SNOW AS STRUCTURAL HABITAT FOR WOLVERINES IN A CHANGING ARCTIC

By

Thomas Rutherford Winder Glass, B.A.

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APPROVED:

Dr. Knut Kielland, Committee Chair
Dr. Greg Breed, Committee Member
Dr. Cory Williams, Committee Member
Dr. Martin Robards, Committee Member
Dr. Diane Wagner, Department Chair
Department of Biology and Wildlife
Dr. Kinchel Doerner, Dean
College of Natural Science and Mathematics
Dr. Richard Collins
Director of the Graduate School

Abstract

Arctic snowpack provides critical wintertime habitat for animals to facilitate thermoregulation and avoid predators. Wolverines (*Gulo gulo*) are iconic among such animals, relying on snow burrows for resting sites and reproductive dens. Most of the knowledge regarding this mesocarnivore's association with snow, however, has so far originated in more southerly latitudes. In this dissertation, I investigated Arctic wolverines' behaviors associated with snow, focusing on how specific snow properties influence resting, habitat selection, and avoiding predators. Motivated by the paucity of published descriptions of wolverine resting burrows and reproductive dens on tundra, I first described terrain features and architecture of such sites. I found that resting burrows typically consist of a single tunnel leading to a resting chamber, sometimes associated with non-snow structure such as stream cutbanks and river shelf ice. By contrast, reproductive dens typically consist of longer tunnels associated with snowdrift-forming terrain. Second, I used GPS collar data from 21 adult wolverines, coupled with snowpack information at 10 meter pixel resolution, to evaluate wolverine habitat selection and movement response to snow depth, density, and melt status. I found that wolverines select deeper, denser snow, except when snow is melting, likely reflecting resting site use. Third, I developed a machine learning model to classify wolverine behaviors using tri-axial accelerometers based on direct observations of three captive wolverines, and applied this model to free-living wolverines in Arctic Alaska. I found that the model performs better when allowed to predict behaviors as "unknown," and that it accurately predicts resting, food handling, running, and scanning surroundings. Finally, based in part on this classification model, I evaluated the extent to which wolverines' use of snow burrows and surface beds for resting sites is influenced by thermoregulatory needs versus predation avoidance. I found evidence in support of both demands driving resting behavior; wolverines trade thermoregulation off against predation avoidance by resting on the snow surface on warm, sunny days, but use snow burrows on cold, dark days to meet both demands simultaneously. Collectively, this dissertation demonstrates the importance of Arctic snowpack to wolverines, a topic of increasing importance as the snow season shortens with climate change, and serves as a model for investigating behavioral processes associated with snow among other species.

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Chapter 1: Introduction

During winter, snow blankets the globe's poleward regions, modifying the physical landscape upon which animals' lives unfold (Boelman et al. 2019). For these animals, seasonal snowfall introduces distinct challenges and opportunities that mediate ecological processes, for example by increasing energetic costs of movement and obtaining food, or by providing a thermally and structurally protective environment (Berteaux et al. 2017). In response, animals evolve behavioral strategies to exploit and contend with this seasonal transformation.

Snow is a complex and dynamic substrate, characterized by dozens of properties that vary at spatial scales spanning centimeters to kilometers, and temporal scales spanning seconds to centuries (Sturm and Holmgren 1994; Liston and Hiemstra 2011; Parr et al. 2020; Sturm and Liston 2021). Regionally, seasonal terrestrial snowpack can be grouped into five classes (prairie, montane forest, maritime, boreal forest, and tundra) according broad differences in depth, stratigraphy, and snow grain type (Sturm and Liston 2021). For example, snow in montane forests is generally deep (50-300 cm) and surficially soft (i.e., susceptible to compression), whereas tundra snow is generally thin (20-80 cm) and mechanically strong on the surface (i.e., resistant to compression). Within each class, local differences in topography, vegetation, and meteorology produce variation as well; tundra snow in topographically rugged areas that decelerate wind is generally deeper than tundra snow in less rugged (and therefore more wind-scoured) areas, for example (Parr et al. 2020).

These snowpack properties, coupled with taxa-specific behavioral and life-history requirements, influence how animals respond to snow. For instance, cricetid rodents in tundra regions select deep snow for its thermoregulatory advantage and protection from predators, exploiting a layer of low-density, easily navigable depth hoar that forms at the snowpack base (Reid et al. 2012; Bilodeau et al. 2013; Poirier et al. 2019). By contrast, rodents in Australia's Snowy Mountains select against deep snow, since meteorological conditions there prevent development of a basal depth hoar layer (Sanecki et al. 2006a, b). In this way, change in one snow property (the presence or absence of depth hoar) results in opposite responses to another (snow depth). The rodents in both cases are faced with similar demands (thermoregulation and avoiding predators), but distinct snow properties result in divergent behavioral patterns. This exemplifies the need to study behavioral patterns associated with snow and how specific snow properties mediate those patterns.

In the Arctic, cricetid rodents are joined by a diverse suite of species using snowpack for structural habitat, including ermine (*Mustela erminea*; Bilodeau et al. 2013), arctic hare (*Lepus arcticus*;

Gray 1993), arctic fox (*Vulpes lagopus*; Prestrud 1991), ringed seal (*Phoca hispida*; Smith and Stirling 1975), polar bear (*Ursus maritimus*; Harington 1968), and wolverine (*Gulo gulo*; Magoun and Copeland 1998). Some of these (ermine and cricetid rodents) spend most or all of the winter under snow, exploiting relative warmth and protection from predators (Pauli et al. 2013). By contract, ringed seals and polar bears use snowdrifts for reproductive dens and occasionally resting sites, whereas arctic fox and arctic hare use snow burrows for resting but not reproduction. Snow properties important to each of these species likely reflect the behaviors animals perform to enhance survival and fitness. For example, ringed seals require snowdrifts that are both suitably resistant to predators and near breathing holes, whereas lemmings require both deep snow and basal depth hoar for thermoregulation and avoiding predators (Smith and Stirling 1975; Furgal et al. 1996; Bilodeau et al. 2013; Poirier et al. 2019). Of the behaviors driving snow use, resting in snow burrows has so far received little attention despite being reported across diverse taxa (Harington 1968; Kelly and Quakenbush 1990; Prestrud 1991; Gray 1993).

Wolverines are iconic among species that, like other mustelids, use snow for structural habitat (Copeland et al. 2010). These mesocarnivores inhabit montane and boreal forests as well as Arctic ecosystems, and female wolverines rear kits in dens between February and May (Magoun and Copeland 1998; Jokinen et al. 2019). In southerly montane environments, these dens are exclusively located in areas of deep, persistent snow, possibly underpinning the close association between the species' distribution and persistent spring snow in that region (Copeland et al. 2010; see also Inman et al. 2012). In boreal forests, where snowpack is thinner, denning wolverines typically exploit non-snow structures such as upturned rootwads, slash piles, or abandoned beaver lodges (Dawson et al. 2010; Jokinen et al. 2019). In Arctic tundra environments, wolverines excavate reproductive dens in wind-blown snowdrifts, although few such structures had been described prior to the work presented in this dissertation (but see Magoun 1985).

In addition to using snowdrifts for reproductive dens, wolverines in the Arctic also excavate resting burrows in snow. Few resting site descriptions from any environment are available for the species; I found only 38 published descriptions prior to this study, of which just 11 sites were snow burrows (Magoun 1985; Copeland 1996; Wright and Ernst 2004; Glass et al. 2021). The present study is motivated by this paucity of information, as well as numerous observations that I and collaborators made during preliminary fieldwork of snow burrows apparently excavated by wolverines for resting rather than reproduction.

