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Terrain Features and Architecture of Wolverine (*Gulo gulo*) Resting Burrows and Reproductive Dens on Arctic Tundra

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ABSTRACT. Burrowing species rely on subterranean and subnivean sites to fulfill important life-history and behavioral processes, including predator avoidance, thermoregulation, resting, and reproduction. For these species, burrow architecture can affect the quality and success of such processes, since characteristics like tunnel width and chamber depth influence access by predators, thermal insulation, and energy spent digging. Wolverines (*Gulo gulo*) living in Arctic tundra environments dig burrows in snow during winter for resting sites and reproductive dens, but there are few published descriptions of such burrows. We visited 114 resting burrows and describe associated architectural characteristics and non-snow structure. Additionally, we describe characteristics of 15 reproductive den sites that we visited during winter and summer. Although many resting burrows were solely excavated in snow, most incorporated terrain structures including cliffs, talus, river shelf ice, thermokarst caves, and stream cutbanks. Burrows typically consisted of a single tunnel leading to a single chamber, though some burrows had multiple entrances, branching tunnels, or both. Tunnels in resting burrows were shorter than those in reproductive dens, and resting chambers were typically located at the deepest part of the burrow. Reproductive dens were associated with snowdrift-forming terrain features such as streambeds, cutbanks on lake edges, thermokarst caves, and boulders. Understanding such characteristics of Arctic wolverine resting and reproductive structures is critical for assessing anthropogenic impacts as snowpack undergoes climate-driven shifts.

Key words: burrow; *Gulo gulo*; reproductive den; resting site; river shelf ice; snow; subnivean; wolverine

RÉSUMÉ. Les espèces fouisseuses dépendent de lieux enfouis sous la terre et sous la neige pour satisfaire leurs importants processus de vie et de comportement, y compris l'évitement des prédateurs, la thermorégulation, le repos et la reproduction. Pour ces espèces, l'architecture des terriers peut avoir des effets sur la qualité et la réussite des processus, car des caractéristiques comme la largeur des tunnels et la profondeur des chambres influencent l'accès aux terriers par les prédateurs, l'isolation thermique et l'énergie dépensée pour creuser. L'hiver, les carcajous (*Gulo gulo*) qui vivent dans les environnements de la toundra de l'Arctique creusent des terriers dans la neige afin de s'en servir comme aires de repos et comme tanières de reproduction. Cependant, peu de descriptions de tels terriers ont été publiées. Nous avons visité 114 terriers de repos, puis nous avons décrit leurs caractéristiques architecturales et les structures connexes n'étant pas recouvertes de neige. Par ailleurs, nous décrivons les caractéristiques de 15 tanières de reproduction que nous avons visitées en hiver et en été. Même si de nombreux terriers de repos ont été uniquement creusés dans la neige, la plupart des terriers incorporaient des structures topographiques, dont des falaises, des talus, de la glace de banquise, des grottes thermokarstiques et des hautes berges de cours d'eau. En général, les terriers étaient composés d'un seul tunnel menant à une seule chambre, bien que certains avaient plusieurs entrées, des galeries, ou les deux. Les tunnels des aires de repos étaient moins longs que ceux des tanières de reproduction, et les chambres de repos étaient généralement situées dans la partie la plus profonde des terriers. Les tanières de reproduction étaient installées dans des caractéristiques topographiques où s'amoncelle la neige, comme les lits de cours d'eau, les hautes berges de lacs, les grottes thermokarstiques et les rochers. Il est essentiel de comprendre les caractéristiques des structures de repos et de reproduction des carcajous de l'Arctique afin d'être en mesure d'évaluer les incidences anthropiques au moment où le manteau neigeux subit des changements liés au climat.

