



Research Article

Habitat Selection of a Re-Colonized Cougar Population in Response to Seasonal Fluctuations of Human Activity

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ABSTRACT Cougar (*Puma concolor*) sightings have increased markedly throughout much of Midwestern North America and breeding populations have re-established in areas where there has not been a viable population of cougars for much of the past century. Using satellite telemetry data, we estimated resource selection functions (RSF) to examine shifts in seasonal habitat selection of a recently re-established population of cougars relative to human activity in Cypress Hills Interprovincial Park (CHIP) in southwest Saskatchewan and southeast Alberta, Canada. We modeled human activity predictors, used in cougar RSFs, from data collected at a network of motion-triggered trail cameras on the road and trail system within CHIP. Using the same network of remote cameras, we quantified cougar use of trails to examine the potential for human–cougar encounters. Cougar habitat selection models that included human activity outperformed models including only environmental variables. Cougars avoided areas near roads and trails during seasonal peaks in human activity but selected those areas during seasons of low human activity. Within each season, we found cougars avoided areas of increased motorized and non-motorized human activity, particularly in spring (motorized and non-motorized) and summer (non-motorized). Although resource selection models did not include covariates for prey, selection results were consistent with the expected distribution of prey on the landscape. Cougar use of trails was prevalent throughout CHIP and use was concentrated during dusk and nighttime periods. Thus, the potential for human–cougar interactions are present throughout the year, although they are likely highest during periods of low human-use and in the evenings. Further, individual variation in habitat selection among cougars makes human–cougar interactions difficult to predict. Our results highlight the adaptable nature of cougars to varying levels of human disturbance, which will facilitate their continued eastward range expansion. © 2014 The Wildlife Society.

KEY WORDS Alberta, cougar, Cypress Hills, habitat, human interaction, *Puma concolor*, remote camera, resource selection function, Saskatchewan, space use.

Cougar (*Puma concolor*) sightings have been on the rise across much of Midwestern North America as cougars re-colonize parts of their former range (Cougar Network 2007, Rosatte 2011, LaRue et al. 2012). Cougar range expansion and growing urbanization is increasing human–cougar interactions (Torres et al. 1996, Sweanor and Logan 2010, LaRue et al. 2012). Understanding the spatial responses of cougars around people and human-developed habitats is

important for mitigating human–cougar interactions, both in terms of evaluating risks to public safety and livelihoods and in terms of managing the impacts of human activity on cougars (Arundel et al. 2007, Kertson et al. 2011). An improved understanding of human–cougar coexistence is particularly pertinent on the eastern front of cougar range expansion where managers and the public have not had to consider the implications of coexisting with cougars for many decades.

As obligate carnivores, cougars require habitats that provide access to prey, which in North America are often deer (*Odocoileus virginianus*, *O. hemionus*) and elk (*Cervus elaphus*; Logan and Irwin 1985, Arundel et al. 2007, Knopff et al. 2009, Bacon et al. 2011). Although cougars are habitat generalists, they tend to prefer rugged terrain with some form of lateral cover, such as forest, shrub, or rocky outcroppings (Logan and Irwin 1985, Arundel et al. 2007), which likely facilitates predation. Strong selection for ecotone edges also

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has been widely documented (Holmes and Laundré 2006, Laundré and Loxterman 2007), which is logical because deer are often associated with edge habitats (Alverson et al. 1988).

To a degree, human-dominated landscapes represent modified, but not necessarily unsuitable, habitats (Burdett et al. 2010, Kertson et al. 2011). In some cases, cougars have been documented using human infrastructure as travel corridors, including gravel roads and trails (Dickson et al. 2005, Kertson et al. 2011). However, cougars are not pliant to all intensities or scales of disturbance. For example, high-density residential development and highways can be effective barriers to movement (Maehr et al. 2002, Dickson et al. 2005, Arundel et al. 2007, Kertson et al. 2011). Additionally, human activity can displace cougars creating prey refugia that can result in trophic cascades (Ripple and Beschta 2006, 2008). Indeed, the effects of human development on cougars are probably more related to human activity than the physical infrastructure (Arundel et al. 2007). Relying on measures of infrastructure as a proxy for human use may therefore oversimplify spatial and temporal complexities of human activity, limiting the effectiveness of management designed to mitigate human-wildlife interactions (Northrup et al. 2012). Despite this, few studies have quantified spatio-temporal variation in human activity to examine the effects on cougar spatial ecology (Sweaner et al. 2008).

Cypress Hills Interprovincial Park (CHIP) was established in 1989 and straddles the Alberta and Saskatchewan border. The Park was re-colonized by cougars around the turn of the 21st century and hosts the eastern-most confirmed breeding population of cougars in Canada. Following the cougars' return to the Cypress Hills Uplands, sightings in CHIP increased substantially in the early 2000s and conflict with human users has occurred (Alberta Justice and Solicitor General, Conservation Officer Service, unpublished data). For example, lethal removal of at least 3 cougars in CHIP has been required because cougars acted aggressively towards people or pets. Additionally, numerous instances of cougars bedding and caching prey under cottages and decks in core areas of the park have been observed, particularly in winter (C. D. Morrison, University of Alberta, unpublished data).

