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ARTICLE

Methods, Tools, and Technologies

How to find a wolverine: Factors affecting detection at wolverine (*Gulo gulo*) bait stations in western Canada

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Abstract

High individual detection success enables precise estimates of density and the ability to monitor trends in abundance for wolverine and other low-density species, information that is critical for the implementation and assessment of conservation measures. We evaluated a dataset that included six different wolverine capture–recapture studies over a large gradient in wolverine (*Gulo gulo*) density to provide recommendations for increasing detection. We examined factors related to bait station components, habitat, and seasonal timing. Accounting for variation in wolverine density and trap duration, our results suggest that bait stations setups having a run pole, frame, and camera to photograph unique ventral color patterns, in addition to hair snag devices, identify more individual wolverine than those without. The presence of snow is a habitat feature that also increases individual detection. Female detection rates were lower than male detection rates at the onset of the reproductive denning season in late February and early March compared with January and early February. We found latency to detection was independent of wolverine density, but greater in areas with human influence. Relatively high rates of genotyping success (55%) were predicted by even a single guard hair left at bait stations, while underfur required ~15 hairs for similar success. Longer

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sampling intervals reduced genotyping success in spring, more so for underfur than guard hair. Hair samples acquired from barbwire were of higher quality than those from either alligator clips or gun brushes. To improve individual detection for wolverine inventory and monitoring, we recommend deploying run pole setups in areas with low human disturbance that will retain snow into late spring. Extending the winter trapping effort into April and May could increase the chances of detecting denning females. Latency to detection suggests that traps should be active for more than a month, especially in human-influenced areas, but genotyping success suggests that traps should also be cleared of hair samples at smaller intervals of a month or less, during late winter/spring.

KEYWORDS

bait station, capture–recapture, detection, genotyping success, *Gulo gulo*, inventory, monitoring, noninvasive sampling, study design

INTRODUCTION

For species at risk, knowledge of population size and trend is a priority for successful management and conservation. Imprecise population estimates can hinder the ability to detect trends over time and preclude effective conservation actions. However, species at risk are distinguished by low or declining density, which can lead to difficulties with estimating remaining populations (Ellison & Agrawal, 2005; Green et al., 2020; Kéry et al., 2011; Schaub et al., 2007).

Wolverine (*Gulo gulo*) are one such species. They are characterized by low population density and inhabit remote and often rugged terrain that makes assessment of population status challenging (Fisher et al., 2022). Population dynamics in North America are largely inferred from harvest records, and reliable knowledge of population trends is almost completely lacking (Fisher et al., 2022; Slough, 2007; see Barrueto et al., 2022 for the exception).

The advent of noninvasive genetic sampling has greatly facilitated the ability to inventory rare species, using DNA from hair, scat, or other material (Schwartz et al., 2007; Waits & Paetkau, 2005). Early attempts to collect wolverine hair for noninvasive genetic sampling with box traps, barbwire corrals, or rub pads detected few wolverine (Mowat et al., 2003). Later bait station designs developed by Magoun et al. (2011) and Mulders et al. (2007) have been deployed with considerable success for estimating wolverine population size and density (Barrueto et al., 2020; Mowat et al., 2020; Royle et al., 2011), as well as distribution and connectivity (Fisher et al., 2013; Heim et al., 2017; Kortello et al., 2019; Sawaya et al., 2019).

Accurate population estimates can be generated using spatially explicit capture–recapture methods (Conner et al., 2016; Pozzanghera, 2015; Royle et al., 2011) but this necessitates individual identification of animals. While modern statistical techniques can account for imperfect detection at bait stations (Efford, 2004; MacKenzie et al., 2017), the power to assess significant population change is facilitated by high detection probabilities (Ellis et al., 2014; Green et al., 2020; Keiter et al., 2017; Morin et al., 2022). Detectability is often related to density (Kéry, 2002; Royle & Nichols, 2003; Walsh et al., 2018) and for low-density species like wolverine, low detection rates add uncertainty to population estimates (Keiter et al., 2017). Consequently, understanding the factors affecting detection is crucial for developing effective sampling designs, but existing information for wolverine has been piecemeal.

Robinson et al. (2017) examined factors affecting multispecies bait station detection in northern Idaho and southeastern British Columbia (BC). This included latency to detection (LTD), seasonal timing, and the influence of habitat on detection. However, low wolverine numbers in their study area and sparse detections limited their conclusions for this species.

Bait stations for wolverine individual genetic identification can be set up in various ways, components include a hair snag device, a bait or lure attractant, and possibly a camera. As wolverine may visit a bait station but not leave a hair sample, Fisher and Bradbury (2014) determined that wildlife cameras increased the effectiveness of bait stations for species identification over genetic sampling alone but did not assess individual identification. Mowat et al. (2020) reported a weak effect of bait type on detection.

Wolverine habitat selection likely affects individual detection success in a hierarchical fashion. While density reflects the location of home ranges within an animal's distributional range, individual detection may also be affected by behavior and habitat use at finer scales, such as foraging or denning habitats. For systematic sampling in remote terrain, safety and logistics often limit bait station placement choices, and habitat features that constrain access (i.e., avalanche terrain, roads) may affect detection (Fisher & Bradbury, 2014). For example, Stewart et al. (2016) showed that wolverine were more inclined to interact with bait stations in protected areas with low anthropogenic disturbance.

As sparsely distributed scavengers that locate carrion, and hence bait stations, using olfactory cues (Green et al., 2012), landscape attributes that aid scent dispersal and facilitate travel or encounter rates may affect detection. Scent dispersal is a diffusive process affected by climate, particularly temperature and wind, and topography (Conti et al., 2020). Cool temperatures retain scent while surface features such as vegetation that provide wind resistance impact odor plumes, affecting scavengers' ability to locate carrion (Ruzicka & Conover, 2012). Wolverine density, distribution, dispersal, and reproduction have all been connected to snow (Copeland et al., 2010; McKelvey et al., 2011; Mowat et al., 2020; Schwartz et al., 2009), and olfactory processes are also affected by snow. Snow crystals readily absorb and retain volatile organic compounds, which are released by carcass decomposition (Herbert et al., 2006; Verheggen et al., 2017). Wolverine have also been shown to select deeper, denser snow for travel (Glass et al., 2021) and prefer travel routes along drainage bottoms (Heinemeyer et al., 2019).

Seasonal timing affects the detection of other carnivores (Lamb et al., 2016) and likely wolverine as well. Bait stations are typically deployed in winter, when alternative food sources are fewer, hibernating bears pose less risk to researchers, and cold temperatures aid DNA preservation (Mulders et al., 2007). Fisher et al. (2013) noted higher wolverine occurrence at bait stations in late winter, but since wolverine readily revisit traps once they have been captured (Barrueto et al., 2020; Mowat et al., 2020; Royle et al., 2011), the link between this seasonal effect and the detection of new individuals is unclear. Wolverine maternal denning occurs from approximately February to April (Inman, Magoun, et al., 2012; Magoun & Copeland, 1998), and females with young have restricted movements during this period, especially in the first few weeks after parturition (Aronsson et al., 2023; Landa et al., 1998). This likely decreases female encounters with bait stations, and detections, during this period.

Understanding how long animals take to arrive at bait stations is useful for gauging species response to sites and determining the minimum length of time for deployment. As scavengers, wolverine have numerous avian and mammalian competitors that may decrease the potential energetic gain per carcass. Hence, rapid arrival times would be advantageous. Robinson et al. (2017) reported a median time to detection of 29 days but did not assess factors affecting latency.

Individual identification also depends on the collection and genotyping of hair samples, although run pole setups may circumvent this requirement by identifying individuals through photographs of distinct ventral patterns (Magoun et al., 2011; Royle et al., 2011). Genetic analysis protocols and error checking produce consistent results, but poor sample quality can preclude successful genotyping (Kendall et al., 2009; Paetkau, 2003). Robinson et al. (2017) found that seasonally colder temperatures during winter retained adequate DNA quality over long trap deployments for multiple species, but sun exposure and frequent melt–freeze cycles in late winter and spring may reduce DNA quality (Stetz et al., 2014). The effect of hair type, numbers, and environmental exposure on genotyping success has been examined for black (*Ursus americanus*) and grizzly bears (*Ursus arctos*) and American marten (*Martes americana*; Lamb et al., 2016; Mowat & Paetkau, 2002; Stetz et al., 2014; Tredick et al., 2007), but not for wolverine.

To aid continued research and monitoring efforts for wolverine, and make effective use of available resources, we used a modeling approach to evaluate the factors affecting individual detection for a network of bait stations across western Canadian mountain ranges, the first time this has been done on a large scale for wolverine. We examined the effects of trap type, habitat, sampling schedule, and sample quality on individual wolverine detections. Six different projects spanning seven winter and spring seasons across a wide range of wolverine densities provided our dataset. Our objective was to assess the most effective methods for noninvasive hair trapping of wolverine and provide recommendations for maximizing detection in future work.