Mots clés : terrier; *Gulo gulo*; tanière de reproduction; aire de repos; glace de banquise; neige; sous la neige; carcajou

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INTRODUCTION

Burrows facilitate many behavioral and life-history processes for animals, including predator avoidance, thermoregulation, resting, and reproduction (e.g., Gray, 1993; Furgal et al., 1996; Milling et al., 2017). A burrow's suitability for each of these processes is determined in part by its architecture and site characteristics. For example, larger burrows and wider tunnels can be less effective in deterring predators and require more energy for excavation and thermogenesis in cold climates, whereas deeper burrows and longer tunnels can permit access to more thermally or structurally advantageous terrain features and restrict access by predators (Vleck, 1979; Bilodeau et al., 2013). Terrain features, such as substrate underlying the burrow, can facilitate or hamper an animal's ability to accomplish these processes (e.g., by providing additional structure or precluding digging; Buskirk et al., 1989; Duchesne et al., 2011; Poirier et al., 2019). Therefore, how animals select and modify burrow characteristics provides insight into the relative influence of various demands that shape animals' lives.

Wolverines (*Gulo gulo*) are circumpolar mesocarnivores inhabiting Arctic and alpine tundra and boreal forests (Copeland et al., 2010). Female wolverines give birth in snow dens between February and mid-March (although they may excavate dens earlier) and occupy these and subsequent dens with kits until snowmelt (Magoun and Copeland, 1998; Inman et al., 2012). Across their global distribution, wolverines exploit a combination of snow and non-snow subnivean structures for reproductive dens (Magoun and Copeland, 1998; Dawson et al., 2010; May et al., 2012; Jokinen et al., 2019). The relative importance of snow versus non-snow structure varies geographically. In taiga, where snow is shallow, of intermediate density (30 – 120 cm, 0.26 g cm^{-3}), and melts early (Sturm et al., 1995; Copeland et al., 2010), wolverine reproductive dens are typically reliant on structure under snow, including root wads of fallen trees, beaver lodges, slash piles from timber extraction, and boulder complexes (Dawson et al., 2010; Scrafford and Boyce, 2015; Jokinen et al., 2019). In alpine habitats, where snow is generally deeper and of similar density (70 – 250 cm, 0.27 g cm^{-3}, Sturm et al., 1995, 2010), wolverines still typically tunnel through the snowpack to access non-snow subnivean structure such as large boulders or woody debris (Magoun and Copeland, 1998). On Arctic tundra, where such structures are less available or absent, the relative importance of snow for reproductive den structure may be higher. We are aware of published descriptions of only eight wolverine reproductive dens on Arctic tundra, all located in deep snowdrifts generally associated with minor drainages and lake cutbanks (Serebryakov, 1983; Magoun, 1985; see also Lee and Niptanatiak, 1996).

To our knowledge, published descriptions of wolverine resting sites are limited to two sites in taiga, 26 sites in the alpine Rocky Mountains, and 10 sites on Arctic tundra (Magoun, 1985; Copeland, 1996; Wright and Ernst, 2004; Glass et al., 2021a). Both taiga sites consisted of beds on the snow surface at the base of large-diameter trees or stumps (Wright and Ernst, 2004), a type of taiga resting site that Scrafford and Boyce (2015) also mention. Alpine resting sites were also primarily surface beds, with only three occurring in snow burrows. On Arctic tundra, wolverines use both surface beds and subnivean burrows for resting (Glass et al., 2021c). Approximately half of wolverine winter and springtime resting sites on tundra occur in snow burrows, which confer thermoregulatory advantages and may reduce predation risk and drive selection for deeper, intermediate density snow (Glass et al., 2021b, c). Magoun (1985) excavated and mapped 14 subnivean burrows on tundra, eight of which were not known or suspected reproductive dens and therefore presumably used as resting sites (Magoun, 1985: b, d, g, j – n in Appendix B). In addition, Glass et al. (2021a) documented two resting sites in thermokarst caves as part of the present study.

