

RESEARCH ARTICLE

Severe environmental conditions create severe conflicts: A novel ecological pathway to extreme coyote attacks on humans

Stanley D. Gehrt^{1,2} | Erich M. Muntz³ | Evan C. Wilson² | Jason W. B. Power⁴ |
Seth D. Newsome⁵ 

¹Max McGraw Wildlife Foundation,
Dundee, Illinois, USA

²School of Environment and Natural
Resources, The Ohio State University,
Columbus, Ohio, USA

³Cape Breton Highlands National Park,
Cheticamp, Nova Scotia, Canada

⁴Nova Scotia Department of Lands and
Forestry, Kentville, Nova Scotia, Canada

⁵Department of Biology, University of
New Mexico, Albuquerque, New Mexico,
USA

Correspondence

Seth D. Newsome

Email: newsome@unm.edu

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Abstract

1. Identifying the circumstances and causes of carnivore attacks on humans is important for prevention of future incidents as well as employing effective wildlife management strategies. Cape Breton Highlands National Park (CBHNP) in Nova Scotia has experienced multiple attacks by coyotes *Canis latrans* on humans, including a fatal attack on an adult in 2009.
2. Here we use a combination of data on space use and diet collected from 2011 to 2013 to reveal that limited resources and a reliance on a large ungulate (moose, *Alces americanus*) as the mechanism leading to aggression by coyotes in CBHNP.
3. Resident coyotes exhibited large home range sizes (mean = 77.5 km²) indicative of limited resources and spatiotemporal avoidance of human activity. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of sub-sampled coyote whiskers ($n = 32$), which provide a longitudinal record of diet over the months before collection, revealed little intra- and inter-individual variation with nearly all individuals specializing on moose, a pattern that agrees with indices of natural resource availability. Specifically, stable isotope mixing models show that moose was the most important prey for most coyotes (25/32), representing between 41% and 78% of dietary inputs. Only four coyotes exhibited use of anthropogenic resources (human foods), and only one of seven coyotes involved in attacks on people had been consuming human foods before the attacks.
4. *Synthesis and Applications:* We have described a unique ecological system in which a generalist carnivore has expanded its niche to specialize on a large prey species, with the unfortunate consequence of also expanding pathways to conflicts with people. Our results suggest extreme unprovoked predatory attacks by coyotes on people are likely to be quite rare and associated with unique ecological characteristics. Extreme management actions such as bounties are unnecessary, but managers may need to employ hazing or lethal removal earlier in the conflict process than under normal circumstances. Also, users of these areas should be made aware of the risks coyotes pose and encouraged to take precautions.

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KEYWORDS

anthropogenic resources, *Canis latrans*, carnivore attack, habitat selection, home range, human–carnivore conflict, stable isotopes

1 | INTRODUCTION

The unprovoked attack and predation of humans by carnivores is arguably the most extreme form of human–wildlife conflict. Although relatively rare, attacks by large mammalian carnivores have increased in North America and Europe in recent years (Penteriani et al., 2016). Various factors may be responsible for attacks beyond a carnivore simply viewing people as prey (Løe & Røskaft, 2004; Quigley & Herrero, 2005), including poor physical condition of the predator (Patterson et al., 2003), habituation via food provisioning by people (Linnell et al., 2002, 2021) and a lack of natural prey or other resources (Yeakel et al., 2009). Such incidents can have important effects on conservation efforts and often result in increased persecution and lethal removal of carnivores (Treves & Karanth, 2003). Thus, assessing the circumstances and cause(s) of such attacks is important for prevention of incidents as well as employing effective management activities to minimize their occurrence (Løe & Røskaft, 2004; Quigley & Herrero, 2005).

Despite their relatively small size, coyotes *Canis latrans* are responsible for most (31%) of the documented attacks on people by large carnivore species in North America (Penteriani et al., 2016), likely due to their extensive range and increasing proximity to people (Hody & Kays, 2018; Poessel et al., 2017). Nevertheless, attacks by canids are rare (Appleby et al., 2017; Løe & Røskaft, 2004; White & Gehrt, 2009), and it is unusual to experience subsequent incidents following the removal of offending individuals, particularly in areas where human population densities are low. For example, both national parks and urbanized areas occasionally have habituated coyotes that become bold or aggressive because of food provisioning and a lack of hunting pressure (Bounds & Shaw, 1994; Carbyn, 1989), although before 2009 there were no reported cases of adult human fatalities resulting from a coyote attack in the United States and Canada. In recent years, Cape Breton Highlands National Park (CBHNP) in Nova Scotia, Canada recorded 32 coyote–human incidents, including 7 independent cases where coyotes bit and injured people. The most extreme case was a 19-year-old female hiking alone who was attacked by coyotes in 2009 and subsequently died from her injuries, thereby representing the only recorded case of an adult fatality from a coyote attack (Sponarski et al., 2015, see Appendix S1 in Supporting Information). Coyote attacks continued in the park for several years following the fatal attack, despite the lethal removal of individual coyotes involved in that incident and other non-lethal attacks.

As coyotes increase their range and colonize virtually every city across North America (Poessel et al., 2017), the incidents at CBHNP and subsequent management responses received international attention and stimulated aggressive management actions in Nova Scotia and elsewhere in Canada (see Appendix S2). Therefore, it is

important to identify the cause(s) of these attacks, which will inform coyote management within CBHNP and possibly other rural or even urban areas faced with managing human–coyote conflicts. A fundamental question is whether the coyote behaviour in and around CBHNP is the result of unique circumstances, such as extreme ecological conditions, or if the incidents are the result of other factors such as anthropogenic resource (i.e. human food) provisioning that are typically associated with canid attacks (Linnell et al., 2021; White & Gehrt, 2009).

We predict that if anthropogenic foods were playing a substantive role in human–carnivore conflicts (*Anthropogenic Resource Hypothesis*), carnivores may shift their spatiotemporal activity patterns in response to the presence of people, would be attracted to areas associated with people (e.g. cities, towns, hiking trails or picnic areas), would exhibit greater reliance on anthropogenic foods and consequently display smaller home ranges in comparison to individuals that do not associate with people. An alternative explanation for human–carnivore conflicts is the lack of natural prey (*Limited Resource Hypothesis*), and this constraint may catalyse the habituation process for carnivores to associate people with sources of food, or even circumvent the habituation process altogether and view people as alternative prey. In this case, carnivores would likely have large home ranges and low population densities associated with resource limitation. Furthermore, if the potential for interactions with humans is seasonal, carnivore responses (attraction or avoidance) to the presence of people might show a seasonal pattern. See Table S1 in Supporting Information for specific predictions generated for these two hypotheses related to human–coyote conflict.

