

RESEARCH ARTICLE

A portable structure for identifying wolverines and Canada lynx using integrated cameras and hair snags

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Abstract

Wolverine (*Gulo gulo*) and Canada lynx (*Lynx canadensis*), listed as threatened under the United States Endangered Species Act, inhabit remote mountainous terrain across multiple western states. To address challenges associated with collecting long-term occupancy and demographic data for both species, we developed and tested a modified non-invasive camera and hair snag (C&H) monitoring system for simultaneous long-term monitoring of wolverine and Canada lynx (lynx hereafter). We aimed to adapt wolverine monitoring for concurrent use with lynx; redesign the data collection framework and station configuration for portability, affordability, and enhanced data capture; and establish the presence of individual wolverine and lynx through integrated photographic identification and genetic sampling. We validated the system over 5 field seasons by linking photographs to genotypes of individuals and identified reproductive status and sex of individuals across 23 stations spread over a non-contiguous grid covering 1,425 km² in western Montana, USA. We obtained individual genotypes for 13 (9 male, 4 female) of 19 wolverines (12 male, 7 female) and 6 (4 male, 2 female) of 12 lynxes (6 male, 4 female, 2 unknown) identified from unique markings

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in photographs. We also obtained photographic detections of bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), and martens (American [*Martes americana*], Pacific [*M. caurina*]). The C&H stations offer an efficient, cost-effective, and non-invasive approach for mesocarnivore monitoring in remote mountainous regions.

KEYWORDS

Canada lynx, *Gulo gulo*, hair snagging, *Lynx canadensis*, mesocarnivores, microsatellite genotyping, Montana, motion-detection cameras, non-invasive monitoring, pattern recognition, pelage, wolverine

Non-invasive wildlife monitoring has gained traction in recent decades (Alonso et al. 2015, Robinson et al. 2017, Golding et al. 2022). Simultaneously, advancements in remote photography and software aid individual animal identification (Ramsey et al. 2019, Clapham et al. 2020, Nipko et al. 2020). Camera trapping and hair snagging (C&H) offer non-invasive ways to monitor populations and assess individual health (Fisher and Bradbury 2014, Harvey et al. 2021), demography (Gardner et al. 2010, Harvey et al. 2021), occupancy and abundance (Lukacs et al. 2020, Anderson et al. 2023, Day et al. 2024), and reproductive status (Magoun et al. 2011a, b; Cunningham et al. 2022) of rare and elusive animals.

Wolverine (*Gulo gulo*) and lynx (*Lynx canadensis*), both threatened species under the United States Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2000, 2023, 2024), are reclusive mesocarnivores that inhabit overlapping alpine and subalpine ecosystems in western Montana, USA (Lukacs et al. 2020, Anderson et al. 2023). Their remote winter habitats and the need for long-term monitoring for recovery make them ideal for C&H monitoring (Magoun et al. 2011a, Lukacs et al. 2020).

Magoun et al. (2011a) developed a wolverine monitoring method using motion-detection cameras and hair snags, identifying animals through ventral pelage patterns and DNA. The authors encouraged testing their method across different wolverine populations and land cover types and solicited design improvements. We aimed to adapt the method for lynx co-monitoring; improve portability, affordability, and data capture; and establish presence or absence of individual wolverines and lynxes through integrated photographic identification and genetic sampling. We predicted that modifications to the stations would enable reliable wolverine and lynx individual identification, reduce costs, improve portability for long-term monitoring programs, expand data collection at C&H stations, and have the potential to monitor the demography of additional mesocarnivore species.

STUDY AREA

Our study area comprised 1,425 km² of forested, subalpine, and alpine ecosystems in western Montana (47.1686° N, to 45.3686° N, and 113.2610° W, to -112.0391° W), encompassing 4 zones representative of land cover types across the region (Figure S1). Forested areas included mixed stands of Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*), whereas subalpine areas included limber pine (*Pinus flexilis*), whitebark pine (*Pinus albicaulis*), Engelmann spruce, and subalpine fir. Alpine areas were characterized by grasses and forbs. We divided the study area into 4 survey zones. Zone 1 was entirely within the Helena National Forest (Lincoln and Helena Ranger Districts [RD]) between the cities of Helena (46.5891° N, -112.0391° W) and Lincoln (46.9549° N, -112.6817° W). Wolverine and lynx were both present in zone 1. Zone 2 was entirely within the Bitterroot National Forest (Stevensville, Darby, and West Fork RDs) on either

side of Montana state Highway 93 between the towns of Victor (46.4166° N, -114.1501° W) and Sula (46.4151° N, -114.1487° W). Zone 3 was entirely within the Beaverhead-Deerlodge National Forest (Wisdom Ranger District) between the towns of Jackson (45.3686° N, -113.4097° W) and Anaconda (46.1281° N, -112.9497° W). Wolverines, but not lynxes, were present in zones 2 and 3. Zone 4 occurred west of the town of Seeley Lake (47.1686° N, -113.4744° W) on land owned and managed by The Nature Conservancy of Montana (Montana Checkerboard, LLC) bordered by Lolo National Forest with both lynx and wolverine present.

The climate in our study area is semi-arid. Accumulated snow depth during the monitoring season did not exceed 1.5 m at monitoring stations, except in 1 isolated instance. Winter temperatures fell as low as -40°C, and highs in early spring reached 5°C. Elevations ranged from 1,670 m to 2,360 m, with all stations on moderate and persistent snowpacks through the early spring months. Logging operations and permitted trapping were active throughout National Forests of the study area and on adjacent private lands. The landscape had a diverse population of large- and medium-sized carnivores typical of the Rocky Mountains. Zones 1 and 4 fell within a federally designated Lynx Recovery Zone, subject to special trapping rules to prevent accidental capture of lynx. Both lynx and wolverine are designated as furbearer animals in Montana but with no trapping season (USFWS 2000). Access to the stations was by snowmobile over semi-established trails, followed by snowshoeing.

METHODS

Sampling design

We deployed 23 C&H stations across the 4 zones (Figure S1): zone 1 (11 stations, 2020–2024), zone 2 (5 stations, 2023–2024), zone 3 (4 stations, 2024), and zone 4 (3 stations, 2024) over the course of 5 field seasons. Zones contained 1–7 monitoring unit grid cells (cells) measuring 8 × 8 km². Each cell within the zones contained 1–3 monitoring stations, and only zone 1 had cells with more than 1 monitoring station. Within zones, we selected station locations based on knowledge of where lynx and wolverine ranges overlap from previous studies and habitat distribution, accessibility of terrain for reasonable station deployment, distribution of stations across the landscape, expanding the database of documented focal species individuals, and placement of stations within approved research boundaries. For these reasons, cells were contiguous in zone 1, cells were separated in zones 2 and 3, and only 1 cell was identified within zone 4. Monitoring seasons ran from December (stations deployed from 28 December–13 February across all years) to April (last genetic data collected from 19 March–14 April across all years). Baiting (described below) ceased by 31 March to minimize bear interaction, following agency recommendations.

Cameras remained operational after we removed the portable framework, subject to access and agency regulations (e.g., spring wheeled-vehicle restrictions vary by National Forest). We repeated all placements in subsequent monitoring seasons, except for the discontinuations of 1 site in 2021, 6 sites in 2023, and 3 sites in 2024, and the addition of 1 site in 2021 (all in zone 1). Repeat placements occurred within approximately 0.5 km of prior deployments. We discontinued stations because of limited resources or absence of focal species and added the station in 2021 to target new focal species individuals. We defined station-years as the total years of station activity.