Motivated by the paucity of such descriptions in published literature, we describe terrain features and architecture of wolverine resting burrows and reproductive dens in an Arctic tundra environment. Because snow is an ephemeral resource and its availability during spring and autumn is declining rapidly with climate change (Callaghan et al., 2011; Box et al., 2019), we include in our descriptions the extent to which wolverines relied solely on snow versus incorporating subnivean structures into dens and resting burrows that could become increasingly important in future climates.

MATERIALS AND METHODS

Study Area

We conducted this study in the vicinity of Toolik Field Station (68.63° N, 149.60° W) and Umiat (69.37° N, 152.13° W), Alaska. The study area transitions from the Brooks Range foothills in the south to the low-elevation Arctic coastal plain in the north, with elevations ranging from 60 to 1000 m above sea level. The region is underlain by permafrost, and trees are absent, but shrubs can grow to more than 2 m in areas, particularly along river corridors (Huryn and Hobbie, 2012).

All water bodies in the study area freeze during winter, at least on the surface, with the exception of a few geothermal spring sites (Huryn and Hobbie, 2012). Water levels beneath the ice drop as winter progresses (Prowse, 2001). In small to mid-size rivers during late winter and spring, shelf ice can form above a waterless cavity, with access often created through cracks that form in the ice as the water level drops and ice shifts.

The snowpack in the study area consists of two functional types: "veneer," and "snowdrift" (Benson and Sturm, 1993). The thinner, lower-density veneer snow, typically under 50 cm deep, comprises approximately 95% of the areal extent of the tundra, whereas snowdrifts, which can be several meters deep, account for the remaining 5% (Benson and Sturm, 1993; Sturm et al., 2001). Wind scours snow from exposed areas and deposits it in areas where terrain features and vegetation decelerate the wind, resulting in high-density, tightly bonded snowdrifts (Colbeck, 1982). These snowdrifts sometimes result in naturally formed cavities (e.g., roll cavities inside cornices). Metamorphism, driven by a temperature gradient between the snow surface and the ground surface, causes the base of the snowpack to transform into low-density, unconsolidated depth hoar, while the upper layer of the snowpack remains hard and tightly bonded (Colbeck, 1982).

Locating and Documenting Wolverine Resting Sites and Reproductive Dens

To locate resting sites, we captured and affixed Global Positioning System (GPS) collars to 21 adult wolverines (11 female, 10 male) near Umiat (6–26 April 2016) and Toolik Field Station (3 March–28 April 2017 and 25 February–18 April 2018) using portable baited wooden box traps (modified from Lofroth et al., 2008). We fitted wolverines with Followit Tellus Ultra Light (Followit Sweden AB, Lindesberg, Sweden) or Lotek LiteTrack 250 Iridium GPS collars (Lotek Wireless, Newmarket, Canada) with a 40-minute fix schedule. Collars transmitted animals' locations via the Iridium satellite network approximately twice per day. All animal capture and handling procedures were approved by University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol 847738 and Alaska Department of Fish and Game scientific permits 16-093, 17-085, and 18-085.

To identify wolverine GPS clusters, we visually investigated recent GPS collar data for any two consecutive locations less than ~20 m apart. We opportunistically visited these clusters in the field during the same periods as collaring efforts. Visiting GPS clusters revealed both surface bed and snow burrow resting sites, but here we only describe resting sites occurring in burrows. We defined a burrow as an excavation in the snow or a naturally occurring cavity with interior dimensions sufficiently large to accommodate a wolverine (approximately 40 cm by 40 cm). Upon locating a subnivean burrow in the field, we used an aluminum avalanche probe to take nine snow depth measurements on a 2 m by 2 m grid, behind the burrow entrance and oriented in the direction of entry into the burrow, such that we sampled the area most likely used by the wolverine. We averaged these snow depths to obtain a representative snow depth for the burrow. We excavated a subset of the burrows opportunistically when time permitted and have no reason to believe that excavated burrows are not a representative sample. At excavated snow burrows, we mapped architecture, measured the total tunnel length, dimensions of chambers, maximum burrow depth, depth to the floor of any chambers, and snow depth at the burrow's deepest location (not all measurements were recorded for every burrow). Additionally, we noted the presence or absence of food items (inside and outside the burrow) and non-snow structure such as boulders, river ice, or stream cutbanks associated with the burrow. In some cases, we could confirm the presence or absence of non-snow structure without excavation.

