



Temporal patterns of wolverine (*Gulo gulo luscus*) foraging in the boreal forest

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The foraging patterns and behaviors of predators can be discerned using GPS data. We used GPS data to investigate the temporal patterns of wolverine (*Gulo gulo luscus*) foraging on large prey in northern Alberta. We built a predictive model of wolverine large-prey events (beaver predation or ungulate scavenging) based on the spatial and temporal patterns of wolverine GPS data at foraging sites we visited in the field in winter. We used this model to predict large-prey events throughout our entire wolverine GPS dataset in winter and summer. We then evaluated how variables related to prey availability, seasonality, competition, and territoriality affected wolverine encounter time, residency time, and return time at predicted large-prey events. We found that wolverines encountered large prey more often in the spring when there is increased beaver and ungulate availability. The total time that wolverines spent at large-prey events was greater in winter (3.11 days [95th percentile = 2.62–3.63 days]) than summer (2.08 days [95th percentile = 1.70–2.51 days]), potentially because prey availability is limited in winter or prey is easier to capture in summer. Wolverines partitioned the total time at events into multiple visits, reducing their residency time and increasing their return time with each revisit, indicating biomass decline through time. The time between visits in winter (10.12 days [95th percentile = 7.99–12.56 days]) and summer (8.39 days [95th percentile = 7.18–9.74 days]) suggests wolverines might be patrolling their home range. We also found that wolverine residency time decreased and return time increased when there were other large-prey events available. Moreover, wolverine residency time at events increased when other wolverines were in the area. Our results suggest that large-prey events are important to the energy balance of wolverines and that wolverine foraging behavior is dynamic in response to environmental change.

Key words: Alberta, *Alces alces*, beaver, *Castor canadensis*, encounter time, *Gulo gulo luscus*, handling time, kill rate, moose, wolverine

The foraging patterns of predators can indicate the availability of prey on the landscape and the behaviors used to exploit them (Charnov 1976; Stephens and Krebs 1987). Predator foraging time can be divided into time spent finding and consuming prey. Researchers measure time spent finding prey as encounter time, or the time between encounters with prey items, whereas time spent consuming prey is measured as handling time, or the time from acquisition to consumption of prey. The time needed by predators to find prey is often dependent on the availability of prey (Holling 1959), whereas the time needed for consuming prey is frequently dependent on prey size (Knopff et al. 2010b; Cristescu et al. 2014). Researchers also have shown that there are a variety of other spatial and temporal variables, unique to the local environment, that have an effect on the time associated

with predators finding (Merrill et al. 2010; Whittington et al. 2011; McPhee et al. 2012) and consuming prey (Shrader et al. 2007; Courant and Fortin 2012; Stewart et al. 2017).

Direct observation is one way to measure encounter and handling times of prey (Stirling 1974; Klinka and Reimchen 2002). For example, observers can follow predators in the field to document the time between predation events (Miller et al. 2013). Although effective, tracking predators to estimate these parameters is time consuming and can be cost prohibitive. Researchers have recently developed statistical techniques that predict predation events from GPS data (Webb et al. 2008; Knopff et al. 2009; Ebinger et al. 2016). To create these models, one must have animal GPS data in tandem with a sample of predation events validated from field surveys. The information

gained from these models can include both predator encounter and handling times of prey (e.g., [Knopff et al. 2010a, 2010b](#)).

Direct observations of wolverine (*Gulo gulo luscus*) foraging on natural prey are rare. Examples include observations of wolverines caching and feeding on eggs in an Arctic goose colony (*Chen rossii* and *C. caerulescens*—[Samelius et al. 2002](#)) or killing Arctic ground squirrels (*Spermophilus parryi*) and other small prey ([Magoun 1987](#)). Scandinavian researchers used extensive field observations to measure wolverine kill rates of caribou (*Rangifer tarandus*—[Mattison et al. 2016](#)). Generally, studies of wolverine diets have been restricted to fecal analysis because these data are easier to acquire ([Lofroth et al. 2007](#); [van Dijk et al. 2008](#); [Inman and Packila 2015](#)). Unfortunately, these studies only provide a coarse spatial and temporal understanding of wolverine foraging behavior.

More detailed knowledge on wolverine foraging ecology would aid in the management of the wolverine population. Wolverines have disappeared from 40% of their range in North America since European settlement ([Laliberte and Ripple 2004](#)) and are considered a Species of Special Concern in Canada ([COSEWIC 2014](#)). Wolverines in Alberta primarily exist in the Rocky Mountains and the northern boreal forest. To date, our knowledge of wolverine foraging behavior in these environments is limited to analyses of food habits from fecal samples ([Lofroth et al. 2007](#); [Scrafford 2017a](#)). For instance, in northern Alberta, food habits analysis showed that wolverines primarily foraged on beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), and moose (*Alces alces*—[Scrafford et al. 2017a](#)). Currently, wolverine encounter and handling times of natural prey have not been reported in this region.