In this dissertation, I explore wolverine behavior associated with snow in a tundra environment, and investigate how specific snow properties influence such behavior. I begin by describing terrain features and architecture of wolverine reproductive dens and resting burrows in Arctic Alaska (Chapter 2). These descriptions provide context for subsequent chapters, in which I investigate behavioral dynamics associated with resting burrows. In chapter 3, I evaluate how snow depth, density, and melt status influence wolverine movement and habitat selection. In chapter 4, I develop a novel method for classifying wolverine behaviors using tri-axial accelerometers which I then use in chapter 5 to assess the relative importance of snow burrows for behavioral thermoregulation versus predation avoidance. I find that wolverines rely extensively on the subnivean space for resting, accounting for approximately half of all wintertime resting sites in this environment. Wolverines select deep, dense, non-melting snow, likely associated with these snow burrows, and burrow use is important both for avoiding predators and thermoregulation during the cold, dark Arctic winter. Collectively, these chapters expand our understanding of the relationship between wolverines and snow in the Arctic, a topic of immediate importance given the rapid pace of environmental change, including advancing snowmelt, in the region (Box et al. 2019).

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Chapter 2: Terrain features and architecture of wolverine (*Gulo gulo*) resting burrows and reproductive dens on Arctic tundra[1]

2.1 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 and/or branching tunnels. 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.

2.2 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

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[1] Glass, T. W., Breed, G. A., Laird, C. R., Magoun, A. J., Robards, M. D., Williams, C. T., & Kielland, K. *In press*. Terrain features and architecture of wolverine (*Gulo gulo*) resting burrows and reproductive dens on Arctic tundra. *Arctic*.

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 structure 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, 2021c). 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 (b, d, g, j, k, l, m, n; Magoun 1985, Appendix B). In addition, Glass et al., (2021a) documented two resting sites in thermokarst caves as part of the present study.

Here, we describe terrain features and architecture of wolverine resting burrows and reproductive dens in an Arctic tundra environment, motivated by the paucity of such descriptions in published literature. 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 included 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.

2.3 Materials and Methods

2.3.1 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 1,000 meters above sea level. The region is underlain by permafrost, and trees are absent, but shrubs can grow to >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 <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).

2.3.2 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 April-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 < ~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 presence/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 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 (Heeres, 2021). 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 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 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, and 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.

2.4 Results

2.4.1 Resting burrows

We visited 114 wolverine resting burrows formed partially or completely in snow (Fig. 2.1). We fully excavated 28 and partially excavated 6 burrows to document subnivean terrain features incorporated into burrows (Table 2.1), map architecture (Fig. 2.2A-E, Table 2.2, Appendix A), measure internal dimensions (Table 2.3), and document food remnants (Table 2.4).

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. 2.1A), use of terrain features including talus (Fig. 2.1B) and stream cutbanks (Fig. 2.1C.) for burrow structure was also common (Table 2.1). 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. 2.1B). These burrows generally exploited naturally formed cavities or depth hoar in snowdrifts underneath overhanging cliffs (Fig. 2.3), 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. 2.1B).

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 entered and exited the burrow used by the wolverine.

2.4.2 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 passing on snowmachine. Three reproductive female wolverines moved their kits between 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*) 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).

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, suggesting 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 2.1, Fig. 2.4). 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. 2.4A), 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. 2.4B). At two dens, along a lake cutbank (Fig. 2.4C) 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; a detailed description is given by Glass et al. (2021a).

We excavated a single reproductive den on 23 April 2016, located in a snowdrift formed on a steep stream bank (Fig. 2.2F). 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.

2.5 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 2.1). 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. 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 it was carried into the burrow by the wolverine for consumption. We found no food remains at 15 burrows (Table 2.4), 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 that wolverines 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 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).

2.6 Conclusions

Describing types of terrain features that animals exploit and modify for resting and reproductive sites is critical, both for parsing the mechanistic drivers underlying habitat selection and to understand 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 fitness implications of these resting/reproductive structures will be crucial as their availability shifts with climate change and encroachment of development activities.

2.7 Acknowledgments

We are grateful to S. Andersen, M. Barrueto, S. Beaudreault, H. Chmura, R. Dorendorf, T. Glass IV, C. Haddad, J. Johnson, M. Keech, R. Kemnitz, R. Klimstra, M. Kynoch, L. Parrett, M. Scrafford, J. Timm, and P. Valkenburg for logistical support. The staff of Toolik Field Station were particularly helpful in field operations. The comments of four anonymous reviewers greatly improved this manuscript. This work was supported by the M.J. Murdock Charitable Trust, Wilburforce Foundation, The Wolverine Foundation, a National Science Foundation Graduate Research Fellowship under Grant No. 1650114, and 69 generous individuals via a crowdfunding campaign.

2.8 References

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2.9 Figures

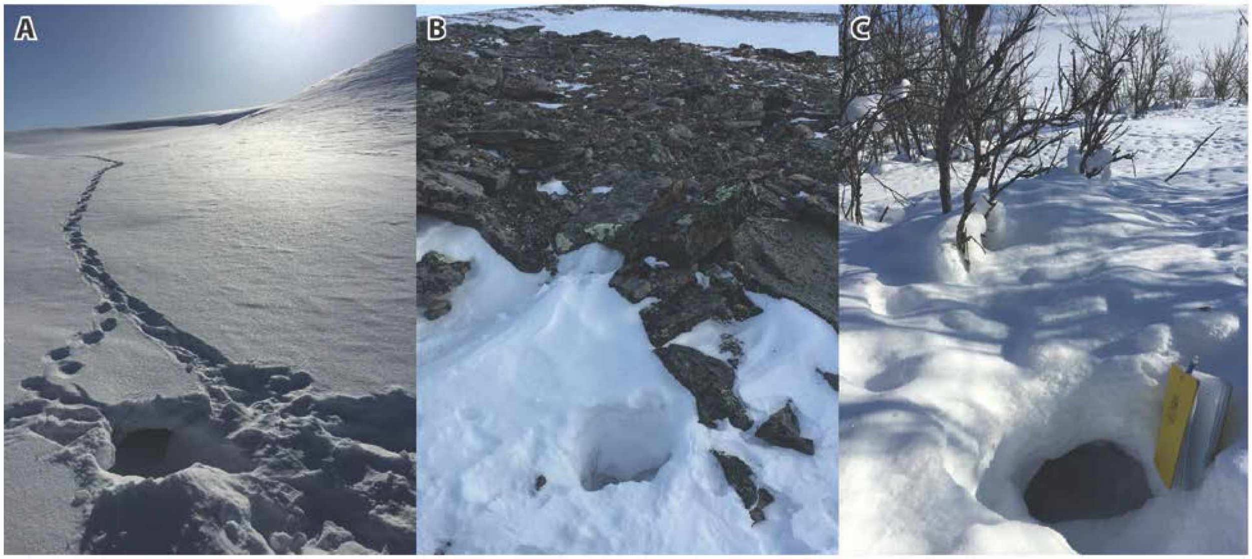

Figure 2.1: Example photographs of wolverine resting burrows in snow only (A), talus (B), and among tall shrubs (C).