Here, we use a combination of space use and diet analysis to identify the potential cause(s) for coyote–human conflicts in CBHNP, with a particular focus on the role of anthropogenic foods. We monitored coyotes in and around CBHNP to determine their space use patterns, particularly with respect to human activities. We used a combination of home range size (Atwood et al., 2004; Mills & Knowlton, 1991), scat analysis, and surveys of potential prey to characterize the type and abundance of resources available to the CBHNP coyote population. We assessed the use of natural versus anthropogenic foods via carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of individual coyotes, which has the potential advantage of identifying the use of anthropogenic foods to a greater degree than scat analysis (Newsome et al., 2010, 2015) and has been used to aid management of human–bear conflicts in national parks (Hopkins et al., 2012) where the availability of anthropogenic foods contribute to such conflicts (Greenleaf et al., 2009). By sub-sampling coyote vibrissae, which is a continuously growing but metabolically inert tissue, we generated longitudinal diet profiles for individual coyotes, including those involved in attacks on humans, which allowed us to ultimately link dietary patterns to space use and conflicts at the individual level.

2 | MATERIALS AND METHODS

2.1 | Study area

Our fieldwork was focused in and along the edges of CBHNP, which is a 948 km² park situated at the north end of Cape Breton Island, Nova Scotia (46°43'0"N, 60°39'35"W). Bounded to the east by the Cabot Strait and to the west by the Gulf of Saint Lawrence, the park is characterized by steep topography and a high central plateau that averages 400 m above sea level and consequently has a distinct taiga and boreal vegetation community (see Appendix S3). The combination of location between two large water bodies and elevation produces a regional climate on the central highland plateau with a shorter growing season, longer periods of snow cover, greater daily temperature extremes and more precipitation than the adjacent lowlands. In addition, the highlands plateau experiences some of the highest mean annual wind speeds (Keys et al., 2017) and annual snowfall (250–300 cm, Patterson et al., 2000) in Nova Scotia. A single 2–3 lane road traverses the perimeter of

CBHNP and connects the few human communities adjacent to the park (Figure 1). Visitation to the park is typically 150,000 annually, with the high-use season occurring from June to October (Parks Canada, 2010). Human activity tends to be concentrated along the perimeter road, regardless of the activity, with low local human densities outside the park and little human presence in the interior.

2.2 | Live-trapping and tracking

From October 2011 to November 2013, we captured and radio-collared 23 coyotes (2 adult females, 2 juvenile females, 15 adult males and 4 juvenile males) using standard live-trapping and immobilization techniques (see Appendix S4); see Table S2 for mean weights (kg) of each sex and age class. We also collected two whiskers from each individual with scissors as close to the muzzle as possible. Animal capture and handling was conducted in accordance with Parks Canada Research Permit 12020, which was

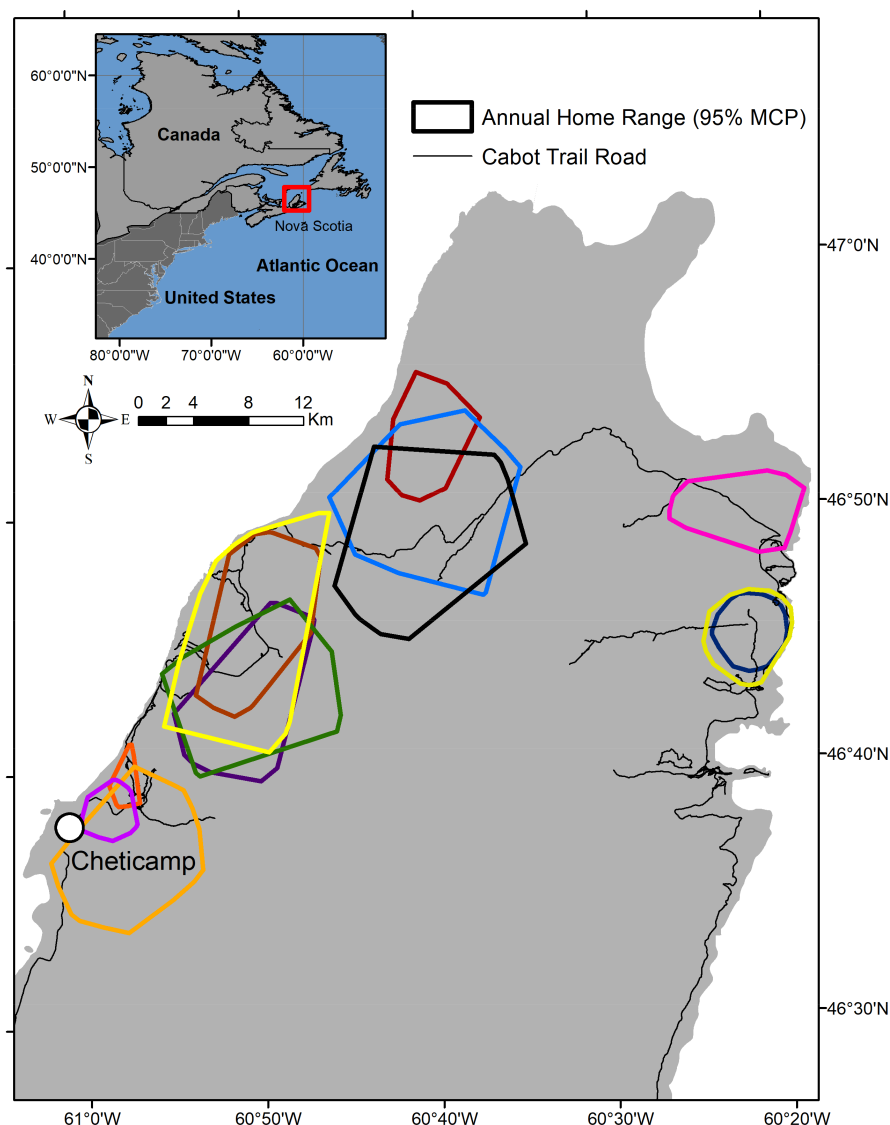


FIGURE 1 Spatial distribution of coyote annual home ranges (coloured polygons) in Cape Breton Highlands National Park, Nova Scotia from 2011 to 2013.

approved by Parks Canada's Animal Care Committee. Of the 23 coyotes captured, 14 (2 F, 12 M) adults (>12 kg) were fitted with Lotek 7000 GPS collars (Lotek Wireless Inc.) with remote communication, or GSC Pinnacle LITE GPS Iridium collars (Sirtrack), and 9 (7 M, 2 F) others with VHF collars. Of the 14 coyotes fitted with GPS collars, four were deployed in late 2011, five in 2012, and five in 2013. Of this sample, one adult male coyote was removed by national park staff in August 2012 during the study because he was exhibiting bold and aggressive behaviour towards people on the Cabot Trail over a 10-day period, behaviour he did not previously exhibit throughout his monitoring period (November 2011–July 2012). Relocation schedules for GPS transmitters were programmed to record a location every 2 h for the first 8 weeks post-deployment, then shifting to 6 or 7 h with intermittent 24-h periods during which locations were obtained with 2-h intervals for the remainder of the transmitter schedule.