Our study took place in the boreal forest of northern Alberta and had 2 objectives. Our 1st objective was to build a model that would allow us to predict large-prey events (beaver predation and ungulate scavenging) from the spatial and temporal characteristics of wolverine GPS data. Our 2nd objective was to determine factors associated with wolverine encounter time, residency time, and return time to large-prey events. We evaluated whether encounter, residency, and return time were best explained by the availability of prey or other variables.

MATERIALS AND METHODS

Study area and animal handling.—Our research took place in the boreal forest surrounding the town of Rainbow Lake (population 870; elevation 500 m), Alberta (119°28'18.705"W, 58°32'22.361"N). The topography of the study area (hereafter, Rainbow Lake) is relatively flat except for narrow valleys surrounding streams. Average annual temperature is -1.3°C with an average annual precipitation of 414 mm ([Strong and Leggat 1981](#)). Rainbow Lake is within the central mixed-wood subregion of the boreal forest. Upland forests in this subregion generally consist of aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). Wetlands cover 30% of the landscape and include peatlands (bogs and fens) with black spruce (*Picea mariana*) forests. Industrial infrastructure in Rainbow Lake includes cutblocks, well sites, processing plants, industrial camps, roads (winter-ice roads and

all-season roads), seismic lines, transmission lines, and pipeline rights-of-way. The mammalian predator community in Rainbow Lake includes gray wolves (*Canis lupus*), black bears (*Ursus americanus*), lynx (*Lynx canadensis*), fishers (*Pekania pennanti*), and pine martens (*Martes americana*).

We used 22 live traps ([Copeland et al. 1995](#)) to capture wolverines over 3 winters (2013–2014, 2014–2015, and 2015–2016) from November to the beginning of April. We spaced live traps 15 km apart and fitted captured wolverines with Telemetry Solutions store-on-board (Quantum 4000) or Tellus Ultralight satellite-GPS collars (Telemetry Solutions, Concord, California) programmed to take GPS relocations every 2 h. All capture and handling procedures were approved by the University of Alberta Animal Care Committee Protocol No. 00000743 and Province of Alberta Collection and Research Permit No. 55714. This study conforms to guidelines published by the American Society of Mammalogists ([Sikes et al. 2016](#)).

Event modeling.—We visited wolverine activity sites in the field in winter if there were 2 consecutive wolverine GPS relocations within 200 m of each other ([Knopff et al. 2009](#)). We searched the site for prey remains or bedding areas. We classified an activity site as a large-prey event if it was clear that a wolverine was feeding on a fresh ungulate or beaver carcass. We classified an activity site as a multi-use event when it was evident that a wolverine killed a snowshoe hare or ruffed grouse (*Bonasa umbellus*), fed on an old carcass (often scattered remains), or rested based on evidence of a bed site.

Our next goal was to describe the spatial and temporal characteristics of each large-prey and multi-use event. We used an algorithm on our wolverine GPS data that identified the location of GPS clusters and calculated their attributes ([Knopff et al. 2009](#)). The attributes of clusters identified by the algorithm included the cluster radius (distance from the center of a cluster to the furthest GPS relocation), actual points (the number of GPS relocations within 200 m of the center of the cluster), away points (the number of GPS relocations outside of 200 m from the center of the cluster), distance (average distance of each GPS relocation to the center of the cluster), and total points (away GPS relocations + actual GPS relocations—[Knopff et al. 2009](#)). We associated large-prey and multi-use events with the attributes of the nearest cluster identified by the algorithm. Because of non-normal error distributions, we derived the average of the attributes of large-prey and multi-use events using a non-parametric bootstrap in R ([boot—R Development Core Team 2017](#)).

We next used logistic regression to create a predictive model that could discern large-prey (designated as a “1”) from multi-use (designated as a “0”) events. We created a candidate set of event models with cluster attributes that were not correlated ($r \leq 0.70$; [Table 1](#)). We used Akaike Information Criterion adjusted for small sample size (AIC_c) to evaluate competing event models and designated the top-event model as the one with the greatest AIC_c weight ([Burnham et al. 2011](#)). We reported coefficient estimates and 95% confidence intervals for explanatory variables from the top-event model.

We evaluated the predictive capacity of the top-event model with k -fold cross-validation ([Boyce et al. 2002](#)) and evaluated

Table 1.—Logistic regression models used to analyze the difference in attributes of wolverine (*Gulo gulo luscus*) multi-use ($n = 74$, designated as “0”) and large-prey events ($n = 33$, designated as “1”) visited in the field between 2013 and 2016 in Alberta, Canada. The attributes of these events were calculated using a GPS data clustering algorithm and included the cluster radius (distance from geometric center of a cluster to further GPS relocation), actual points (the number of GPS relocations within 200 m of the geometric center of the cluster), away points (the number of GPS relocations outside of 200 m of the geometric center of the cluster), distance (average distance of each GPS relocation to the geometric center of the cluster), and total points (away GPS relocations + actual GPS relocations). K = number of parameters included in the model; AIC_c = Akaike Information Criterion corrected for small sample size; ΔAIC_c = difference between the model score and the score of the top-ranked model; ω_i = model weight.