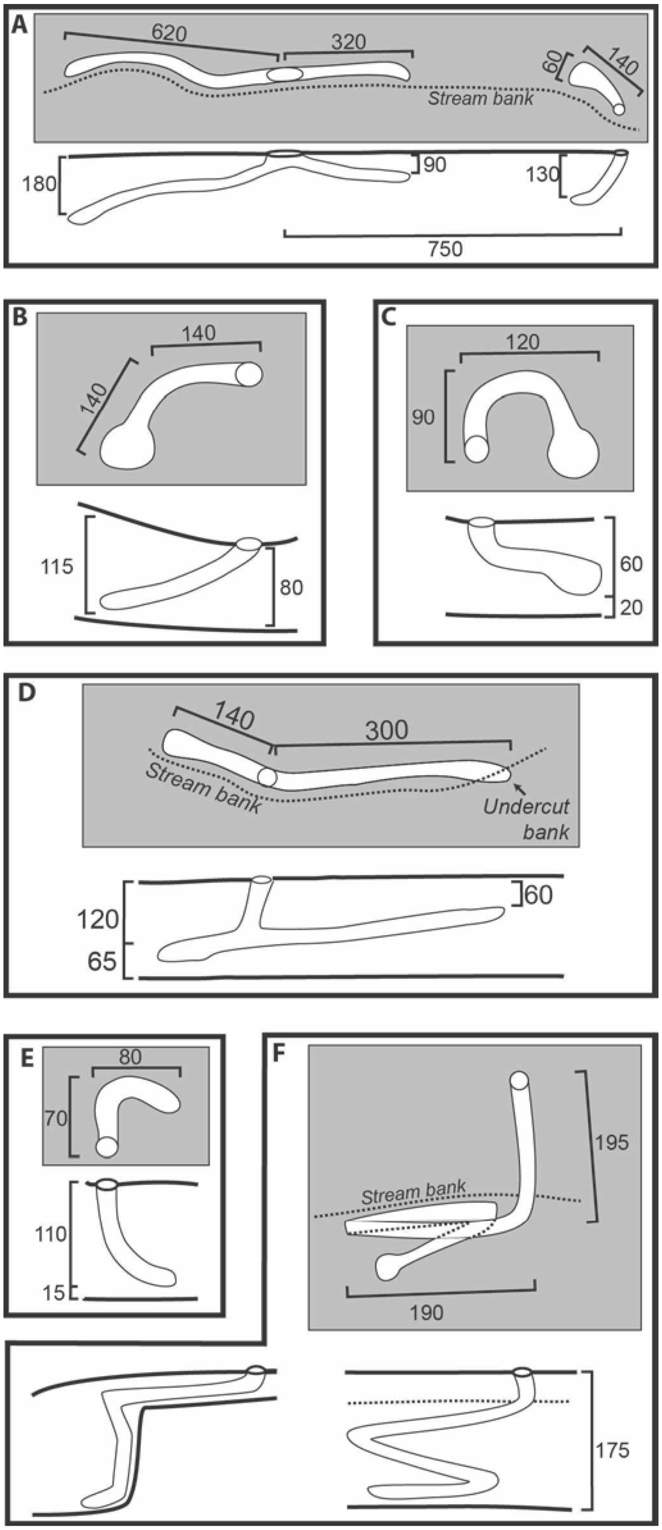

Figure 2.2: Example architecture of wolverine resting burrows (A through E) and a reproductive den (F). Each panel shows the view from the top looking down (grey background), and the view from the side (white background). Panel F shows two side-views, perpendicular to one another. Distances are shown in centimeters. Diagrams of all excavated burrows are in Appendix A.

Figure 2.3: Wolverine resting burrow, created under an overhanging cliff.

Figure 2.4: 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).

2.10 Tables

Table 2.1: Subnivean terrain features used by wolverines in 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 structure 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

Table 2.2: 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 <20 meters away	4
Single entrance, multiple tunnels, no auxiliary burrow	1
Multiple entrances, tunnels converge	1
Unknown (did not excavate)	82

Table 2.3: 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 2.4: 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

Chapter 3: Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator[2]

3.1 Abstract

Climate change is rapidly altering the composition and availability of snow, with implications for snow-affected ecological processes, including reproduction, predation, habitat selection, and migration. How snowpack changes influence these ecological processes is mediated by physical snowpack properties, such as depth, density, hardness, and strength, each of which is in turn affected by climate change. Despite this, it remains difficult to obtain meaningful snow information relevant to the ecological processes of interest, precluding a mechanistic understanding of these effects. This problem is acute for species that rely on particular attributes of the subnivean space, for example depth, thermal resistance, and structural stability, for key life-history processes like reproduction, thermoregulation, and predation avoidance. We used a spatially explicit snow evolution model to investigate how habitat selection of a species that uses the subnivean space, the wolverine, is related to snow depth, snow density, and snow melt on Arctic tundra. We modeled these snow properties at a 10 meter spatial and a daily temporal resolution for three years, and used integrated step selection analyses of GPS collar data from 21 wolverines to determine how these snow properties influenced habitat selection and movement. We found that wolverines selected deeper, denser snow, but only when it was not undergoing melt, bolstering the evidence that these snow properties are important to species that use the Arctic snowpack for subnivean resting sites and dens. We discuss the implications of these findings in the context of climate change impacts on subnivean species.

3.2 Introduction

Climate change is rapidly altering the quality and availability of snow at Earth's high latitudes (Callaghan et al. 2011). Increasing air temperatures are driving reductions in snow accumulation and contractions in the snow-covered period, and the snow that does accumulate is generally wetter and denser. Since snow directly alters physical landscape features such as the energy landscape (e.g.,

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[2] Glass, T. W., Breed, G. A., Liston, G. E., Reinking, A. K., Robards, M. D., & Kielland, K. (2021). Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. *Oecologia, 195*, 887–899. https://doi.org/10.1007/s00442-021-04890-2

Crête and Larivière 2003) and availability of resources (e.g., Aars and Ims 2002), these changes are dramatically rearranging the drivers of wildlife movement, habitat selection, and life-history events.

However, the way that snow influences such ecological processes varies with spatiotemporally dynamic snowpack properties, so understanding wildlife response to the changing snowpack relies on a mechanistic understanding of the link between these properties and ecology (Berteaux et al. 2017). For example, snow depth and surface hardness influence the energetic costs associated with locomotion in a variety of terrestrial taxa (Crête and Larivière 2003), with cascading effects on spatial distribution, habitat selection, survival, and overall population processes (Mahoney et al. 2018; Reinking et al. 2018). Similarly, hardness at the base of the snowpack can influence population cycling and survival among small mammals and ungulates, often resulting from freeze-thaw or rain-on-snow events that prevent animals from accessing forage (Aars and Ims 2002).

For species that rely on the subnivean space for reproductive dens, thermoregulation, or to avoid predators, the influence of spatiotemporal snow dynamics on ecological processes can be particularly acute. Rain-on-snow and mid-winter melt events, which reduce the thermoregulatory and structural integrity of snow, can have profound effects on animals using subnivean birth lairs or dens, such as polar bears (*Ursus maritimus*), ringed seals (*Phoca hispada*), and wolverines (*Gulo gulo*), sometimes resulting in den collapse and mortality (Clarkson and Irish 1991; Stirling and Smith 2004). Changes in snow density can influence the availability of suitable burrowing habitat, since density is negatively related to thermal insulation but positively related to structural stability (Colbeck 1982); therefore, animals might be expected to seek intermediate snow densities. Similarly, deeper snow confers more thermal insulation and protection from supranivean predators, but requires more energy to access, so changes to snow depth can alter the capacity of animals to effectively thermoregulate or avoid predators. Neglecting to account for such snow properties in ecological studies risks mischaracterizing a crucial component of ecosystem dynamics.

Despite this, incorporating snow data into studies of wildlife ecology remains a nascent field, in part due to the considerable logistical difficulty in collecting accurate snow-related data at biologically-relevant resolutions across temporal and spatial scales of interest (Magoun et al. 2017; Boelman et al. 2019). Further difficulty arises from the inherent complexity of the snowpack, which can change rapidly at fine resolutions in response to weather conditions, terrain, and vegetation (Colbeck 1982; Sturm et al. 1995). Animals may respond to a wide range of such dynamic snowpack characteristics, including depth, density, hardness, structural integrity, and phenology (Berteaux et al.

2017), and identifying and measuring the characteristics that are relevant to the biological process of interest for a particular species can present a considerable challenge.

