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Den Use and Activity Patterns in Female Canada Lynx (*Lynx canadensis*) in the Northern Rocky Mountains

Abstract

Knowledge of female behavior while rearing young can have important implications for species conservation. We located dens and analyzed activity (defined as movement between consecutive GPS locations) for nine female lynx with kittens in the north-central Rocky Mountains in 2005 and 2007. We used GPS tracking collars to quantify the percentage of time a female spent active and her daily distance traveled for each of three reproductive stages, classified as predenning, denning, and postdenning. We also described the use and placement of maternal dens for these females. Female lynx in our study used one to six dens per breeding season, and increased both frequency of den relocation and distance between dens as kittens matured. Females typically left the den twice a day, and were gone for an average of five hours at a time. Females were active for 56% of a given 24 hour period during predenning, 48% during denning, and 61% during postdenning. Females traveled greater distances in 24 hours during predenning than denning. We conclude that reproductive female lynx alter the amount of time they spend active and daily distance traveled based on reproductive status.

Introduction

Understanding a species' reproductive behavior is often critical for successful conservation planning. The extent and type of habitat needed by female mammals for successful reproduction can differ from that needed by a species in general (Morris 1984, Chamberlain et al. 2002). Animals may also be especially sensitive to anthropogenic disturbance when they are breeding or rearing young (Weaver et al. 1996). Thus, it is important to understand the timing and duration of reproductive activities so that appropriate conservation actions can be implemented.

Canada lynx (*Lynx canadensis*) are a federally threatened species in the United States (U.S. Fish and Wildlife Service 2000) and yet much remains unknown concerning their maternal and denning behavior. Previous work on denning in the Canada lynx has focused on den site selection or habitat requirements (Koehler 1990, Slough 1999, Moen 2008, Squires et al. 2008). Lynx establish dens in young to mature forest with dense cover and large amounts of coarse woody debris (Mowat et al. 2000, Organ et al. 2008, Squires et al. 2008). In Montana, lynx predominantly den in complex mature forest stands with high horizontal cover (Squires et al. 2008). Lynx give birth in a natal den and often move kittens to one or more subsequent dens, known as maternal dens (Slough 1999, Squires et al. 2008). Detailed information on the timing and duration of Canada lynx natal and maternal den use is currently lacking from the literature.

Maternal behavior and den use may also impact female lynx activity and movement patterns. Female mammals undergo large changes in daily energy requirements depending on their reproductive stage (Gittleman and Thompson 1988). Reproductive females have higher energy demands during the early rearing period due to gestation, lactation, and an increased hunting effort necessary to feed offspring (Oftedal 1984, Gittleman and Thompson 1988). In species with altricial young, the need to protect young from predators, aid in thermoregulation, and carry young can also increase a female's energy needs (Altman and Samuels 1992, Laurenson 1994, Walton and Wynne-Edwards 1997). The extent to which female lynx adjust their movements and activity patterns to account for the increased cost of supporting young kittens is unclear.

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Figure 1. Two- to three-week-old Canada lynx kittens in a maternal den in the northern Rocky Mountains (photo by Zachary Wallace).

Canada lynx produce litters of three to four semi-altricial kittens once a year (Brand and Keith 1979, Aubry et al. 2000) (Figure 1). Kittens of most *Lynx* species are weaned at 12 weeks (McCord and Cardoza 1982), but may eat meat at four weeks (Tumlison 1987). Eurasian lynx (*Lynx lynx*) begin walking at 24 to 30 days (Tumlison 1987), and Iberian lynx (*Lynx pardinus*) are mobile enough to leave the den at around two months (Fernández et al. 2002). Canada lynx kittens remain with their mothers until they are approximately 9–10 months old (Parker et al. 1983, Koehler 1990), after which time most kittens disperse (Mowat et al. 1996, Poole 1997).

Here we investigate den use and seasonal and diel activity patterns of female Canada lynx with kittens in the north-central Rocky Mountains of Montana. We describe natal and maternal den use and date of parturition for lynx in this population. We also describe how activity patterns (including percentage of time spent active and daily distance traveled) differ as kittens mature. We test the prediction that females will increase the proportion of time spent away from the den and distance traveled from the den as kittens mature, since newly born kittens are semi-altricial and require more parental care, and older kittens may have greater energetic requirements, necessitating more foraging effort.