METHODS

Study area

The ~74,000 km^2 study area included the Columbia and Rocky Mountain ranges and foothills of southeast BC and southwestern Alberta (Figure 1). All of the study area was within the wolverines' contemporary range in

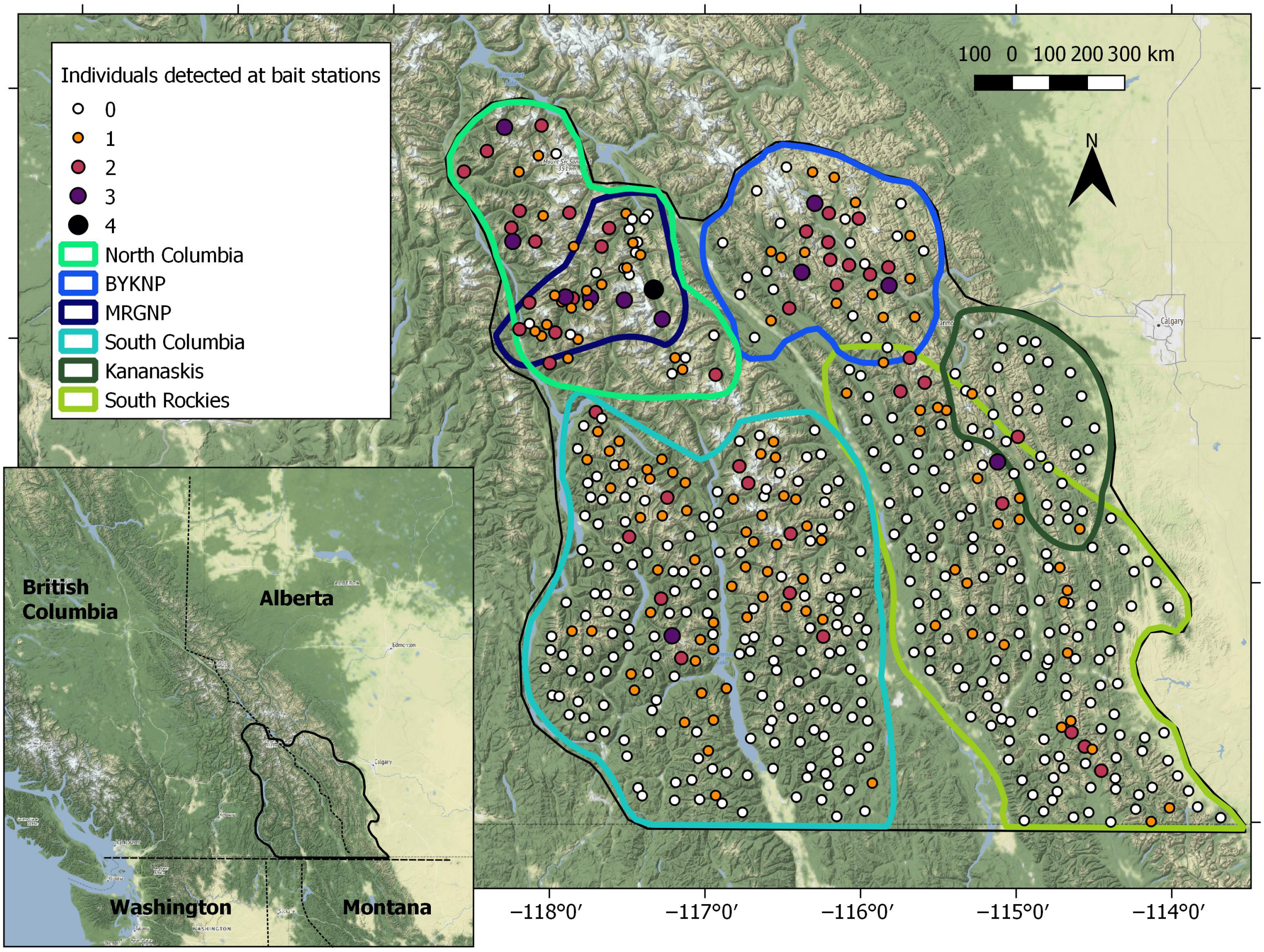

FIGURE 1 Wolverine winter sampling areas in southeast British Columbia and southwest Alberta, Canada, showing sampling area boundaries, bait station locations, and the number of different individuals detected. BYKNP, Banff, Yoho, and Kootenay National Parks and nearby crown lands; MRGNP, Mount Revelstoke and Glacier National Parks and nearby crown lands.

western Canada, as defined by recent harvest records (Lofroth & Ott, 2007; Webb et al., 2013) but wolverine density varied considerably, generally increasing from south to north and east to west (Mowat et al., 2020). Elevations ranged from 400 to >3000 m, with large regional variation in seasonal precipitation. At lower elevations, forests consisted of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and western larch (*Larix occidentalis*). At higher elevations, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests give way to treeless alpine meadows, rock, and ice (MacKillop & Ehman, 2016).

Major transportation corridors crossed the study area latitudinally, including the TransCanada highway (Hwy 1) in the northern portion of the study area and the Crowsnest highway (Hwy 3) in the south. Smaller highways and human settlements were located in low elevation valleys. Extensive forest harvesting has occurred throughout the area and mining was widespread historically, less so currently. Both industries left a legacy of road networks extending to subalpine areas in many watersheds. Winter recreation (snowmobile use, ski resorts, helicopter or snowcat-access skiing, ski lodges, backcountry skiing) was prevalent in the area. Regulated trapping of wolverine occurred on crown lands in Alberta and BC during the years sampled. Parks and protected areas made up ~25% of the land base.

Sampling

We used noninvasive techniques in winter and spring to collect hair samples from wolverines in six sampling areas (Figure 1, Table 1) between 2011 and 2018. Sampling occurred on public lands in habitat consistent with wolverine use. Each study area was partitioned

TABLE 1 Wolverine sampling effort and detection success across six sampling areas in southeastern British Columbia and southwestern Alberta, Canada, between 2011 and 2018.

Sampling area	Year	Area sampled (km^2)	No. sites sampled	No. sessions	Setup	Bait	Camera present	Total no. individuals (F/M)
BYKNP	2011	8400	44	3	Tree	Beaver	Yes	22 (9/13)
Kananaskis	2012	4500	34	4	Tree	Beaver	Yes	4 (2/2)
MRGNP	2011, 2012, 2014, 2015	3900	33	3	Tree	Beaver or domestic animal	Yes	26 (15/11)
South Rocky Mountains	2014–2016	21,400	163	3	Tree	Beaver	Yes	23 (15/8)
South Columbia Mountains	2012–2016	25,000	228	2	Tree	Ungulate or beaver	Rarely	40 (24/16)
North Columbia Mountains	2018	9900	25	2	Runpole	Beaver	Yes	25 (17/8)

Note: Year was the year at the end of the sampling winter. Within a sampling area, different years sampled different subranges or areas. Sessions were the number of intervals that the bait stations were checked during the deployment, and detections were the total number of times wolverine was detected at different sites. We only include data for the first detection of each individual at a site, but some individuals were detected at multiple sites.
Abbreviations: BYKNP, Banff, Yoho, and Kootenay National Parks and nearby crown lands; F, female; M, male; MRGNP, Mount Revelstoke and Glacier National Parks and nearby crown lands.

into 10 × 10 km or 12 × 12 km cells that approximated the minimum size of a female home range. One or, rarely, two bait sites were placed in each cell, and bait sites were checked between two and four times over the course of the winter at approximately three- to four-week intervals.

Hair traps prior to 2018 followed Fisher et al. (2013), consisting of a tree wrapped in barbwire, with bait nailed above the wire ~2 m from the ground or snow surface. We refer to these as tree traps because trees were the primary structural component (Figure 2). Most tree setups included a camera attached to a second nearby tree to photograph animals that visited the site, except in the south Columbia mountains, where few cameras were deployed.

In 2018, we used a different configuration, with a 1.2 m horizontal piece of lumber attached to a tree ≥1 m from the snow or ground (Magoun et al., 2011). A frame was mounted to the distal end of the lumber and bait was positioned on a cable strung between that tree and another tree, ~4 m away, such that the wolverine must climb onto the frame to access the bait, exposing its ventral side. A camera was mounted to photograph distinct individual markings on the wolverine's throat and chest. Alligator clips tethered to the frame collected hair samples when triggered and the run pole support tree was wrapped in barbwire. For more details refer to Magoun et al. (2011). We refer to this as a run pole setup.

For bait we used a beaver carcass (*Castor canadensis*), ungulate head or quarter. In Mount Revelstoke and Glacier National Parks (MRGNP), meat from domestic animals, a pig head or beef roast, was used during 2014, and beaver otherwise. We used a commercial scent-based long-distance lure (Caven's Gusto Long Distance Call, Minnesota Trapline Products, Pennock, MI, USA), smeared on a rag and suspended from a tree branch at all sites.

During each check the barbwire was examined for hairs and the bait replenished if necessary. Hair was collected and stored in paper envelopes in a dry environment.

For our evaluation of genotyping success from wolverine hair samples, we used additional hair sample data from a concurrent study in the United States that was adjacent to the study area for the detection analysis. This study used beaver bait and tree setups with 30 caliber bronze gun brushes arranged in two concentric circles, at 30 and 45 cm below the bait, instead of barbwire, to remove hair (Robinson et al., 2017).