Our research examined how spatial patterns in the seasonal activity of humans affected cougar spatial ecology in Cypress Hills Interprovincial Park. Specifically, our objectives were to 1) quantify seasonal variation in the amount of motorized and non-motorized human use and model its within-season spatial distribution; 2) model the seasonal effects of motorized and non-motorized human activity on cougar habitat selection; and 3) assess human-cougar shared-use of roads and trails because this is where direct encounters are most likely to occur. We used an information-theoretic approach to assess alternative models of seasonal cougar habitat selection and we predicted that models that included inputs of human activity would have more support than a null model that included only environmental covariates. We expected that the most supported models would indicate a shift in cougar space use seasonally, corresponding with seasonal patterns of human activity. Finally, we expected

cougar use of roads and trails to be prevalent in CHIP and to reflect natural patterns of cougar activity.

STUDY AREA

Cypress Hills Interprovincial Park (400 km²; Fig. 1) is located in southeastern Alberta and southwestern Saskatchewan, Canada. The park encompasses a large portion of the Cypress Hills Uplands, an insular formation of foothills that rise several hundred meters above the surrounding grassland landscape. The Hills are further distinguished from their surroundings by tree cover consisting primarily of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*). The matrix surrounding the Hills is an expanse of mixed grasslands, ranchlands, and agriculture development. The Cypress Hills' relatively high elevation (1,234 m, Elkwater, AB) results in cooler summers and warmer winters than the surrounding lowlands with an average temperature of 19.1°C in July and -3.3°C in January. Also, annual precipitation is 533.5 mm, which is greater than the surrounding area.

Cypress Hills Interprovincial Park is managed by 2 provincial government agencies: Saskatchewan Tourism Parks Culture and Sport, and Alberta Tourism Parks and Recreation. The Saskatchewan portion is comprised of 2 separate areas known as Center Block and West Block. The Alberta portion is a single protected area known as CHIP Alberta (Fig. 1). An estimated 650,000 people visit CHIP annually, although this visitation is highly seasonal with the greatest visitation occurring in summer (Ministry of Tourism, Parks, Culture and Sport - Parks Service, unpublished data; B. Seifert and M. Nagel-Hisey, Parks Service, personal communication). Human activity is concentrated in 2 core areas with 1 on the Alberta side (Elkwater) and 1 on the Saskatchewan side in Center Block. Over 1,000 campsites, 500 cottages, and multiple business leases operate in CHIP with most occurring in these 2 core

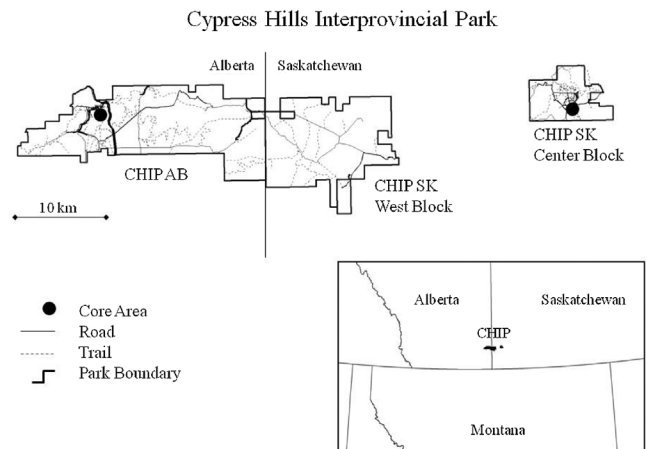


Figure 1. Study area: Cypress Hills Interprovincial Park (400 km²) located in southeast Alberta and southwest Saskatchewan. Core areas, consisting of cottages, campgrounds, and commercial development, are located in both provincial sides of the park. An extensive network of roads and trails exist throughout the park.

areas. An extensive network of roads and trails (hereafter collectively referred to as trails) is maintained for visitors. Based on a random sample of 4,000 locations in CHIP, average distance to the nearest trail is 509 m (SD = 550 m, min. = 0 m, max. = 3,900 m). Trails are categorized into 5 types: winter roads (usually paved and actively plowed during winter), summer roads (usually paved but not plowed), secondary roads (usually gravel), truck trails, and hiking trails, some of which are track-set for cross-country skiing in winter. Motorized traffic is restricted to roads and truck trails while hiking, biking, cross-country skiing, and equestrian use comprise the bulk of non-motorized activity on trails. In winter, gates and/or snow conditions limit motorized access to most trail types (except winter roads), although some trails become popular for non-motorized activities.

Outside the Cypress Hills, the closest known breeding populations of cougars are 200 km south in the Bear Paw Mountains in Montana and 250 km west in the Rocky Mountains of southwestern Alberta. Primary diet of cougars in the Cypress Hills is white-tailed deer, mule deer, porcupines (*Erethizon dorsata*), and elk (Bacon et al. 2011, C. D. Morrison, unpublished data). No deer hunting is permitted in CHIP and only a limited-entry elk management hunt exists to help mitigate conflicts with adjacent landowners (Hegel et al. 2009). Prior to the re-colonization by cougars, no large carnivore had been present in this system during the past century. Wild ungulates are therefore present in high densities and are widely distributed throughout CHIP.