Spatially explicit snow evolution models promise to reduce some of the logistical hurdles of accurately building snow properties into ecological models (Boelman et al. 2019). Snow evolution models are numerical models that estimate snow characteristics based on meteorological, topographic, and land-cover inputs. These models have typically been developed to address hydrological questions and for avalanche forecasting, though their broad applicability to other disciplines, including wildlife biology, is increasingly possible (Liston et al. 2016; Mahoney et al. 2018; Reinking et al. 2018). For example, SnowModel (Liston et al. 2020) can be flexibly applied to diverse landscapes and snow regimes such as tundra, coastal regions, forested areas, and sea ice. Further, it produces daily (or sub-daily) outputs of snow characteristics including depth, density, snow water equivalent (SWE), runoff volume, solid- and liquid-precipitation, and sublimation. The model is capable of assimilating field observations of SWE (Liston and Hiemstra 2008) to correct errors in precipitation datasets; precipitation can be difficult to measure accurately and is frequently inaccurate in meteorological reanalysis products used for model forcing (e.g., Liston and Hiemstra 2008, Liston et al. 2020). The spatial resolution of the SnowModel outputs can range from 1 meter to 10 kilometers, depending on the application of interest, and is defined by the resolution of the underlying digital elevation model (DEM) and land-cover raster. SnowModel's flexibility and diverse outputs make it broadly applicable to studies of wildlife ecology, and it has been applied to diverse systems and ecological processes including polar bear denning in the Arctic (Liston et al. 2016), Dall sheep (*Ovis dalli*) habitat selection in alpine Alaska (Mahoney et al. 2018), and pronghorn (*antilocapra americana*) mortality risk in sagebrush steppe (Reinking et al. 2018).

Here, we demonstrate the value of including spatiotemporally variable snow properties (and not simply presence or absence) in ecological models of species that rely on the subnivean space. Further, we provide a mechanistic context for understanding the impacts of climate change on such species by assessing habitat selection and movement of wolverines in response to physically based snow property representations. Specifically, we investigated whether habitat selection and movement among wolverines not associated with reproductive dens (hereafter non-denning wolverines) are altered by relatively fine-scale (<30 meters) spatiotemporally variable tundra snowpack characteristics. We focused on non-denning wolverines to evaluate snow's importance to the species apart from its well-documented role in reproductive denning (Magoun and Copeland 1998). We evaluated (1) the utility of including high-resolution snow property data in models of wolverine habitat selection, and (2) whether wolverine habitat selection and movement in relation to snow indicate the excavation of subnivean cavities. Observations from published works (Magoun 1985) and our own fieldwork indicate that non-denning wolverines on Arctic tundra dig resting cavities in deep snowdrifts during winter and spring. Building on this, we predicted that high-resolution snow property data would substantially improve the ability of a statistical model to evaluate wolverine habitat selection and movement, and that wolverines would select areas of deeper, intermediate-density snow, when the snow is not melting. We further predicted that these snow attributes would reduce wolverine movement rate, reflecting the importance of these attributes for resting sites. We based these predictions on the assumptions that deep snow provides more structural protection, higher-quality food caching habitat, and more abundant subnivean prey (Duchesne et al. 2011), and that denser snow offers better structural integrity for snow caves and tunnels. Further, we assumed that these snow properties would be reduced during melt, since meltwater reduces the thermal resistance and structural stability of the snowpack (Colbeck 1982).

3.3 Methods

3.3.1 Study Area

We collected data in the vicinity of Umiat (69.37° N, 152.13° W) and Toolik Field Station 68.63° N, 149.6° W), Alaska (Figure 3.1). This region encompasses the transition from the Brooks Range in the south, through the foothills region, north to the Arctic coastal plain. The study area is treeless, although shrubs can grow to >2 meters tall along riparian corridors (Figure 3.2; Huryn and Hobbie 2012). The Brooks Range is characterized by steep, rugged terrain with elevations ranging from 700 to 2,700 m. The foothills region is characterized by low rolling hills with elevations ranging from 60 to 1,000 m. The coastal plain is mostly flat, but broken by stream cuts, permafrost-related terrain features such as polygons and pingos, and eroded lake edges (Huryn and Hobbie 2012).

Snowpack in the study area is typically categorized as either “veneer,” a relatively thin layer, or “snowdrift,” a deeper, wind-deposited layer (Benson and Sturm 1993). Snowdrifts are associated with topographic features that decelerate wind, such as incised stream channels, cut-banks along lake edges, ridgelines, vegetation, and degrading permafrost features. As the snow-transporting winds slow, snow grains accumulate on the snow surface. During wind transport, snow grains deteriorate into small particles that become densely packed and highly bonded upon deposition (Colbeck 1982). Additionally, veneer snow undergoes metamorphism driven by the temperature gradient and associated vapor pressure gradient between the ground surface and the air, whereby water vapor is transported from the bottom toward the top of the snowpack, resulting in a large-grained, low-density snow crystals called depth hoar (Colbeck 1982). The combination of these two processes leads to a largely binary snowpack with a dense wind slab overlying softer, low density snow. This process happens to a lesser extent in snow drifts, where deeper snow results in a less pronounced temperature gradient and the higher density wind-transported snow is less permeable to vapor flow through the snowdrift. As such, wind-drifted snow is typically of higher density (roughly 250-550 kg m^{-3}), while veneer snow is typically lower density (150-250 kg m^{-3}, Benson and Sturm 1993). Up to 50% of snow deposited on tundra is blown by wind into snowdrifts, up to several meters deep, that cover approximately 5% of the surface area of the landscape (Benson and Sturm 1993; Sturm et al. 2001). The remaining 95% of the landscape is covered by veneer snow, typically less than 50 cm deep. The period of continuous snow cover typically initiates in September or October. Snowmelt begins in late April or early May (although this date is advancing with climate change), and proceeds rapidly as day length and air temperature increases (Hinzman et al. 2005; Callaghan et al. 2011). The tundra is mostly snow-free by late May or early June (Macander et al. 2015).

3.3.2 Study Species

Wolverines occur across the study area, although their occupancy is non-uniform and correlates with rugged terrain and the presence of well-drained soils (Poley et al. 2018). Generally, wolverines are considered a snow-associated species, and on the Arctic tundra, which comprises a considerable portion of the wolverine's global distribution, the relative importance of snow as a structural habitat component may be higher than in other ecosystems. Non-snow structures that are associated with reproductive dens and resting sites elsewhere, such as trees, boulders, and beaver lodges (May et al. 2012; Jokinen et al. 2019), are sparse or absent on tundra, and although studies of wolverine habitat associations on tundra are limited (but see Magoun 1985; Poley et al. 2018), all reproductive dens documented on the tundra have been in deep, drifted snow (Magoun and Copeland 1998), and non-reproductive wolverines have been documented excavating cavities in snow to avoid predators, behaviorally thermoregulate, and cache food (Magoun 1985, Glass et al. *unpublished manuscript*). With few exceptions (e.g., Magoun and Copeland 1998, Pozzanghera et al. 2016, Magoun et al. 2017), only snow presence/absence data at >500m pixel resolution has been used to inform the relationship between wolverines and snow, although the ways in which this and other species (e.g., ringed seals, Stirling and Smith 2004) are affected by snow is almost certainly mediated by more complicated dynamically evolving snow properties at much finer spatial resolutions (Magoun et al. 2017).

3.3.3 Wolverine Capture and Collaring

We captured wolverines near Umiat (06-Apr-2016 – 26-Apr-2016) and Toolik Field Station (03-Mar-2017 – 28-Apr-2017 and 25-Feb-2018 – 18-Apr-2018), Alaska using portable baited wooden box traps (modified from Lofroth et al. 2008). We moved traps opportunistically to maximize trapping yield, resulting in minimum convex polygons surrounding our trapping areas of 715 km^2 and 3,100 km^2 at Umiat and Toolik, respectively. We fitted wolverines with 250-300g Followit Tellus Ultra Light (Figure 3.2; Followit Sweden AB, Lindesberg, Sweden) or Lotek LiteTrack 250 Iridium GPS collars (Lotek Wireless, Newmarket, Canada) with a 40-minute fix schedule. 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.

We limited analyses to GPS data collected during the snow-covered period (i.e., when the majority of the landscape was snow covered, subjectively defined as ending May 10; collars were deployed mid-winter, so we did not define a fall starting date). Because we were interested in non-denning habitat selection, we excluded 538 (3% of total) steps of denning females and their mates within 1 km of their den site. Steps with intervals longer than 43 minutes also were excluded from analysis.