2.3 | Spatial analysis

We distinguished resident and transient status for radiocollared coyotes based on space use. Residents maintained exclusive territories, whereas transients exhibited home ranges that overlapped multiple territories (Gese et al., 1996; Wilson & Shivik, 2011). Transients were excluded from seasonal and annual home range estimates but were included with measures of activity. We estimated annual home ranges with 95% minimum convex polygons (MCP; Shivik & Gese, 2000) for individuals with at least 100 locations recorded over a minimum of 3 months using the R (R Core Team, 2015) package *ADEHABITATHR* (Calenge, 2006). For all seasonal comparisons, we partitioned the data into two seasons—high use (June 1–October 31) and low use (November 1–May 31)—corresponding to the patterns of high and low human activity in and around the park (Parks Canada, 2010). We used individual 95% MCP home range boundaries to calculate available habitat at the third level of selection (Johnson, 1980) for each coyote. All seasonal estimates included individuals with >100 locations from a period of at least 1.5 months during a season (Gese et al., 1990). We used the Nova Scotia Department of Lands and Forestry Forest Inventory to identify habitats (https://novascotia.ca/natr/forestry/gis/dl_forestry.asp), which we simplified by pooling into the following five classes: Bog/Barren, Open, Forest, Developed, and Water. Because we were specifically interested in coyote response to humans, we created the Developed habitat representing a layer of human use or activity by adding a 100-m buffer to paved roads and buildings. Compositional analysis (Aebischer et al., 1993) was used to determine relative habitat selection within each season using *adehabitatHS* (Calenge, 2006). In addition, we calculated the proportion of locations for each coyote that occurred within the Developed category each season and compared this use between seasons using a paired t-test. To compare activity levels between seasons, we used movement rates as a proxy for activity (Lowe et al., 2010; Patterson et al., 1999; Rhoads et al., 2010) by

calculating the linear distance between sequential GPS fixes. We only included time steps of ≤2 h between GPS fixes in analyses to avoid failed GPS fixes and limit the likelihood of underestimating movements that could occur in longer intervals between fixes. Distances were calculated using *adehabitatLT* (Calenge, 2006) and movement rates were estimated as meters/hour and attributed to the midpoint in time between sequential points rounded to the nearest hour. Sample sizes between time periods and seasons was relatively consistent and ranged from 185 to 207 movement rates per time interval. We performed a one-way analysis of variance (ANOVA) by season to compare mean movement rates between seasons across all time intervals, then performed t-tests corrected for multiple comparisons using a Bonferroni adjustment between each seasonal hourly measurements to determine where differences in movement rates occurred.

2.4 | Stable isotope analyses

We analysed vibrissae from 32 (17 F, 15 M) coyotes (Table S3), including 19 whiskers from coyotes that were live-captured and radiocollared, 5 from the 2009 lethal attack including 2 that were confirmed to be involved in the attack, 4 from coyotes lethally removed following human-coyote incidents including attacks, and 4 from unmarked individuals captured during trapping or recovered as roadkill. We also opportunistically collected hair from potential coyote prey items that occurred in the study area during 2012–2014 for stable isotope analysis (Table S4), including southern red-backed voles *Myodes gapperi* ($n = 27$), shrews *Sorex* spp. ($n = 49$), snowshoe hare *Lepus americanus* ($n = 17$), white-tailed deer *Odocoileus virginianus* ($n = 20$), and moose *Alces americanus* ($n = 21$). Red-backed voles and shrews were grouped as small mammals because they had statistically indistinguishable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Samples were collected during unrelated small mammal surveys or from roadkill animals within the study area. We also analysed the isotopic composition of local human residents to serve as a proxy for a consumer of anthropogenic resources that could be directly compared to measured coyote isotope values; human hair samples were collected opportunistically from local barbershops.

Keratin samples from coyotes (vibrissa), potential prey (hair) and humans (hair) were rinsed in 2:1 chloroform:methanol solution to remove surface contaminants. Hair samples were homogenized with surgical scissors and vibrissa were sub-sampled into 0.2–0.3 mg segments using nail clippers; this weight range represents the lowest weight for which we can reliably generate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for keratin. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured with a Costech 4010 elemental analyser (Valencia, CA) coupled to a Finnegan Delta Plus XL isotope ratio mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, WY). Isotopic results are expressed as δ values: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1000 \times [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] - 1$, where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively; units are parts per thousand or per mil (‰). Analytical precision

was determined via repeated analysis of internal reference materials calibrated to international standards; within-run standard deviation of an acetanilide standard was $\leq 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. We applied tissue-specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic discrimination factors (TDF) of 2‰ and 3‰ (Figure 3), respectively, reported for captive wolves *Canis lupus* (Derbridge et al., 2015) to directly compare isotope values of keratin tissues from coyotes (vibrissae) to that of potential prey (hair); we also used these TDFs in the mixing model analysis (see below). Lastly, experiments on captive canids and other mammalian carnivores show that vibrissae growth rates likely scale with body mass (Hirons et al., 2001; Robertson et al., 2013; Stanek, 2014; Tyrrell et al., 2013). Based on these studies, we assume that coyotes (15–20 kg) will have mean vibrissae growth rates in the range of 8–12 cm/year. Since the mean (\pm SD) length of a vibrissa collected from the CBHNP was 6.2 ± 0.5 cm, we estimate that our sub-sampling approach produces a 6- to 9-month longitudinal record of dietary information for each individual coyote but acknowledge that seasonal variation in vibrissae growth rates (McLaren et al., 2015) could impact this estimate.

We used a one-way ANOVA with a post hoc Tukey–Kramer HSD test to assess differences in hair $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values between male and female coyotes and among potential prey types consumed by coyotes in this area. For post hoc Tukey–Kramer HSD pairwise comparisons, significance was assigned at a p -value of < 0.05 . ANOVAs were performed in JMP (v14; SAS Institute). We also used the package Stable Isotopes Mixing Models in R (simmr; Parnell, 2019) to quantify the relative contributions of prey to the diets of individual coyotes (Table S5). Models were run separately for coyotes ($n = 28$) that consumed natural prey, and the four individuals whose whisker isotope profiles clearly show they switched between natural and anthropogenic resources (Figure 3b) were not included in the mixing model analysis because no isotope data were available for local human foods. Model inputs included isotope data for each whisker segment and included mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for four resources: moose, white-tailed deer, snowshoe hare and small mammals (Figure 3). The latter resource combined isotope data for southern red-backed voles and shrews. We used mean (\pm SD) TDFs of $2.0 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$ and $3.0 \pm 0.5\text{‰}$ for $\delta^{15}\text{N}$ (Derbridge et al., 2015).