Methods

Study areas were located in the Purcell Mountains of northwest Montana near the Canada and Idaho borders (115° W, 48° N) and near Seeley Lake, Montana (113° W, 47° N), approximately 200 km to the southeast. In May and June 2005 and 2007, we used radio-telemetry to locate nine active dens from previously marked Canada lynx females and GPS to determine the activity patterns of these nine females. We used radio-telemetry to locate 50 other dens from these nine and 16 additional female lynx from 1999 to 2009 to characterize the timing of parturition in western Montana. Females were captured and collared as part of a larger research effort. Trapping, handling, and den location methods followed Squires et al. (2008) and an Institutional Animal Care and Use Committee permit (# 4-2008). Lynx were collared with GPS radio-collars (Sirtrack Ltd, Havelock North, New Zealand) also equipped with VHF-transmitters to enable location on the ground. Collars were programmed to record a location every 30 minutes for 24 hours, every other day. Females in 2005 were re-located in December 2005 or January 2006 and from snow-tracks were determined to have at least one surviving kitten. Females in 2007 were not relocated due to funding constraints; therefore we assumed that kitten survival was similar to 2005.

We used GPS data and ArcMap (ArcGIS 9.2, ESRI, Redlands, CA) to confirm dens located on the ground and to determine subsequent maternal den locations. Lynx were considered to have localized at a natal (parturient) den when their GPS positions were first clustered within a 100 m radius of one location for longer than 24 hours (Koehler 1990, Moen et al. 2008). We quantified the number of subsequent maternal dens a female used by counting additional distinct locations where female telemetry relocation points were clustered for longer than 24 hrs. We used ArcMap to determine the distance between consecutive dens and the number of days spent in each den. We also determined the age of kittens (in days) when each den relocation occurred. We then used mixed effects regression to test whether the length of time a den was used and the distance between consecutive dens was correlated with kitten age.

Analysis was conducted with StataIC version 10.1 (StataCorp 2007, College Station, TX) with distance or days per den as the dependent variable, kitten age as a fixed effect, and individual female as a random effect. We estimated the date that localized denning ended for each female as the last date that females repeatedly visited any one location for > 48 hrs. During the time that females were localized at a den, we also quantified mean number of times females left dens per 24 hr period and duration of consecutive time spent away from dens in 24 hrs. To qualify as away from the den, females had to be > 100 m from the den for at least two consecutive GPS locations.

To examine female activity patterns at different stages of reproduction, we divided GPS movement data into three seasons: *predenning* (February - April, females breeding/pregnant), *denning* (May-July, parturition/lactation, non-mobile kittens), and *postdenning* (August - October, provisioning, kittens able to travel). We categorized lynx behavior at each GPS location into 'active' or 'resting' states using step length and turn angle data from movement paths (Johnson et al. 2002, Morales et al. 2004). 'Active' locations occurred when lynx were moving, whereas 'resting' locations occurred when lynx were stationary. To distinguish true movement from that induced by GPS error, we compared the step length and turn angles leading to each GPS location to the distribution of step lengths and turn angles from test collars known to be in a stationary position. Segments that had a length or turn-angle within the 70th percentile of the stationary test collar's segment distribution were classified initially as 'resting'; the remaining segments were classified as 'active'. Among the remaining 'active' segments, we removed GPS points which spiked abruptly away from clusters of consecutive 'resting' points. Finally, to account for the autocorrelation in animal behavior monitored with systematic telemetry (Forester et al. 2007, Gurarie et al. 2009) we also reclassified 'active' points as 'resting' when an individual point was between 2 'resting' points, each within 123 m (the 95th percentile of consecutive distances between known stationary locations).

We analyzed differences in the percentage of time females spent active for each season (predenning, denning, postdenning) and time of day (dawn, day, dusk, night). Percentage of time spent active was determined by the number of active 30 minute track segments divided by the total number of segments in a 24 hr GPS track. To control for changing hours of daylight during each season we determined the times of sunrise and sunset on the 15th day of each month and classified each hour in a month into 4 time of day categories: *dawn* (1 hr before and after sunrise), *day*, *dusk* (1 hr before and after sunset), and *night*. We examined the total minimum distance females traveled while active (sum of all active 30 min segments) during a 24 hr period as well as the net displacement distance (straight line distance from start to end of a GPS track) from 0600 hr to 0600 hr of the next day for each of the three reproductive seasons.