Station design

We adapted the C&H station design of Magoun et al. (2011a, b) for monitoring wolverines (Figure 1 and S2; Appendix A). Briefly, we constructed frames from inexpensive and readily available materials that were lightweight (2.3 kg) and packable before beginning fieldwork (Appendix B, Table B1). Frame dimensions were designed to

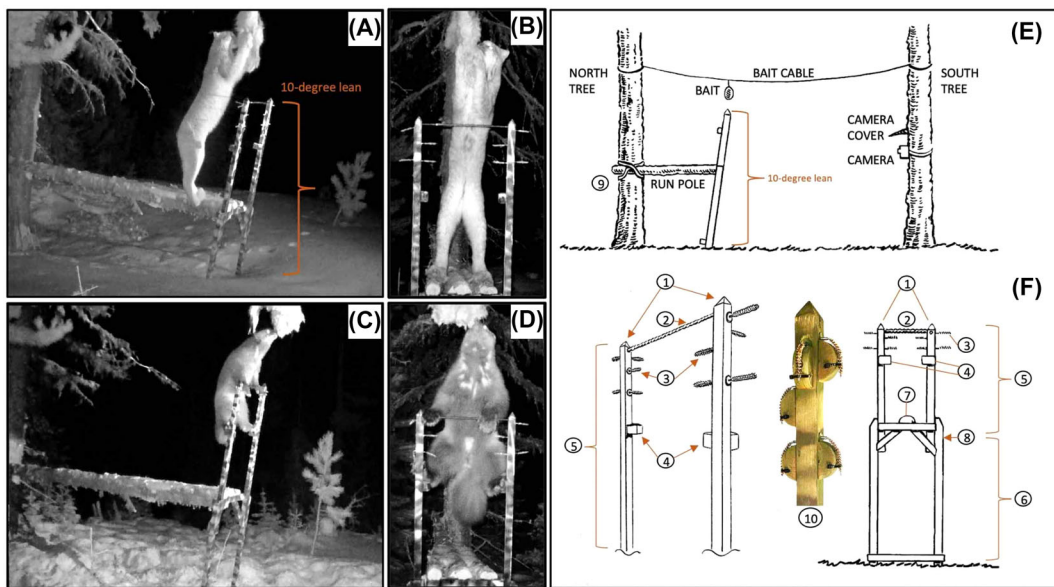


FIGURE 1 Layout and configuration of a station and frame design used for wolverine and lynx in Helena National Forest, Montana, USA, in 2021. We provide example photographs from camera B of lynx and wolverine visiting the monitoring station and mounting the frame (A, C), highlighting the 10-degree lean of the frame towards camera A, and the frontal view from camera A of lynxes (B) and wolverines (D) mounting the frame. We show the components and setup of the portable data collection framework from multiple angles (E, F), which includes 1) a pyramid-shaped upper support post top, 2) an upper horizontal support bar, 3) bore brush hair snags, 4) wolverine hindfoot supports, 5) the upper support system, 6) the lower support system, 7) a run pole, 8) the central hinging point, 9) the run-pole attachment system (ratchet strap or hardware), and 10) lynx-safe snags with spacer.

position mesocarnivores in a bipedal stance, exposing their ventral region to cameras. Hair snags continuously facilitated repeated genetic sampling. To account for expected seasonal snowfall accumulation in our study area, we adjusted the height of the lower support posts to 61–107 cm initially and as needed throughout the winter to accommodate heavy or light snowfall. After construction, we finished the frame with camouflage spray paint.

Two lynx entanglements in 2021 (where the long hairs on the bottom of the lynx's feet appeared to get caught as they wrapped their feet around a wire bore brush) prompted a design change to create a lynx-safe design by securing wire bore brushes around a semi-circular spacer (Figure S2E). This eliminated entanglements; 2 occurred before the modification (6 stations, 121 active days) and 0 occurred after (5 stations, 106 active days) the design modification.

We chose camera models Reconyx® HyperFire 2 (model HF2X), Reconyx® UltraFire (model XR6), Reconyx® HyperFire HD Covert IR (model HC600), and Bushnell® Core DS 30 MP Low Glow (model 119975 C) for their ability to operate reliably in extreme cold temperatures and capture high-quality images (Reconyx, Holmen, WI, USA; Bushnell, Overland Park, KS, USA). Energizer® lithium-ion batteries (Energizer, Clayton, MO, USA) powered the cameras and operated well at low temperatures, generally lasting the duration of the season. A passive infrared sensor, triggered by moving heat, activated cameras. Animal contact bent labeled bore brushes that could repeatedly capture hair from one or more animals. This aided in linking photos to corresponding hair samples. Camera A captured all bore brushes except numbers 5 and 10, located on the back of the framework, where animals often interacted with the top of each support post.

Cameras operated continuously, using an infrared flash at night to capture 10-photograph bursts. Camera A recorded still photographs with 8-megapixel resolution at 72 dots/inch (dpi) vertical and horizontal resolution. Camera B recorded 1080p high definition (HD) resolution, 30–60-second videos with audio and auxiliary

photographs. We used 32-gigabyte secure digital (SD) cards with capacity for approximately 2 hours of video or 15,000 JPEG photographs, which provided sufficient memory.

We checked the C&H stations every 2–3 weeks to minimize the number of individuals interfacing with the frame between checks, maintain fresh bait, and balance these needs with the costs of station checks (Appendix B, Table B1). Station checks involved replacing SD cards, collecting and replacing hair snags (i.e., bore brushes), replacing bait, and deploying lures. Wearing nitrile gloves to prevent contamination, we placed recovered hair snags individually in labeled coin envelopes with collector ID, date, station, and bore brush position, and then stored the envelopes in a dark, dry, cool location until season's end for processing.

Photographic analysis

We processed camera A images using 3 Python scripts. We searched for animal passes that did not trigger camera A in downloaded images (assumed to be exclusively instances where the animal did not mount the frame) and video footage from camera B and used concurrent time stamps to link camera B footage to camera A photographs. We binned photographs with continuous time stamps (by the minute) together into detection events labeled with the date and time stamp of the first photograph (Script 1, available in Supporting Information). Next, we sorted the events by station ID, time, and triggering agent (i.e., an animal species or focal species individual; Script 2, available in Supporting Information). For focal species, we categorized events based on the visibility of distinguishing pelage marks: no marks (no visible distinguishing marks, i.e., ventral region entirely obscured), partial marks (some visible marks, i.e., ventral region partially obscured), and full marks (all identification marks visible, i.e., entire ventral region visible). We copied detection events with all associated metadata (date, time, location, agent, and visibility of marks) to a spreadsheet (Excel, Microsoft Corporation, Redmond, WA, USA; Script 3, available in Supporting Information). To develop Python script, we prompted ChatGPT (OpenAI, San Francisco, CA, USA) with a description of the script's desired output from the given input of data. For example, we prompted ChatGPT to create a Python script (Script 3) that would generate a table from metadata within labeled directories of detection events, then tested all scripts for consistent functionality.

To identify the source of hair on each snag, we first visually linked the hair sample to the individual using photos, then identified the species, sex, and individual by pelage marks. We defined isolated events as a single individual of a species visiting the station between checks. For non-isolated visits (multiple individuals), we assessed the targeted individuals via photo identification; the individuals' interactions with the frame, indicating likely hair snags; and the percentage of time each individual interacted with specific bore brushes. This assessment yielded percent odds of hair-snag capture per individual, informing hair selection for lab samples. We also considered which initially upright bore brushes were bent after being rubbed, as seen in photographs.

Pelage pattern matching and individual characteristics

Following procedures for recovering and matching human fingerprints and Magoun et al. (2011b), we developed protocols to match a known ventral pelage pattern to a photographed wolverine or lynx individual. First, we located ≥ 1 high-quality photographs of an individual that clearly showed distinguishing pelage marks from the ventral region. For wolverines, an ideal position was standing on the hindfoot supports in a push-up position with front paws on the upper horizontal support. For wolverines, recognizing the pattern of highly contrasting light-colored marks on otherwise dark pelage was straightforward. Additionally, some wolverines had unique patterns of white on their forelegs, paws, and toes that further distinguished individuals (Figure 2A–F).