Hair samples were sent to Wildlife Genetics International (WGI) in Nelson, BC, for microsatellite genotyping. Only samples that had ≥1 guard hair with a root or ≥5 underfur were selected for analysis, and we used up to 10 guard hairs or approximately 30 underfur in an extraction when available. DNA was extracted using QIAGEN DNeasy Tissue kits, following the manufacturer's instructions (Qiagen, Toronto, ON). Species identification was based on a sequence-based analysis of a segment of the mitochondrial 16S rRNA gene (Johnson & O'Brien, 1997). For samples that yielded wolverine DNA, WGI utilized multilocus genotyping, consisting of a ZFX/ZFY sex marker, and seven additional microsatellite markers for individual identification. Individual identifications were error-checked, following established rules that yield very low error

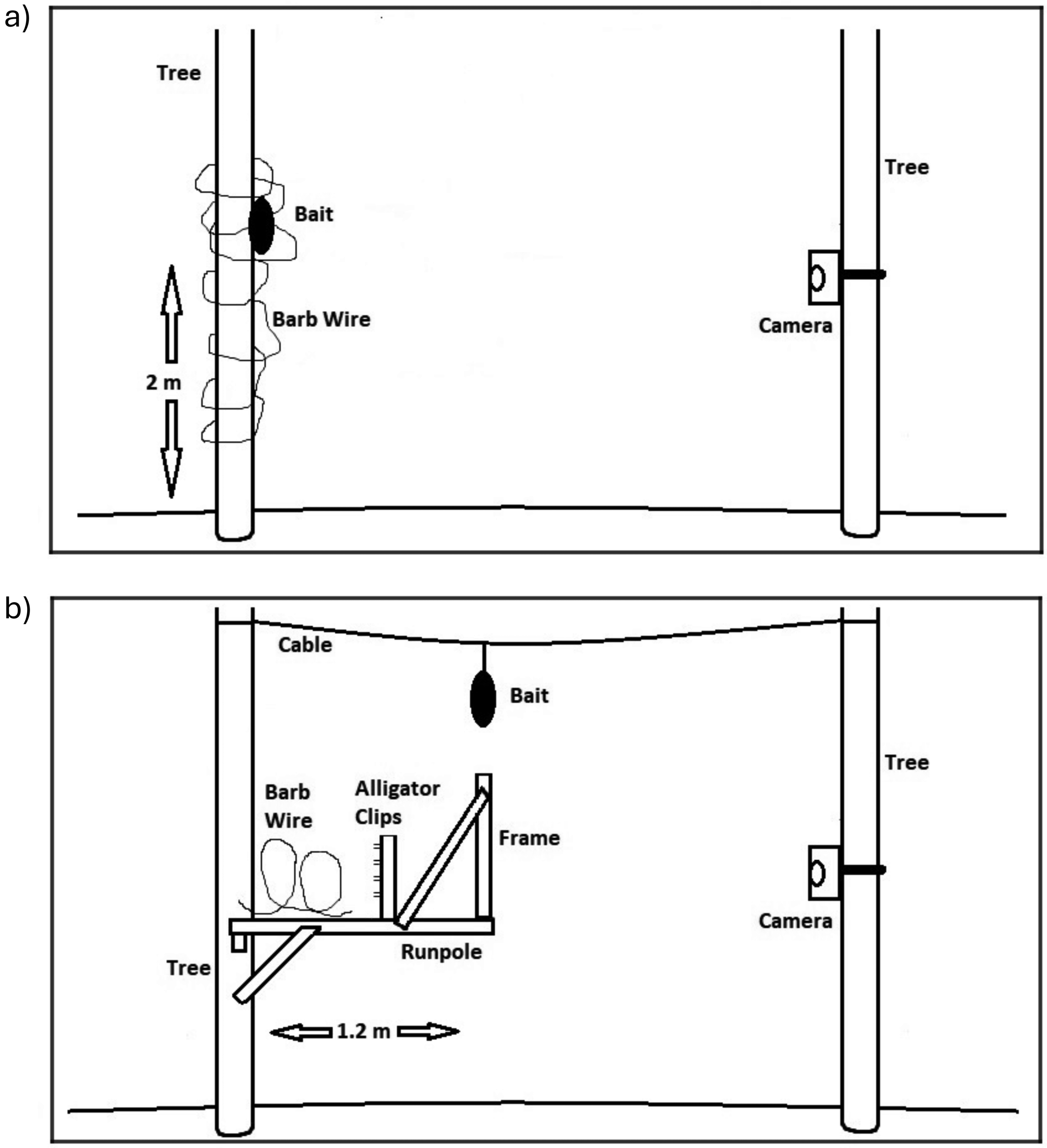

FIGURE 2 (a) Tree bait station setup for noninvasive hair snagging of wolverine. Cameras were present in Banff, Yoho, and Kootenay National Parks and nearby crown lands, Mount Revelstoke and Glacier National Parks and nearby crown lands, Kananaskis and almost all south Rockies sites, but were used only occasionally in south Columbia. (b) Runpole bait station setup used in north Columbia.

rates (Kendall et al., 2009; Paetkau, 2003). The studies in the national parks were analyzed at the Rocky Mountain Research Station laboratory in Missoula, Montana, using nearly identical methods. One sample from each individual was reanalyzed at WGI, to verify individual identities were comparable between the labs (Mowat et al., 2020).

To preclude learned behaviors affecting the independence of our observations for our analysis of wolverine detection at bait stations, we only used bait stations deployed in areas where wolverine were thought to be naïve; that is, we included only data from the first of multiple years of sampling and only included the first detection of an individual at a particular bait station within years. The sample unit for the genotyping analysis was the hair sample collected from the snagging device and this potentially included multiple detections of the same individual.

Detection variables

We used variables related to timing, habitat, and methodology. To examine the broad-scale effect of the timing of bait station deployment on detection, we assigned a value for the week of year that a bait station was first deployed (FIRSTWEEK), sequentially, with the last week of November as week 1, and increasing with subsequent weeks to 31 March, week 18, and included this in our models.

Our habitat variables considered vegetation, snow, and anthropogenic factors. In montane environments, wolverine occupy upper elevation forests and females den near treeline (Inman, Packila, et al., 2012; Krebs et al., 2007; Magoun & Copeland, 1998). We predicted that bait stations situated near open, alpine terrain would have increased scent dispersal and higher detections than those in closed forest habitat. We separated mapped vegetation communities into two broad zones: (1) alpine, including rock, alpine tundra and grassland, alpine parkland and woodland ecosystems; and (2) forest, grouping Engelmann spruce–subalpine fir typical of subalpine areas and lower elevation forests of pine, Douglas fir, cedar, and hemlock. We calculated the percent area of alpine vegetation types in a 10-km radius from the sampling location to index the influence of alpine versus forest on detection (ALPINE).

To assess the influence of snow cover and depth on wolverine detection, we measured late winter snow depth (SNOW) at each site when it was last checked in April or early May. This period is the onset of spring melt, when snow depths were highly variable among sites. We predicted that the amount of snow at each bait station would positively influence detection.

Landscape topographic position influences movement (Heinemeyer et al., 2019) and scent dispersal (Conti et al., 2020), conceivably affecting detection. From a sampling standpoint, topographic position can also affect the difficulty in deploying and accessing a site. For our categorical topography variable, we classified trap locations as valley bottom, ridgetop, mid-slope, or on a pass, if the site was located at or near the apex of major watersheds or terrain breaks (TOPO: valley, ridge, mid-slope, pass). Passes concentrate travel routes between watersheds and funnel air movement. We expected higher detection on passes than other topographic features.

Stewart et al. (2016) found that wolverine behaviors at bait stations varied with human footprint on the landscape. Wolverine in areas with high human use were less inclined to climb the tree to the bait. We used Human Influence Index (HUMANII) mapping as a generalized measure of anthropogenic disturbance (http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic) to test this hypothesis in our area. We created a measure of human disturbance by calculating the mean HUMANII in a 10-km radius window around each site.

In steep montane habitats, safety and access limit the location of traps on the landscape. All bait station locations required avalanche terrain avoidance. Traps deployed using trucks or snowmachines were limited by proximity to plowed or unplowed roads, respectively, while traps deployed using helicopters were limited by the availability of safe landing sites (openings in forest). Ski access was limited by distance (typically <6 km from roads). However, Heinemeyer et al. (2019) found that wolverine avoided areas with human recreational disturbance, both motorized and nonmotorized, and Scrafford et al. (2018) found that wolverine avoided roads. We compared detection among bait stations with ski, truck, snowmachine and helicopter access (ACCESS: ski, truck, snowmachine, heli). We predicted that helicopters would access terrain with less human disturbance, and this would result in more wolverine detections. We recognize that access is related to the HUMANII index described in the previous paragraph, at a different scale.

For variables related to methodology, we considered both bait type and trap configuration. Bait is a critical component of hair trap stations. Although wolverine are opportunistic scavengers, fat content, odor, and familiarity might all potentially affect the attractiveness of bait and hence detection. We compared detection when using beaver, ungulate heads, domestic meats (beef roasts and pig heads) and ungulate quarters, in a categorical variable BAIT.

The two different categories of trap configurations for our bait stations, run pole and tree, comprised our SETUP variable. In tree setups, cameras (CAMERA) may or may not be used, but their use provides additional information on wolverine presence (Fisher & Bradbury, 2014) and could conceivably affect the search effort for cryptic hair samples. However, the presence of a camera is an integral part of run pole setups, and in this context can provide individual identification independent of hair samples. Since wolverine may visit a bait station without leaving hair, we predicted higher detection for run pole bait stations versus the reference tree setups.

Analytic approach

We approached the question of wolverine detection from several different angles. First, we modeled methodological and spatial factors affecting individual detection at bait stations. Next, we examined fine-scale temporal variation in detection over the onset of reproductive denning in females. Then we evaluated the same detection factors as predictors of LTD because we felt that it might provide insight into the behaviors driving detection. Finally, we assessed the impact of sample quality (type and number of hairs, length of exposure to environmental conditions) on genotyping success and compared sample quality between different hair-snagging devices.

Individual detection

Although SECR models allow the estimation of covariates for detection probability concurrent with density, models become intractable with large numbers of covariates. Instead, we modeled variables affecting wolverine detection using generalized linear models (GLM; Poisson errors, log link). Our response variable was the number of unique individuals (0–4) identified at each bait station, scaled by the offset terms, DENSITY and DURATION. These terms account for unbalanced sampling between trap sites with respect to both underlying densities and the length of time that traps were deployed, as both are known to functionally influence detection. We used the estimates of wolverine density (DENSITY) presented in Mowat et al. (2020), taking the mean density in a 10-km radius window. Since the onset, duration and number of sessions among sampling areas was highly asynchronous, we measured the total number of days that a station was operational (DURATION) and used this as a second offset term in all detection models.