Model	K	ΔAIC_c	ω_i	Log-likelihood
Away + actual	3	0	0.9	-34.33
Total	2	5.21	0.07	-37.99
Total + distance	3	6.67	0.03	-37.66
Actual	2	14.16	0	-42.47
Away + radius	3	19.19	0	-43.92
Intercept only	1	59.37	0	-66.11

model accuracy by calculating the area under the receiver operator characteristic curve (AUC; pROC—R Development Core Team 2017). We determined the probability threshold for distinguishing a large-prey event from a multi-use event after investigating the AUC. We then used the top-event model to determine whether clusters, identified throughout the entire winter and summer wolverine GPS dataset using the clustering algorithm (Knopff et al. 2009), could be classified as large-prey events. To do this, we used the top-event model to calculate the probability that each cluster was a large-prey event. We classified a cluster as a large-prey event if the estimated probability was greater than or equal to the probability threshold. We further evaluated the predictive ability of the top-event model by calculating the number of large-prey and multi-use events visited in the field in winter that were correctly classified at the probability threshold. We also did this analysis for a limited sample of known foraging sites we visited in summer. We then used the predicted large-prey events for further analyses described below.

Encounter time.—We used a mixed-effects model of Cox proportional hazards (CPH) to identify explanatory variables related to wolverine encounter time with large-prey events (Harrell 2001). The CPH model measures the risk that an encounter (detection of a large-prey event) will occur with an increase in risk corresponding to a decrease in encounter time. We defined encounter time as the time (days) between the 1st GPS-collar relocations at consecutive large-prey events. We right-censored an event if the wolverine only had a single large-prey event or if it was the last event in the monitoring period. Many wolverines had gaps in monitoring when GPS collars were not operational. When there was a gap in monitoring, the time of origin was based on the 1st GPS relocation at a large-prey event after a new GPS collar was deployed on the wolverine. We used a non-parametric bootstrap to calculate the average encounter time in winter and summer seasons for non-censored events.

We created 3 candidate models representing hypotheses related to wolverine encounter time with large-prey events (Table 2). Our 1st hypothesis was that encounter time was best represented by a baseline hazard unaffected by explanatory variables (Model #1). Our 2nd hypothesis was that encounter time decreases when prey were most available (Model #2). Our hypothesis predicted that wolverine prey were most available in spring and that encounter time was negatively associated with days until spring (20 March). This is because beavers are likely more available to wolverines in the spring because they are often out of their lodges foraging and dispersing (Sun et al. 2000). Moreover, large predators often kill ungulates in the spring that are weakened by winter conditions (Smith et al. 2004), which provides carcasses to wolverines. Our 3rd hypothesis (Model #3) was that encounter time was associated with more than just the seasonal availability of prey. This model includes the density of streams and roads in a wolverine’s 80% minimum-convex polygon (MCP). Our hypothesis predicted that encounter time decreased with stream density (beaver habitat) because of more abundant prey and increased with road density because roads can occlude the foraging movements of wolverines (Scrafford et al. 2017b).

We used individual wolverines as a random intercept to account for pseudo-replication and we used AIC_c for model selection. We designated the top model as the one with the greatest AIC_c weight and report an estimate of the relative hazard and 95% confidence interval for explanatory variables from the top model. The analysis of encounter time, as well as analyses of residency and return times discussed below, were completed in R (coxme—R Development Core Team 2017).

Residency time.—We modeled residency time with a mixed-effects CPH. An increase in risk equates to a decrease in residency time. We first identified all GPS relocations that were within the radius (“actual points”, see description above) of the large-prey event up to 90 days after the time of origin. We designated the 1st GPS relocation at a large-prey event as the time of origin. We identified separate visits to a large-prey event if a wolverine was outside the radius of the event for ≥ 1.9 days (average duration that a wolverine was at an event during its 1st visit). We calculated residency time for each visit as the time from the 1st to last GPS relocation of a visit (before the wolverine left for ≥ 1.9 days).

We created 3 candidate models representing hypotheses of wolverine residency time at large-prey events (Table 2). Our 1st hypothesis was that residency time was best represented by baseline hazards (Model #1). Our 2nd hypothesis was that residency time was best represented by the cumulative time a wolverine was at an event up until that visit and by the season (Model #2). We suggest both of these variables are related to prey availability. Our hypothesis predicted that wolverine residency time decreased with the cumulative time a wolverine was at a large-prey event because of prey-biomass depletion. The hypothesis also predicted that wolverines increased residency time in the winter when prey were less available to wolverines on the landscape (Inman et al. 2012b). We used a Boolean term to indicate season (based on start of residency time; 1 = winter [1 November to 1 April], 0 = summer [2 April to 31 October]). Our 3rd

Table 2.—Cox proportional hazards models used to explain wolverine (*Gulo gulo luscus*) encounter time, residency time, and return time (days) to large-prey events between 2013 and 2016 in Alberta, Canada. AIC_c = Akaike Information Criterion corrected for small sample size; ΔAIC_c = difference between the model score and the score of the top-ranked model; ω_i = model weight; LCL = lower confidence limit; UCL = upper confidence limit.