For lynx, the ideal position was standing on the run-pole with front paws reaching for bait (Figure 2G–L). Matching pelage patterns was more nuanced because they have fewer contrasting marks, and long-haired winter pelage can partially

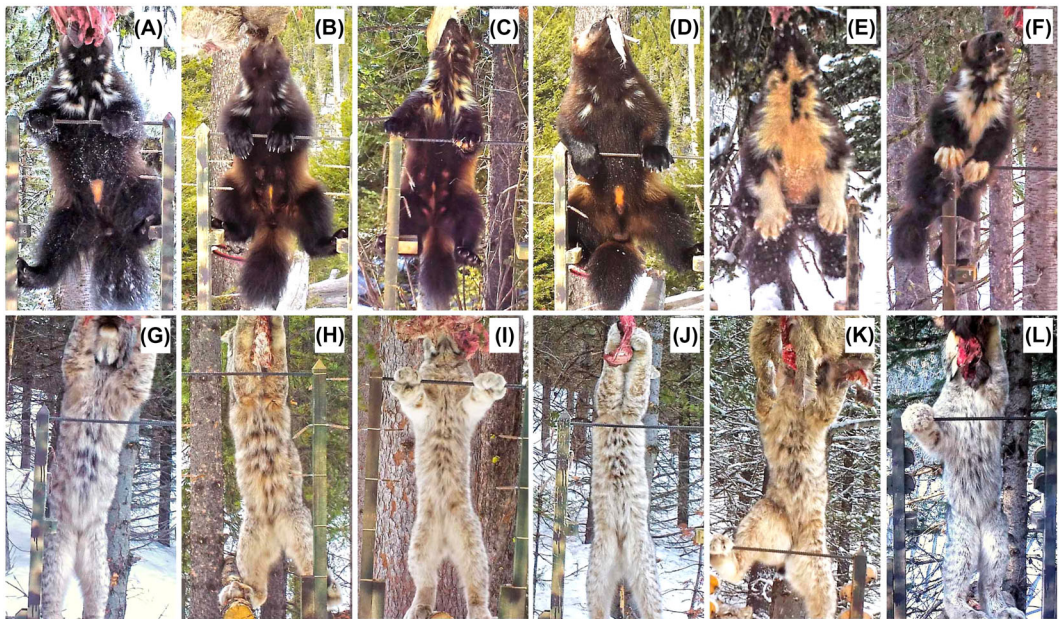


FIGURE 2 Examples of 6 individual wolverines (A–F) and 6 individual lynxes (G–L) whose ventral pelage patterns were linked to unique individual genotypes analyzed from hair samples in zones 1–4 of Montana, USA, in 2020–2024. We photographed wolverines in the ideal push-up position (A–F) required for individual photographic identification, with the ideal outstretched position for lynxes facilitated by a frame design that requires animals to reach their front paws toward the bait.

obscure marks (Anderson et al. 2023). As a result, we used multiple photographs from the same detection of an individual to map the complete pattern. We drew closed polygons overlaying the ventral area and enhanced this subset of high-quality images in Adobe Photoshop (Adobe, San Jose, CA, USA) to increase the contrast of distinguishing marks (Figure 3). Next, we split the ventral region into 4 quadrants (centering the dotted line across the median portion of the abdomen) and extracted the pattern of dark marks contrasted against the lighter background from each quadrant as individual polygons (Figure 3). We identified an individual lynx match by determining a similar characteristic polygon, or grouping of polygons, oriented within a quadrant for at least 3 of the 4 quadrants that was additionally consistent with the overall ventral region pattern when compared with photographed individuals (Figure 3). If we found a match to a known wolverine or lynx, we assigned that individual to the specific photo-identification. If we did not find a match, we assigned the animal a new photo-identification and added it to the database of known individuals. We verified each match by confirming consistency with sex, age class, and last known location and time of detection in the existing database following the method detailed in Magoun et al. (2011a, b) and Ramsey et al. (2019).

Images also provided information on sex, age class, reproductive status (i.e., lactation cycle stage), health status, interactions, and relatedness. We identified sex of wolverines per Magoun et al. (2011a, b; Figure S3) and determined lynx sex by genitalia (scrotum or vulva) and anogenital distance following Marti and Ryser-Degiorgis (2018; Figure 4). We assessed the lactation cycle of reproducing female wolverines by the progression of swelling teats (Figure S3; Carbyn and Patriquin 1983, Brainerd 1985, and Magoun et al. 2011a). We categorized lynxes as adults or kittens based on relative size (Figure 5) when individuals were detected in a family group (Figure S4), an assessment that was corroborated by confirming those individuals were new to the database. Kittens of the year were presumed to be 1 winter old, thereby establishing an inferred age timeline. Zone 1 lynxes were previously identified genetically, confirming any non-kitten as an adult. We investigated potential relatedness using detailed genetic analysis. We identified genitalia in other mesocarnivores without genetic corroboration.

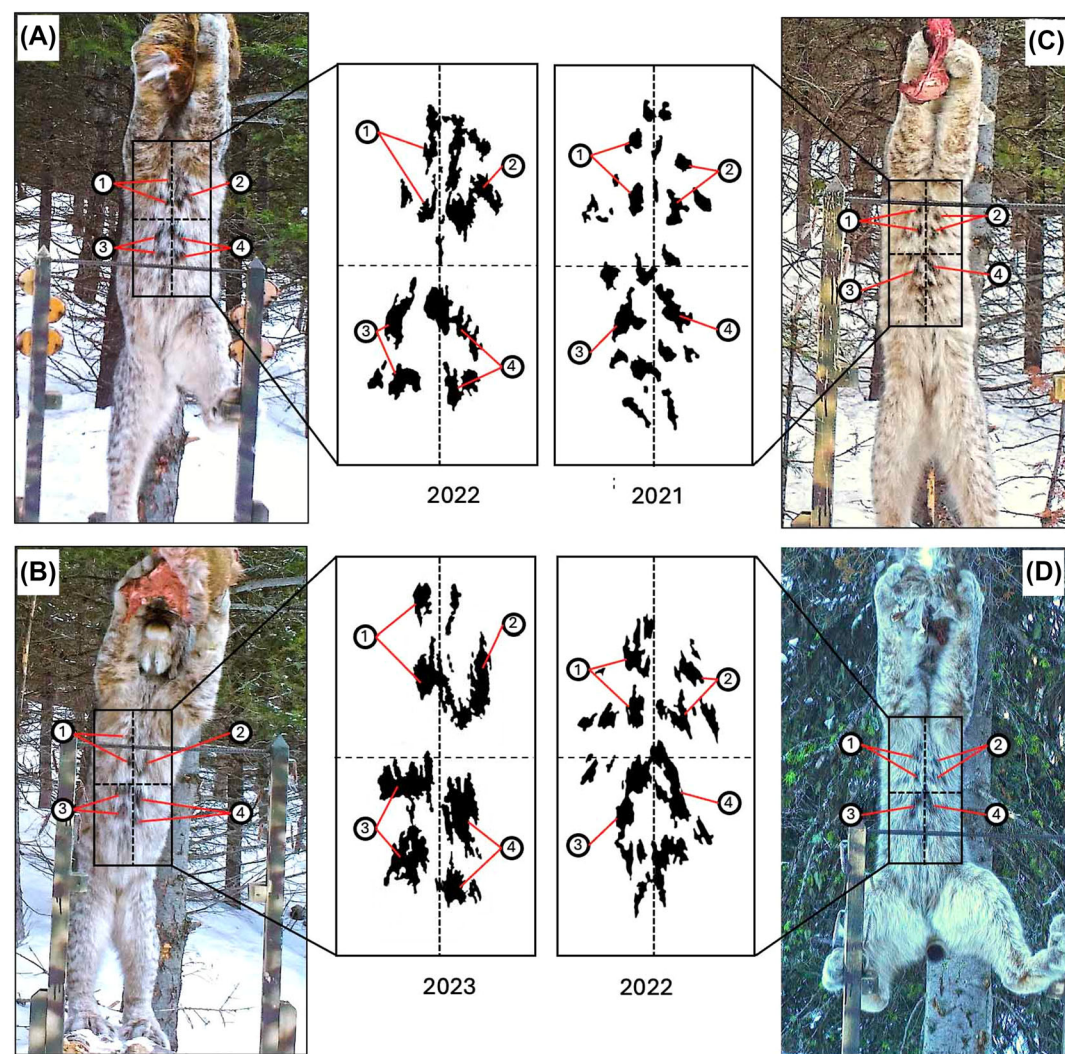


FIGURE 3 Identification, extraction, evaluation, and comparison of ventral pelage patterns from photographs of 2 lynx individuals from the Helena National Forest, Montana, USA, across multiple years. To characterize the distinguishing patterns of lynx, we split the ventral region into 4 quadrants and then extracted the pattern of dark marks contrasted against the lighter background from each quadrant as individual polygons. We identified an individual lynx match by determining a similar characteristic polygon, or grouping of polygons, consistently oriented within a quadrant for at least 3 of the 4 quadrants and additionally consistent with the overall ventral region pattern when compared to photographed individuals. Photographs of the first (A and B) and second (C, D) lynx individuals across years include insets of extracted distinguishing pelage patterns. For each detection event, we confirmed the identities of each lynx by genetic analysis of linked hair samples.