We used residual plots and checked for over- or under-dispersion to determine the most appropriate type of error distribution. We ran nested models to evaluate sex-based differences, using the number of unique males or unique females. All analyses were conducted in software package R version 4.1.1 (R Core Team, 2021).

We checked for potential nonlinear relationships between detection and its covariates by plotting univariate response curves. Where a nonlinear relationship was suggested, we transformed the original data and selected the form of the covariate having the lowest corrected Akaike information criterion for small sample sizes (AIC_c) in subsequent analyses (Burnham & Anderson, 2002). The variables HUMANII, ALPINE, and SNOW were $\log_{10}$-transformed to normalize their relationship with the number of individuals detected. A small constant (0.0001) was added to each to facilitate handling of zeros.

We assessed collinearity and multicollinearity using Spearman's correlation coefficients and variance inflation factors (VIF) using cutoff values of $\rho > 0.6$ or $\text{VIF} > 3$, respectively (Glasser & Winter, 1961; Zuur et al., 2010). Comparisons between bivariate and continuous covariates used a Pearson's point-biserial correlation, to avoid tied values. For pairs of correlated covariates, we retained the one with the most direct causal link to the response. When this was not clear, we used the covariate with the lowest AIC value.

We calculated AIC_cs and log likelihoods for univariate models of all variables. Our global model included ALPINE, SNOW, TOPO, CAMERA, ACCESS, BAIT, FIRSTWEEK, and SETUP, with offset terms DENSITY and DURATION. We constructed candidate models by evaluating all subsets of the global model using the R package MuMIn (Barton, 2016; Doherty et al., 2012). We used AIC_c weights and log-likelihoods to compare the relative support for each model, and regarded all models within two AIC_c points of the top-ranked model as having empirical support, while possibly containing uninformative parameters (Arnold, 2010; Burnham & Anderson, 2002). We calculated parameter estimates for the top-ranked model and plotted effects in the original scale, with non-focal variables held at typical values using the R package Effects (Fox, 2003; Fox & Weisberg, 2018; Fox & Weisberg, 2019). We report beta coefficients (β) and SEs for variables of interest. Since variables with weak effects may still help to improve sample methods, we noted effect sizes for variables in other models within two AIC points of the top-ranked model.

Temporal comparison

To assess fine-scale and sex-specific temporal effects of denning on individual identification at bait sites that were deployed and monitored in asynchronous time intervals, we used an index of relative detection (RDI; Lamb et al., 2016). We calculated an RDI for each day and site sampled. This was accomplished by taking the number of new individuals detected at a site and dividing by the length of the session where the bait site was operational to obtain a daily detection probability. Individuals previously detected at the site were not counted again. We accounted for variation in wolverine density across the sampled landscape by further dividing this number by the sex-specific density at that location (from Mowat et al., 2020). For example, two new females identified over a 30-day sampling session with a female density of $0.7/1000\ \text{km}^2$ would derive a value of 0.095 for each of the 30 days that the trap was operational in that session. We then averaged these daily detections across all sites (Lamb et al., 2016) and calculated SEs for each day. To increase temporal resolution, we removed any sessions that were >50 trap nights.

Since some bait stations were deployed in November and others remained operational until the end of May, we truncated the analysis period, selecting date intervals to maximize the number of sampling sites that were operating simultaneously. We compared male and female relative detection over two time periods, pre-denning, from 9 January to 9 February; and early denning, from 10 February to 6 April. To control for nontemporal factors that may affect detection, we only included data from sites that were monitored continuously through each time interval, so that the variation in the relative detection of sites was a function of time only, not the addition or removal of more or less successful sites.

Latency to detection

Using a similar approach to the detection models, we used the subset of bait stations that included a wildlife camera to calculate a LTD, the time (in days) from when the bait station was first established to the first detection of a wolverine. This measure was the response variable in a Gamma-distributed (log link) GLM with a similar set of covariates as our detection analysis. For latency, including DURATION was nonsensical, we used the correlated FIRSTWEEK to reflect the timing of sampling onset. We included DENSITY as a covariate rather than as an offset term, because, unlike detections, we did not expect latency was a proportion of density. We added a new variable, SEX (male, female, unknown). We predicted that the same variables associated with detection would also influence LTD times.

Genotyping success

We evaluated genotyping success rates for wolverine guard hair and underfur hair samples as a function of the number of hairs in the sample (HAIRCOUNT), the length of the interval between trap checks (DAYS_OUT), and the month the samples were collected (MONTH_COLLECTED; January as the first month), using the binomial family of general linear models. We used MONTH_COLLECTED as an indication of increasing sun exposure, temperatures, and increasing frequency of melt/freeze cycles. We included an interaction term for DAYS_OUT and MONTH_COLLECTED because we expected that colder months would show less deterioration of genetic material for a given period of time. We $\log_{10}$-transformed HAIRCOUNT because we expected increasing hair numbers to have an asymptotic effect on genotyping success. This analysis only used data from samples at WGI, where HAIRCOUNT information was available. To compare the effectiveness of different hair snag devices in capturing hair samples, we used coefficients from these models to calculate a guard hair equivalent (GHE) for underfur and mixed samples (Lamb et al., 2016), using DAYS_OUT = 30 and MONTH_COLLECTED = 1 as reference levels. Since hair samples were sometimes collected from snow, tree pitch, or branch stubs, we used GHE as our response on a set of samples from sites in north Columbia (all years, 2018–2020) where both barbwire and alligator clips were used simultaneously and the location of the hair sample was explicitly recorded. Additional data obtained from six bait stations outside the study area provided the gun brush comparison (Robinson et al., 2017).

RESULTS

We installed 527 sample sites and detected between zero and four individuals at each site for a total of 151 individual wolverine, 90 females and 61 males, across 6 winters. We examined 10 variables potentially related to individual detection and LTD. Some variables had collinear relationships. The variables ALPINE and HUMANII were correlated with DENSITY (0.81, −0.61) and unstable in models containing DENSITY. As density was a key component of the individual detection model framework, we did not consider either ALPINE or HUMANII further in the detection analysis. ACCESS was only weakly correlated with HUMANII (−0.4). For the latency analysis we included DENSITY, HUMANII, and ALPINE as variables, but not in the same model. DURATION was highly correlated with FIRSTWEEK (0.97), we used DURATION in all detection models for its strong causal link. The categorical variable CAMERA was confounded with BAIT and SETUP, in that the majority of tree setups that lacked cameras also had bait other than beaver, while all run pole setups necessarily had cameras. As the effect of CAMERA was not significantly different from zero in models that also contained SETUP and BAIT, whereas coefficients on the other two variables changed little, we considered that the effect of CAMERA on individual detection, independent of SETUP and BAIT, was negligible and dropped this variable.

We simplified some of our categorical variables after running univariate models. For ACCESS, the only significant contrast to the reference level snowmachine was heli; grouping ski and truck with snowmachine resulted in a heli versus ground comparison for that variable. For BAIT, beaver performed better than other levels, and significantly better than ungulate heads. We grouped ungulate head, ungulate quarter, and domestic meat into a reference level, resulting in a beaver versus other comparison for BAIT. The variable TOPO did not generate any significant contrasts or logically justifiable groupings between categories.

Individual detection

The variable set for predicting individual detection included TOPO, SNOW, SETUP, BAIT, and ACCESS, scaled using DENSITY and DURATION as offsets. The highest ranked model predicting individual detection included variables related to both habitat and methods:

TABLE 2 Model selection results to compare covariates predicting wolverine detection at bait stations.

Model set	Variables	Model	df	LL	AIC$_c$	ΔAIC$_c$	ω_i
Habitat	TOPO	1	4	−414.51	837.01	13.18	0.00
	Log(SNOW)	2	2	−410.33	824.69	0.85	0.23
Method	SETUP	3	2	−413.07	830.17	6.34	0.00
	BAIT	4	2	−415.47	834.95	11.12	0.00
	CAMERA + SETUP + BAIT	5	4	−412.07	832.22	8.39	0.00
	ACCESS	6	2	−413.97	831.97	8.14	0.00
Combined factors	**Log(SNOW) + SETUP**	**7**	**3**	**−408.90**	**823.83**	**0.00**	**0.35**
	Log(SNOW) + SETUP + ACCESS	8	4	−408.75	825.58	1.75	0.15
	Log(SNOW) + SETUP + BAIT	9	4	−408.77	825.62	1.78	0.14
	Log(SNOW) + ACCESS	10	3	−409.82	825.69	1.85	0.14

Note: Wolverine density and sampling duration are included in all models as offset terms. TOPO-contrasted topographical locations, valley, ridge, mid-slope and pass; SNOW was the snow depth (in centimeters) at each site when it was visited in April or early May; SETUP-contrasted baited trees wrapped in barbwire with sites having suspended bait and run poles with frames fixed to trees and integrated with cameras for ventral photographs; BAIT-contrasted sites baited with beaver versus other baits (ungulate heads, ungulate quarters, and domestic meat); CAMERA-contrasted sites with and without remote cameras present; and ACCESS-contrasted sites visited from the ground (by snowmachine, ski, or truck) with helicopter-accessed sites. Bold values indicate the model with the lowest AIC$_c$.

Abbreviations: AIC$_c$, corrected Akaike information criterion for small sample sizes; LL, log-likelihood; ΔAIC$_c$, difference in AIC$_c$ from the top model; ω_i, Akaike weight for the model.

SNOW and SETUP (Table 2). The habitat variable SNOW was a strong and consistent predictor of detection, indicating a positive effect of the amount of late winter snow (Figure 3) present on the ground at the site.

