel 1990; Blundell et al. 2002; Gorman et al. 2006a; Jenkins 1980; Rock et al. 1994; Serfass 1995). Sociality likely varies by biological season and influences activity patterns of otters living in groups through mechanisms such as risk of predation, foraging efficacy, and competition for resources such as dens, food, or mates.

Finally, we suggest using caution when directly comparing results among studies of animal activity. Differences might reflect true ecological variation among study sites, but direct comparisons can be confounded by differences in the temporal resolution of the sampling scheme or the measure of activity used (e.g., PLA versus the rate of movement). Thus, it remains crucial for future studies of activity to track animals at a temporal resolution that is appropriate for the questions being asked (Pace 2001).

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