We located reproductive dens, which we define as burrows where kits-of-the-year were present, both by investigating GPS clusters of suspected reproductive wolverines and conducting aerial surveys from fixed-wing aircraft in late April 2016 and 2017. Aerial surveys consisted of two aircraft, each containing a pilot and observer, flying at low altitude searching for wolverine tracks in snow. Both pilots and observers had experience snow-tracking wildlife on tundra from aircraft. Upon encountering tracks, the aerial crew followed those tracks until infeasible, it was judged that the tracks were unlikely to lead to a potential reproductive den, or a potential reproductive den was located. We identified potential reproductive dens according to abundance of wolverine activity in the area without other obvious reasons for that activity such as a carcass, and the qualitative appearance of the entrance to the den, which we expected to be well-used. To access potential reproductive dens on the ground, we landed planes on the tundra (> 400 m away), or approached by snowmachine (> 100 m away, sometimes closer if exact den location was unknown), and finished our approach by snowshoe. To avoid disturbing reproductive wolverines, we maintained quiet voices while near potentially occupied reproductive dens and remained in the vicinity less than 15 minutes. We deployed a motion-activated camera approximately 5–10 m from the den entrance and verified reproductive dens by the presence of wolverine kits in photos. At two sites, we verified reproductive dens without photos of kits. At one of these, we verified the den based on extensive use by a female wolverine that had been lactating during her capture that season; at the other, we found deceased kits at the site after snowmelt.

We excavated one reproductive den, a site where we confirmed abandonment by the mother and kits prior to excavation. We visited reproductive den sites during summer by helicopter to retrieve cameras and document subnivean terrain structures within the area used by wolverines. To estimate minimum tunnel length, we measured the maximum distance between wolverine sign, including latrines, prey remains, remnant tunnels, and beds. We note that this metric of tunnel length is inherently biased low since it does not account for any tunnels extending beyond wolverine sign that persisted into summer.

RESULTS

Resting Burrows

We visited 114 wolverine resting burrows formed partially or completely in snow (Fig. 1). We fully