For variables related to sampling methods, run pole setup methods appeared to be more effective than tree setups. A typical run pole setup detected 0.38 ± 0.07 (SE) individuals per site, compared to 0.27 ± 0.02 individuals per site for tree setups. Effect sizes for BAIT and ACCESS were small (ACCESS: heli $\beta = 0.08 \pm 0.14$, $p = 0.6$, model 8; BAIT: beaver $\beta = -0.07 \pm 0.15$, $p = 0.6$, model 9) and not significant. The variable TOPO did not appear in the top models. Sex-specific analyses generated top-ranked models similar to the combined-sex analysis; however, both snow and run pole setups were more important for female than for male detections (Table 3). Run pole setups detected more females (0.22 ± 0.05 per site) and a higher proportion of females (61%) than tree setups (0.14 ± 0.01 females per site; 55%).

Temporal comparison

For the pre-denning period, 9 January to 9 February, 118 sites were monitored continuously in four sampling areas. Male and female RDI were similar with no discernable temporal trend (Figure 4). For the first 2 months of the reproductive denning period, 10 February to 6 April, 195 sites in six sampling areas were in continuous operation. Temporal trends show diverging RDI in males and females beginning in late February and continuing through most of March, with male RDI generally increasing and females having both lower RDI and lower variability in RDI. Female RDI approached male RDI again by late March.

Latency to detection

We were able to evaluate LTD for 132 sites in a camera-monitored subset of our sites that retained consistency with the full dataset with respect to factors predicting individual detection. All LTD data necessarily had at least one detection; we were interested in how long it took for that detection to happen. Average time to detection at bait stations was ~32 days (range 1–95).

The top combined model for latency included HUMANII and ACCESS (Table 4). Bait stations located in areas with low human influence were visited much more quickly than areas with anthropogenic impact ($\beta = 0.07 \pm 0.02$; model 12). Additionally, bait stations set up using helicopters had shorter latency times than those accessed by ground travel (Table 5, Figure 5). For example, we estimated 10.6 ± 2.4 days for LTD in helicopter-accessed sites with no human infrastructure within 10 km, while ground-accessed sites having very minimal infrastructure nearby (HUMANII = 1) had an LTD of 35.0 ± 3.2 days.

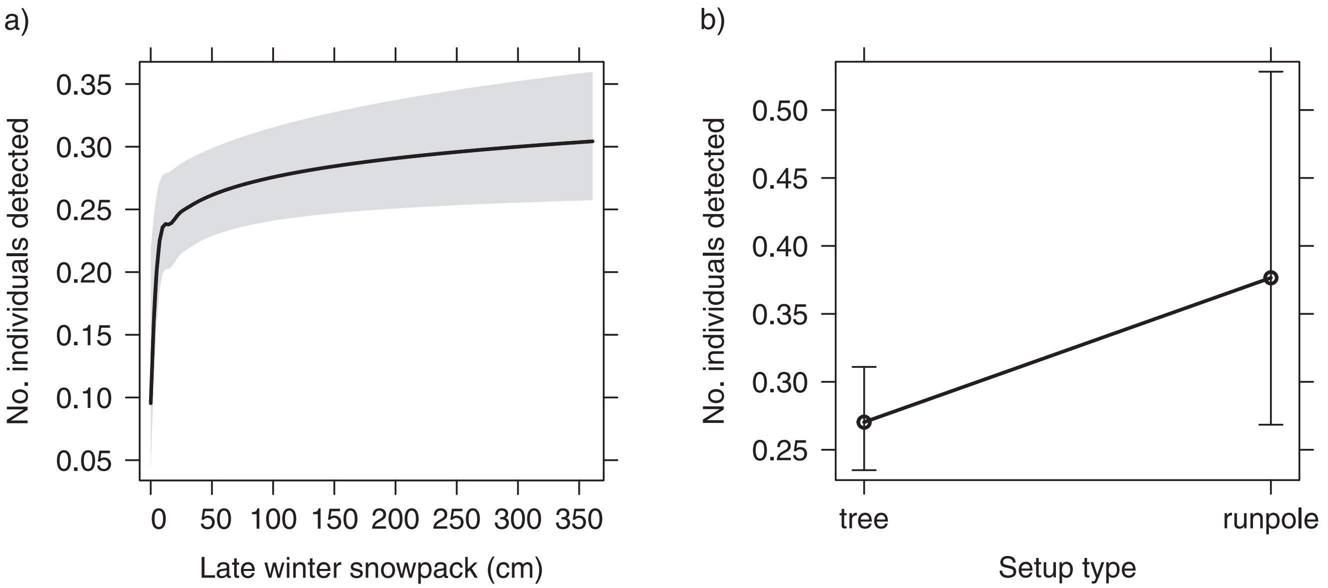

FIGURE 3 Covariates derived from the best multivariate model (model 7, Table 2, Table 3) predicting wolverine detection success at bait stations, back-transformed to original scale. Shaded areas indicate 95% CI. The response, number of individuals, is scaled by wolverine DENSITY, measured within a 10-km radius of the bait station, and DURATION, the number of days that a trap was operational. (a) SNOW was the snow depth (in centimeters) at each site when it was visited in April or early May. (b) SETUP-contrasted baited trees wrapped in barbwire with sites having suspended bait and run poles with frames fixed to trees and integrated with cameras for ventral photographs.

TABLE 3 Parameter estimates and significance levels for variables appearing in the top wolverine detection model (model 7 in Table 2).

	Both sexes		Female		Male	
Model variable	**Estimate (SE)**	***p***	**Estimate (SE)**	***p***	**Estimate (SE)**	***p***
(Intercept)	−6.16 (0.15)	<0.0001	−6.34 (0.22)	<0.0001	−5.93 (0.19)	<0.0001
Log(SNOW)	0.08 (0.03)	0.0133	0.09 (0.05)	0.0501	0.06 (0.04)	0.1260
SETUP:runpole	0.33 (0.19)	0.0783	0.44 (0.23)	0.0631	0.17 (0.31)	0.5950

Note: SNOW was the snow depth (in centimeters) at each site when it was visited in April or early May; and SETUP-contrasted baited trees wrapped in barbwire with sites having suspended bait and run poles with frames fixed to trees and integrated with cameras for ventral photographs.

Other variables in competing models with AIC < 2 had weak effects that were also potentially of interest from a study design perspective. Latency times for sites with beaver as bait had a nonsignificant advantage ($\beta = -0.25 \pm 0.32$; model 13) over domestic bait, and LTD had a nonsignificant declining trend throughout the sampling season, indicated by the FIRSTWEEK variable ($\beta = -0.02 \pm 0.02$; model 14), such that the typical site set up in late November was visited 10 days later (42.3 ± 6.1 days) than those in March (32.2 ± 7.8 days). We did not find strong differences between sexes, but females averaged shorter latency times (27.6 ± 3.2 days) than males (30.3 ± 3.7 days) and wolverine of unknown sex (i.e., caught on camera but no viable genetic sample or definitive ventral photographs) took the longest (33.8 ± 3.6 days). Surprisingly, DENSITY, despite being negatively correlated with HUMANII, did not have a significant effect on latency ($\beta = -0.12 \pm 0.08$; model 2) and did not appear in the top models. The top variables predicting detection, SNOW and SETUP, were also poor predictors of LTD, and so was topography (TOPO).

Genotyping success

With the exception of run pole setups, successful individual identification depended on the hair samples used for genetic analysis. We obtained 4642 genetic samples. Of these, 742 hair samples were wolverine, suitable for genotyping, and 529 of these generated successful wolverine genotypes. On average, sites with wolverine DNA detected had 3.6 samples per site that contained wolverine hair and 1.5 samples per site with successful genotypes.

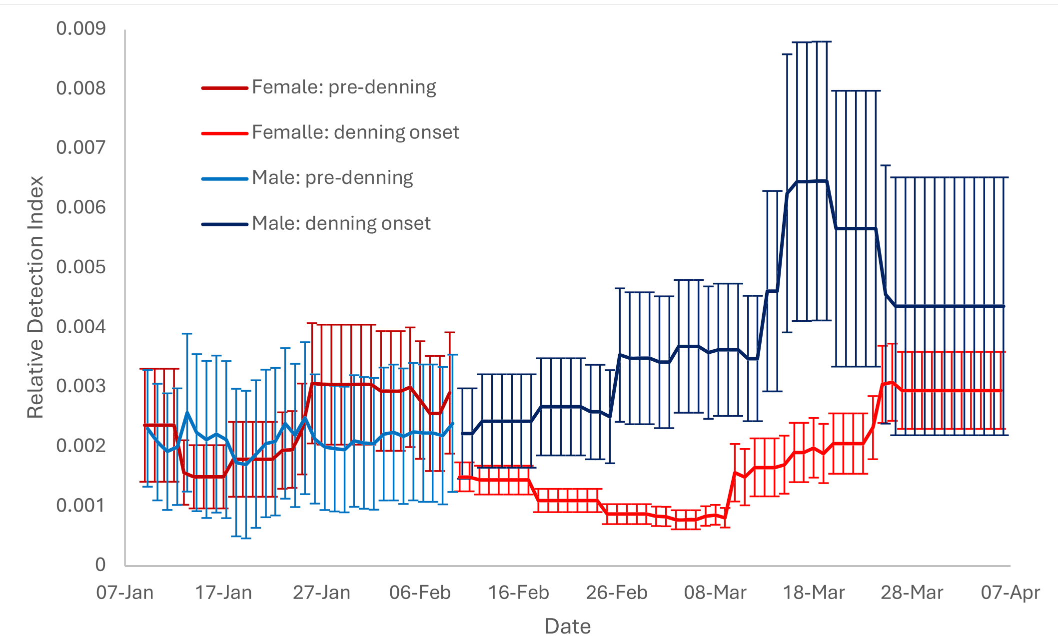

FIGURE 4 Relative detection index for wolverine bait sites with SE bars for male and female wolverine, for 118 sites monitored continuously in the pre-denning period (9 January—9 February) and 195 sites monitored continuously during the onset of the denning season (10 February–6 April).