3.3.4 Environmental Covariates

We estimated snow depth at 10 meter spatial resolution using SnowModel, a numerical model that incorporates topography, land-cover, meteorological data, and ground measurements of SWE to recreate snowpack spatial distribution and temporal evolution. For a detailed description of SnowModel, see Liston et al. (2020), Appendices A-H. We simulated snow depth, SWE, and SWE melt at a daily time step, enabling us to link snow characteristics with wolverine relocations both temporally and spatially (Figure 3.3). We used an Interferometric Synthetic Aperture Radar (IfSAR) 5 meter DEM, resampled to 10 meter resolution, for topography data. We used National Aeronautical and Space Administration (NASA) Modern Era Retrospective-analysis for Research and Applications Version 2 (MERRA-2) for meteorological data, and we used the model MicroMet (Liston and Elder 2006) to downscale these data to the 10 meter resolution required for the

SnowModel simulations. We corrected MERRA-2 precipitation values using 21 ground measurements of SWE (Arp 2018; Pedersen et al. 2019; Stuefer et al. 2019), by assimilating them into SnowModel using the model SnowAssim (Liston and Hiemstra 2008).

SnowModel has a variety of user-defined parameters that enable flexible application to different environments; we qualitatively compared SnowModel outputs to high resolution structure-from-motion (SfM) maps of snow depth (Matthew Sturm, *unpublished data*) at focal sites within our study area to fine-tune these parameters. The structure-from-motion technique uses aerial photogrammetry to create three-dimensional maps of the snow surface elevation, from which the terrain elevation is subtracted to obtain snow depth. To accommodate the relatively high spatial resolution of our simulations and our interest in snowdrifts that occur on a scale of 10s of meters (Figure 3.3), we adjusted the MicroMet wind parameters (Liston and Elder 2006) until the SnowModel simulated snowdrifts visually matched those observed in the SfM data. Since vegetation height data at the resolution of our simulations (10 meters) were unavailable, and rescaling coarser land-cover data introduced clear artifacts to snow depth predictions, we used a uniform vegetation height of 5 cm for the entire domain. This decision reflects the dominance of tussock-tundra in our study area, though precludes the effect of shrubs on capturing snow. Additionally, to better match SfM snow depth maps, we uniformly increased the MERRA-2 wind speeds by a factor of 1.5 (Mahoney et al. 2018).

We calculated snow density as SWE divided by snow depth for a given pixel. We calculated the daily fraction (0-1) of seasonal snow melt as

$$\frac{\mathrm{SSMT_k} - \mathrm{SSMT_{k-1}}}{\mathrm{SSMT_{end}}}$$

Where $\mathrm{SSMT_k}$ is the season's total amount of SWE (cm) that has melted for a given pixel on date *k*, and $\mathrm{SSMT_{end}}$ is the season's total SWE that melts for a given pixel by the end of the season. We then converted this into a binary indicator variable representing whether or not any snow had melted during the preceding 24 hours.

In addition to snow covariates, we investigated terrain ruggedness, distance to streams/rivers, and distance to lake edges (Table 3.1, Figure 3.1), because these are commonly related to wolverine habitat selection elsewhere (Poley et al. 2018; Scrafford et al. 2018), or because we expected them to be influential based on our field observations. We decided against including distance to roads as a covariate, since the Dalton Highway is the only road in the study area (Figure 3.1), and most collared wolverines never directly encountered it. Although we are unaware of other studies that have investigated the response of wolverines to lake edges, we included this as a covariate since many lake edges on the North Slope are characterized by steep, eroded cut banks and tall shrubs, making them attractive for ptarmigan, snowshoe hares, and other potential prey species (Ehrich et al. 2012). We used the National Hydrology Dataset for lake data, and converted the lake polygons into polylines to assess habitat selection in relation to lake edges (i.e., to permit non-zero values for locations occurring within the original polygons on frozen lakes). We derived terrain ruggedness as the square root of the summed squared deviations in elevation between each cell and every neighboring cell (Riley et al. 1999), based on an IfSAR 5 meter resolution DEM and included it in our models as a continuous variable. We derived stream and river data from the IfSAR 5 meter resolution DEM using ESRI's Flow Accumulation tool in the Spatial analyst ToolPak (ESRI ArcMap 10.3.1). This tool allows users to define flowlines according to the number of pixels that have accumulated upstream. In this way, we set accumulation values for streams and rivers as greater than 300 pixels to best capture our perception of what constituted a "stream" on the landscape. We used the ESRI's Erase tool to exclude flowlines that overlapped lakes, and we clipped the resultant layer to include data only within the coastline. We calculated distances from wolverine GPS locations to streams and rivers using ESRI's Near tool.

We assessed all predictor covariates for collinearity and found the highest degree of correlation to be 0.58, so we removed no covariates. We also standardized all continuous predictor variables (subtracted the mean and divided by the standard deviation).

3.3.5 Habitat and Movement Modeling

3.3.5.1 Step Selection analysis

To assess how wolverine space use responds to spatially and temporally variable environmental conditions, we used integrated step selection analyses (iSSA; Avgar et al. 2016). iSSA describes animal movement as a series of discrete "steps" which represent movement between two locations in space. We matched each realized step (time *t*) with five available steps, each originating at the previous location (time *t*-1) but having a step length and turn angle drawn from gamma and Von Mises distributions, respectively, which were parameterized empirically from the observed data of that animal. Matched sets of one realized and five available steps form a stratum. For each step, we extracted environmental covariates at the start and end of the step to test hypotheses regarding movement and habitat selection, respectively. We fit step selection functions (SSF) for each wolverine individually using the R package *survival* (Therneau et al. 2020). We included the natural logarithm of step length (lnSL) as a covariate in all models to explicitly account for the resource-independent movement kernel, thereby reducing bias in the estimation of our habitat-related parameters (Forester et al. 2009; Avgar et al. 2016).

3.3.5.2 Modeling Approach

We employed a two-step model evaluation process. In the first step, we built a "base" model describing wolverine habitat selection in the absence of snow by evaluating all possible combinations of non-snow covariates (distance to stream/river, distance to lake edge, and terrain ruggedness). Because we expected non-linear responses to all covariates, we log-transformed the distance terms and included terrain ruggedness as a quadratic term. As such, there were three separate terms included in our candidate base models, generating seven possible models: *ln*(distance to stream/river), *ln*(distance to lake edge), and [terrain ruggedness + terrain ruggedness^2]. To evaluate population-level model performance, we calculated Akaike weights (Burnham and anderson 2002) for each set of candidate models for each wolverine, and then calculated the mean Akaike weight across individuals using a non-parametric bootstrap, weighted by sample size (Scrafford et al. 2018). We designated the model with the highest population-level Akaike weight our "base" model.

In the second phase of our modelling process, we evaluated the effect of including snow-related covariates, and investigated our hypothesis that wolverines' selection for snow properties is consistent with the excavation of subnivean cavities for resting sites, food caches, and/or subnivean hunting sites. To do so, we built a candidate model set including all three possible combinations of the covariates "Snow depth + Snow depth^2 + lnSL:Snow depth + lnSL:Snow depth^2" and "Snow density + Snow density^2 + lnSL:Snow density + lnSL:Snow density^2," where snow covariates interacting with lnSL were extracted at the step's start to evaluate their influence on wolverine movement (Avgar et al. 2016). We added these covariates to those of the base model, and fit these candidate models separately to strata that contained at least one step during which snow had undergone melt ("melt" models) and strata that did not contain any steps with melting snow ("no melt" models). We then used the same bootstrapped mean Akaike weight procedure described above to evaluate model performance. We calculated average population-level coefficient estimates and 95% confidence intervals using a non-parametric bootstrap of individual estimates, weighted by their inverse variance (Scrafford et al. 2018).