We used SAS, version 9.2, (SAS Institute, Cary, NC) to estimate a generalized linear mixed model (GLMM) of percentage of time spent active, with individual females and GPS track date as random factors to control for a potential lack of independence within lynx tracks. We considered season and time of day fixed factors and used the containment method to determine denominator degrees of freedom (West et al. 2007). We used a logistic GLMM to analyze percentage of time spent active since the outcome variable was binary (active or resting; Hosmer and Lemeshow 2000). We conducted pair-wise comparisons in the GLMM using the difference in least square means (DLSM) between all levels of each factor (season, time of day, and season by time of day interaction), and adjusted for multiple comparisons using the Tukey-Kramer adjustment. We compared total distance traveled and net displacement distance for each season using repeated measures ANOVA, with distance as the dependent variable, season as the independent variable, and individual lynx as a random factor. Post-hoc comparisons to estimate differences between seasons were performed using a Tukey-Kramer pairwise comparison, with differences considered significant if $P < 0.05$. Summary statistics were first calculated within a given female's GPS track data and then averaged across all females to control for sampling variation among females. All averages are means ± standard deviations.

Results

In 2005, movement data were collected from February to October on four females, each for varying amounts of time. GPS data were measured in lynx-days (one day of GPS tracking for one lynx); 108 lynx-days were recorded for 'predenning' (February–April), 152 for 'denning' (May–July), and 23 for 'postdenning' (August–October). In 2007, data were collected on five different females from February to July. The predenning period had 170 lynx-days recorded and denning had 223 lynx-days. Each female was tracked for an average of 75.5 ± 7.7 days (range: 62–84 days).

Lynx gave birth from 26 April to 23 May (median date: 9 May, n = 59), except for one adult female who gave birth on 11 July, based on GPS data and field-estimated kitten age. Female den use ended from 22 June to 31 July (excluding the July birth). Thus the average length of localized den use was 59 ± 5 days (range = 50–66 days, n = 8). While females were localized at a den, they left the den (> 100 m) an average of 2 ± 0.2 times per 24 hour period (range = 1–4, n = 9). An average bout away from the den lasted 5 ± 1 hrs (range = 1–21 hrs, n = 9).

Females used an average of 3 ± 2 maternal dens in a given year (range = 1–5, n = 9 females). The time spent in subsequent dens decreased with time since parturition (mixed-effects regression: β = -0.32, std. err. = 0.07, $z_{9, 37}$ = -4.69, P < 0.001). Lynx stayed in natal dens for an average 21 ± 17 days (range = 8–52 days, n = 9), 14 ± 10.4 days in the first maternal den (range = 2–32 days, n = 8), 5 ± 2.8 days in the second maternal den (range = 2–10 days, n = 7), 11 ± 8.9 days in the third maternal den (range = 2–22 days, n = 6), 4 ± 0.8 days in the fourth den (range = 2–4 days, n = 5), and 4 ± 2 days in the fifth den (range = 2–6, n = 2) (Figure 2). The average distance between consecutive den locations for all females was 786 ± 156.3 m (range = 133–1553 m, n = 9). The distance between consecutive dens increased with kitten age (mixed-effects regression: β = 17.17, std. err. = 6.55, $z_{9, 29}$ = 2.62, P = 0.01). The distance from natal den to first maternal den averaged 709 ± 532.2 m (range = 133–1479 m, n = 9), second to third den was 568 ± 396.6 m (range = 93–1288 m, n = 7), third to fourth was 543 ± 357.6 m (range = 210–1058 m, n = 6), fourth to fifth was 1539 ± 1121.9 m (range = 216–3057 m, n = 5), and fifth to sixth was 797 ± 53.0 m (range = 759–834, n = 2).

Time spent active by females with kittens was influenced by both season and time of day (season: $F_{2, 15}$ = 5.86, P = 0.013; time of day: $F_{3, 68}$ = 6.85, P < 0.001), as well as their interaction ($F_{6, 68}$ = 17.31, P < 0.001) (Figure 3). Time spent active was greater during predenning than denning (DLSM: t = -3.26, P = 0.013; Figure 3). Females spent an average of 56 ± 3% of a given 24 hr period active during predenning, 48 ± 8% active while denning, and 61 ± 5% active during postdenning. The sample size of GPS tracks collected during postdenning was markedly smaller than in either of the other two seasons, so the lack of a difference between postdenning and denning may have been due to lack of statistical power. Across seasons, females spent slightly more time active during dawn than day or night (DLSM: day: t = 3.42, P = 0.006, night: t = 2.71, P = 0.041), and during dusk than day or night (DLSM: day: t = 3.41, P = 0.006, night: t = 2.69, P = 0.043). Females spent 56 ± 10% of their time active at dawn, 54 ± 9% at dusk, 50 ± 6% at night, and 50 ± 7% during the day.