METHODS

Human Activity

We maintained a network of 90 motion-triggered trail camera stations between 1 July 2011 and 30 June 2012 to quantify human use on trails in CHIP. To ensure an adequate spatial distribution of sample locations, we used a geographic information system (GIS) to overlay the Park with a 500-m × 500-m grid and randomly selected 90 cells (13%; total $n = 708$) for sampling. Within each selected cell, we determined camera locations by first generating a random point in the GIS and then relocating the point to the nearest trail. Type of trails available to be sampled included secondary roads, truck trails, and hiking trails. We did not include sites on winter and summer roads to reduce the potential of camera theft and vandalism because these roads received relatively high amounts of traffic, based on expert opinion from Park staff. In the field, we established camera stations adjacent to the trail on the nearest suitable tree to the GIS-determined location. We identified trees with a metal tag and recorded locations with a handheld global positioning system (GPS) so we could relocate them for subsequent sampling periods throughout the year.

We divided the calendar year into 6 consecutive 2-month sampling periods beginning with January–February (i.e., sampling period 1) and ending with November–December (i.e., sampling period 6). We cycled 30 cameras (Reconyx

HC600, Holmen, WI) on a 20-day rotation to sample all 90 camera stations during each 2-month period. We made the assumption that data recorded during the 20-day sampling session would be representative of the 2-month period. We chose the order of sampling for camera stations at random within each period. In the field, we positioned cameras at a height approximately 1 m above the surface of the trail and aimed cameras at roughly 60° across the trail. We cleared branches and brush from the camera's field of view to limit the number of environmental triggers. We programmed cameras at the highest sensitivity and to take 3 photos at 3-second intervals every time the camera was triggered by movement. We then programmed a 15-second quiet period between triggers. At the end of the sampling period, we replaced memory cards and batteries and relocated the camera to the next station to be sampled.

We processed all camera data using Timelapse Image Analyzer (Greenberg and Godin 2012). We categorized detections of human activity as motorized (vehicles, all terrain vehicles, and snowmobiles) or non-motorized (foot, bike, ski, and equestrian) and documented the date, time, and number of individuals observed (e.g., 2 hikers = 2; 1 car regardless of passengers = 1). We recorded consecutive detections, where the individual(s) was clearly attracted to the camera, only once. On occasion, sampling sessions did not last the entire 20-day duration because of environmental disturbance, human tampering, or equipment malfunction. In these cases, the sampling period ended on the date of the last recorded photo or when the field of view was altered significantly. We included in the analysis only sampling sessions that were operational for a minimum of 13.5 days. This ensured the greater portion of each day of the week was included in the sampling session at least twice to smooth out any isolated variability in human activity and to ensure data would be more representative of the 2-month season.

To assess seasonal variation in overall human relative activity (individuals/day) we summed the number of motorized and non-motorized individuals observed at each camera station for each 2-month sampling period and divided it by the number of trap days that the camera was operational (George and Crooks 2006). Because human-use data were right skewed, we performed a natural log transformation prior to statistical analysis. We used a Friedman's rank sum test to test for mean differences in overall activity among 2-month periods. Following a significant result, we used a pair-wise Wilcoxon tests with a Bonferonni corrected $P = 0.003$ to determine which specific periods differed. We pooled periods that did not differ significantly and had similar weather conditions into a single season. The resulting seasonal definitions formed the basis of subsequent models of human activity and cougar habitat selection.

To estimate within-season spatial variation of human activity, we calculated indices for motorized (MRA) and non-motorized (NMRA) relative activity separately, using the same method described above for overall activity. We developed generalized linear models (Gaussian distribution) for MRA and NMRA within each season using candidate

Table 1. Names and descriptions of candidate variables available to model seasonal motorized and non-motorized relative human activity in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada.

Covariates	Description
dist_camp ^a	Distance to nearest campground (m)
dist_core ^a	Distance to nearest core area measured from visitor centers (m)
dist_park ^a	Distance to nearest parking (m)
dist_entr ^a	Distance to nearest entry gate (m)
dist_mentr ^a	Distance to nearest main entry gate (m)
dist_sentr ^a	Distance to nearest secondary entry gate (m)
dist_trailh ^a	Distance to nearest trailhead (m)
dist_fclty ^a	Distance to nearest facility which included campground, core area, parking, and entry gates (m)
prox_core	Euclidean distance to core area
smmr_main ^a	Distance to nearest junction with main road (m)
wntr_main ^a	Distance to nearest junction with winter main road (m)
ski	Binary variable indicating if trail was maintained for cross-country skiing (1 = track set; 0 = not track set)
sled	Binary variable indicating if snowmobiling was permitted on trail (1 = permitted; 0 = not permitted)
trail_type	Categorical variable for trail types: Secondary roads, truck trails, hiking trails. Secondary roads was the reference category.

^a Calculated as distance along the trail using Network Analyst in ArcGIS10.

explanatory variables expected to influence human activity, as identified by park managers (Table 1). If explanatory variables were highly correlated ($|r| > 0.7$), we restricted them from entering the same model. In each season, we determined the most-supported model for MRA and

NMRA based on the model structure with the lowest Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

Using the most-supported models for each season (Table 2), we predicted MRA and NMRA for each 30-m segment of the trail network in CHIP using a GIS. For winter roads and summer roads that were not included in the camera survey (approx. 18% of cumulative trail network length), we assigned the maximum value of MRA, based on the opinion of park staff that these trails were the most heavily used. For NMRA, we combined winter and summer roads with secondary roads based on the assumption that non-motorized human activity would be similar on trail types that were intended for motorized traffic. We then used the resulting spatial layers as candidate variables for modeling seasonal cougar habitat use.