To visualize our results, we calculated the linear predictors based on the population-level coefficient estimates from the best performing “no melt” model and fit generalized additive models (GAMs) of exponentiated linear predictors against predictor covariates of interest, then plotted the result (termed a "relative probability of use plot," Avgar et al. 2017). We used the fitted values from these GAM functions to evaluate relative probability of use at specific values of covariates (Avgar et al. 2017). We selected the number of knots in our GAMs using Generalized Cross Validation (Craven and Wahba 1978). In addition, we used the habitat weighting function generated by our SSF to calculate the relative probability of use for habitat pixels in the vicinity of Toolik Field Station, creating a spatial visualization of our results.

We calculated the mean movement rate for each wolverine using the equation (Ladle et al. 2019)

$$\text{Movement rate } \left(\frac{\text{meters}}{40 \text{ minutes}}\right) = b_2 * \left[b_1 + \beta_{\text{lnSL}} + \left(\beta_{1\ldots n} * x_{1\ldots n}\right)\right]$$

Where b_1 and b_2 are the tentative individual-level shape and scale parameters, respectively, β_{lnSL} is the population-level coefficient for lnSL, and $\beta_{1\ldots n}$ are the population-level coefficients for the interaction between lnSL and snow covariates. To evaluate the influence of specific covariates, we held all other snow covariates constant at their median values, and varied the covariate of interest across its range. We then calculated a population-level mean using a non-parametric bootstrap, weighted by sample size (Scrafford et al. 2018).

Finally, we evaluated both the base model and the top performing “no melt” model for their ability to predict habitat use patterns among out-of-sample data by adapting the k-fold cross validation approach described in Boyce et al. (2002), using individual animals as “folds.” Specifically, for each model we iteratively withheld the data of one individual, fit the model to the data of the remaining individuals, and used the fitted model to generate linear predictors for the withheld data. We exponentiated these linear predictors and partitioned them into ten bins of equal sizes, then divided the number of realized steps by available steps in each bin. This provided a frequency for each bin (analogous to the “area adjusted frequency”; Boyce et al. 2002), which we expected to increase for higher bins, since the proportion of realized to available steps should be greater for higher values of linear predictors. We then averaged frequencies across iterations and calculated the Spearman’s Rank correlation coefficient for bin versus frequency. Validating the model in this way assesses how well it can be generalized to the population as a whole.

3.4. Results

We captured and GPS-collared 21 adult wolverines (11 female, 10 male), obtaining 16,167 steps, of which 15,493 (across all 21 individuals) were included in the "no melt" models and 674 (across 11 individuals; 6M 5F) were included in the "melt" models.

3.4.1 Base Model

Akaike weight rankings for candidate base models and coefficient estimates for the top performing base model are found in Tables B.1 and B.2, respectively. We found support for including streams and rivers, lake edges, and terrain ruggedness in our base model (Table B.1). Wolverines generally selected more rugged areas closer to streams, rivers, and lakes (Table B.2). Distance to lake edge only improved model performance marginally over the next best model (Akaike weight evidence ratio = 1.04, Table B.1), and as such had minimal effect compared with other predictors on the relative probability that a wolverine selected a resource unit (Table B.2). Wolverines were twice as likely to use a resource unit 10 meters from a stream or river than one 400 meters away, and were nearly four times more likely to use a resource unit with a terrain ruggedness index of 150 (characteristic of the mountain slopes in the southern portion of the study area and the higher-relief foothills) than one of 20 (typical of valley bottoms and the rolling tundra, Figure 3.5).

3.4.2 Influence of Snow on Habitat Selection and Movement

For non-melting snow, adding any snow covariate improved model performance above the base model, and the model including both snow density and snow depth performed best among all candidate models (bootstrapped mean Akaike weight = 0.4, Table 3.2). In general, wolverines selected deeper and denser snow (Figure 3.4, Table 3.3). Specifically, wolverines were twice as likely to use a resource unit characterized by snow that was 250 cm deep than a unit with snow 20 cm deep, and were similarly twice as likely to use a resource unit with snow of density 450 kg m^{-3} than 250 kg m^{-3} (Figure 3.4). Wolverine movement rate was negatively influenced by snow depth but positively influenced by snow density across the range of densities available to wolverines, although confidence bands generated from bootstrapped means of individual coefficient estimates suggest uncertainty in these trends (Figure 3.4). For melting snow, adding any snow covariate to the base model substantially reduced performance (Table 3.2).

Both the base model and the top performing "no melt" model had high cross-validation scores (0.95 and 0.93 Spearman's Rank correlation coefficient, respectively).

3.5 Discussion

This study demonstrates the importance of including spatiotemporally variable snow properties in ecological models of species that rely on the subnivean space, and provides a mechanistic context for understanding nuanced, but important impacts of climate change on these species (Mahoney et al. 2018; Boelman et al. 2019). Our findings are broadly consistent with our predictions; specifically, we found that (1) including snow properties in habitat selection models for snow-associated species would improve model performance, and (2) that wolverines select deeper, denser snow, but only when that snow is not undergoing melt. Our results are ambiguous regarding the importance of denser snow for subnivean cavities, suggesting that selection for denser snow may instead (or also) be driven by reduced energetic costs associated with movement. These results have important implications for wolverines and other subnivean species in the context of a rapidly changing Arctic snowpack.

3.5.1 Snow as a Component of Habitat

The subnivean zone is important to diverse taxa for its thermoregulatory and structural benefits (Pauli et al. 2013). Species such as polar bears, ringed seals, marten (*Martes americana*), ermines (*Mustela erminea*), and cricetid rodents occupy this zone for part or all of the winter. As such, studying the ways in which variable snow properties influence the quality of this habitat is an important component of understanding a species' broader ecology. Our finding that snow depth is important to wolverines using the subnivean zone is consistent with results from other taxa. Ringed seals, polar bears, and Arctic hares all select deep, structurally stable snow for dens associated with resting and reproduction (Gray 1993; Furgal et al. 1996; Liston et al. 2016).

Snow density may also be important to subnivean species. Since denser snow caused by wind drifting is characterized by higher structural integrity and mechanical resistance to digging, but lower thermal resistance (Colbeck 1982), we expected wolverines to select an intermediate level of snow density for subnivean dens, as has been qualitatively reported for other species (Harington 1968). However, our results do not support the existence of an upper limit to selection for denser snow within the range of densities available to wolverines (Figure 3.4), suggesting that any decrease in thermal resistance conferred by denser snow has negligible consequences for wolverines.

Moreover, although our results indicate a clear preference for denser snow among wolverines, (Figure 3.4), the mechanism underlying this selection is unclear. The slight positive influence of snow density on wolverine movement (Figure 3.4) suggests that this selection may be driven by reduced energy expenditure associated with traveling over dense snow (Crête and Larivière 2003) rather than the use of dense snow for subnivean structures. This trend is somewhat unexpected, since dense snow is generally found to be important for over-snow travel among taxa with higher footloads (body mass/foot surface area; Whiteman and Buskirk 2013), but less so for wolverines which have a lower footload (Pozzanghera et al. 2016). However, the wide 95% confidence band for this relationship suggests that both processes (i.e., subnivean structures and movement) may contribute to wolverines' selection for denser snow.

3.5.2 Wolverines and Snow

Although there is considerable evidence supporting the importance of snow as an attribute of wolverine habitat (Magoun and Copeland 1998; Aubry et al. 2007; Pozzanghera et al. 2016; Heinemeyer et al. 2019), the exact nature of this relationship is unresolved and varies geographically. The global distribution of wolverine reproductive dens and telemetry locations overlaps broad-scale (>500m resolution) spring snow persistence (Copeland et al. 2010), although it has been argued that this relationship may arise from uneven sampling effort (Aronsson and Persson 2017), and may not capture snow properties at a spatial scale relevant to the species (Magoun et al. 2017). Additionally, reproductive dens and individuals are increasingly being found in areas without substantial spring snowpack (Webb et al. 2016; Aronsson and Persson 2017; Jokinen et al. 2019). Regardless, the high proportion of reproductive dens that have been located in deep snow suggests an important, if not obligatory, use of this substrate by the species (Webb et al. 2016). In addition to the use of deep, persistent snow for reproductive dens, snow may play an important role in food preservation for wolverines, enabling the species to thrive in relatively low-productivity, unpredictable environments (Inman et al. 2012).