Model	Response	Explanatory variables	ΔAIC_c	ω_i	Log-likelihood
#2	Encounter time	Spring	0.00	0.83	-915.48
#3		Spring + road density + stream density	3.31	0.16	-915.59
#1	Residency time	Intercept only	9.86	0.01	-924.25
#3		Cumulative time + concurrent events + season + wolverine	0.00	1.00	-3372.03
#2		Cumulative time + season	13.42	0.00	-3368.51
#1	Return time	Intercept only	97.87	0.00	-3459.27
#3		Cumulative time + concurrent events + season + wolverine	0.00	1.00	-1999.59
#2		Cumulative time + season	13.82	0.00	-2008.56
#1		Intercept only	17.59	0.00	-2012.45
			Hazard ratio	LCL	UCL
#2	Encounter time	Spring	0.80	0.70	0.91
#3	Residency time	Cumulative time	1.36	1.20	1.54
		Concurrent events	1.48	1.18	1.86
		Season	0.73	0.57	0.94
		Wolverine	0.79	0.63	0.99
#3	Return time	Cumulative time	0.82	0.71	0.95
		Concurrent events	0.70	0.59	0.82
		Season	0.81	0.65	1.00
		Wolverine	1.00	0.81	1.23

hypothesis was that wolverine residency time was best explained by additional explanatory variables including the number of concurrent foraging opportunities and whether another wolverine was detected at the event (Model #3). The number of concurrent events was a count of the number of times the range of dates the wolverine visited a specific large-prey event intersected the range of dates of all other large-prey events visited by that wolverine. To allow time for visiting additional foraging sites, our hypothesis predicted that wolverine residency time decreases with concurrent events. Our hypothesis also predicted that wolverines increased residency time during a visit if another wolverine was present at a large-prey event to reduce loss of prey to the wolverine. We used a Boolean term to indicate whether another wolverine was detected at the event (1 = wolverine, 0 = no wolverine). We caution that strength of the conclusions that can be drawn from the wolverine covariate is weak because not all wolverines in the population wore GPS collars.

We included a random intercept for the event nested within a term for individual wolverine to account for pseudo-replication. We designated the top model as the one with the greatest AIC_c weight and reported the relative hazard and 95% confidence interval of explanatory variables from the top model. For summary statistics, we calculated a non-parametric bootstrap of the average residency time during a visit in winter and summer seasons, the average number of visits to a large-prey event, the total time spent at each large-prey event (sum of residency time across visits), the average number of concurrent events that a wolverine visited, and the average residency time with and without another wolverine present using R (boot—R Development Core Team 2017).

We also used these methods to calculate and then compare the residency time of wolverines at beaver-predation ($n = 21$) and ungulate-scavenging events ($n = 12$) visited in the field.

We used a non-parametric bootstrap to calculate the total time wolverines spent at these events and the number of visits. We suggest that the value of these metrics differs between events if there are non-overlapping 95th percentile confidence intervals.

Return time.—We modeled wolverine return time to large-prey events with a mixed-effects CPH. An increase in risk equates to a reduction in return time. Similar to our methods for calculating residency time, the GPS relocations identified within the radius of the large-prey event were used to estimate return time. We calculated return time (days) to large-prey events by subtracting the date of the last wolverine GPS relocation before departing during a visit from the date of the 1st GPS relocation the following visit.

We created 3 candidate models representing hypotheses of wolverine return time to large-prey events (Table 2). Our 1st hypothesis was that return time was best represented by baseline hazards (Model #1). Our 2nd hypothesis was that return time was best explained by the cumulative time a wolverine spent at a large-prey event and season (Model #2). Our hypothesis predicted that wolverine return time increased as the cumulative time spent at an event increased because there is less reward (biomass) to incentivize a quick return. The hypothesis also predicted that return time increased in winter because wolverines increased their residency time at each large-prey event. Our 3rd hypothesis (Model #3) was that wolverine return time also was affected by presence of other wolverines and other foraging opportunities. Our hypothesis predicted that return time decreased when other wolverines were present to reduce biomass loss to competitors and increased as concurrent events increased because of the time required to visit additional events.

We included a random intercept for the event nested within a term for individual wolverine to account for pseudo-replication. We designated the top model as the one with the greatest

AIC_c weight and report the relative hazard and 95% confidence interval of explanatory variables from the top model. For summary statistics, we calculated a non-parametric bootstrap of the average return time after a visit in winter and summer seasons, the average number of departures from a large-prey event, the average number of concurrent events visited, and the average return time with and without another wolverine present using R (boot—R Development Core Team 2017).

RESULTS

Wolverine GPS data.—Our GPS dataset consisted of 2,456 wolverine days of GPS-collar monitoring in winter (1 November to 1 April) and 1,999 wolverine days of monitoring in summer (2 April to 31 October). In winter, we monitored 11 females for an average (calculated with a non-parametric bootstrap) of 99 days (95th percentile = 60–139 days) and 13 males for an average of 70 days (95th percentile = 50–89 days). In summer, we monitored 11 females for an average of 98 days (95th percentile = 75–125 days) and 11 males for an average of 126 days (95th percentile = 89–178 days).