Cougar Habitat Selection

Between 2008 and 2011, we captured cougars in the CHIP area. We pursued and treed cougars with the assistance of a professional houndsmen and trained tracking hounds, chemically immobilized cougars, and fitted them with a GPS radiocollar (Lotek Model 4400, Newmarket, Ontario, Canada; ATS Iridium, Isanti, MN). Trained personnel completed all animal handling in accordance with Animal Use Protocol 568-02-11 approved by the University of Alberta Animal Care Committee. We programmed GPS radiocollars to take a fix every 3 hours. Although many cougars in our study used home ranges in all seasons that extended beyond the provincial park boundary, we included only GPS relocations that occurred within CHIP in this analysis because this was the extent of the human-activity

Table 2. Most-supported seasonal models based on Akaike's Information Criterion (AIC) for estimating natural log transformed motorized and non-motorized human relative activity in Cypress Hills Interprovincial Park, Alberta, Saskatchewan, Canada. We determined human relative activity (people/day) using a network of motion-triggered cameras. Delta AIC is in reference to the intercept only (null) model to evaluate relative performance of the selected models.

Season	Model structure	AIC	Δ AIC
Winter			
Motorized	trail_type ^a + dist_core ^b + dist_entr ^c + dist_park ^d	-56.81	36.95
Non-motorized	trail_type + dist_core + ski ^e	-14.71	39.36
Spring			
Motorized	trail_type × dist_trailh ^f	59.79	82.82
Non-motorized	trail_type + dist_fclty ^g + dist_entr	126.65	40.09
Summer			
Motorized	trail_type + dist_fclty + dist_entr	66.46	176.44
Non-motorized	trail_type + dist_entr + dist_core + dist_park + trail_type × dist_core + trail_type × dist_park	171.4	51.11
Fall			
Motorized	trail_type × dist_core	100.17	76.12
Non-motorized	trail_type × smmr_main ^h	82.83	57.37
Late fall			
Motorized	trail_type + dist_core	151.34	24.45
Non-motorized	trail_type + dist_core + ski	10.92	26.84

^a Categorical variable for trail types: secondary roads, truck trails, hiking trails.

^b Distance along trail to nearest core area measured from visitor centers (m).

^c Distance along trail to nearest entry gate (m).

^d Distance along trail to nearest parking (m).

^e Binary variable indicating if trail was maintained for cross-country skiing (1 = track set; 0 = not track set).

^f Distance along trail to nearest trailhead (m).

^g Distance along trail to nearest facility, which included campground, core area, parking, and entry gates (m).

^h Distance along trail to nearest junction with main road (m).

models. We included only cougars that registered a minimum of 50 GPS relocations in the study area, in a particular season, in the resource selection analysis for that season.

We used a 2-stage modeling approach that first quantified the seasonal response of individual cougars to human activity and then averaged the individual cougar responses to obtain a population-level response (Nielsen et al. 2002, 2009; Fieberg et al. 2010). For each season, we used resource selection functions (RSF) of individual cougars to quantify the relative probability of a site being selected based on multiple explanatory variables (Manly et al. 2002). We determined use data by cougar GPS locations that fell within the CHIP boundary and separated locations into human-activity defined seasons based on local date and time (Central Time Zone; GMT-6). Within each season, we delineated the domain of availability for each cougar by buffering each GPS location by 2,062 m, which was the 95th percentile of 3-hour step lengths observed within the CHIP boundary (Morrison 2013). We dissolved these buffers to create a polygon representing a seasonal home range for an individual cougar. We clipped this polygon by the CHIP boundary and used the extent of the resulting polygon to draw a sample of available points at a 5:1 ratio to observed points. We repeated this process for each cougar in each season and estimated the individual-level responses required for the 2-stage modeling approach. This use-availability design provided a measure of selection within the seasonal home-range scale (third-order selection; Johnson 1980).

We developed 5 a priori candidate models, to evaluate our prediction that the inclusion of anthropogenic variables would have more support than environmental variables alone (Table 3). We chose environmental covariates based on landscape characteristics deemed important to the biology of the species from past research (Logan and Irwin 1985, Arundel et al. 2007, Kertson et al. 2011). The model including only environmental variables served as the

biologically relevant null model. The trail model expanded on the environmental model to include distance to the nearest trail, which accounted for between-season variation in human activity but assumed within-season human activity to be uniform across space. The MRA, NMRA, and combined activity (MRA and NMRA) models expanded on the trail model to include estimates of motorized and non-motorized human activity, separately and combined, and therefore incorporated within-season estimates of spatial variation of human activity types (Table 3).

For the population-level models, we averaged AIC weights (w_i) across individuals to identify the best-ranked population-level models in each season. In all seasons, 1 model consistently ranked as most supported based on AIC w_i (Table 3). Therefore, we averaged beta coefficients across individual models for this single model structure to estimate population-level coefficients (Fieberg et al. 2010). Based on the sample of individual betas, we then calculated 95% and 85% confidence intervals for coefficients to examine population-level trends in selection and levels of significance.