TABLE 4 Model selection results to compare covariates predicting wolverine latency to detection at bait stations.

Model set	Variable	Model	df	LL	AIC$_c$	ΔAIC$_c$	ω_i
Null	NULL	1	2	−587.83	1179.8	19.2	0
Density	Log(DENSITY)	2	3	−586.87	1179.9	19.3	0
Sex	SEX	3	4	−585.93	1180.2	19.6	0
Habitat	Log(ALPINE)	4	3	−587.70	1181.6	21	0
	Log(SNOW)	5	3	−587.41	1181.0	20.4	0
	TOPO	6	5	−587.35	1185.2	24.6	0
	Log(HUMANII)	7	3	−580.86	1167.9	7.3	0.01
Method	ACCESS	8	3	−579.43	1165.1	4.5	0.05
	SETUP	9	3	−581.51	1169.2	8.6	0.01
	BAIT	10	3	−586.95	1180.1	19.5	0
Timing	FIRSTWEEK	11	3	−580.26	1166.7	6.1	0.02
Combined	**ACCESS + Log(HUMANII)**	**12**	**4**	**−576.12**	**1160.6**	**0**	**0.48**
	ACCESS + BAIT + Log(HUMANII)	13	5	−575.86	1162.2	1.6	0.22
	ACCESS + FIRSTWEEK + Log(HUMANII)	14	5	−575.95	1162.4	1.8	0.20

Note: ALPINE was the percent area of alpine vegetation within a 10-km radius of the sampling location, SNOW was the snow depth (in centimeters) at each site when it was visited in April or early May; TOPO-contrasted topographical locations, valley, ridge, mid-slope and pass; HUMANII was an index of human use; ACCESS-contrasted sites visited from the ground (by snowmachine, ski, or truck) with helicopter-accessed sites; SETUP-contrasted baited trees wrapped in barbwire with sites having suspended bait and run poles with frames fixed to trees and integrated with cameras for ventral photographs; BAIT-contrasted sites baited with beaver versus other baits (ungulate heads, ungulate quarters, and domestic meat); and FIRSTWEEK was the week of the year the bait stations were deployed, sequentially, with the last week of November as week 1. Bold values indicate the model with the lowest AIC$_c$.

Abbreviations: AIC$_c$, corrected Akaike information criterion for small sample sizes; LL, log-likelihood; ΔAIC$_c$, difference in AIC$_c$ from the top model; ω_i, Akaike weight for the model.

We were able to evaluate the effect of hair type, number of hairs, sampling interval length, and month collected on genotyping success for 500 wolverine samples. To be conservative, we constrained our analysis to values of DAYS_OUT <60 and MONTH_COLLECTED <6, representative of typical sampling times and intervals; however, the dominant trends in our results were reinforced when we also included longer and later outlier events.

We found strong relationships between genotyping success and the number of hairs, the length of the sampling interval, and the month the hairs were collected, for both hair types (Table 6). Guard hairs were much more likely to generate a genotype (Figure 6). At median levels of DAYS_OUT (30 days) and MONTH_COLLECTED (4, April), the probability of a successful genotype for one guard hair was 55 ± 5%. Two guard hairs increased the probability to 69 ± 3%, equivalent to approximately 30 underfur hairs (68 ± 6%, Figure 6). Ten guard hairs had a probability of 91 ± 2%.

We observed declining genotype success over the length of the sampling interval, and this effect became more pronounced as the season progressed. Genotyping success for five guard hairs declined negligibly for different length sampling periods that ended in January, from 92 ± 3% at 30 days to 90 ± 2% at 60 days. In contrast, genotyping success dropped more substantially over equivalent sampling periods that ended in May, from 80 ± 4% at 30 days to 50 ± 18% at 60 days. For underfur hairs this decline was even steeper, so that even with 30 underfur hairs the probability of a successful genotype after 60 days, ending in May, was 11 ± 9%.

In 120 run pole sites having both barbwire and alligator clips on the same setup, the number of possible wolverine hair samples we got from each snagging device was roughly equal (barbwire = 761, alligator clips = 763), but we were unable to make a similar comparison with gun brushes. In samples identified to wolverine, barbwire collected more hair, 4.9 ± 0.2 GHE per sample ($n = 182$), compared with 4.2 ± 0.9 GHE per sample ($n = 16$) for gun brushes, and 3.1 ± 0.3 GHE per sample ($n = 131$) for alligator clips. However, gun brush samples had the highest proportion of underfur hairs, averaging 71 ± 12% underfur per sample, whereas alligator clips had 58 ± 0.4% underfur per sample and barbwire was the lowest at 47 ± 0.3% underfur per sample. Since underfur hair DNA quality declined more rapidly with environmental exposure, barbwire samples tended to have the highest genotyping success, 74 ± 3%, followed by alligator clips, 63 ± 4%, and gun brushes, 50 ± 13%. On average, female wolverine left better hair samples (5.3 ± 0.3 GHE) than males (4.3 ± 0.3 GHE).

TABLE 5 Parameter estimates for variables appearing in the top model predicting latency to detection.

Model variable	Estimate (SE)	*p*
(Intercept)	3.555 (0.0917)	<2e-16
Log(HUMANII)	0.074 (0.0240)	0.002750
ACCESS:Helicopter	−0.520 (0.1471)	0.000574

Note: HUMANII was an index of human use; and ACCESS-contrasted sites visited from the ground (by snowmachine, ski, or truck) with helicopter-accessed sites.

DISCUSSION

Optimizing individual detection facilitates estimates of density and the ability to monitor population trends

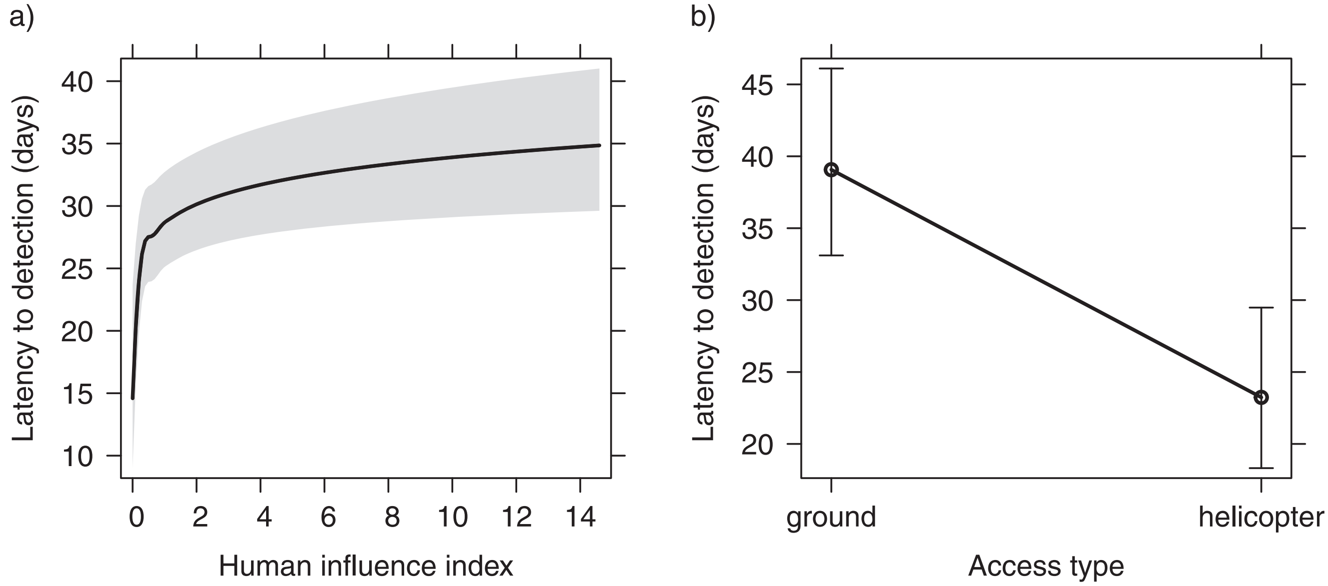

FIGURE 5 Covariates from the top model predicting wolverine latency to detection at bait stations, back-transformed to original scale. Shaded areas indicate 95% CI. (a) Human Influence Index (HUMANII), measured within a 10-km radius of the bait station. (b) ACCESS, access to the bait station, that is, ground (snowmachine, ski, or truck) versus helicopter access.

TABLE 6 Parameter estimates for variables affecting sample genotyping success of wolverine guard hairs and underfur.

	Guard hair		Underfur	
Model variable	**Estimate (SE)**	***p***	**Estimate (SE)**	***p***
(Intercept)	1.302 (0.459)	0.005	−0.605 (1.010)	0.549
Log(HAIRCOUNT)	0.899 (0.166)	6.09e-8	0.950 (0.342)	0.0054
DAYS_OUT:MONTH_COLLECTED	−0.009 (0.004)	0.012	−0.015 (0.005)	0.0008

Note: HAIRCOUNT was the number of hairs in the genetic sample; DAYS_OUT was the length of sampling interval; and MONTH_COLLECTED was the month of the year, January = 1, February = 2, etc.