Analysis of genetic samples

We compiled hair samples from single or combined hair snags. We grouped putative wolverine and lynx hairs morphologically. Lynx have banded hairs that are thinner and finer, whereas wolverine hairs do not have distinct banding and are darker, coarser, and typically longer. For DNA extraction, we targeted snags with at least 10 hairs with follicles but used fewer when necessary. We stored hairs on identifying slides (300 series Bristol paper;

Strathmore[®], West Springfield, MA, USA) with double-sided tape in sterile 50-mL polypropylene centrifuge tubes (Non-pyrogenic, DN/RNase-free, Membrane Solutions LLC, Auburn, WA, USA) with 2-gram desiccant packets (Orange silica gel, Interlock Packaging[®], Kent, WA, USA).

To maximize economy, we did not analyze redundant samples from individuals identified in photographs while still addressing stated research goals. We labeled samples with presumed identities for subsequent genetic verification by the National Genomics Center (Missoula, MT, USA). In cases where genetic results disproved evaluations by photographic analysis, we reevaluated the photographic analysis.

We extracted genetic DNA from hair samples in a dedicated laboratory for non-invasive samples using the QIAGEN DNeasy[®] Blood and Tissue kit (Qiagen, Valencia, CA, USA) according to manufacturer's instructions for tissue and using modifications for hair samples (Mills et al. 2000). To determine species we amplified 360 base-pair (bp) mtDNA fragments using modified 16S rRNA universal primers (16sL-TAAACGGCCGCGGTATCC and 16sR-GAATTACGCTGTTATCCCT; Hoelzel and Green 1992). Reaction volumes of 30 μ L contained 50–100 ng DNA, 1 $\times$ reaction buffer (Life Technologies, Grand Island, NY, USA), 2.5 mM MgCl₂, 200 μ M each dNTP, 1 μ M each primer, and 1 U Amplitaq Gold polymerase (Life Technologies). The polymerase chain reaction (PCR) program was 94°C for 10 minutes, followed by 34 cycles of 94°C for 1 minute, 50°C for 1 minute, and 72°C for 90 seconds, and a final elongation step at 72°C for 5 minutes. We determined the quality and quantity of template DNA by 1.6% agarose gel electrophoresis. We used ExoSap-IT (Affymetrix-USB Corporation, OH, USA) to purify PCR products according to manufacturer's instructions.

Reactions were sequenced at Eurofins Genomics (Louisville, KY, USA) using standard Sanger sequencing protocols. We used Sequencher (Gene Codes Corp, Ann Arbor, MI, USA) to view and align DNA sequence data and compared sequences to reference sequences from known species.

Microsatellite DNA amplification and analysis

We analyzed wolverine samples at 19 microsatellite loci used in previous mustelid studies: Gg3, Gg4, Gg7, Gg14, Ma2, Ma8, Tt1, Tt4 (Davis and Strobeck 1998); Mp0120, Mp0182, Mp0197 (Jordan et al. 2007); Ggu101, Ggu216, Ggu234, Ggu238 (Duffy et al. 1998); Mvis020, Mvis72, Mvis075 (Flemming et al. 1999); and Lut604 (Dallas and Piertney 1998). We genetically identified sex using the dbxy-215 primers and digest (Sekiguchi et al. 2010).

We analyzed lynx samples at 10 microsatellite loci: Lc106, Lc109, Lc110, Lc111, Lc118, Lc120 (Carmichael et al. 2000); Fca43, Fca57, Fca132 (Menotti-Raymond et al. 1999); and PcoA208 (Kurushima et al. 2006). We identified genetic sex using the amelogenin region (Pilgrim et al. 2005).

The PCR reaction volumes (10 μ L) contained 1.0 μ L DNA, 1 $\times$ reaction buffer (Applied Biosystems, Foster City, CA, USA), 2.0 mM MgCl₂, 200 μ M of each dNTP, 1 μ M reverse primer, 1 μ M dye-labelled forward primer, 1.5 mg/ml BSA, and 1U Taq polymerase (Applied Biosystems). We multiplexed 3–4 loci per reaction, and the PCR profile used for all multiplexes was 94°C for 5 minutes, followed by 45 cycles of 94°C for 1 minute, 55°C for 1 minute, 72°C for 30 seconds. We amplified DNA from hair samples using the multi-tube approach (McKelvey and Schwartz 2004) by amplifying each sample at least twice at each locus and followed protocols outlined in Elbroch et al. (2024) for generating concordant genotypes. We removed any sample that failed at more than 20% of the loci panel from further consideration. We visualized the resultant products on a LI-COR DNA analyzer (LI-COR Biotechnology, Lincoln, NE, USA). We used the program Dropout (McKelvey and Schwartz 2005) and GenAIEx (Peakall and Smouse 2006, 2012) to error-check the genotype data. We compared resulting genotypes to regional DNA databases for lynxes ($n = 80$) and wolverines ($n = 50$) housed at the National Genomics Center to determine new and recaptured individuals.

We used GenAIEx and the program CERVUS 3.0 (<https://cervus.software.informer.com/3.0>) to calculate standard genetic measures (probability of identity (PID), probability of identity given siblings (PIDsib), polymorphic information content (PIC), observed heterozygosity (Ho), expected heterozygosity (He), and number of alleles) for

animals identified from this study and the regional dataset. We performed tests for Hardy-Weinberg equilibrium on the loci using the regional datasets.

RESULTS

Photographic detections

We photographed wolverines at 16 stations and in every year of the study, totaling 36 station-years (Table 1). We photographed lynxes at 9 stations and in every year of the study, totaling 23 station-years (Table 1). We photographed martens (*Martes* spp.), red foxes (*Vulpes vulpes*), and bobcats (*Lynx rufus*) at 8, 12, and 6 stations, respectively (Figure 6). We photographed wolverines, lynxes, and martens mounting the frame every year they were detected at all stations, except in the case of one wolverine at site 11 in zone 1. We photographed red foxes mounting the frame in 6 station-years and bobcats in 5 station-years.

Over 5 field seasons, we identified 19 unique individual wolverines from photographic evidence (Figure S5), assigning sex (12 male, 7 female) and determining unique ventral patterns and patterns of white on the forelegs, feet, and toes for each wolverine (Figure 2, S3, and S6A–E). During successive monitoring seasons between 2020–2024, we identified 2 (1 male, 1 female), 3 (2 male, 1 female), 2 (1 male, 1 female), 8 (6 male, 2 female), and 12 (5 male, 7 female) wolverine individuals, respectively (Table 2). Photographs of 5 of the 19 wolverines' individual pelage patterns were recaptured from previous monitoring records, 2 were first identified during this study and 3 in other monitoring studies. We recovered photographs of wolverine ventral patterns from 67% of station-years (Tables 1 and 2). We documented 5 lactating female wolverines during 3 monitoring seasons.