3 | RESULTS

We used GPS locations collected from November 2011 through December 2013 for space use and activity patterns. Annual home ranges were arranged in a largely exclusive pattern (Figure 1), consistent with territories, but extraterritorial movements were common, especially for coyotes residing on the central highland plateau. We obtained sufficient data from 11 GPS-collared coyotes for annual home range estimates (Table S6). Annual home ranges varied in size from 13 to 134 km² (mean = 77.5 km²) and the smallest estimates were for two coyotes (13 and 23 km²) residing in or near villages adjacent to CBHNP (Figure 1).

3.1 | Habitat selection

Coyotes exhibited overall selection for habitat types during the winter–spring season when human use of CBHNP is lowest ($n = 8$, Wilks' $\lambda = 0.285$, $p = 0.04$), and to a lesser extent during the summer–fall season when human use is highest ($n = 11$, Wilks' $\lambda = 0.466$, $p = 0.08$). Selection of habitat types ranked (most to least) during the low- and high-use season was nearly identical; Bog/Barren, Forest, Open, Water, Developed in low use and Bog/Barren, Forest, Open, Developed, Water in high use. Importantly, Bog/Barren, Forest, and Open habitats were consistently ranked as the most selected and Developed as the least selected for both seasons. Selection ratios provided insight regarding patterns of seasonal habitat selection (Figure 2a). Habitats, Bog/Barren and Forest had mean ratios consistently near or > 1 each season, with relatively little variation about the means. However, Developed had the greatest variability among individuals compared to other habitat categories, particularly during the high-use season. Consequently, there was considerable individual variation among coyotes in seasonal selection of Developed habitat, ranging from 0% to 51% for those with sufficient locations. This variability among individuals during the high use area likely caused the low ranking among habitat types, as the selection for Developed did not differ from any habitat type. Although mean use of Developed habitat was higher during the high use season (13.7%, SE = 5.4) than the low use season (3.7%, SE = 1.0), this difference was largely influenced by two coyotes and was not significant ($t = -1.56$, $p = 0.137$).

3.2 | Activity patterns

Movement rates of coyotes varied between low-use and high-use seasons ($F_{1,11} = 5.1$, $p = 0.02$). During the low-use season, hourly movement rates were comparatively low during nocturnal hours but peaked during diurnal hours (Figure 2b). The pattern inverted during the high-use season when hourly movement rates were lowest during diurnal hours and highest during nocturnal hours. Overall, movement rates differed between seasons in 8 of the 12 time periods sampled (Figure 2b). During crepuscular hours (0600–1000 and 1800–2000), there was no difference in movement rates between the seasons (Figure 2b).

3.3 | Stable isotope analysis and individual coyote diets

Mean vibrissa $\delta^{13}\text{C}$ ($F_{1,32} = 1.0$, $p = 0.32$) and $\delta^{15}\text{N}$ ($F_{1,32} = 0.3$, $p = 0.58$) values for male and female coyotes were statistically indistinguishable. In contrast, prey types had significantly different $\delta^{13}\text{C}$ ($F_{3,124} = 35.1$, $p < 0.001$) and $\delta^{15}\text{N}$ ($F_{3,124} = 47.0$, $p < 0.001$) values; Table S7 reports results of post-hoc Tukey–Kramer HSD pairwise comparisons of prey types. The mean (\pm SD) number of segments sub-sampled from each coyote vibrissa was 16 ± 7 (range: 6 to 41).