Event modeling.—We visited 107 wolverine activity sites over the winters of 2013–2014, 2014–2015, and 2015–2016. We visited a site if there were at least 2 GPS relocations within 200 m of each other. We then categorized these sites into 33 large-prey events (12 ungulate scavenging and 21 beaver predation) and 74 multi-use events (48 beds, 9 snowshoe hare kills, 2 grouse kills, and 15 small-scavenging sites). We used a clustering algorithm (Knopff et al. 2009) to calculate the spatial and temporal attributes of large-prey and multi-use events (Table 3). The top-event model indicated that large-prey events had a greater number of actual ($\beta = 0.181$, $SE = 0.041$) and away points ($\beta = 0.734$, $SE = 0.020$; Table 1, Fig. 1). We found the 10-fold cross-validation prediction error for the top-event model was 0.12 (88% accuracy) which indicated the model was good at predicting large-prey events. The AUC (0.83) also indicated good predictive capacity. We found that the optimal probability threshold from the ROC curve was 0.7. At a probability threshold of 0.7 or greater, the top-event model correctly classified 84% of large-prey events we visited in the field in the winter. The top-event model also correctly classified 2 large-prey events (1 beaver predation and 1 ungulate scavenging) and 5 multi-use events (1 small scavenging and 4 small prey) that

we visited in the field during the summer. We then used the probability threshold of 0.7 or greater to predict whether clusters identified by the clustering algorithm (Knopff et al. 2009), throughout all the wolverine GPS-collar data, were large-prey events. Overall, the model identified 265 large-prey events from these clusters: 113 in winter and 152 in summer. In winter, 13 males had 49 large-prey events and 11 females had 64 large-prey events. In summer, 11 males had 79 large-prey events and 11 females had 73 large-prey events.

Encounter time.—The encounter time CPH model included 109 encounter times in winter and 134 encounter times in summer. There were fewer encounter times used for the encounter time CPH model than the total number of large-prey events identified by the top-event model because the 1st event of each monitoring period (e.g., new GPS collar deployed) was considered the time of origin and therefore did not have an encounter time. In winter, we identified 46 encounter times for 12 males and 63 encounter times for 11 females. In summer, we identified 71 encounter times for 11 males and 63 encounter times for 11 females. The average of 92 encounter times in winter (not including censored events) was 19.5 days (95th percentile = 16.1–23.1 days) and the average of 109 encounter times in summer was 12.8 days (95th percentile = 10.0–16.0 days; Fig. 2). Stream density in the 80% MCP of wolverines was 0.72 km² (95th percentile = 0.62–0.82 km/km²) and road density was 0.56 km² (0.48–0.64 km/km²).

We found that encounter time was best represented with a reduced model that included days until spring as an explanatory variable (Model #2, Table 2). The hazard ratio from the top model indicated that wolverine encounter time with large-prey events decreased nearer to spring (Table 2, Fig. 3).

Residency time.—Wolverines visited large-prey events 235 times in winter and their average residency time per visit was 1.5 days (95th percentile = 1.24–1.77 days). Wolverines visited large-prey events 415 times in summer and their average residency time per visit was 0.74 days (95th percentile = 0.61–0.88 days). The average total time spent by wolverines in winter at 113 large-prey events was 3.11 days (95th percentile = 2.62–3.63 days) and the average total time spent by wolverines in summer at 152 large-prey events was 2.08 days (95th percentile = 1.70–2.51 days; Fig. 2). Wolverines made 401 return visits to large-prey events and the average number of return visits per large-prey event was 1.62 return visits (95th

Table 3.—The average spatial attributes of wolverine (*Gulo gulo luscus*) beaver-predation events, ungulate-scavenging events, resting events, and other events (small-scavenging events, grouse and snowshoe hare kills) identified in the field between 2013 and 2016 in Alberta, Canada. The attributes of events were calculated using a GPS data clustering algorithm and included the actual points (the number of GPS relocations within 200 m of the geometric center of the cluster), away points (the number of GPS relocations outside of 200 m of the geometric center of the cluster), cluster radius (distance from geometric center of a cluster to farthest GPS relocation), and distance (average distance of each GPS relocation to the geometric center of the cluster). Averages were calculated using a non-parametric bootstrap (10,000 iterations), numbers in parentheses are 95th percentile range.