Cougar Use of Trails

To investigate the variation in the use of trails by cougars during each 2-month sampling period, we summarized camera data for cougar activity following the same protocols used to quantify seasonal human activity. To ensure equal detectability, we included only camera stations that were operational in all six 2-month sampling periods in this analysis ($n = 61$). We determined how many camera stations detected a cougar, the average relative activity of cougars (detections per day), and the distribution of detections with respect to diel period: morning, day, evening, and night. We determined the start and end times of diel periods based on sunlight and twilight hours published for the mid-date of each trapping session for Medicine Hat, Alberta (www.nrc-cnrc.gc.ca). We defined daytime as 1 hour after sunrise to 1 hour before sunset, nighttime by the start and end times of

Table 3. Candidate cougar habitat models and corresponding composite Akaike's Information Criterion (AIC) weights (AIC w_i) in each season. We calculated composite AIC w_i by averaging AIC w_i of the individually fit models in each season. The combined activity model ranked highest in AIC w_i across all seasons; therefore, we used it for population-level modeling.

Model name	Model structure	Seasonal composite AIC w_i				
		Winter	Spring	Summer	Fall	Late fall
Environment	tri ^a + cover ^b + edg_inopn ^c + edg_infrst ^d + dist_water ^e	0.04	0.00	0.00	0.01	0.00
Trail	(Environment) + dist_trail ^f	0.02	0.01	0.09	0.06	0.05
Motorized activity	(Trail) + MRA ^g	0.06	0.15	0.21	0.28	0.14
Non-motorized activity	(Trail) + NMRA ^h	0.25	0.08	0.10	0.23	0.32
Combined activity	(Trail) + MRA + NMRA	0.63	0.76	0.59	0.43	0.49

^a Topographic roughness index; 90-m resolution.

^b Binary variable indicating forest cover (1 = conifer, deciduous, mixed forests, and shrub) or open cover (0 = grassland, cropland, exposed land); 30-m resolution.

^c Distance to edge for points in open (m).

^d Distance to edge for points in forest (m).

^e Distance to nearest water course (m).

^f Euclidean distance to nearest trail (m).

^g Estimated motorized relative activity (MRA) of nearest trail from human MRA models (people/day). Estimate changed by season according to seasonal human use model.

^h Estimated non-motorized relative activity (NMRA) of nearest trail from human NMRA models (people/day). Estimate changed by season according to seasonal human use model.

civil twilight, and morning and evening as the periods falling between night and day accordingly. In each season, we multiplied the total number of detections by the proportional duration of each diel period to obtain the expected distribution of detections assuming indiscriminate temporal use of trails. We calculated ratios of observed to expected frequencies in each diel period in each season to examine cougar selection for those periods. We averaged these selection ratios across all seasons to examine in which diel period cougar use of trails was most concentrated. To examine the trail-level effects of seasonal human activity on cougar use of trails, we compared average MRA and NMRA at camera sites that detected a cougar versus sites that did not detect a cougar using *t*-tests. Because we did not make cross-season comparisons in this latter analysis, all camera stations that were operational in each 2-month period were eligible to be included in the analysis for that period.

RESULTS

Measuring and Modeling Human Activity

We operated camera stations for an average of 19.3 days during each 2-month period and recorded 28,997 total human activity events. We excluded 5 camera stations from the analysis because they were compromised in some way (e.g., changes in route access during the year-long sampling period).

Overall human activity measured during 2-month sampling periods in CHIP fluctuated significantly throughout the year ($\chi^2_5 = 141.98$, $P < 0.005$). Human use was higher in July and August than other periods and these months accounted for 58% of the total year-round observations of human use of trails (Fig. 2). Human use in May–June and September–October was moderate and represented 14% and 15% of the annual total observations, respectively. Human use in January–February and March–April was lowest (2%),

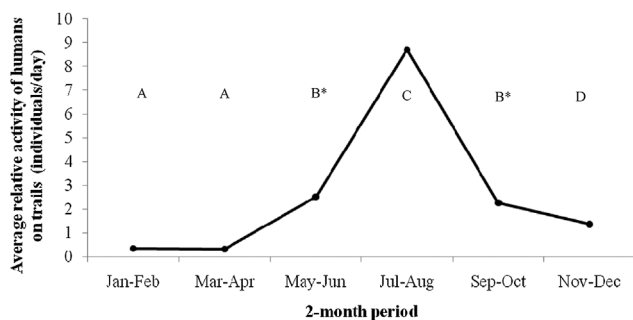


Figure 2. Average human activity (motorized and non-motorized combined) detected at camera locations in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada, 1 July 2011–30 June 2012. Average human activity is reported here as real data, but we natural-log transformed data for statistical analysis. Periods with the same letter indicate no significant differences between 2-month seasons based on pair-wise Wilcoxon tests using a Bonferonni corrected *P*-value (0.003) for multiple comparisons. We pooled periods (Jan–Feb and Mar–Apr) that did not differ significantly into 1 season for modeling motorized and non-motorized human activity and cougar habitat selection, but did not pool periods that had considerable environmental differences (*).

whereas human use in November–December (8%) represented a transition between fall and winter. We pooled data from January–February and March–April into 1 season because we did not find a difference in human activity, and environmental conditions (e.g., weather) were similar. We kept September–October and May–June separate despite similar human activity because of considerably different environmental conditions between spring and autumn. For all subsequent human activity and cougar RSF models, we therefore considered 5 seasons: winter (Jan–Feb, Mar–Apr), spring (May–Jun), summer (Jul–Aug), fall (Sep–Oct), and late-fall (Nov–Dec). Trail type was the only covariate to consistently appear in both MRA and NMRA models across all seasons. Otherwise structures of the most supported models used to estimate the spatial distribution of MRA and NMRA differed in all seasons (Table 2).