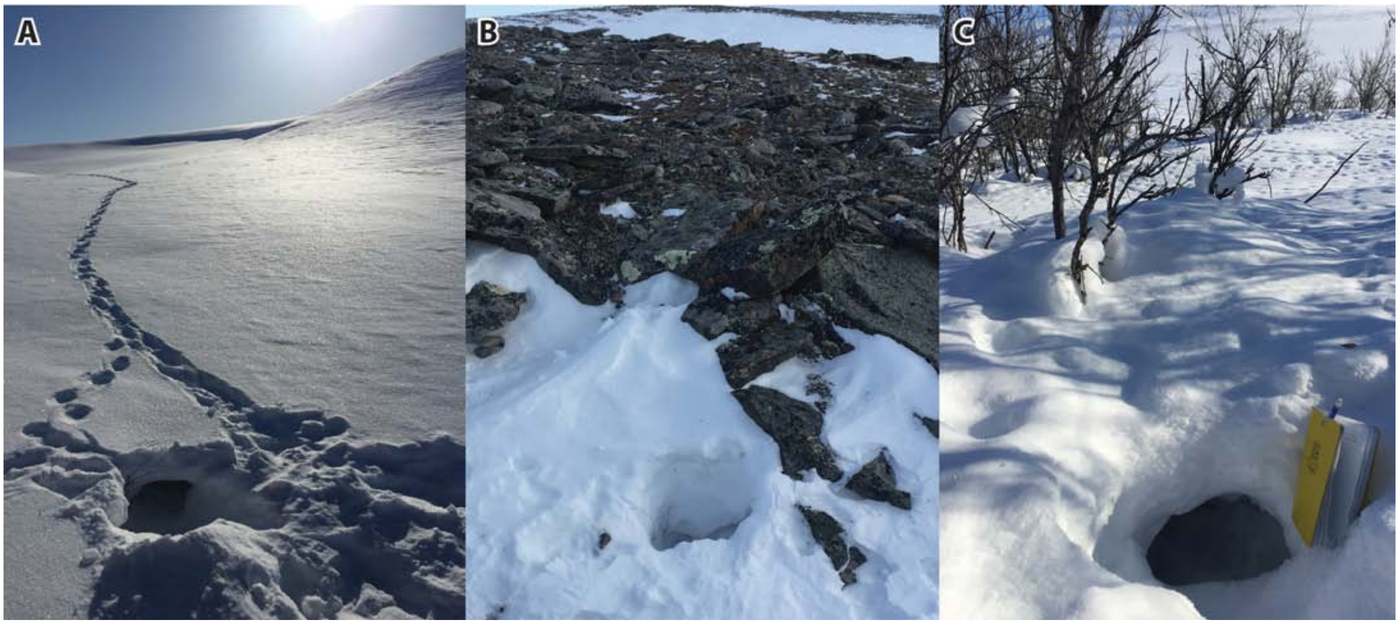

FIG. 1. Wolverine resting burrows in snow only (A), talus (B), and among tall shrubs (C).

TABLE 1. Subnivean terrain features used by wolverines as resting burrows and reproductive dens. Some "snow-only" burrows and dens were in snowdrifts formed by terrain features (e.g., stream beds) but did not exploit these features as part of their structure. These figures underrepresent snow-only burrows since verifying that a burrow solely exploited snow required excavating the burrow in its entirety or being able to see the burrow's full interior from the surface, whereas verifying non-snow structures was often possible without excavation.

Terrain feature	Resting burrows	Reproductive dens
Snow only	29	5
River ice	15	0
Cliff	14	0
Stream cutbank	11	1
Lake cutbank	0	2
Talus	7	0
Thermokarst cave	2	1
Boulder	0	1
Unknown	36	5

excavated 28 and partially excavated 6 burrows to document subnivean terrain features incorporated into burrows (Table 1), map architecture (Fig. 2A–E; Table 2; Supplementary Appendix), measure internal dimensions (Table 3), and document food remnants (Table 4).

Most burrows descended to within 5–10 cm of the subnivean ground surface, but wolverines rarely cleared snow from the ground surface and instead made beds on snow. We did not document more than one chamber per burrow. Chambers were typically located at the end of a tunnel, at or near the deepest part of the burrow.

Most food remnants were small (e.g., a single bone fragment or tuft of hair), although in one case the remains of a whole caribou (*Rangifer tarandus*), which had been buried in snow, were in a burrow chamber. In another case, a collared wolverine dug a burrow adjacent to a mostly intact unburied caribou. Caribou hair along the length of this burrow's tunnel and in the chamber suggested that the wolverine carried caribou remains inside the burrow for consumption, and GPS collar data indicated that the animal remained within 300 m of the site for 50 hours.

Although many burrows were excavated solely in snow (Fig. 1A), use of terrain features including talus (Fig. 1B) and stream cutbanks (Fig. 1C) for burrow structure was also common (Table 1). Resting burrows associated with cliffs and boulders occurred exclusively on tops of hills in the southerly portion of the study area, where such features are more abundant (Fig. 1B). These burrows generally exploited naturally formed cavities or depth hoar in snowdrifts underneath overhanging cliffs (Fig. 3), on the leeward side of cliffs, or underneath boulders. Wind speeds are high on these ridges, so snow is shallow or absent except in cracks between boulders or in deep drifts on the lee side of cliffs. Therefore, burrows associated with boulders typically descended through 30 cm or less of snow into spaces between or beneath boulders (Fig. 1B).