Event characteristic	Beaver-predation event ($n = 21$)	Ungulate-scavenging event ($n = 12$)	Resting event ($n = 48$)	Other event ($n = 26$)
Actual points	23.13 (16.81, 30.19)	20.25 (12.50, 29.08)	7.31 (5.94, 8.92)	5.04 (4.08, 6.20)
Away points	14.28 (5.62, 24.47)	36.40 (25.17, 47.17)	4.15 (1.69, 7.10)	0.69 (0.11, 1.50)
Radius	134.29 (106.00, 165.10)	157.30 (118.80, 194.60)	72.00 (58.94, 84.92)	62.31 (46.16, 80.73)
Distance	51.90 (38.90, 65.71)	71.57 (56.75, 84.92)	35.46 (29.21, 42.42)	38.54 (28.42, 49.20)

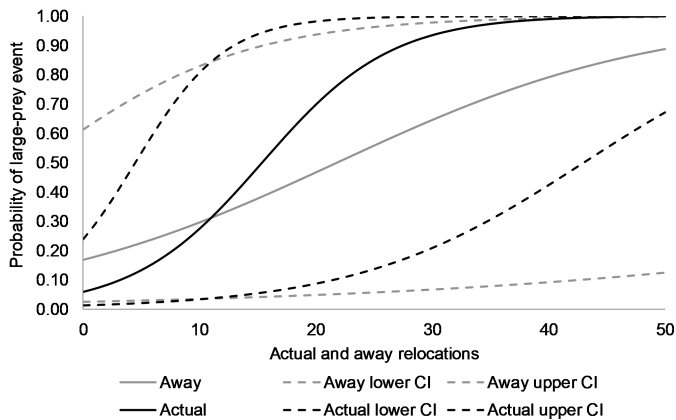


Fig. 1.—Logistic regression model that measures the effect of an increasing number of actual and away points on whether an event would be classified a large-prey (designated “1” in logistic model; $n = 33$) or multi-use event (designated “0” in logistic model; $n = 74$). Actual points are the number of GPS relocations within 200 m of the geometric center of the cluster and away points are the number of GPS relocations outside of 200 m of the geometric center of the cluster.

percentile = 1.45–1.80 return visits). There were 248 visits to large-prey events where another wolverine had been detected at the event and the average residency time during these visits was 1.12 days (95th percentile = 0.99–1.45 days). There were 402 visits to large-prey events where another wolverine was not detected at the event and the average residency during these visits was 0.89 days (95th percentile = 0.73–1.06 days). The average number of concurrent events visited per large-prey event was 3.25 concurrent events (95th percentile = 3.07–3.44 concurrent events).

We found that residency time was best explained by a full model that included cumulative time, concurrent events, season, and wolverine (Table 2). As predicted, wolverine residency time decreased as the cumulative time at a large-prey event increased (Fig. 4) and as the number of concurrent sites visited by the wolverine increased. We also found that wolverines increased their residency time at large-prey events in the winter and when other wolverines were present at the event (Table 2).

We did not find a difference in the residency time of wolverines at beaver-predation ($n = 21$) and ungulate-scavenging events ($n = 12$) visited in the field. We found that the total time (residency time across visits) wolverines spent at beaver-predation events was 2.9 days (95th percentile = 2.09–3.87 days) spread across an average of 1.7 visits (1.10–2.45 visits). Wolverines spent 3.15 days (95th percentile = 1.57–4.90 days) at ungulate-scavenging events spread across 2.1 visits (1.5–3.1 visits).

Return time.—Wolverines left large-prey events and eventually returned 138 times in winter and their average return time was 10.12 days (95th percentile = 7.99–12.56 days). Wolverines left large-prey events and eventually returned 264 times in summer and their average return time was 8.39 days (95th percentile = 7.18–9.74 days) (Fig. 2). The average number of departures from large-prey events was 2.89 departures (95th percentile = 2.77–3.01 departures) and the average number of concurrent events visited while away was 3.55 concurrent

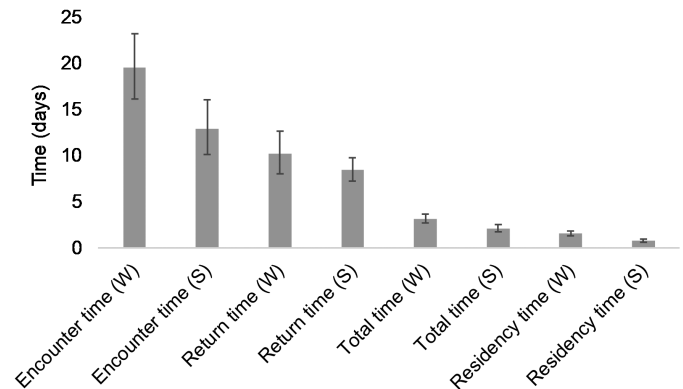


Fig. 2.—Winter (1 November to 1 April) and summer (2 April to 31 October) averages of encounter time, return time, total time (sum of residency time across visits), and residency time per visit at large-prey events. Averages were calculated using a non-parametric bootstrap (10,000 iterations). Averages for all variables except encounter time were identified with 109 large-prey events in winter (W) and 134 large-prey events in summer (S). There were 92 (W) and 109 (S) large-prey events used for the encounter time averages because there was no encounter time leading up to the 1st encounter with a large-prey site during a monitoring period.