Over 5 field seasons, we identified 12 unique lynxes (6 male, 2 female, 4 unknown) from photographic evidence (Figure S5), assigning sex or determining unique ventral patterns for 10 lynxes (6 male, 2 female, 2 unknown; Figures 2, 4, and S6F–I). From photographs, we identified 3 (2 male, 1 female), 3 (2 male, 1 female), 3 (2 male, 1 female), 6 (3 male, 1 female, 2 unknown), and 3 (1 male, 2 unknown) lynx during successive monitoring seasons between 2020–2024, respectively. Photographs of 3 of the 10 lynxes' individual pelage patterns were recaptured, all of which were first identified during this study. We recovered photographs of lynx ventral patterns from 33% of station-years (Tables 1 and 2). We photographed both wolverine and lynx ventral patterns at the same monitoring site for 17 station-years, all in zone 1. We did not use ventral patterns on martens, red foxes, or bobcats for individual identification, as these mesocarnivores were not the primary focus of this study. We photographed a morphologically distinct cross fox (i.e., with a partially melanistic coat pattern) at 1 site in 2023.

Genetic detections

From 29 station-years (601 hair snags collected during 89 checks) with wolverine hair recovered, we compiled 126 DNA samples composed of 127 hair snags (21%; Tables 3 and 4). From 126 presumed wolverine hair samples analyzed, 118 (93.7%) were identified as wolverine, 6 were identified as marten, and 2 did not yield DNA for analysis. Of these, we chose 99 (88%) for further individual and sex identification with 89 samples (90%) yielding an individual genotype. From 164 presumed lynx hair samples analyzed, 154 (94%) were identified as lynx, 3 samples were from the bait, and 7 did not yield DNA for analysis. Of these, we further analyzed 118 (77%) for individual and sex identification, with 83 samples (70%) yielding an individual genotype. Fifteen of the lynx hair samples analyzed from 2023 were a mixed sample with more than one individual present (>2 alleles observed at several loci) and were not used for analysis. We used a genotype for a sample if the sample successfully amplified with consistent allele scores at 80% of the loci. The loci used

TABLE 1 Number of years wolverines, lynxes, martens, red foxes, and bobcats were photographed at monitoring stations and wolverine and lynx genotypes were recovered at monitoring stations for each year of the study (2020–2024) across all 4 study area zones of Montana, USA: zone 1 is Helena National Forest, zone 2 is Bitterroot National Forest, zone 3 is Beaverhead-Deerlodge National Forest, and zone 4 is Lolo National Forest. The red fox detection at station 3 in zone 3 represents a single detection of a cross fox (partially melanistic color variant of typical red fox coat). The total row includes the numbers of stations and station-years.

Study area	Station	Station-years	Number of years detected					Number of years genotypes recovered	
			Wolverine	Lynx	Marten	Red fox	Bobcat	Wolverine	Lynx
Zone 1	1	3	3	0	0	2	0	2	0
	2	4	3	4	0	0	1	1	4
	3	4	4	4	0	1	0	2	4
	4	3	1	3	0	2	0	1	2
	5	3	2	0	0	3	0	0	0
	6	3	3	3	0	1	0	3	1
	7	3	2	0	0	1	0	0	0
	8	4	4	3	0	2	0	2	1
	9	4	4	0	0	0	1	3	0
	10	3	3	3	0	2	0	0	0
	11	1	1	0	0	0	1	0	0
Zone 2	1	2	0	0	2	1	2	0	0
	2	2	1	0	2	0	0	1	0
	3	2	0	0	2	1 ^b	0	0	0
	4	2	2	0	2	2	0	2	0
	5	2	0	0	2	0	2	0	0
Zone 3	1	1	1	0	0	0	1	1	0
	2	1	1	0	1	0	0	1	0
	3	1	0	0	1	0	0	0	0
	4	1	1	0	1	1	0	1	0
Zone 4	1	1	0	1	0	0	0	0	1
	2	1	0	1	0	0	0	0	1
	3	1	0	1	0	0	0	0	1
Total	23	52	36	23	13	18	8	20	15

for genotype analysis had high power to discern individuals, while observed heterozygosity for both species in this study were higher than expected, though this is likely because of sampling and small numbers of individuals (Table 5). One locus in each dataset deviated from Hardy-Weinberg equilibrium: Mvis72 (wolverine; $P = 0.028$) and Lc118 (lynx; $P = 0.016$; Table 5). We identified 15 unique wolverine genotypes (11 male, 4 female), with 4 unique wolverine genotypes recaptured from previous monitoring records: 2 first identified from this study and 2 from other monitoring projects. We recovered unique wolverine genotypes from 38% of station-years (Tables 1 and 5).

TABLE 2 Summary of monitoring success based on photographic analysis results for wolverines and lynxes each year of the study (2020–2024) across all 4 study area zones of Montana, USA: Helena National Forest (NF), Bitterroot NF, Beaverhead-Deerlodge NF, and Lolo NF. Totals represent cumulative values across years.

Year	Stations with wolverine ventral patterns identified	Wolverine individuals	Wolverine recaptures	Stations with lynx ventral patterns identified	Lynx individuals	Lynx recaptures
2020	7	2	1	4	3	0
2021	9	3	2	4	3	2
2022	8	2	1	4	3	3
2023	6	8	4	2	6	1
2024	5	12	4	3	3	0
Total	35	27	12	17	18	6

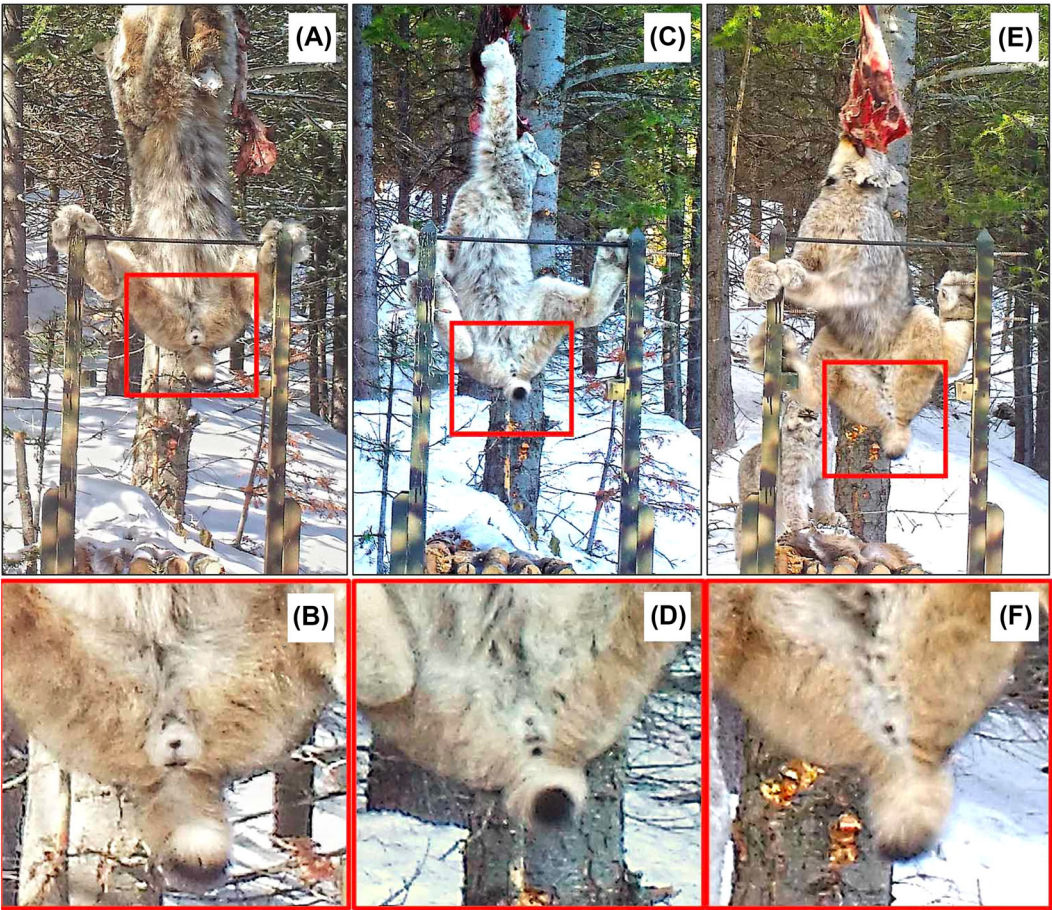


FIGURE 4 Example of sex determination in 3 lynxes in Helena National Forest, Montana, USA, in 2021, including an adult male (A, with closeup of genital area in enlarged photo for same individual shown in B); a sub-adult male (C, with closeup of genital area in enlarged photo for same individual shown in D); and an adult female (E, with closeup of genital area in enlarged photo for same individual shown in F). The scrotum is less pronounced in the sub-adult male (C, D) than in the adult male.