Resting burrows associated with river shelf ice descended through 30–200 cm of snow to cracks in shelf ice formed as ice settled. At three shelf-ice burrows, tracks of river otter (*Lontra canadensis*) were also present and, in one case, showed that an otter had entered and exited the burrow used by the wolverine.

Reproductive Dens

We located 15 reproductive dens: eight by aerial survey, six by investigating GPS clusters of collared wolverines, and one by opportunistically observing a wolverine at its entrance while we passed by on snowmachine. Three reproductive female wolverines moved their kits between

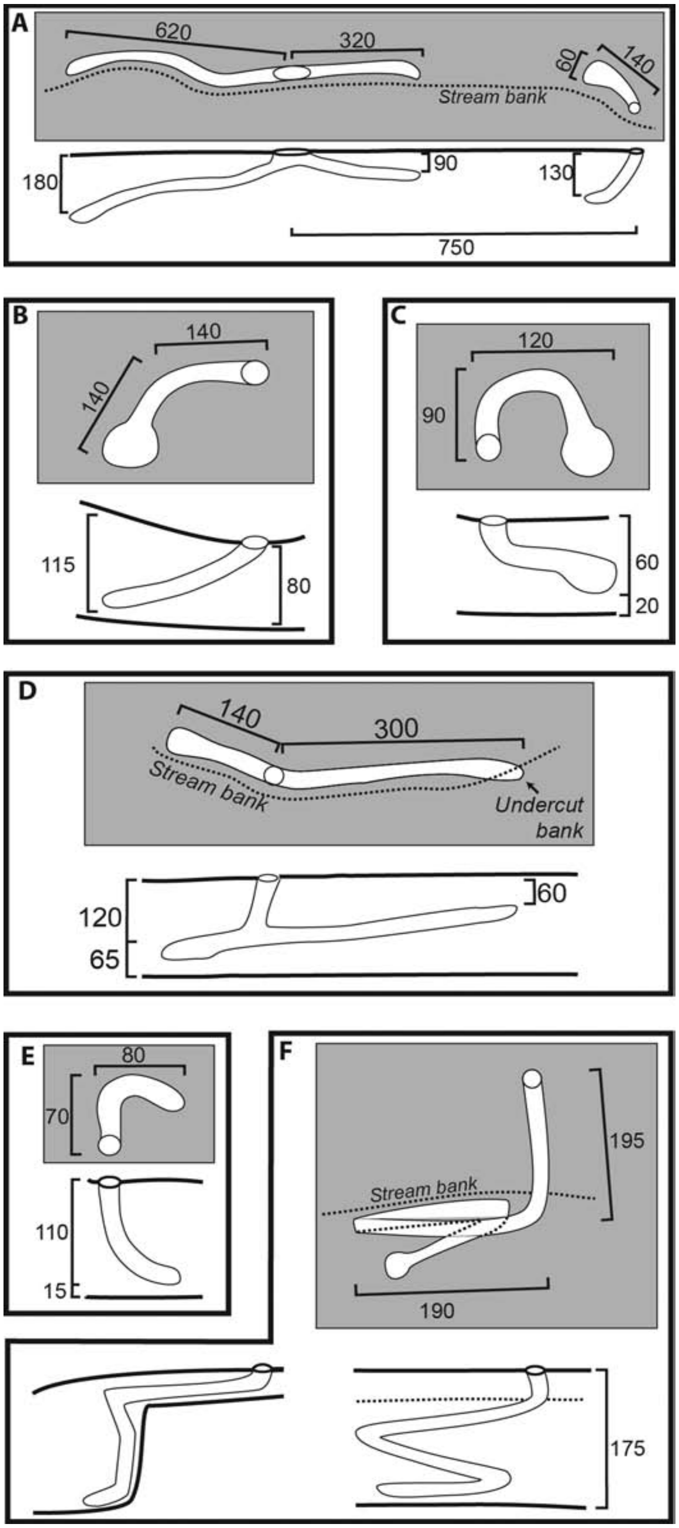

FIG. 2. Example architecture of wolverine resting burrows (A through E) and a reproductive den (F). Each panel shows the view from the top looking down (grey background), and the view from the side (white background). Panel F shows two side views perpendicular to one another. Distances are shown in centimeters. Diagrams of all excavated burrows are in the supplementary appendix.