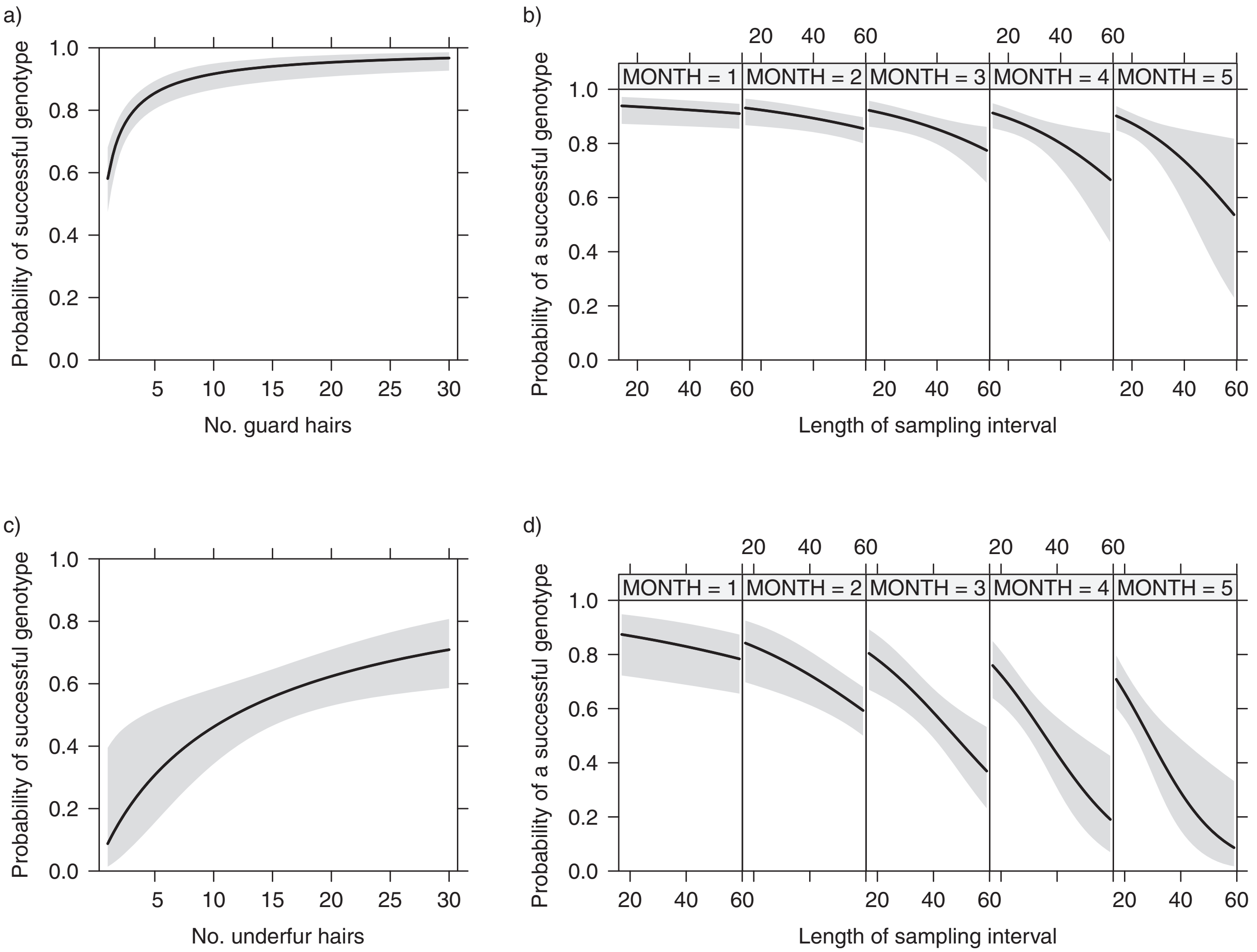

FIGURE 6 Factors affecting genotyping success of wolverine hair samples for guard hair: (a) hair quantity and (b) length of sampling interval by month of year (January = 1, February = 2, etc.), and for underfur hair: (c) hair quantity and (d) length of sampling interval by month of year (January = 1, February = 2, etc.). Laboratory analysis spanned a range of 1–10 hairs for guard hairs and 5–30 hairs for underfur; values were extrapolated to aid comparison.

for wolverine and other low-density species. This information is critical for the implementation and evaluation of conservation measures. Using a large dataset of noninvasive genetic sampling sites with broad geographic extent and variable wolverine density, we demonstrated that several factors related to methods, habitat, and seasonal timing are important to wolverine individual detection and LTD at bait stations. We also provided information on factors affecting genotyping success, including hair type and exposure, and the effect of different hair snag devices on sample quality.

Individual detection

The configuration of bait station components was an important predictor of success. Magoun et al.'s (2011) run pole setup was more effective at detecting individuals than the tree or pole setup first described by Mulders et al. (2007). Ventral photographs facilitate the identification of individuals that do not leave hair samples, and can also be cross-referenced between sites or sessions having better hair samples.

The run pole setup had higher detection for females than the tree setups. The proportion of females detected by run poles, 61%, closely matched the spatially explicit capture–recapture estimated proportion of females in the population, 62% (Mowat et al., 2020), and was greater than the proportion detected by tree setups, 55%, suggesting that females are overrepresented in the animals missed by tree setups. The run pole setup confers other advantages including the identification of sex and breeding condition and reductions in genetic laboratory costs once a particular ventral pattern is linked with a particular genotype. Run poles can be left in place for multi-year studies, and re-baiting is easy. Disadvantages include more materials and complexity, with longer setup times, higher initial costs, and difficulties in transporting materials and tools. Run poles also require cameras and incur the cost of analyzing photos.

In montane environments, access can preclude randomized placement of bait stations. Most studies opt for a systematic deployment within grid cells of varying dimensions (Fisher et al., 2013; Lukacs et al., 2020; Robinson et al., 2017), although clustered sampling designs may allow field workers to sample inaccessible areas more efficiently (Clark, 2019; Efford & Boulanger, 2019). While we did not find an effect of access method or topography on detection, we did find that snow at bait stations mattered, even when we controlled for density effects.

Wolverine have been linked strongly with snow presence (Copeland et al., 2010; Inman, Magoun, et al., 2012). Although the broad-scale extent of multiyear spring snow predicted wolverine density in our study area (Mowat et al., 2020), we also showed that local snow amounts affected wolverine detection, independently of density. Our results suggest that the presence of snow improved detection more than snow depth, because detection increased little after about 40 cm snow depth. The importance of this variable may be related to higher encounter rates resulting from fine-scale habitat use. Snow is used for reproductive dens and food caches (Inman, Magoun, et al., 2012; Magoun & Copeland, 1998) and Glass et al. (2021) showed that wolverine selected deeper, denser snow for travel routes. Snow also retains scent, and this might provide a "scent pathway" facilitating encounters with bait stations. Future workers should select sites and sampling periods that will remain snow covered.

As befits a generalist scavenger, wolverine were not selective about bait. However, beaver had a weak trend for shorter latency times, compared to other baits. Beaver are generally considered a good bait for winter trap sets because they are fatty and remain pliable and pungent even in cold temperatures, and in many places the skinned carcasses can be purchased from local trappers.

Temporal comparison

The timing of bait station deployment affected detection. Other studies have noted a trend toward increasing species-level detections over late winter (Fisher et al., 2013; Kortello et al., 2019), but our fine-scale temporal comparison indicated a reduction in daily RDI for females at the onset of the maternal denning period, in approximately mid-February (Inman, Magoun, et al., 2012; Magoun & Copeland, 1998). Wolverine kits are altricial, and this observation is consistent with limited foraging movements by the female beyond the den during the early denning period (Aronsson et al., 2023). Similarly, our observed difference in RDI was more pronounced in the early denning period, and female RDI approached male RDI by late March. Male detection generally increased through the winter, and late winter had the highest RDI. Trends toward increasing detection and decreasing LTD suggest that sampling later in the winter, into April or May, would generate higher detection for both male and female wolverine although care must be taken to choose sites that will retain snow during this time and bear encounters become a concern. Future analysts should test for lower detection probabilities for females from February to mid-March.

Latency to detection

LTD for bait stations averaged 32 days, rather a long period given potential losses from other scavengers. We observed many baits reduced to skeletons by other scavengers over this length of time. Wolverine use olfaction to detect carcasses, and scent plumes travel rapidly as a function of air movement and diffusion processes (Farrell et al., 2002). Since our traps averaged 7–8 km apart, and wolverine travel upward of 20 km/day, essentially covering the area of their annual home range over a similar 32-day period of time (Copeland, 1996; Inman, Packila, et al., 2012), this latency suggests either poorly directed search efforts with respect to bait stations or, perhaps initially, active avoidance. The latter is supported by the poor relationship between density and LTD since, even under a random search pattern, more wolverine in an area would be expected to translate to faster encounter rates with bait stations. Naïve latency does not preclude a subsequently positive trap response, as detected in previous noninvasive baited wolverine studies (Barrueto et al., 2020; Mowat et al., 2020; Royle et al., 2011), because trap response is a learned behavior and bait is a substantive reward.

Wolverine avoidance of human activity has been noted previously (Barrueto et al., 2022; Heinemeyer et al., 2019; Scrafford et al., 2018), and our results suggest a strong effect of anthropogenic influence on LTD. Our HUMANII variable mapped generalized human influence at broad scales, and we suggest that ACCESS method is another proxy for human use and influence at a finer resolution, in that helicopters are typically reserved for remote areas where difficulty in access provides little alternative. Our latency-modeling results indicated that remote sites without human influence were visited almost a month earlier than sites more proximal to human infrastructure, suggesting increased wariness in human-modified landscapes. These results are consistent with Stewart et al.'s (2016) observations of changes in wolverine behavior around bait stations associated with anthropogenic influence. Many other carnivores show behavioral avoidance of human presence, presumably due to risk associations (Muhly et al., 2011; Ordiz et al., 2021; Suraci et al., 2019). For wolverine, such behaviors might also be related to avoidance of competitive interactions with species associated with anthropogenically modified environments such as coyotes, rather than human presence per se (Chow-Fraser et al., 2022; Heim et al., 2017). In general, future workers should try to set their sites in areas removed from human disturbance.