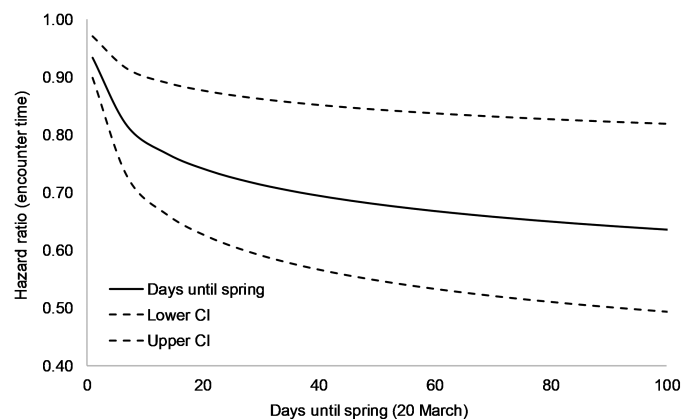


Fig. 3.—Cox proportional hazards model of wolverine (*Gulo gulo luscus*) encounter time (days) with large-prey events ($n = 234$) as a function of days until spring (20 March). An increase in the hazard ratio (risk) equates to a decrease in encounter time.

events (95th percentile = 3.31–3.78 concurrent events). There were 248 departures from large-prey events where another wolverine was detected and the average return time was 8.89 days (95th percentile = 7.25–10.73 days). There were 402 departures from large-prey events where another wolverine was not detected and the average return time was 9.04 days (95th percentile = 7.63–10.63 days).

We found support for the hypothesis that return time is best explained by a model that included cumulative time, concurrent events, season, and individual wolverine (Table 2). Wolverine return time increased as the cumulative time spent at a large-prey event increased (Fig. 4), increased with the number of concurrent events, and increased in winter. The confidence interval for individual wolverine crossed zero indicating a variable effect on residency time of having another present at the large-prey event (Table 2).

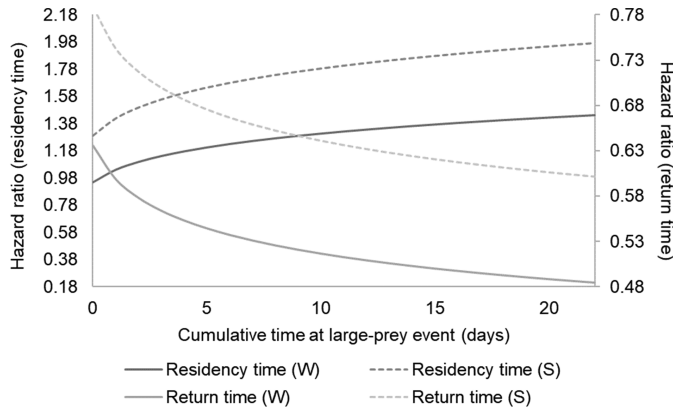


Fig. 4.—Wolverine (*Gulo gulo luscus*) residency and return time (days) to large-prey events in winter (W, 1 November to 1 April) and summer (S, 2 April to 31 October) seasons in relation to the cumulative time spent by a wolverine at an event. Hazard ratios were calculated using models of Cox proportional hazards. An increase in the hazard ratio (risk) equates to a reduction in return time and an increase in residency time.

DISCUSSION

We show that wolverine foraging behavior is dynamic in response to environmental change. Our analysis of encounter time indicates that the availability of large prey to wolverines is not uniform throughout the year. We found that wolverines encountered large prey more often in the spring. We suspect that during spring, wolverines have greater access to beavers that are outside of their lodges or dispersing (Sun et al. 2000; Gable et al. 2016). Moreover, ungulate carcasses are more available to wolverines in the spring when large predators often kill ungulates weakened after winter and from poor-snow conditions (e.g., DelGiudice et al. 2002; Smith et al. 2004). The increased availability of prey to wolverines during spring is hypothesized to be important to their reproductive success (Inman et al. 2012b). Large prey also might increase in availability in the fall when beavers are building structures for winter and hunters are killing ungulates and leaving carcass remains. However, we were not able to predict large-prey events in late-September and October because batteries on GPS collars were depleted.

Our metric of encounter time is similar to kill rate calculated for other predators. We found that the rate of wolverine encounters with large prey was approximately 0.36 encounters/week in winter and 0.55 encounters/week in summer. Cougars (*Puma concolor*) in Alberta killed approximately 0.8 ungulates/week with some of these “kills” likely being scavenging events (Knopff et al. 2009). Without including scavenging, Amur tigers (*Panthera tigris*) made 1.08 kills/week (Miller et al. 2013) and wolves in Yellowstone National Park made 0.48 kills/week (Smith et al. 2004). Although wolverine encounter time with large prey is lower than that of the other predators discussed above (especially considering that our metric included predation and scavenging), wolverines also are much smaller in size than these predators and likely require less energy. Wolverines also are adept at subsidizing their diet with small

prey such as snowshoe hares and grouse (Lofroth et al. 2007). The most comparable estimate of a kill rate for wolverines is from Scandinavia, where wolverines killed between 0.23 and 0.47 semi-domestic reindeer/week. We note that wolverines in Scandinavia would likely encounter large prey at a similar or greater rate than what we observed in Alberta if they included scavenging and feeding on other large-bodied prey (Mattison et al. 2016).