TABLE 2. Branching structure of wolverine resting burrows. Both burrows at each of the four auxiliary burrow sites were counted elsewhere, resulting in 114 total burrows elsewhere but only 110 here.

	Count
Single entrance, single tunnel	22
Single entrance, multiple tunnels, auxiliary burrow under 20 m away	4
Single entrance, multiple tunnels, no auxiliary burrow	1
Multiple entrances, tunnels converge	1
Unknown (did not excavate)	82

TABLE 3. Dimensions of wolverine resting burrows and reproductive dens.

	Median	Range	N
Resting burrows:			
Tunnel length (cm)	160	0 – 1600	34
Chamber area (m^2)	0.5	0.2 – 1.4	15
Chamber depth (cm)	90	50 – 210	18
Snow depth at deepest tunnel's deepest location (cm)	115	60 – 330	23
Reproductive dens:			
Minimum tunnel length (cm)	1000	200 – 2000	9

TABLE 4. Food remnants on the snow surface surrounding resting burrow entrances ("outside") and in burrow tunnels or chambers ("inside").

		Food outside	
		Yes	No
Food inside	Yes	2	9
	No	3	15
	Unknown	6	79

multiple dens included in our count, such that these 15 dens belonged to 10 reproductive female wolverines. Of the three wolverines that used multiple dens, one used four dens along a stream and headwater lake (distance between dens: 500 – 12,000 m), and the other two used two dens each (distance between dens: 330 m and 6000 m).

Entrances to reproductive dens were clean in appearance, with no scat or food items. We did not find any evidence of large prey remains such as caribou or moose (*Alces alces*) on the snow surface near any reproductive dens. At two dens, we found a recently used bed on the snow surface approximately 30 m from the den entrance. At three den sites, we found additional burrows within 350 m of the main entrance, with well-used trails connecting the burrows. We did not excavate these dens to determine subnivean connectivity. At one site, we placed motion-activated cameras at two such entrances located 330 m apart and documented the female moving kits between the two dens on 22 April 2016. At this location, we included both dens in our total den count. The four dens located along 12 km of a stream and its headwater lake were used by a collared female wolverine with kits. She moved her kits between the dens over the course of five days in late April 2017, spending 63, 2, and 15 hours at the latter three dens (including time spent on an apparent foraging trip away from the den). The first den was used for at least six days (beginning on her capture date, which was our first knowledge of this den).

FIG. 3. Wolverine resting burrow created under an overhanging cliff.

At three dens, each used by a different wolverine, we observed a wolverine emerge from or enter the den while we were placing cameras. In all three instances, the female removed her kits from the den within a day and did not return (one of these was the 330 m movement described above). In a separate instance, the first photograph from the camera (13 hours after placement) was of the female wolverine emerging from the den, which suggests that she was inside the den at the time of camera placement. She and three kits continued to use the den until snow deteriorated 22 days later.

We documented terrain features associated with 10 reproductive dens during summer visits (Table 1; Fig. 4). At five, underlying terrain was sufficiently rugged to decelerate wind and create snowdrifts but lacked terrain features that could have enclosed any of the den structure. Four of these five dens were in snowdrifts formed by small streambeds (Fig. 4A), and the fifth was on a low-angle tussock hill. The remaining five dens showed evidence, including bone fragments and latrines, that wolverines had used terrain features to complement snow for den structure. At one, a 25 cm deep overhang of a partially buried boulder formed the roof of a tunnel used by a wolverine (Fig. 4B). At two dens, along a lake cutbank (Fig. 4C) and a stream cutbank, wolverines incorporated small (< 2 m long) tunnels and caves formed in eroding soil. At a den associated with a thermokarst cave, a wolverine used both the cave (at least 15 m^2) and snowdrifts formed in an erosional trench network (see detailed description in Glass et al., 2021a).