Seasonal Cougar Habitat Selection

Of the cougars with >50 GPS locations in CHIP for at least 1 season, we used 15 individuals (5 males; 10 females) to assess seasonal habitat selection and response to human activity. Although the number of cougars included in each seasonal sample varied (Table 4), the geographic extent of the study area was well sampled in all seasons because of the wide-ranging nature of cougars and a high degree of home-range overlap (Fig. 3). Average GPS success rate of cougar-borne collars in this study was 80.8%.

At the individual level, models in all seasons that included anthropogenic measures had considerably more empirical support than the environmental model (Table 3). Also, models that included any metric of human activity (MRA, NMRA, and combined activity) at the nearest trail consistently outperformed models that included only distance to nearest trail (Table 3). The model that included estimated MRA and NMRA (combined activity) was the most supported in all seasons and thus we used this model to estimate population-level models (Table 3).

Variation in selection at the individual level was apparent for most covariates, although we found population-level trends. Overall, cougars selected rough terrain in all seasons except spring. Forest cover was selected by cougars only during winter with selection for proximity to forest edge in all seasons. Selection of hydrological features varied between seasons (Table 5). In response to anthropogenic features, cougars were strongly associated with proximity to trails in

Table 4. Sample size of cougars and average number of global positioning system (GPS) locations that contributed to seasonal resource selection function models. We monitored cougars between 2008 and 2012 in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada.

Season	Sample size	GPS locations		
		Average	Min.	Max.
Winter	11	304	59	710
Spring	11	281	82	494
Summer	8	235	57	376
Fall	6	260	79	467
Late fall	7	241	104	515

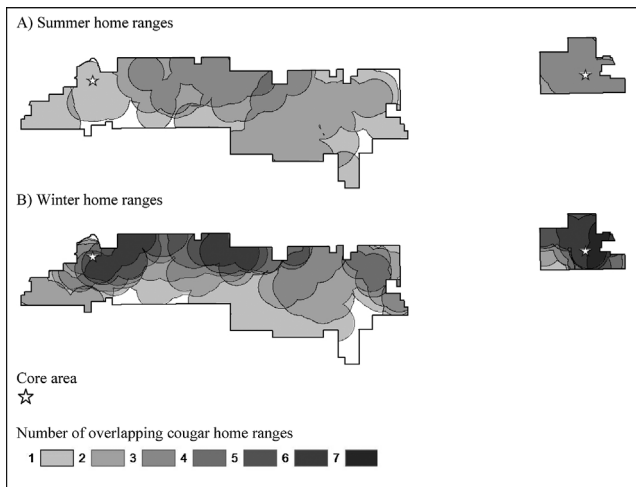


Figure 3. Summer (A) and winter (B) home ranges of cougars in Cypress Hills Interprovincial Park (CHIP) Alberta and Saskatchewan, Canada, between 2008 and 2011. Maps delineate only the portion of cougar home ranges that were located within CHIP to illustrate the between-season distribution and overlap of home ranges with the study area (summer home ranges, $n = 8$; winter home ranges, $n = 11$).

winter and avoided proximity to trails in summer. During spring, fall, and late-fall, proximity to trails was not supported in habitat selection models (Table 5). Across all seasons, cougars avoided areas in proximity to greater levels of MRA and NMRA, although this response was significant only during spring for MRA and in summer and spring for NMRA (Table 5).

Cougar Use of Trails

Remote cameras recorded 267 cougar detections at 50 (82%) of the camera stations ($n = 61$). Number of cougars detected per day was highest during July–December (Fig. 4). Averaged across all seasons, cougars were detected

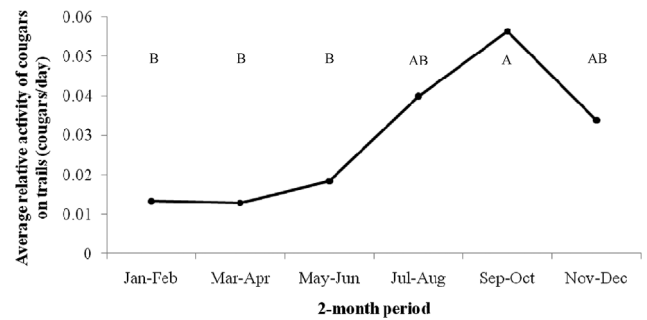


Figure 4. Average relative activity of cougars detected at camera locations in Cypress Hills Interprovincial Park Alberta and Saskatchewan, Canada, 1 July 2011–30 June 2012. Periods with the same letter indicate no significant difference based on pair-wise Wilcoxon tests using a Bonferroni corrected P -value (0.003) for multiple comparisons.

2.03 ± 0.23 times more than expected in the evening and 1.42 ± 0.47 times more than expected during the night. They were detected less than expected in the morning and day by 0.94 ± 0.47 and 0.55 ± 0.11 times, respectively. Average seasonal MRA was higher at camera stations that detected a cougar in January–February ($P = 0.029$). Otherwise, within-season MRA and NMRA did not differ significantly between locations that detected a cougar and those that did not (in all cases $P > 0.05$).

DISCUSSION

Seasonal Cougar Habitat Selection

Our results provide insights into the spatial ecology of a recently re-established cougar population in the Cypress Hills. Consistent with findings elsewhere, selection by cougars was influenced by habitat covariates that met their biological requirements, including access to prey. For

Table 5. Population-level coefficients for most-supported seasonal models based on Akaike's Information Criterion (AIC) weights. We calculated population coefficients by averaging individual-level betas for each model, respectively. Double asterisks (**) and single asterisks (*) indicate 95% and 85% confidence levels do not overlap 0, respectively.