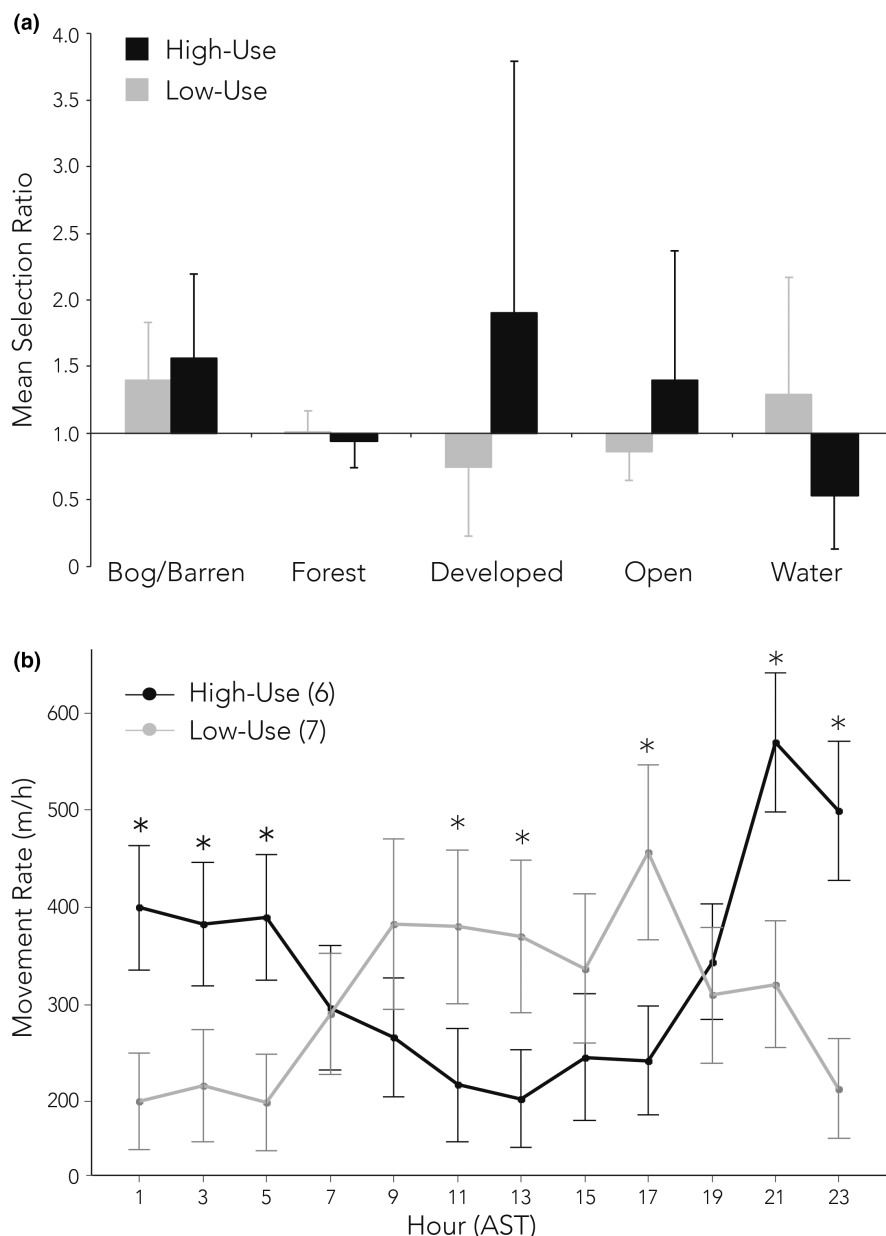
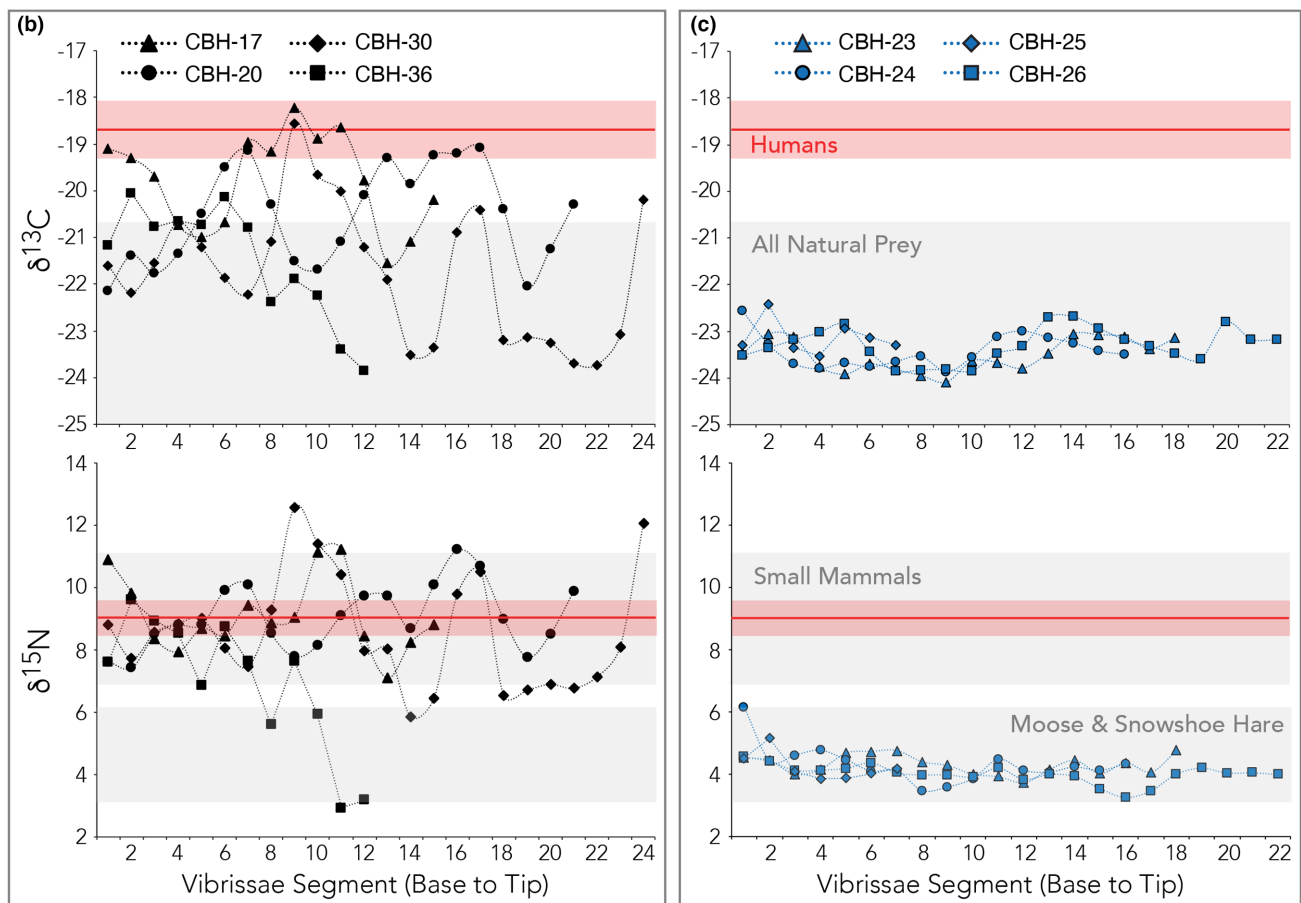
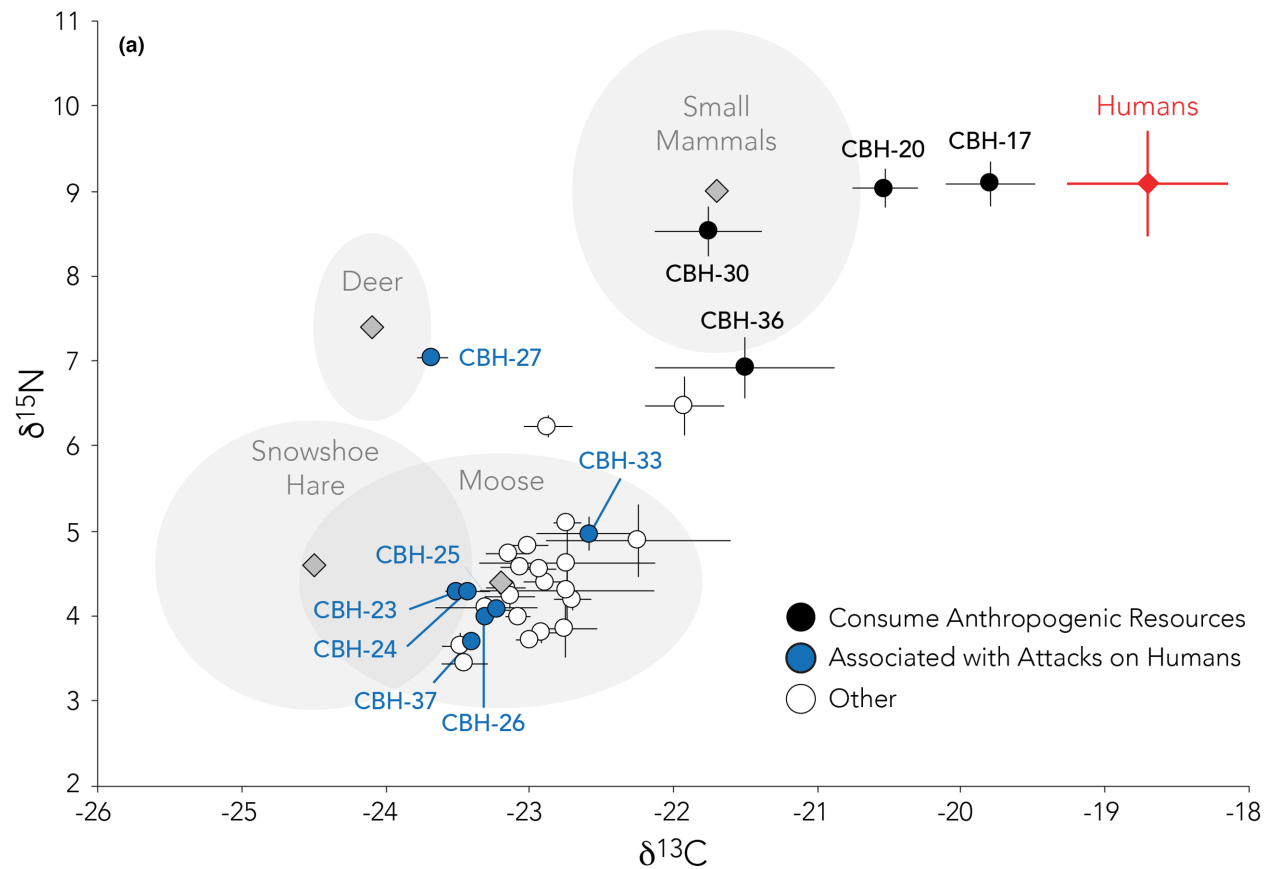