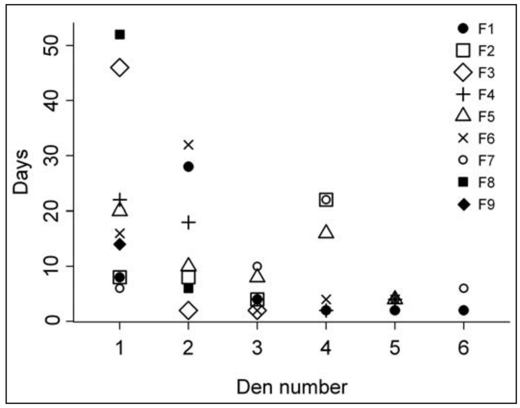

Figure 2. The number of days each lynx remained in a given den, from natal den (Den number 1) to final maternal den (Den number 6). All dens for all nine lynx (identified here as F1–F9) studied in 2005 and 2007 in the northern Rocky Mountains are shown.

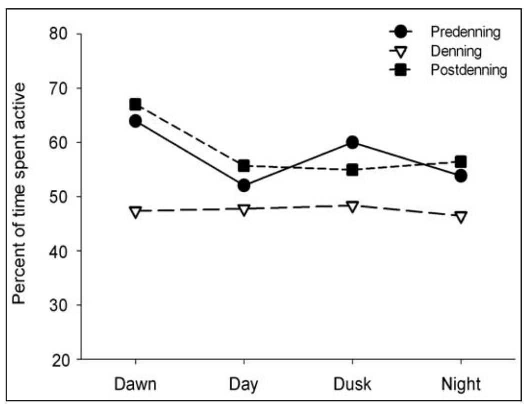

Figure 3. Average percent of time spent active interaction plot for Canada lynx (plotted by time of day) as related to season (predenning, denning, or postdenning), in the northern Rocky Mountains, 2005 and 2007.

Time spent active was more variable throughout a 24 hr day during postdenning and predenning than during denning (Figure 3).

Female lynx traveled a greater minimum distance per 24 hr period during predenning (7.0 ± 3.2 km, *n* = 278) than during denning (6.3 ± 3.8 km, *n* = 375; $F_{2,8}$ = 4.04, *P* = 0.02). There was no difference in the distance that females traveled between predenning and postdenning (6.0 ± 2.6 km, *n* = 24) or denning and postdenning. There was also an effect of season on net displacement ($F_{2,8}$ = 41.14, *P* = 0.001). After kittens were born, females had shorter net displacement distances (denning: 2.1 ± 1.2 km, *n* = 375; postdenning: 1.9 ± 0.98 km, *n* = 24) than before kittens were born (predenning: 2.9 ± 1.3 km, *n* = 278). There was no difference in net displacement distance between denning and postdenning.

Discussion

Canada lynx in the northern Rocky Mountains relocated their kittens to as many as five maternal dens per year. For most *Lynx* species, maternal dens are little more than temporary sheltered locations, which offer protection to the kittens from extreme temperatures, precipitation, or predators (Fernández and Palomares 2000, Boutros et al. 2007, Moen et al. 2008). Relocating kittens to a series of maternal dens from the natal den occurs in all *Lynx* species (Iberian lynx, Fernández et al. 2002; Canada lynx, Moen et al. 2008; bobcat, *Lynx rufus*, Kitchings and Story 1984; and Eurasian lynx, Schmidt 1998). Similar numbers of maternal dens are used by Iberian and Eurasian lynx (5–6 and 1–4 dens per year, respectively; Schmidt 1998, Fernández et al. 2002). Females appeared to stop caching kittens at dens for extended periods of time when kittens were approximately two months old. At two months of age, kittens are still nursing (McCord and Cardoza 1982), but are also eating solid food and are mobile enough to travel with their mothers (Tumlison 1987, Fernández et al. 2002).