Additionally, snow may play a role in wolverine food acquisition. Cricetid rodents are an important component of wolverine diet on tundra during the snow-covered spring (Dorendorf et al. 2018). Cricetids are generally associated with deep snow on tundra; winter nest density and activity are higher in areas with deeper snow (Duchesne et al. 2011), and snow fence experiments have found that cricetids select areas with experimentally increased snow depth, subsequently returning to pretreatment levels upon fence removal (Reid et al. 2012). Little data are available regarding wolverine hunting of cricetids, but studies of Arctic fox (*Vulpes lagopus*) suggest that supranivean predators may not be impeded by deep snow, employing a digging technique instead of pouncing to capture subnivean cricetids in deeper snow (Bilodeau et al. 2013). Our field observations suggest that in some cases wolverines travel short distances along the subnivean ground surface through the soft depth hoar layer, possibly implying a use of this space besides resting and food caching. Therefore, in addition to its importance for resting sites and food caching, deep snow may afford wolverines greater subnivean hunting opportunity.

Despite the ample evidence that snow is important to wolverines, this study is the first of which we are aware to systematically address the way in which within home-range habitat selection by wolverines is driven by the spatially and temporally variable snowpack. As such, we have identified several relevant issues that could aid our understanding of the relationship between wolverines and snow.

First, we show that snow is important to non-denning wolverines in the Arctic. Much of the existing literature regarding wolverines and snow focusses on its importance for thermoregulation, predation avoidance, and food caching among neonates and mothers (Magoun and Copeland 1998; Copeland et al. 2010; Inman et al. 2012). These mechanisms linking wolverines to snow are undoubtedly important. However, by focusing on non-denning wolverines in our analysis, we have shown that snow characteristics are important to wolverines for reasons other than solely creating reproductive dens, a result that finds support in other snow-denning species, including polar bears and ringed seals (Harington 1968; Kelly and Quakenbush 1990). This has important implications when considering the impact of climate change on such snow-associated species, since the way in which the changing snowpack affects these species depends on the mechanism linking them to snow. Our findings suggest that snowpack changes may impact fitness across demographics, not only among reproductive females and neonates. However, for wolverines this relationship likely varies across the species' geographic range, since ecosystems with more ample non-snow resting habitat (e.g., downed trees and large boulders), different wolverine diet compositions, and different snow regimes, are likely characterized by a different mechanistic link between wolverines and snow. Wolverines in areas with taiga snow, for example, which is characterized by extremely low densities and depths (Sturm et al. 1995), likely excavate fewer subnivean cavities than wolverines on tundra (Jokinen et al. 2019). Explicitly accounting for the well-described and highly variable snow regimes (Sturm et al. 1995) that occur across wolverines' global range should be a part of any conversation regarding the relationship between the species and snow.

Second, we found three specific snow characteristics to be important to wolverines: depth, density, and melt. Due to logistical limitations associated with collecting snow data (Boelman et al. 2019), most previous studies investigating wolverines and snow rely on snow metrics derived from satellite imagery, and are restricted to >500m pixel resolution (Aubry et al. 2007; Heinemeyer et al. 2019). Additionally, such studies typically incorporate snow as a temporally summarized statistic, such as number of years with snow within a given date range (e.g., Copeland et al. 2010). In contrast, by explicitly accounting for the complex nature of the snowpack, and incorporating multiple snowpack properties, our study provides insight regarding the specific mechanism linking the substrate and the species, specifically wolverine's use of snow for excavating subnivean cavities, and possibly the use of denser snow for reducing energy expenditure associated with over-snow travel. Additionally, studying specific snow properties enables a more informed understanding of how climate-induced changes to the Arctic snowpack may be affecting this species.

3.5.3 Climate Change Implications

Ongoing climate change is rapidly altering the Arctic snowpack. In northern Alaska, historical climate analyses and projections indicate that more snow is falling now during winter, but that the duration of the snow-covered season is contracting in both spring and fall (Callaghan et al. 2011). Indeed, the duration of the snow covered season has decreased by three days per decade since 1951, with accelerating loss in the most recent decades (Callaghan et al. 2011). With these changes in mind, the results of this study are best interpreted not as a "baseline," but rather as a snapshot in time, documenting wolverines' relationship with snow in the midst of accelerating directional change.

Increased snow depth in the Arctic could positively influence species using subnivean cavities for resting sites and hunting during winter. For this to occur, the snow would need to be of sufficient density to maintain cavities and tunnels, and/or increased snow depth would need to positively influence cricetid populations. However, we suspect that the most direct snow-mediated impact of climate change on these species results from earlier spring melt and increased frequency of midwinter melt events, since these changes require animals to seek alternate structural protection and reduce food caching opportunities. Our finding that wolverines in the Arctic are sensitive to the melt status of the snow suggests that the date of snow disappearance, as is reflected in the remotely sensed presence/absence data commonly used for assessing snow-associated species' response to snow, may be less biologically important than melt initiation date.

3.5.4 Wolverine Habitat Selection in Relation to Non-Snow Environmental Features

Our findings indicate that the environmental features driving wolverine habitat selection on tundra are similar to those elsewhere. Wolverines have previously been found to select streams during winter in alpine habitats (Aubry et al. 2007). We extend this finding to Arctic tundra, likely due to the use of frozen streams and rivers as travel corridors and/or habitat for prey species such as snowshoe hare and ptarmigan. Previous studies have also found that wolverines prefer more rugged terrain in montane regions (Krebs et al. 2007), as well as in tundra regions at the occupancy level of selection (Poley et al. 2018). Our study extends this finding to habitat selection operating at the within home-range level on tundra. Care should be taken in making direct comparisons between studies, however, since the spatial resolution at which a study defines terrain ruggedness alters what is considered "rugged." In our study, at 5 meter resolution, rugged terrain includes, for example, an incised stream 10 meters in width; such a feature would not be captured by a terrain ruggedness index defined at a 50 meter resolution.

3.6 Conclusions

Here we highlight the importance of explicitly accounting for snowpack spatial and temporal variability, rather than simply the presence or absence of snow, in studies of subnivean species (Boelman et al. 2019). Climate change is rapidly altering the duration and quality of the snow-covered period, and the way in which these changes influence ecological processes is mediated by the specific snow properties that are important to a given process. We demonstrate that for wolverines, which rely on the subnivean space, the depth, density, and melt status of snow are important drivers of habitat selection and movement. Further, we demonstrate that such snow properties, which vary over fine spatial and temporal scales, can be incorporated into ecological models using a physically based snowpack evolution model. Continuing to parse the mechanistic relationship between animals and snow using tools such as these will be a crucial component of understanding the response of high-latitude and high-elevation species to climate change.