FIGURE 2 Estimates of habitat selection and movement rates for coyotes in CBHNP (2011–2013) during months of high human use (summer/fall) and low human use (winter/spring) within the park. (a) Mean selection ratios of habitats; error bars represent SD. Ratios <1 reflect avoidance of that habitat type, whereas ratios >1 reflect selection for that habitat. (b) Seasonal patterns of activity, as measured by movement rate, at hourly intervals for coyotes. Asterisks indicate a significant ($p < 0.05$) difference between seasons for each hour.

Once corrected for trophic discrimination, most (28/32 or 88%) coyotes had low mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that indicate they primarily consumed moose and snowshoe hare (Figure 3a). Mixing models show that mean (\pm SD) contributions of natural resources (in order of importance) for these 28 individuals were $52.5 \pm 13.9\%$ for moose,

$24.4 \pm 8.6\%$ for snowshoe hare, $11.7 \pm 7.4\%$ for small mammals and $11.4 \pm 9.9\%$ for deer. Resource contributions vary among individuals (Figure 4), especially in the consumption of moose (range: 10.0%–77.5%), snowshoe hare (range: 8.5%–39.1%) and deer (range: 5.3%–58.1%).

FIGURE 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results for coyotes and potential prey from CBHNP. (a) Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual coyotes (circles) and potential prey (grey diamonds) in CBHNP; for graphical clarity, error bars for coyotes are standard error, while ellipses around prey represent standard deviation (SD). Isotope values of potential prey have been corrected for trophic discrimination by adding 2‰ and 3‰ to measured mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively (45). Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of human hair (red diamond) collected from local towns are shown for direct comparison to coyotes. Individual coyotes associated with attacks on people (blue circles) or had isotope values that indicated they consumed human foods (black circles) are labelled. (b and c) vibrissae $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ profiles of individual coyotes in or adjacent to CBHNP. The four coyotes in panel (b) consumed some anthropogenic foods based on similarity with mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of humans (red line and shaded area). In contrast, the four coyotes in panel (c) only consumed natural prey (grey line and shaded area) and had relatively low intra-individual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in comparison to the coyotes shown in panel (b). Note that small mammals and humans have overlapping $\delta^{15}\text{N}$ but distinct $\delta^{13}\text{C}$ values (panel a), enabling identification of anthropogenic resource consumption. Whisker segments are presented in order from base to tip of the vibrissa representing a longitudinal record of the most recent to oldest dietary information, respectively.



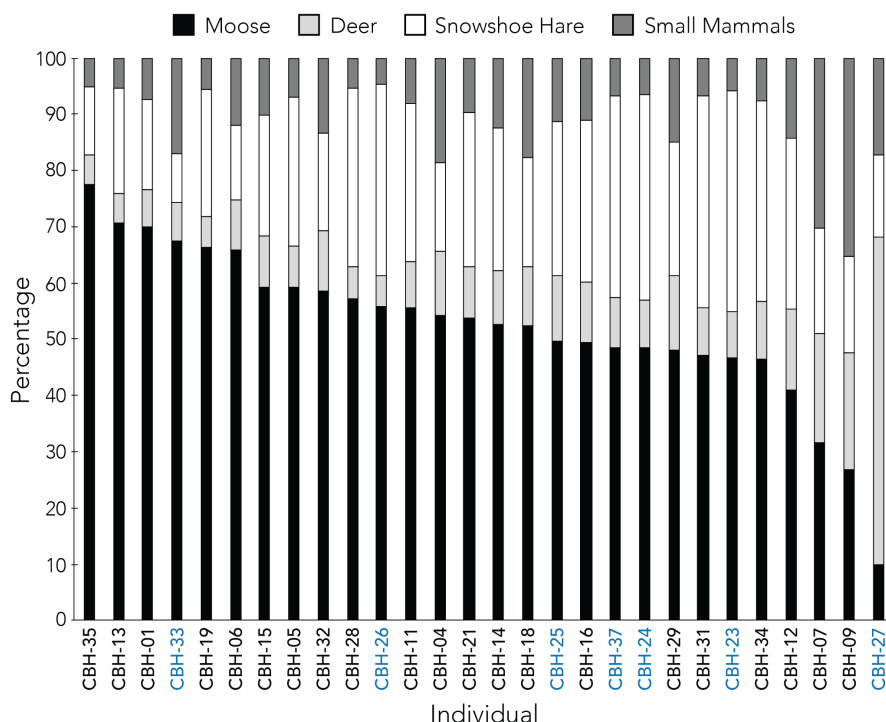


FIGURE 4 Estimates of mean contributions of four natural prey types to the diet of individual coyotes ($n = 28$) based on a stable isotope mixing model. Error in contributions varies by individual coyote and prey type but the mean error (SD) is equivalent to $\pm 9\%$. Individual coyotes associated with attacks on people are labelled in blue. Note that the four individuals whose whisker isotope profiles clearly show they switched between natural and anthropogenic resources (Figure 3b) were not included in the mixing model analysis because no isotope data are available for local human foods.