We found a weak trend toward lower LTD as winter progressed. This could reflect snow conditions and ease of travel in compacted, late winter snowpacks, although as previously mentioned, given the proximity of bait stations and the average daily travel distances of wolverine, we suspect travel times were not a limiting factor. Shorter latency times could also reflect a shift in alternative food availability and a stronger food drive or warming temperatures which leads to stronger smelling baits. Although little is known about annual energy budgets for wolverine, in late winter rodent availability is low, food caches may have become depleted and wolverine may be more dependent on less reliable resources—ungulates in poor condition and carrion caught in late winter avalanche cycles (Inman, Magoun, et al., 2012). Persson (2005) showed that female wolverine are food limited, with reproductive success tied to food availability. Certainly, for reproductive females, after the initial period of restricted activity around parturition, there will be increasing energetic demands associated with lactation (Blecha et al., 2018; Clutton-Brock, 1991; Gittleman & Thompson, 1988) that could reduce their caution around bait stations. This is consistent with the weakly shorter time to detection for females.

Our SETUP variable was not a good predictor of latency, suggesting that potential disturbance impacts associated with trap setup (i.e., noise, human presence, odor) were consistent between trap types, despite the higher amounts of infrastructure and longer initial construction times required for run poles. In general, the important variables in latency models were not the same as the important variables in detection models, suggesting that a long sampling interval can overcome wolverines' initial reluctance to visit bait stations, especially if it extends past late March. Since longer trap deployments will generally lead to more detections, we suggest future workers leave traps out for several months and remind the reader that we checked most sites monthly and added new bait and lure when needed.

Genotyping success

While visiting bait stations, wolverine leave highly variable amounts of hair behind. The number of hairs in most samples is much fewer than most bear studies because wolverine hair have deep roots attached to the skin, and unlike bear hair sampling, sampling occurs in winter when natural shedding is minimal (Mowat et al., 2017). To reduce lab costs for genotyping, hair samples are frequently subsampled, thereby increasing the possibility that an individual may be missed. Conversely, generating two genotypes for the same animal at the same sampling period adds costs but no add information. Wolverine hair has higher genotyping success than that of grizzly bears, wolves, or pine marten (Lamb et al., 2016; Mowat & Paetkau, 2002; Stenglein et al., 2011); one guard hair provided a genotype more often than not, while underfur had a much lower likelihood of success. A negative effect of environmental exposure is well documented in studies of summer bear DNA genotyping success (Lamb et al., 2016; Stetz et al., 2014), but like Robinson et al. (2017), we found little loss in genotyping success rates for samples left for long periods in midwinter. However, as the season progressed toward spring, successive months showed an increasingly negative relationship between genotyping success and the number of days in the sampling interval. This loss was more pronounced for underfur than for guard hairs. Consequently, we suggest future workers should plan to check traps at 20- to 30-day intervals if they are deployed during late winter or spring. However, since LTD can easily be as long as a month, access may be difficult, and little is gained from checking a trap that has not been visited yet, workers might consider longer intervals between trap checks in midwinter.

Although many factors can potentially influence whether a snag device is successful in capturing hair, wolverine hair samples obtained from barbwire tended to be larger, have proportionately more guard hair, and were more likely to generate an individual genotype than those from either gun brushes or alligator clips. However, we point out that our sample from gun brushes was relatively small and may not be representative. Different snag devices may confer other advantages. For example, gun brushes facilitated rapid collection of samples during trap checks. Additionally, alligator clips in the run pole setup allow hair capture in a specific clip to be documented on camera and associated with a particular individual and chest pattern, even if more than one animal visits the site and leaves hair (Magoun et al., 2011). This can save on genetic analysis costs. We recommend subsampling based first on sample quality. Samples with two or more guard hairs are most likely to generate a genotype. Next, we suggest field staff use the location of different samples on the tree or run pole and camera data to help decide whether more than one animal may have visited the site and hence whether it is worth running more samples from that site visit.

Monitoring wolverine using noninvasive capture–recapture is a tremendous improvement over snow tracking or harvest data for abundance estimation (Mowat, 2001). Yet, the resources required to access large areas of wolverine habitat are considerable and detection success is variable. To maximize individual detection within a selected area (e.g., predetermined grid cell), we recommend using run pole and camera bait station setups deployed in areas of persistent snow. Longer deployments had higher success, but we caution that detection for females may be lower temporarily during the reproductive denning period. We suggest using longer deployment times in areas that experience human influence, to account for longer LTD. Barbwire tends to provide better quality hair samples and laboratory subsampling protocols for genetic analysis should consider that even one guard hair from a wolverine has a reasonable chance of yielding a genotype, but use of more guard hairs can greatly increase genotyping success. Longer sampling intervals between trap checks will negatively affect genotyping success in warmer months. Consideration of these factors should provide better individual detection rates and thus, estimates of density to inform conservation measures for wolverine.

We attempted to control for systematic differences among sampling protocols and study areas using density and trap duration; however, we acknowledge the potential for unexamined confounding factors. Given the observed responses to snow, there may have been annual climatic effects on detection that we were unable to assess. Additionally, wolverine residency status within home ranges potentially affects behavior around bait stations and this could shift the context of our observations on detection and latency. We sampled wolverine in a montane environment at the southern end of their range in North America. The increase in detection that we observed in late winter may not occur, or may occur later, in more northern environments. Similarly, the use of run poles in arctic environments may be more difficult due to the lack of trees. Our study assessed factors affecting the initial capture of individual wolverine. However, recaptures are essential for density estimation. We assumed that the food reward associated with bait stations will reduce the caution and selectivity of wolverine in subsequent encounters with similar structures, facilitating recaptures.

CONCLUSIONS

We can make several suggestions to help field biologists to improve inventory results in the future:

1. Detections are higher in areas with greater wolverine density, but for a spatial design, it is important to sample the range of densities in a study area, especially if one intends to use a model to extrapolate density to unsampled areas.
2. Sample in areas that will remain snow covered through spring and away from human influence.
3. Run pole set-ups to improve individual detection, especially for females, as well as generating other data such as breeding condition. Tree setups trade off somewhat lower detection for less cost and effort to implement.
4. Beaver as bait may confer a slight advantage in the shorter term, but other baits have similar success. Larger baits last longer so are preferable.
5. While longer trap periods lead to greater detections, trapping later in the winter, and perhaps into early spring (May), has the potential to generate more captures and increase the chance of detecting females that are raising young that winter.
6. Analysts may want to allow for sex-based detection probabilities and accommodate lower detection for females during February to mid-March.
7. Longer deployments (>35 days) are necessary for detection in human-influenced areas.

8. Genotyping success was greater than 50% with one guard hair, and nearly 70% when two guard hairs are included in the sample. Studies that generate many samples may prefer to only genotype samples with two or more guard hairs to reduce genetic analysis costs.
9. Monthly, or more frequent (20–30 day), trap checks yield better DNA quality during late winter and spring, but longer trap check intervals could be used in midwinter with negligible quality loss.
10. Barbwire yielded more individual genotypes per sample than either alligator clips or gun brushes, but a combination of barbwire and alligator clips confers some advantages. In instances where multiple wolverine visited a bait station, the visual cue of displaced alligator clips can reduce genetic costs by allowing samples to be linked via a photograph to individuals.

AUTHOR CONTRIBUTIONS

Garth Mowat, Andrea Kortello, Doris Hausleitner, Mirjam Barrueto, and Anthony Clevenger conceived the ideas for this paper. Andrea Kortello led the analysis and writing. All authors provided data and input that shaped the analysis and manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are sensitive and are not publicly available due to the conservation status of wolverine in Canada. Wolverine bait station data and genetic data were compiled from numerous sources under data sharing agreements that did not include public dispersal of data. Ownership resides with the following researchers and agencies and data are available to qualified researchers. For data requests regarding the south Columbia wolverine bait stations and associated genetic data, please contact Andrea Kortello (kortello@yahoo.com), Grylloblatta Ecological Consulting or Doris Hausleitner (dorishaus78@gmail.com), Seepanee Ecological Consulting. For north Columbia bait stations and genetic data, please contact Mirjam Barrueto (mirjam.barrueto@ucalgary.ca), Department of Biological Sciences, University of Calgary. For south Rockies and Banff, Yoho, Kootenay Nation Park data, please contact Anthony Clevenger (apclevenger@gmail.com), Western Transportation Institute, Montana State University. For Kananaskis data, please contact Nikki Heim (heimnikki@gmail.com), Nikki Heim Consulting. Mount Revelstoke and Glacier National Park portions of the data were obtained under license from Parks Canada Agency. Contact Mount Revelstoke and Glacier National Parks Ecological Integrity Monitoring Coordinator, Lisa Larson (lisa.larson@pc.gc.ca). Contact Michael Lucid (michael@selkirkwildlife.com), Selkirk Wildlife Science LLC, for wolverine genetic data from Idaho. Other datasets used for this research included Human Influence Index mapping (https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic/maps) and Biogeoclimatic Ecosystem Classification (BEC) Zone mapping (https://catalogue.data.gov.bc.ca/dataset/f358a53b-ffde-4830-a325-a5a03ff672c3).

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