Foraging theory provides a basis from which to interpret wolverine handling time once large prey is found. Optimal foraging theory relates predator behavior in habitat patches to prey availability. According to the law of diminishing returns, a predator reduces time in a patch as prey become more scarce and difficult to obtain (Charnov 1976). We suggest that sites where large prey are found or killed by wolverines have similar characteristics to prey patches: both can be depleted and ultimately exhausted by the predator. We found that wolverines decreased residency time and increased return time with each revisit to a large-prey event as their cumulative time at the event increased. These patterns suggest that biomass becomes harder for wolverines to acquire over time, which reduces the reward for wolverines to stay long or return quickly after multiple visits. Wolverines might eat much of the available tissue in the 1st visit to large-prey events and return for cached bones and other scattered remains during subsequent visits.

Wolverine handling time also was affected by the winter and summer seasons. We found that residency time (per visit), total time (sum of residency time across visits), and return time were all greater at large-prey events in the winter relative to the summer. We speculate that these patterns are related to prey availability. For example, less abundant prey in winter might cause wolverines to reside at large-prey events longer to make use of available energy. Moreover, decreased residency time in summer could be because beavers are easier for wolverines to capture (e.g., Knopff et al. 2010b) or because large-prey tissues deteriorate more quickly due to warmer temperatures (Farwig et al. 2014). The combination of decreased residency time in summer and good traveling conditions without snow might decrease wolverine return times to large-prey events. Future research could attempt to better understand the drivers of these patterns.

Our results indicate that territoriality and competition might influence wolverine foraging behavior. Researchers hypothesize that wolverines defend their food supply and mates (Bischof et al. 2016). If wolverines were not territorial, they might reside at foraging sites until all biomass was consumed to increase energy intake. However, we found that wolverines often left large-prey events after 1–2 days and did not return for 8–10 days. This return time is similar to the estimate of time needed by wolverines to travel the circumference of their home range (~1 week—Inman et al. 2012a), suggesting that wolverines are leaving carcasses of large prey to defend their territories. If another wolverine was detected at a carcass, we found evidence that wolverines would increase their residency time. Similar to red foxes (*Vulpes vulpes*—Mukherjee et al. 2009), detection of competitors might cause the wolverine to reside in

the area longer to defend the kill, consume more, or to cache food items in the surrounding area before departing to other parts of its territory.

Territoriality also might affect how wolverines allocate time to foraging when they have multiple large prey available to them. We found that wolverines reduced residency time and increased return time at large-prey events with each additional site they were visiting concurrently. If wolverines kept residency and return time constant as more foraging sites were found, it would mean other aspects of the wolverine's time budget would likely have to be reduced. By reducing their foraging time at large-prey events when prey are more available, wolverines can visit all of the events while still leaving time for other activities important to their fitness, such as searching for mates and defending territorial boundaries.

Our predictive modeling did not differentiate wolverine behavior based on the prey species at an event because there were too few large-prey events of specific species that could be used for model development. However, we did summarize wolverine residency time and revisits at beaver-predation and ungulate-scavenging events but did not find a statistical difference in these values. If handling time was related to biomass consumption (Knopff et al. 2010b), our results indicate that wolverines acquire equal amounts of biomass when killing a beaver and scavenging on an ungulate carcass. We note, however, that handling time is related to finding, accessing, and consuming prey. In this case, wolverines might have to dig through beaver lodges in winter to kill beavers, increasing handling times. We also documented wolverines residing in beaver lodges or under ice after killing them. Our methods did not allow us to determine how wolverines allocated their time to each of these activities and therefore might not provide an accurate estimate of biomass consumption.

Another weakness of our methods was that we used the spatial and temporal attributes of field-visited foraging events in winter to predict foraging events in the summer. For example, it is possible that we under-predicted the number of large-prey events in summer because winter residency times at large-prey events, which were used to develop the models, tend to be greater than those in summer. However, our top-event model did successfully predict the 7 foraging sites we visited in the summer (2 large-prey and 5 multi-use events), providing validation of our methods.

We also used a clustering algorithm designed for cougars (Knopff et al. 2009) to detect foraging sites for wolverines. Cougars may have unique behaviors during feeding that would make the clustering algorithm ineffective at identifying wolverine feeding sites. However, like wolverines, cougars also have been documented to behave as scavengers that cache prey (Knopff et al. 2010a).

Our results provide insight into the foraging behavior of wolverines and provide evidence of the seasonal availability of prey in northern Alberta. We found that wolverines spent considerable amounts of time foraging for large prey, which suggests they are important to the energy balance and reproductive success of the wolverine population. Managers should ensure that large prey, such as beavers and moose, are managed sustainably in boreal

habitats used by wolverines. For instance, in industrial landscapes, borrow pits can serve to increase the beaver population (Scrafford et al. 2017b) and hunting and trapping quotas can be used to manage the availability of moose and other large prey to wolverines.

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