Only four coyotes (CBH-17, -20, -30, -36) had relatively high mean $\delta^{13}\text{C}$ ($> -22\text{‰}$) and $\delta^{15}\text{N}$ ($> 7\text{‰}$) values that indicated some use of anthropogenic resources (black circles, Figure 3a), and three of these individuals were associated with Cheticamp, a small town bordering the park (Figure 1). None of these four coyotes had mean $\delta^{13}\text{C}$ values that overlapped with mean $\delta^{13}\text{C}$ values for humans (Figure 3a), but some sub-sampled vibrissa segments had $\delta^{13}\text{C}$ values that overlapped with that of human hair (Figure 3b). Coyotes CBH-17 and CBH-20 were adult females located outside the park in Cheticamp and had the highest degree of isotopic overlap with humans of any coyotes we analysed (Figure 3a,b), but had no records of conflicts with humans. Coyote CBH-17 was a radiocollared adult female and had a territory that encompassed Cheticamp and the western periphery of the park. Coyote CBH-20 was not radiocollared, but was killed in a trap set near the Cheticamp municipal golf course. The other two coyotes (CBH-30, -36) with vibrissa segment $\delta^{13}\text{C}$ values indicating partial use of anthropogenic resources reportedly bit people (Figure 3b). Coyote CBH-30 was identified as a pup that was food conditioned and was observed repeatedly along the road during the day and exhibited little fear of people. It eventually bit a person on the ankle/foot and was lethally removed, but vibrissae segments reflecting the period before the incident did not have $\delta^{13}\text{C}$ values indicating use of anthropogenic foods. Coyote CBH-36 (adult male) had a more severe interaction with humans and bit a teenage human on the head causing serious injury, but isotope data also showed that this individual was not reliant on anthropogenic foods before the attack (Figure 3b).

Of the five coyotes initially implicated in the 2009 fatal attack that were lethally removed, only CBH-25 and CBH-26 were subsequently linked directly to the attack, while the other three individuals (CBH-23, CBH-24 and CBH-27) were removed from the

area soon after the incident and their involvement in the attack is unknown. It is notable that all five individuals lethally removed after the attack, including those directly linked to the attack (CBH-25 and CBH-26), exhibited little isotopic variation (Figure 3c) and had mean isotope values indicating consumption of moose, deer and snowshoe hare (Figure 3a) with no indication that these individuals were utilizing human foods before the fatal attack (Figure 3). For example, mixing models show that the two individuals directly linked to the 2009 fatal attack primarily consumed moose (CBH-25: 49.7%, CBH-26: 55.8%) and snowshoe hare (CBH-25: 27.2%, CBH-26: 34.2%). Two other coyotes (CBH-33 and CBH-37) were involved in incidents with humans unrelated to the fatal attack. Coyote CBH-33 attacked and bit a person while CBH-37 attacked a person on a bicycle, but both individuals have isotope values indicative of consumption of moose and snowshoe hare (Figure 3a) with combined proportions of these two resources contributing $> 75\%$ to their diets (Figure 4).

There was a general pattern of relatively low intra-individual variation as indicated by intra-vibrissa standard deviations in $\delta^{13}\text{C}$ of $< 0.5\text{‰}$ for most coyotes that had low mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicative of consumption of natural prey, including individuals associated with attacks on people (Figures S2A). Intra-individual variation in $\delta^{13}\text{C}$ values increased as mean whisker $\delta^{13}\text{C}$ values increased (Figure S2A), which suggests individuals that consumed a high proportion of anthropogenic foods were switching between natural and anthropogenic resources. Intra-individual variation in $\delta^{15}\text{N}$ values was less predictable; however, most individuals with low mean nitrogen isotope values indicating consumption of natural prey also had low within-vibrissa variability (SD $< 0.7\text{‰}$) in $\delta^{15}\text{N}$, including individuals associated with attacks on people (Figure S2B).

4 | DISCUSSION

Multiple lines of evidence support the Limited Resource Hypothesis for explaining coyote–human conflicts in CBHNP, which expands the known causes of coyote attacks on humans, while also describing a unique system with a coyote population specializing on moose as food throughout much of the year. Support for the Limited Resource Hypothesis includes large home ranges for coyotes on the plateau, the overall lack of selection for Developed habitat, and a shift to a more nocturnal activity pattern during high human use periods, presumably to avoid people. The observed patterns of space use suggest that small prey abundance was low and although there was substantial individual variation, most coyotes largely avoided areas of the park frequently used by people (e.g. picnic areas, hiking trails, towns). Mean MCP home range size for residents in our study was in the upper range of published estimates (e.g. 30–101 km²) for coyotes in northeast North America (Parker, 1995; Patterson & Messier, 2001; Tremblay et al., 1998), which are larger compared to coyotes found in Midwestern or Western regions of the continent (Ellington & Murray, 2015). Larger home range size in the northeast of the continent has been attributed to a lack of prey abundance or diversity (Parker, 1995; Patterson & Messier, 2001), although other factors may also play a role, such as social interactions (Wilson & Shivik, 2011) or genetic hybridization (Ellington & Murray, 2015). In contrast, coyote home ranges tend to be smaller in urbanized areas, partially because of the availability of anthropogenic food subsidies (Atwood et al., 2004; Gehrt et al., 2009; Gehrt & Riley, 2010; Poessel et al., 2016).

Our isotope-based diet data were perhaps the strongest line of evidence in support of the Limited Resource Hypothesis and were consistent with space use in suggesting limited prey availability within the park. Once corrected for trophic discrimination, nearly all (28/32 or 88%) coyotes had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were similar to natural prey, with little evidence of reliance on anthropogenic foods. Mixing models show that mean contributions of moose (52.5%) and snowshoe hare (24.4%) combined to contribute ~77% to the diets of these 28 individuals, but there was significant variation in resource proportions among individuals (Figure 4) with some consuming relatively high proportions of deer (CBH-27) or small mammals (CBH-07 and CBH-09) in comparison to other coyotes. A concurrent study of coyote scats collected in the park during our field work (Power et al., 2019) revealed that moose was the most frequent diet item with an annual frequency of occurrence of 57% with some seasonal (winter/spring) frequencies exceeding 70%, patterns that mirrored the mean contribution of moose derived from isotope mixing models. The annual frequency of occurrence of snowshoe hare in scats was 18%, which was slightly lower than estimated via mixing models (24.4%). Low consumption of deer and small mammals suggested by our isotope analysis was also consistent with scat analysis, that produced annual frequencies of occurrence of 5% and 10% for each prey type, respectively (Power et al., 2019). While moose were abundant in the park during our study, we rarely observed snowshoe hare or white-tailed deer tracks or pellets in the study area. On

a larger scale, Provincial pellet routes for the region encompassing our study area were low for snowshoe hare and deer, but high for moose during the study period with an estimated population density of 2.24/km² in 2011 (Figure S1). We also conducted limited small mammal trapping on the central plateau within the territories of our collared coyotes, and captured few small mammals (Table S8), which suggested low availability of this prey type.