Covariate	Population-level coefficients by season				
	Winter	Spring	Summer	Fall	Late fall
tri ^a	40.40**	13.16	38.40**	37.59**	30.75**
cover ^b	0.52**	0.16	0.10	0.28	-0.36
edg_inopn ^c	-0.008**	-0.009**	-0.006**	-0.003**	-0.02*
edg_infirst ^d	-0.0005	-0.001**	-0.00009	-0.002	-0.003**
dist_water ^e	-0.001**	-0.00002	0.00002	0.0004**	-0.0009**
dist_trail ^f	-0.0007**	-0.0001	0.0005*	0.0002	-0.0003
NMRA ^g	-0.26	-0.96**	-0.93*	-0.12	-6.50
MRA ^h	-1.77	-0.43*	-0.10	-0.52	-0.03

^a Topographic roughness index; 90-m resolution.

^b Binary variable indicating forest cover (1 = conifer, deciduous, mixed forests, and shrub) or open cover (0 = grassland, cropland, exposed land); 30-m resolution.

^c Distance to edge for points in open (m).

^d Distance to edge for points in forest (m).

^e Distance to nearest water course (m).

^f Euclidean distance to nearest trail (m).

^g Estimated motorized relative activity (MRA) of nearest trail from human MRA models (people/day). Estimate changed by season according to seasonal human use model.

^h Estimated non-motorized relative activity (NMRA) of nearest trail from human NMRA models (people/day). Estimate changed by season according to seasonal human use model.

example, cougar selection for edge habitats is logical because the primary prey of cougars in the Cypress Hills are deer and elk (Bacon et al. 2011), which are often associated with edge habitats (Alverson et al. 1988; M. M. Bacon, University of Alberta, unpublished data).

Our primary objective, however, was to examine cougar space use relative to temporal (between seasons) and spatial (within season) variation in human activity. Human activity in Cypress Hills Interprovincial Park fluctuated considerably between seasons with a marked spike in July and August, accounting for 58% of the total year-round activity. This exemplifies the oscillating pattern of human activity expected to occur in many parks with seasonal climates. By stratifying cougar habitat analyses into 5 seasons based on this oscillation, we accounted for the effects of seasonal variation in human activity on cougar space use. As predicted, models that included anthropogenic variables performed substantially better than a null model that included only environmental covariates. Likewise, Burdett et al. (2010) found strong support for models that incorporated human-influence variables versus only natural variables, indicating human-disturbed landscapes influence cougar habitat selection.

At population levels, cougars appeared to shift their habitat selection corresponding with seasonal fluctuations of human activity. The shifts were most apparent in summer and winter when overall average human activity was highest (8.7 people/day) and lowest (0.3 people/day), respectively. Associated with observed fluctuations in human activity, cougars selected areas farther from trails during the summer and closer to trails in winter. Moderate rates of human activity, ranging from 1.4 to 2.5 people/day, did not reveal significant trends in selection and appear to have less influence on cougar habitat selection. Seasonal shifts in selection in this study implicate human-cougar interactions because it indicates that the potential for overlap of people and cougars could be maximized at moderate or low levels of human activity. Similarly, Kertson et al. (2011) found the greatest potential for human cougar interactions occurred at moderate levels of rural development.

Infrastructure-based measures of human disturbance (e.g., Kertson et al. 2011), however, often do not account for temporal variation in human activity. One of the few studies to quantify human activity and cougar responses observed that individual cougars responded differently to weekly fluctuations in human activity in a California park (Sweaner et al. 2008). Some cougars avoided areas of high human use, whereas others appeared to use the park randomly (Sweaner et al. 2008). Quantifying human activity at a longer temporal scale (i.e., seasonally vs. weekly) may account for the time required for cougars to adjust their selection of habitats. Similar to our results, cougars in Florida avoided roads during the hunting season coinciding with an expected increase in human activity during this period (Janis and Clark 2002).

An alternative, though not necessarily mutually exclusive, explanation for the seasonal shift in cougar habitat selection is the seasonal distribution of prey. Pierce et al. (1999)

documented migratory patterns in cougars following prey between summer and winter range. However, the effects of prey distribution on cougar habitat selection do not operate in isolation from the effects of people. Janis and Clark (2002) postulate that some of the shift in space use of Florida panthers might have been attributable to a corresponding shift in the space use of prey that also were responding to increased human activity. Our observations of a population-level shift in space use corresponding with spatio-temporal variation in human activity might be indicative of the cougar's attempts to limit human interactions while obtaining prey.