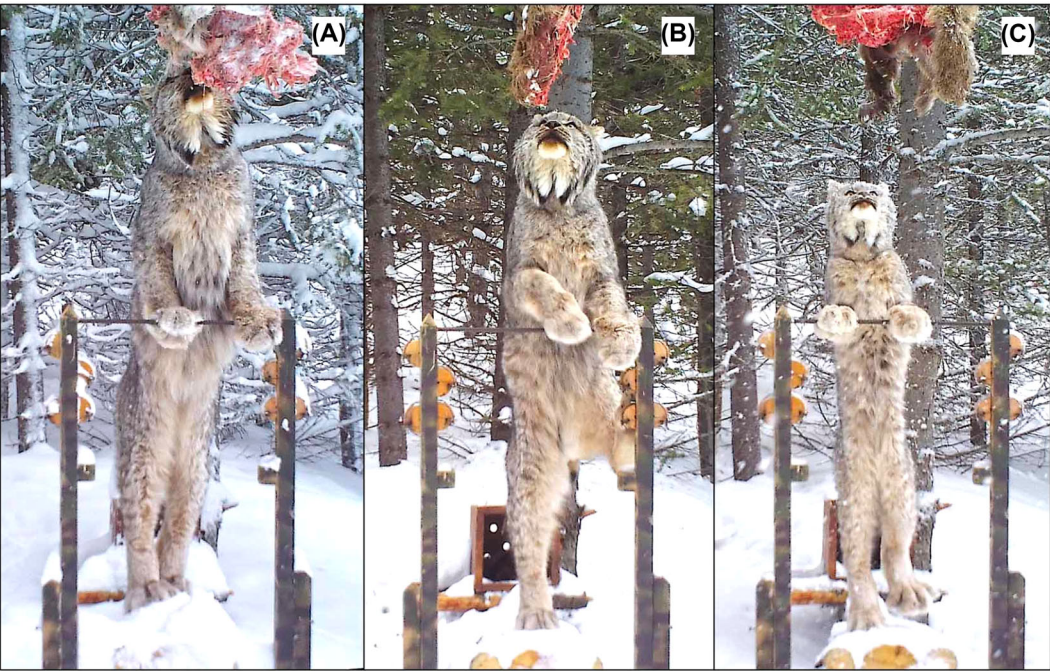


FIGURE 5 Sexual dimorphism between adult male (A) and adult female (B) lynxes photographed in Helena National Forest, Montana, USA, in 2023. We also used body size differences relative to the frame to assess age classes, which included adult lynxes (A, B) and lynx kittens in their first winter (C).

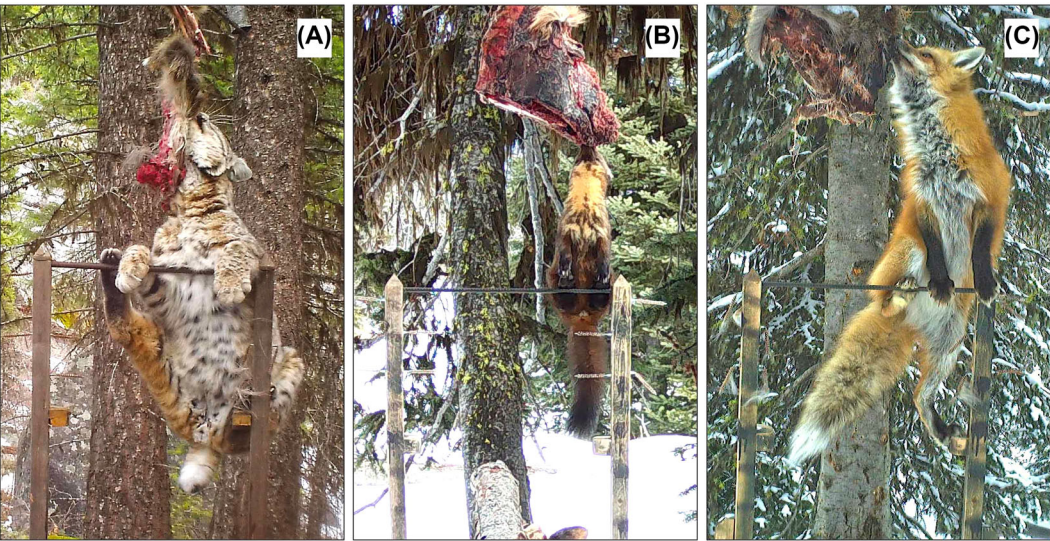


FIGURE 6 Additional mesocarnivore species detected at monitoring stations included (A) bobcats, (B) martens, and (C) red foxes. Genitalia and ventral patterns are visible on the A) male bobcat and B) male marten.

TABLE 3 Summary of monitoring success based on genetics analysis for wolverines and lynxes each year of the study (2020–2024) across all 4 study area zones of Montana, USA: Helena National Forest (NF), Bitterroot NF, Beaverhead-Deerlodge NF, and Lolo NF. Totals represent cumulative values across years.

Year	Stations with wolverine genotypes	Wolverine genotypes	Wolverine recaptures	Stations with lynx genotypes	Lynx genotypes	Lynx recaptures
2020	2	2	1	3	3	0
2021	3	3	2	2	3	2
2022	5	2	1	5	3	3
2023	5	8	4	2	5	2
2024	5	8	4	3	1	1
Total	20	23	12	15	15	8

TABLE 4 Summary of quality of DNA samples analyzed based on amplification of DNA results for wolverine and lynx each year of the study (2020–2024) across all 4 study area zones of Montana, USA: Helena National Forest (NF), Bitterroot NF, Beaverhead-Deerlodge NF, and Lolo NF. Totals represent cumulative values across years.

Year	DNA samples	Samples positive for the species	Samples analyzed for DNA individual and sex identification	Samples yielding DNA individual and sex identification
Wolverine				
2020	4	4	4	4
2021	12	11	11	11
2022	46	46	27	24
2023	39	38	38	32
2024	25	19	19	18
Total	126	118	99	89
Lynx				
2020	9	8	8	7
2021	18	15	15	11
2022	61	61	25	20
2023	60	58	58	34 ^a
2024	16	12	12	11
Total	164	154	118	83

^aFifteen lynx samples tested for individual and sex identification from the 2023 collection were from >1 individual.

From 15 station-years (393 hair snags collected during 44 checks) with lynx hair recovered, we compiled 164 DNA samples composed of 95 hair snags (24%) and identified 9 lynx genotypes (6 male, 3 female; Tables 3 and 4). Five lynx genotypes were recaptured: 3 first identified from this study and 2 from other monitoring projects. We recovered unique lynx genotypes from 29% of station-years (Tables 3–5). We recovered both wolverine and lynx individual genotypes at the same monitoring site 5 station-years, all in zone 1.

TABLE 5 Standard genetic measures for the individuals used in this study (9 lynx and 15 wolverine) in Montana, USA, 2020–2024, and a larger regional DNA databases used for comparison. Measures provided are number of individuals (*n*), number of loci, mean number of alleles per locus, observed heterozygosity (*Ho*), expected heterozygosity (*He*), mean polymorphic information content (*PIC*), probability of identity (*PID*), and probability of identity given siblings (*PIDSibs*).