Female mammals may relocate dens to reduce the accumulation of excrement or parasites at dens (Butler and Roper 1996, Larivière and Messier 1998), as well as prey remains that may attract predators (Prestrud 1992). We used trained scat dogs at several dens and did not locate any scat from adults or kittens around the immediate den area (J. Squires, personal observation), while Saunders (1963) found that captive lynx kittens bury their feces. Adult lynx also do not generally leave prey uneaten at the den, instead consuming between 78% and 95% of hare carcasses (O'Donoghue et al. 1998). Females may also relocate dens because of den disturbance (Fernández et al. 2002). We approached eight females' dens on foot in this study; of these, four females relocated dens within four days, according to GPS data. The other four females, however, did not relocate dens for at least 20 days after the disturbance. Lynx in our study were also in remote areas unlikely to be accidentally approached by humans, so subsequent den relocations were not likely due to human disturbance. Thus, while it appears that some lynx may relocate dens in response to human interaction, this is not the primary factor. Den relocation may also occur to gain access to areas with increased prey availability (Laurenson 1993), and as kittens mature, their increased ability to keep up with their mother may facilitate den relocation for this purpose (Kitchings and Story 1984, Fernández et al. 2002). Our data support this hypothesis, as duration of time spent at maternal dens decreased as kittens grew and required more food, while the distance between dens increased as kittens became more able to travel. A similar pattern of juvenile relocation occurs in wolves (*Canis lupus*), with pups kept in a natal den until they become more mobile, at which point they are moved to one or a series of rendezvous sites while adults hunt (Ballard and Dau 1983, Fuller 1989).

Female lynx traveled shorter daily distances and had smaller net displacement distances when kittens were newborn to two months old than before kittens were born. While kittens have limited mobility, females appear to act as central-place foragers (Orians and Pearson 1979) that return to the den to accommodate the restricted movements of young kittens. When females are not limited by the mobility of their offspring, however, they tend to cover greater daily distances. A reduction in movement for females with young kittens has been found in other populations of lynx. For example, female lynx in Minnesota limit their daily foraging movements during the 50 days after parturition (Moen et al. 2008), with home ranges during summer and fall 1.5 times bigger than during denning, and winter home ranges 3.6 times bigger than during the denning season (Burdett et al. 2007). Although females in our study restricted their movements during early denning, they still left their kittens approximately twice per day for an average of five hours per day.

The percentage of time females spent active before kittens were born was greater than while kittens were restricted to a den site. While denning, females may decrease their activity to be present at dens for thermoregulation and protection from predators. When kittens are older, females may increase their time spent active, and likely their time spent foraging, to meet the increased caloric demands of kittens as they mature. The increased mobility of offspring by two or three months of age (Tumlison 1987) may also influence female activity.

During predenning and postdenning, when kittens were either absent or less dependent, females were more active during dusk or dawn and less active during the day, similar to Kolbe and Squires (2007) finding on adult males and females without kittens. The primary prey species of lynx, the snowshoe hare (*Lepus americanus;* Aubry et al. 2000), is crepuscular or nocturnal (Foresman and Pearson 1999); thus we would expect lynx to forage more at night, or during dusk and dawn. While denning, however, females exhibited approximately equal levels of activity from dawn to dusk, with a slight drop in activity at night. The roughly continuous diel activity of females while denning may be due to an adjustment in hunting patterns to accommodate the needs of kittens for thermoregulation and protection from predators. There is evidence from other studies that lynx adjust their prey seasonally, with a decrease in dependence on hares in the summer, although the reasons for this adjustment are not well understood (Mowat et al. 2000). We observed denning females hunting Columbian ground squirrels (*Spermophilus columbianus*), which are diurnal (Elliott and Flinders 1991), on several occasions (J. Squires, personal observation). Ground squirrels may provide an important alternate prey for females in the northern Rockies when denning; on several occasions we located dens in close proximity to ground squirrel colonies (J. Squires, personal observation).

Canada lynx in the northern Rocky Mountains give birth in late April to mid-May, with an average parturition date of 9 May, and thus are potentially restricted to dens from late April to late July. While we did not formally evaluate disturbance to lynx in this study, our data and that of others suggests Canada lynx, as well as other lynx species, may respond to anthropogenic disturbance while denning by relocating kittens to a new den (Mowat et al. 1996, Fernández et al. 2002). The impact of den relocation on kitten survival in Canada lynx is unknown, although the continued presence of kittens at first snow for all females whose dens were approached in 2005 suggests that survival may not be greatly affected. Nevertheless, if managers are concerned with limiting potential disturbance to denning lynx in the northern Rocky Mountains, the most effective period will be from late April to late July.

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