Other studies have addressed prey distributions in the Cypress Hills (Hegel et al. 2009, M. M. Bacon, unpublished data) but there are few data pertaining to the seasonal variation in prey distribution at scales appropriate for our cougar habitat models. However, field observations hint at some possible 3-way interactions between people, predators, and prey. People providing feed for deer were prevalent in CHIP and feeding resulted in an abundance of prey in the core areas of the park (C. D. Morrison, unpublished data). During winter, when human activity was low, several instances of cougars killing and caching deer under cottages and decks were observed (C. D. Morrison, unpublished data), which likely contributed to the positive selection for proximity to roads, which were associated with cottages, in the most-supported winter habitat model. In summer, when human activity peaked, cougar activity was limited in the core area and no deer kills were observed in this area, despite the relatively high density of deer (C. D. Morrison, unpublished data). In this case, human activity probably had a more direct effect on cougar habitat selection resulting in avoidance of trails. Unlike edge habitats, for example, that were consistently selected by cougars presumably to locate prey, observations of seasonal use of the core area by cougars indicate that human activity is affecting cougar space use; otherwise, we would expect cougars to use the core areas throughout the year. These seasonal patterns of selection are consistent with apparent patterns in the seasonal distribution of home ranges. Most notably, all winter home ranges overlapped with at least 1 core area, whereas only half of summer home ranges overlapped with the core area (Fig. 3). At minimum, this pattern indicates that some degree of tolerance for human activity in low-human-use seasons was common across individual cougars. However, we are limited in our ability to identify the mechanisms underlying the seasonal distribution of home ranges because this is beyond the scale of our analysis (i.e., second-order selection; Johnson 1980).

Habitat selection models that included estimates of MRA and NMRA greatly outperformed all other models. At the population level, cougars avoided areas with high levels of motorized and non-motorized human activity and their response was strongest in spring and summer, when human activity was highest. Within-season avoidance of areas with higher levels of human activity indicates that cougars are more sensitive to the actual human activity rather than physical infrastructure (Arundel et al. 2007) and that cougars

are able to adapt their space use at different spatial or temporal scales. However, the relatively weak avoidance of areas with human activity in seasons when human disturbance is low indicates that the spatial variation of human activity on trails is not sufficiently predictable, or variable enough to detect a response from cougars at the population level. Although population trends may be apparent, we noted considerable variability among individual cougars regarding direction of selection for MRA and NMRA, thus the weak population-level selection associated with human-activity in most seasons. This highlights an advantage of a 2-stage modeling approach to habitat selection (Fieberg et al. 2010), which facilitates an assessment of the individual variation among animals that is aggregated in population-level results.

Individual variation in selection has been documented for cougars in other habitat selection studies in response to anthropogenic development (Sweaner et al. 2008, Kertson et al. 2011). Our sample of cougars included a range of demographics (males and females; sub-adults and adults) and behaviors, which could account for differences in space use (Kertson et al. 2011). For example, our sampling design assigned the estimated MRA and NMRA of the nearest trail to each GPS point, so feeding behavior, which localizes a cougar for several days (Knopff et al. 2009), could influence selection for that individual cougar. Behavior or demographic-specific models might reveal different patterns in space use, but because we were interested in habitat selection at a population level (i.e., across all behaviors and age classes), our models included GPS data collected from all cougars and during all behaviors.

Cougar Use of Trails

Examining cougar use of trails provides insights into the potential for direct interactions with people. Although we were limited to 1 year of data on cougar use of the trails, and therefore the generality of our results is limited, these findings provide baseline information on potential human-cougar interactions. Cougars were detected at 82% of randomly distributed camera stations indicating cougar use of trails is prevalent in CHIP. Cougars were slightly more active on trails (although not significantly) during the summer and fall periods even though our habitat-selection results indicate that they tend to avoid areas near trails during peak tourist months. Although cougars may avoid proximity to trails at larger spatial scales during periods of increased human activity, trails still may be important travel corridors to facilitate movement through dense vegetation (Beier 1995, Dickson et al. 2005, Kertson et al. 2011). Similarly, camera stations that detected a cougar in January-February had higher levels of motorized human activity, which could result from cougars using plowed or user-maintained roads to facilitate travel in snow. Also, we detected cougars more than expected during evening and night, which is a logical activity pattern based on the crepuscular (or vespertine in this case) and nocturnal ecology of the species (Van Dyke et al. 1986, Sweaner et al. 2008). As such, cougar use of trails might be more indicative of cougar

activity patterns and energetic requirements rather than a reflection of cougar habitat selection at larger spatial scales. In this case, cougar activity might be less affected by variation in human activity, as compared to cougar habitat selection. Similarly, other researchers found no correlation of cougar activity patterns compared to weekly (Sweaner et al. 2008) and seasonal (Janis and Clark 2002) variation in human activity, even when a shift in cougar space use was observed (Janis and Clark 2002).

MANAGEMENT IMPLICATIONS

We documented seasonal changes in space use in a recently re-established cougar population in an isolated, inter-provincial Park in Alberta and Saskatchewan. Human-cougar interactions can occur throughout the year, although the likelihood of interaction is not spatially or temporally constant. Rather there are periods, such as low to moderate human-use seasons, when the spatial overlap between people and cougars is greatest, which increases the potential for interactions. Furthermore, cougar use of roads and trails is prevalent, especially in the evening, which represents another time with a higher likelihood of human-cougar interaction. Increased understanding of human-cougar coexistence can assist with mitigating the risks posed by cougars to people and can also aid in managing the effects of human activity on cougars. This has useful applications throughout cougar range and is particularly pertinent for managers and the public in areas that have recently been re-colonized by cougars and who are facing novel challenges associated with coexistence. Education initiatives will be important for disseminating accurate information regarding cougar ecology and for promoting a peaceful coexistence. For example, managers can encourage human use during periods of low cougar activity (e.g., daytime) and can promote, or enforce, public safety precautions at times of heightened risk (e.g., evenings and off-seasons). Although population trends provide valuable information for management and education, individual variation underlying these population-level results makes the potential for human-cougar interactions difficult to predict.

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