Species	Dataset	<i>n</i>	Loci	Alleles/locus	<i>Ho</i>	<i>He</i>	<i>PIC</i>	<i>PID</i>	<i>PIDSibs</i>
Lynx	This study	9	10	2.90	0.59	0.48	0.42	1.4E-05	5.4E-03
	Regional	80	10	5.60	0.64	0.65	0.59	2.4E-08	5.3E-04
Wolverine	This study	15	19	3.37	0.53	0.50	0.44	9.3E-11	2.6E-05
	Regional	50	19	3.95	0.51	0.50	0.45	3.3E-11	2.0E-05

TABLE 6 Summary of concordance between results of genetic and photographic analyses for wolverine and lynx each year of the study (2020–2024) across all 4 study area zones of Montana, USA: Helena National Forest (NF), Bitterroot NF, Beaverhead-Deerlodge NF and Lolo NF. Totals represent cumulative values across years.

Year	Wolverine photo IDs linked to unique genotype	Wolverine photo IDs linked to multiple genotypes	Wolverine photo IDs not linked to a genotype	Lynx photo IDs linked to unique genotype	Lynx photo IDs linked to multiple genotypes	Lynx photo IDs not linked to a genotype
2020	2	0	0	3	0	0
2021	3	0	0	3	0	0
2022	2	0	0	3	0	0
2023	6	2	0	2	4	0
2024	8	0	4	1	0	2
Total	21	2	4	12	4	2

Concordance between methods

We linked 15 of 19 photographed wolverine individuals (78%) to genotypes (11 male, 4 female), with 100% consistency between genetic and photographic analysis for species, sex, and individual ID (Table 4). Two wolverine genotypes were associated with ventral patterns for 2 male wolverines, giving each a 50% chance of matching either genotype. All other wolverines were linked to unique genotypes, and all but 1 of these were linked to isolated visits. We could not identify the remaining 4 wolverines because we did not have genetic samples or the samples did not amplify (Table 6).

Photographic identification with integrated genetic sampling proved more complex for lynx. Of 10 lynxes with fully visible ventral pelage, we linked 6 (60%) to individual genotypes (4 male, 2 female; Table 4). All but 2 of these were linked to isolated visits. The remaining 4 lynxes were kittens (2 male, 1 female, 1 unknown) in the family group of 6 in 2023. Although camera B video confirmed 2 male kittens, those males could not be linked to ventral patterns recorded by camera A. Three lynx genotypes (2 male and 1 female) were linked to the 4 kittens' ventral patterns, giving each a 25% chance of matching any of the genotypes. Genetic analysis confirmed the kittens were related to the 2 adults in the photos (Table S1). Two other lynxes photographed in 2024 had an insufficient genetic sample for amplification for unique IDs.

Species and sex identification by photographic analysis for lynx matched linked genotypes in 100% of cases. However, photographic analysis incorrectly identified 1 adult female lynx in 2023; subsequent genetic analysis showed she was a different adult female. Photographic analysis aligned with genetic results across multiple years in all other cases (98% Figure 2G–L; Figures S4 and S6). From 2020–2024, 15 lynx samples yielded unusable genotypes because of the presence of more than 1 individual. We successfully matched ventral patterns and linked genotypes to all recaptured wolverines and lynxes.

Marten hair can be mistaken for wolverine hair because it has similar morphology. Despite this challenge, determination of species, sex, and individual ID by genetic analysis verified and was consistent with identifications made by photographic analysis alone for all but 6 samples (mistaken as marten hair) in wolverines (94%) and for all but 2 samples (mistaken as the wrong individual but correct in species and sex) in lynxes (98%). The greater number of samples analyzed to secure a unique genotype in lynx (8.1 samples per unique genotype) compared to wolverine (4.7 samples per unique genotype) reflects the complexities of linking lynx hair samples to photographic identifications.

DISCUSSION

Our redesigned monitoring system of motion-detection cameras and hair snares improves wolverine and lynx monitoring by reducing costs, increasing portability, and expanding data collection to include reproductive status, relatedness, age class, behavior, and health. Final modifications, based on trial and error over 5 monitoring seasons, demonstrated the durability and adaptability of the Magoun et al. (2011a) system for multiple mesocarnivore species. We confirmed that photographic analysis is a viable alternative to solely genetic analysis for identifying and monitoring a rare, elusive mesocarnivore species, the wolverine. For lynx, photographic analysis complements genetic analysis. The wolverines' solitary nature and distinct pelage markings create ideal conditions for repeated, reliable photographic identification. Matching genotypes to each photographed lynx was more challenging because of their less-distinct pelage patterns and frequent multi-animal visits. We misidentified 1 female lynx using ventral patterns from photographs, but she was already in the United States Forest Service database. Advancements in digital camera technology and artificial intelligence (AI) uses (e.g., pattern recognition, extraction, matching) may soon solve challenges in identifying species with more complex ventral pelage patterns.

We reduced laboratory costs associated with genetic analyses by using the photographic evidence to pick a subset of collected samples for analysis. This offset the additional operating costs of running a station incurred by including the cameras. After 4 years of testing, we found the most valuable modifications to the portable C&H station were a 10-degree lean (frontal-facing photo capture), strategic bore brush placement (multi-species sampling), a portable frame design, optional ratchet strap tree connection for deployment where connection hardware (i.e., lag bolts and screws) is not allowed, pyramidal caps on upper supports (reduced perching), and adding a second camera (additional data). Reduced station material costs created an accessible and efficient method for monitoring rare carnivores over large landscapes. Researchers adapting this methodology should tailor techniques to regional variations in winter snow cover, temperatures, and the mesocarnivore community and validate with genetic methods alongside photographic analysis.

A key adaptation of the Magoun et al. (2011a, b) method included replacing alligator clips, which collect a single hair sample from a definite single individual, with wire bore brushes, which continuously collect hair between station checks. Because genotype is matched to both species and sex, which is also identified from photographs, we could match multiple genotypes from snags to multiple individuals visiting between checks. For example, it would be possible to match 1 male wolverine, 1 female wolverine, 1 female lynx, and 1 male lynx. This maximizes genotype recovery and linked photographic identifications from a station. If a single sample contains hair from multiple individuals, or if multiple undocumented individuals of the same species and sex are linked to a sample collection, individual genotype may not be identifiable. We see the potential value of including both bore brushes (our

modification) and adding alligator clips (Magoun et al. 2011a, b) as hair snags to maximize repeat sampling, while alligator clips provide single-individual samples.

The shortcomings of C&H monitoring stations include the risk of introducing diseases and creating conflict with bears at bait sites. Also, the cameras use lithium-ion batteries, a sensitive resource (McGlamery 2023, Long et al. 2024). We discovered that wire bore brushes have the potential to present previously unreported problems with lynx entanglement (e.g., Robinson et al. 2017, Golding et al. 2022) but that the deployment of lynx-safe hair snags appeared to completely eliminate these issues. Potential risks to animal safety associated with the use of bore brushes can be easily mitigated and do not outweigh the benefits of an efficient, effective, low-impact, and non-invasive method of long-term demographic monitoring in remote locations, particularly in areas where federally listed species are present.

Piloting the use of our modified data collection framework with more common mesocarnivore species confirmed that martens, bobcats, and red foxes will use the station as designed, allowing long-term collection of photographic and genetic data. Despite martens and bobcats mounting the frame far more often than red foxes, we were able to successfully link photographed individuals to DNA samples amplified to the species level (but did not assess individual identity or sex). The use of similar techniques has been reported in other mustelid species (Hofmeester et al. 2024), highlighting the application of this methodology for additional species that have individually distinct pelage markings, with the cost-effectiveness of this design increasing with each additional species that is monitored simultaneously. Future testing and possible further modifications to the portable integrated monitoring system design described here could increase the quality and quantity of non-invasive data collection for red foxes, bobcats, and martens, and are an exciting and logical next step for researchers.