Although the extreme environmental conditions and topography of the park represented a risky and challenging landscape for coyotes (Ellington et al., 2020), it also likely provided opportunities and facilitated the exploitation of moose. On the plateau, high snowfall and extreme winds produce ever-shifting snow drifts, and provide opportunities for coyotes to depredate moose, similar to lowlands where snow cover facilitates coyote predation on white-tailed deer (Patterson et al., 2000). Indeed, during winter fieldwork, study personnel occasionally found moose immobilized in drifts. Snow cover has been observed to be important in facilitating coyote predation on large ungulates like elk *Cervus elaphus* and moose (Benson & Patterson, 2013; Gese & Grothe, 1995).

Of note is the limited intra-individual variation in diet among most coyotes living within the park, which in conjunction with the observed patterns in mean isotope values and scat analysis suggests that coyote diets contain large proportions of moose throughout much of the year. This diet specialization is remarkable for coyotes, given that data from a wide range of systems show they frequently switch prey that results in considerable inter- and intra-individual variation in diet (Bekoff & Gese, 2003; Newsome et al., 2015). The homogeneity in diet among coyotes in our sample is consistent with a general picture of a system with limited availability of alternative prey, and a strong dependence on moose, which is unique compared to other systems where coyotes are the dominant top predator. We assume that most moose consumption resulted from scavenging (Kays et al., 2008; Parker, 1995), but some level of predation also occurred. At least one carcass located during winter coyote tracking showed signs of predation, and on other occasions live, adult moose were observed with fresh wounds consistent with coyote bites, in addition to coyote tracks leading to the moose. Coyotes are capable of depredating large ungulates including elk and caribou *Rangifer tarandus* in favourable winter conditions (Boisjoly et al., 2010; Gese & Grothe, 1995; Paquet, 1992), and recent accounts have described coyote predation of adult moose (Benson & Patterson, 2013). However, coyote use of moose as a diet item appears to be minimal in multi-prey systems. For example, in central Ontario only 11% of ungulate biomass consumed by coyotes was moose, while 89% was white-tailed deer, and scavenging was uncommon (Benson et al., 2017). Although we were unable to measure frequencies of ungulate kills in our system, our results clearly indicate that the foraging strategies of coyotes in CBHNP differ from previous studies.

We found little evidence that anthropogenic foods were an important part of coyote diets in CBHNP, and consequently limited support for the Anthropogenic Resource Hypothesis to explain coyote–human conflicts. Only four coyotes had isotope values indicating partial use of human foods, and two of these were associated

with a local town. Our results contrast with reports of conflicts involving coyotes and other carnivores from national parks and urban areas where food provisioning has typically been implicated as the mechanism leading to those incidents (Bounds & Shaw, 1994; Carbyn, 1989; Penteriani et al., 2016; White & Gehrt, 2009). Thus, our results extend the range of mechanisms through which coyotes may become aggressive towards people.

We suggest that the unprovoked, severe attacks on people in CBHNP are at least partially the result of prey-switching by coyotes that had specialized on a very large prey species in the absence of alternative smaller prey and an extreme resource-limited environment. Coyotes in the park are not subjected to hunting or trapping, and without these negative stimuli they may not view humans with the fear that typifies the coyote-human relationship elsewhere. Given the size of moose, their primary prey, combined with limited alternative prey, it seems coyote attacks on humans may be a unique circumstance leading to attempts at switching to a novel prey. Although rare, this ecological pathway to carnivore attacks on humans has occurred with other species (Linnell et al., 2021; Packer et al., 2005). The use of stable isotope ratios demonstrated that the case of the lions *Panthera leo* of Tsavo, where multiple people were killed by a pair of lions, was also the result of dietary specialization on a novel prey during a time of natural prey limitation (Yeakel et al., 2009).

4.1 | Synthesis and management implications

We have described a unique ecological system in which a generalist carnivore has expanded its ecological niche to specialize on a large prey species, with the unfortunate consequence of also expanding pathways to conflicts with people. These results have multiple implications for management. Previously, coyote predation of moose in the Northeast was not considered possible because of the size of the prey, until definitive cases of coyote predation of mature moose were reported from Quebec (Benson & Patterson, 2013). Although it is unlikely that coyote predation has an appreciable effect on the moose population in CBHNP, managers of small populations of threatened large ungulate species should not ignore the potential role coyote predation may have in conservation efforts (Benson & Patterson, 2013).

Similarly, it appears the ecological expansion of the ecological niche for coyotes has also revealed a rare form of risk of attack for humans and leads to the following points regarding the management of human-carnivore conflicts. First, extreme, unprovoked predatory attacks by coyotes on people are likely to be quite rare. In the initial aftermath of the human fatality in CBHNP, there was a concern that similar threats may occur elsewhere (see Appendix S1), especially as coyotes became residents in metropolitan areas where the potential for coyote-human conflicts is high. However, our results provide context, and suggest that the frequency of attacks on people in CBHNP is a result of a unique combination of environmental conditions, limited small prey and protection from human persecution.

Indeed, since the fatal incident in 2009, there have been no additional fatal attacks by coyotes, despite coyotes being responsible for the greatest number of attacks on people in North America among carnivore species (Penteriani et al., 2016).

Second, it is important that, while rare, managers and the public are aware that coyotes are capable of serious, unprovoked attacks on people under rare circumstances. This awareness would be important in areas with similar ecological characteristics to CBHNP, in which coyotes may prey-switch to large prey in the absence of alternative foods. In systems with limited prey, people using parks should be aware of carnivores, even coyotes, and take appropriate precautions, such as hiking with a partner and carrying a stick or bear spray, even when coyotes may represent the largest resident carnivore species.

The third implication from our results is that managers of human-carnivore conflicts in areas with extreme ecological conditions may need to employ hazing, or especially lethal removal, earlier in the conflict process than under normal circumstances. National parks or other areas protected from hunting or trapping and characterized by seasonal or persistent resource limitation may require modification of management strategies including careful monitoring of coyote behaviour and use of a lower threshold for removal of coyotes exhibiting bold or aggressive behaviour.

AUTHOR CONTRIBUTIONS

Stanley D. Gehrt, Erich M. Muntz and Seth D. Newsome designed the research; Stanley D. Gehrt, Erich M. Muntz, Jason W.B. Power and Seth D. Newsome performed the research; Stanley D. Gehrt, Evan C. Wilson and Seth D. Newsome analysed the data; Stanley D. Gehrt and Seth D. Newsome wrote the paper. Our study includes authors from two countries, the United States and Canada, including scientists based in the country (Canada) where the study was conducted. All authors were engaged with the research and study design to ensure that the diverse set of perspectives and skillsets they have were considered throughout the project.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.d51c5b06t> (Gehrt et al., 2022).

ORCID

Seth D. Newsome  <https://orcid.org/0000-0002-4534-1242>

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