On 23 April 2016, we excavated a single reproductive den located in a snowdrift formed on a steep stream bank (Fig. 2F). The entrance was in shallow (50–60 cm) veneer snow on top of the bank, 195 cm from the edge. In vertical profile, the tunnel formed a "Z" shape, descending downhill 175 cm along the stream bank through shrubs. The tunnel did not branch and contained a single chamber with no latrine.

DISCUSSION

This study expands the published accounts of wolverine resting burrows and reproductive dens on Arctic tundra and documents the use of snowdrifts, talus, cliffs, and river shelf ice for these sites. Most resting burrows incorporated terrain features that complemented snow for structure, although burrows using only snow were more common than any single terrain feature class (Table 1). Reproductive dens generally relied less on non-snow subnivean structure, although sometimes included limited use of subnivean earthen caves. Low-angle gullies of intermittent streams and associated snowdrifts were the most common terrain features for reproductive dens, a finding consistent with Magoun and Copeland (1998), although reproductive dens were also located in snowdrifts formed by cutbanks on lake edges and on open tundra in areas with less pronounced snowdrift-forming terrain.

Burrow architecture documented in this study likely reflects a trade-off between reducing energy spent during excavation and improving insulation and security from predators such as wolves (*Canis lupus*). Although we observed considerable variation in tunnel length and chamber size, wolverines consistently used deeper snow than generally available in the veneer layer (Benson and Sturm, 1993). The fact that tunnels at resting burrows were generally shorter than the minimum tunnel length at reproductive dens suggests that female wolverines invest more energy in creating a secure environment for themselves and their particularly vulnerable kits.

Tunnel length could also be influenced by food location in snowpack, if burrows are used to access buried or cached food. We found strong evidence that food access was the primary burrow function at one burrow, since the tunnel terminated at the remains of a whole caribou that could not have been brought into the burrow. Otherwise, the small size and high transportability of food remnants precluded evaluation of whether the wolverine dug burrows to access food or if food was carried into the burrow by the wolverine

FIG. 4. Examples of snowdrift-forming structures associated with wolverine reproductive dens: intermittent stream (A), 1 m tall partially buried boulder (B), and cutbank on lake edge (C).

for consumption. We found no food remains at 15 burrows (Table 4), suggesting that resting is often the primary burrow function, although we may have missed feeding events that could be identified through other forensic methods (e.g., environmental DNA analysis of snow taken from burrows to detect prey species).

Despite our cautious protocol for den visits, directly observing a wolverine while deploying a camera at the den site may have prompted the female to abandon the den with her kits in three instances. Abandonment following such direct interaction with humans is consistent with previous observations (Copeland, 1996; Jokinen et al., 2019). However, observations here and elsewhere that wolverines sometimes continue to occupy dens following some level of disturbance (Magoun, 1985) and move between dens apparently unprompted by human disturbance (Copeland, 1996; Jokinen et al., 2019; Heeres, 2021) suggest nuance in the fitness consequences of and resilience to human activity at den sites. Better understanding the causes and consequences of den abandonment is important for designing ethical research protocols and mitigating the impacts of industrial development to this species, as is the case for denning polar bears (*Ursus maritimus*) in the same region (Wilson and Durner, 2020).

CONCLUSIONS

Describing types of terrain features exploited and modified by animals for resting and reproductive sites is critical, both for parsing the mechanistic drivers underlying habitat selection and understanding how animals respond to environmental change. We have highlighted the use of deep, extensive snowdrifts by wolverines in Arctic tundra habitats, as well as the use of several types of subnivean structure not previously known to be used by wolverines, including earthen caves and river shelf ice. Working to understand the fitness implications of these resting and reproductive structures will be crucial as their availability shifts with climate change and encroachment of development activities.

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