CONSERVATION IMPLICATIONS

Our redesigned monitoring system of motion-detection cameras and hair snares improves managers' ability to collect comprehensive, long-term demographic data on rare mesocarnivore species across remote terrain and prioritizes portability and cost savings to facilitate management and conservation efforts at landscape scales. The benefits of collecting demographic, occupancy, and connectivity data for multiple wildlife species simultaneously are pronounced for species listed under the Endangered Species Act and are becoming increasingly important for more common species in the face of accelerating climate change, habitat fragmentation, and disease impacts. We incorporated new lynx-safe modifications to hair snags into our modified C&H monitoring stations while increasing the richness and quality of data collected on individual identity, sex, relatedness, reproductive status, health, and behavior. We anticipate that ongoing advancements in AI applications will enhance the efficiency and effectiveness of using non-invasive monitoring for both rare and common wildlife species in the near future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All study methodologies were reviewed and approved by relevant authorities, including United States Forest Service wildlife biologists and district rangers, ensuring adherence to ethical standards for research involving federally listed species. Lynx-safe hair snags were specifically designed and tested to eliminate the risk of entrapment, prioritizing animal safety while allowing effective genetic sampling. Bait was collected under a Montana Fish, Wildlife and Parks permit from roads adjacent to study areas to avoid the spread of chronic wasting disease in deer carcasses.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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APPENDIX A: STATION SETUP INSTRUCTIONS

For ease of transport, we created a foldable frame by using a central hinge and loosening screws that fixed lower and upper support sections together. The frame folded so that the upper support nested within the lower support. Fully deployed, the frame measured 57 cm wide and 104 cm tall. Folding reduced the dimensions to approximately half the fully deployed size. Upper horizontal support consisted of 1 51-cm piece of 0.95-cm #3 rebar that was secured to the tops of the upper support posts by tapping into 0.95-cm pre-drilled holes and glued in place with marine epoxy. We added wolverine hindfoot supports to the upper support posts 30.5 cm below the upper horizontal support and cut the tops of the upper supports to pyramids. We constructed all components from 3.8 × 3.8-cm furring lumber that was fastened together with 7.6-cm and 10-cm star wood deck screws.

We secured 10 wire 30-caliber bore brushes (7.62 × 63 mm Brownells®, Montezuma, IA, USA) to the frame by screwing into 0.64-cm T-nuts that were attached strategically (i.e., to facilitate focal species rubbing against the bore brushes) to the outside and inside profile and backside of the upper support posts and drilled the T-nuts in place before securing them with marine epoxy. Each hair snag position was labeled 1–10 for ease of linking specific hair snags to specific hair snagging events documented in photographs. We provide additional frame component details that can assist other researchers in building the portable structure (Figure S2).

In the field, we procured run poles from standing dead trees with diameter range of 10.2–15.2 cm but with milled lumber dimensions of 10.2 × 10.2 cm and a minimum length of 1.2 m given existing management restrictions at some sites that prevented harvest of materials or because of the scarcity of forest resources in some areas. We secured frames on site with 10-cm deck screws to the end of a run pole attached with 10–15-cm deck screws to a standing tree (north tree), or optionally with a 3.8-cm-wide ratchet strap where regulations forbade inserting mounting hardware into trees. We set the framework with a 10° lean towards a camera (camera A) affixed to a second standing tree (south tree). We adjusted the length of the run pole until the distance between the framework and camera A was approximately 3.4 m to provide a consistent photographic field of view across stations. We chose the north tree and south tree on an approximate north-south line so that the subject of camera A was south-facing for optimal natural lighting conditions before establishing a minimum distance between the 2 trees of 4.3 m. We set a minimum distance of 0.9 m between the bait and north tree to decrease the likelihood of focal species jumping onto the bait from the tree instead of using the run pole. To ensure a wide view of the C&H station and create a backup in case of failure of

camera A, we fixed a second camera (camera B) to a third tree at a right angle to the line between the north tree and the south tree. Like Magoun et al. (2011a, b), we added camera covers to prevent snow from accumulating on lenses. Between the north tree and south tree, we strung a wire bait cable (composed of 3 strands of 16-gauge wire) from which we hung a road-kill-sourced unskinned quarter from white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), or elk (*Cervus canadensis*) by a similar wire cable approximately 41 cm above the upper horizontal support (Figure 1). City of Helena Animal Control also provided white-tailed and mule deer that had been culled and tested negative for chronic wasting disease (CWD). We supplemented these deer with deer collected using a Montana State roadkill animal salvage permit. In addition to the bait, we applied a long-distance call lure (Caven's® Gusto Long Distance Predator Lure, Minnesota Brand, Minnesota Trapline Products, Pennock, MN, USA). To assist researchers in constructing and using our portable structure, we have provided step-by-step instructions (Video 1).

Key changes to the C&H station design in Magoun et al. (2011a, b) included a foldable frame for transport, a 10° lean of the frame towards camera A, wire bore brushes with T-nut anchors as hair snags, ratchet straps to secure run poles to live standing trees, wood frame materials for upper and lower support, a stable tripod configuration for supporting the frame and run pole, adapted frame dimensions, an improved rigid upper horizontal support, pyramidal caps on vertical uprights, wire bait cable assembly, and a side view camera B. Modifications specialized for wolverines included hind foot supports.

APPENDIX B: PROJECT COST COMPARISON ANALYSIS

See Table B1.

TABLE B1 Typical approximate project costs (in US dollars as of 2024) for materials and lab services to maintain a camera and hair snag (C&H) monitoring station for wolverine and lynx for the startup year and an additional year in Montana, USA.

Material or supply	Unit cost	Quantity	Vendor	Purpose	Total cost, year 1	Total cost per additional year
1.5" x 1.5" furring lumber (8' strip)	\$1.75	3	Home Depot	Frame construction	\$5.25	0
3" star flathead wood deck screws (365 pack)	\$35.97	20 pieces	Home Depot	Frame construction	\$1.97	0
4" star flathead wood deck screws (237 pack)	\$35.57	2 pieces	Home Depot	Frame construction	\$0.30	0
Tee-nuts (M5) (3 pack)	\$2.75	10 pieces	Home Depot	Frame construction	\$9.17	0
#3 rebar 48" (12 pack)	\$30.97	1 piece	Home Depot	Frame construction	\$2.58	0
Green exterior wood spray paint 12 oz	\$6.98	0.25 oz	Home Depot	Frame construction	\$0.15	0
8 oz marine epoxy	\$4.97	1 oz	Home Depot	Frame construction	\$0.62	0
Coin envelope (500 pack)	\$35.09	30 pieces	Staples	Hair snag storage	\$2.11	\$2.11
0.30 caliber bore brushes (12 pack)	\$32.99	30 pieces	Brownells	Hair snags	\$82.48	\$82.48
Nitrile gloves (100 pack)	\$21.87	10 pieces	Home Depot	Handling genetics	\$2.19	\$2.19
16.5 gauge rebar tie wire (400 ft.)	\$11.97	55 ft	Home Depot	Bait cable and attachment	\$1.65	\$1.65
Caven's Gusto Long Distance Predator Lure (4 oz)	\$25.00	1	IronTrail Trapline Supply	Focal species attractant	\$25.00	\$25.00
SanDisk Ultra 32 GB SDHC memory card	\$16.93	4	Staples	Memory card for photo storage	\$67.72	0
Reconyx® UltraFire (model XR6)	\$599.95	1	TrailCamPro.com	Camera A	\$599.95	0
Bushnell® Core DS 30 MP Low Glow (model 119975 C)	\$199.95	1	TrailCamPro.com	Camera B	\$199.95	0
3 g desiccant sachet (100 pack)	\$19.59	10 sachets	Interlock packaging	Preparing genetic samples	\$1.96	\$1.96

(Continues)

TABLE B1 (Continued)

Material or supply	Unit cost	Quantity	Vendor	Purpose	Total cost, year 1	Total cost per additional year
50 mL centrifuge tubes (100 pack)	\$49.99	10 tubes	Sigma Aldrich	Preparing genetic samples	\$5.00	\$5.00
Acid-free paper (20 8.5" x 11")	\$21.99	2 pieces	Staples	Preparing genetic samples	\$2.20	\$2.20
Nuclear DNA assays	\$50	10	RMRS, USFS	Genetics analysis	\$500	\$500
Mitochondrial DNA assays	\$25	10	RMRS, USFS	Genetics analysis	\$250	\$250
Totals					\$1,760.25	\$872.59