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3.9 Figures

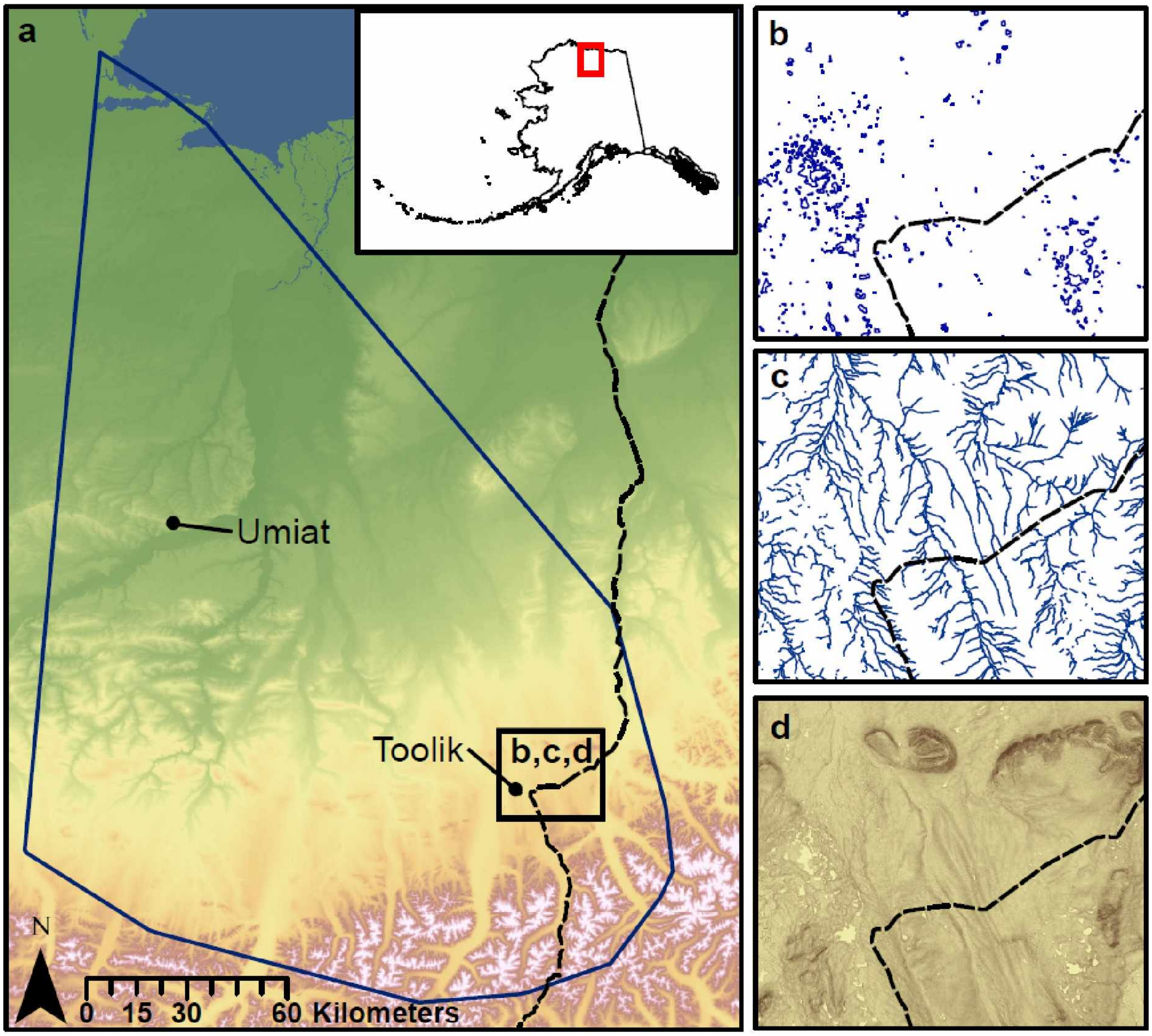

Figure 3.1: Study area in Arctic Alaska (a). The blue polygon in (a) indicates the minimum convex polygon containing all wolverine relocations used in the analysis, the broken black line shows the Dalton Highway, and the black box indicates the extent of panels (b), (c), and (d) within the study area, providing detailed views of lake edges (b), streams/rivers (c), and terrain ruggedness (d; darker colors indicate more rugged terrain).

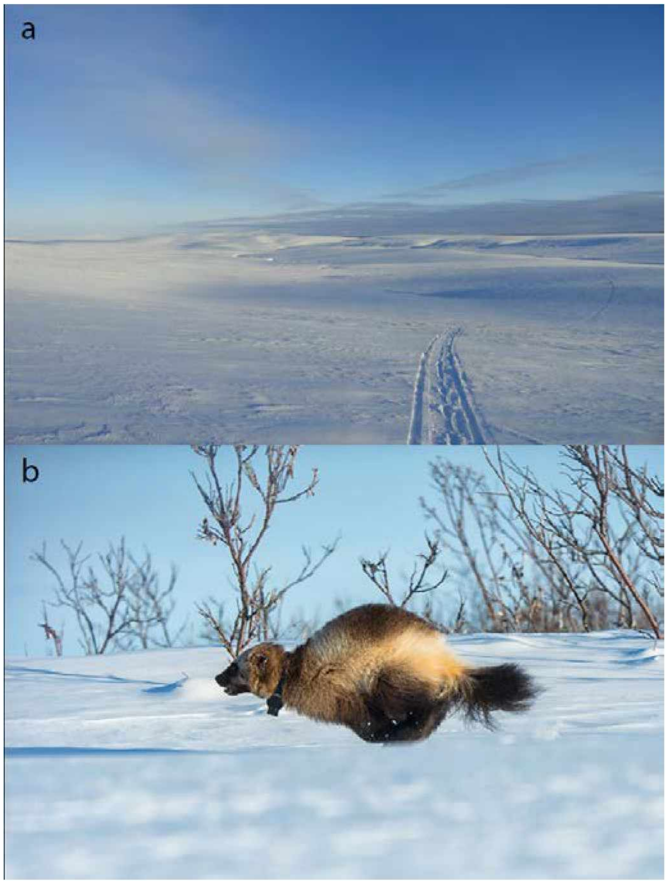

Figure 3.2: Rolling tundra near Umiat, characteristic of the North Slope foothills (a), and a collared wolverine traveling along a river corridor (b; photograph courtesy of Peter Mather).

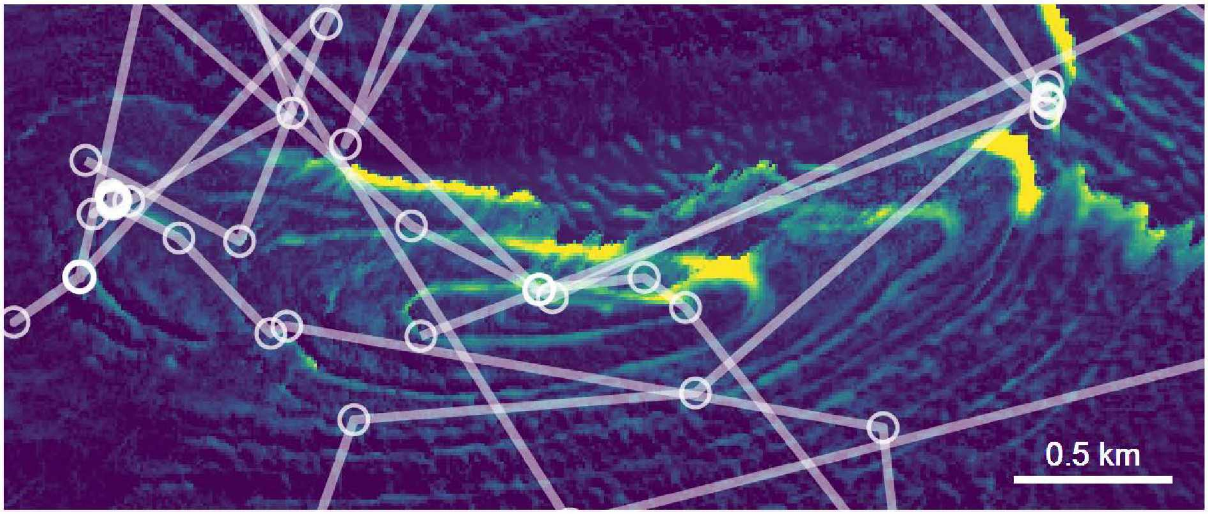

Figure 3.3: Example SnowModel output for 18-Apr-2017 illustrating the fine spatial scale over which snow depth varies within the study area, overlaid with wolverine movement data (open circles and lines) during spring 2017. Circles are opaque, so overlapping circles (indicating multiple GPS locations) appear brighter. Pixels are 10 m x 10 m.

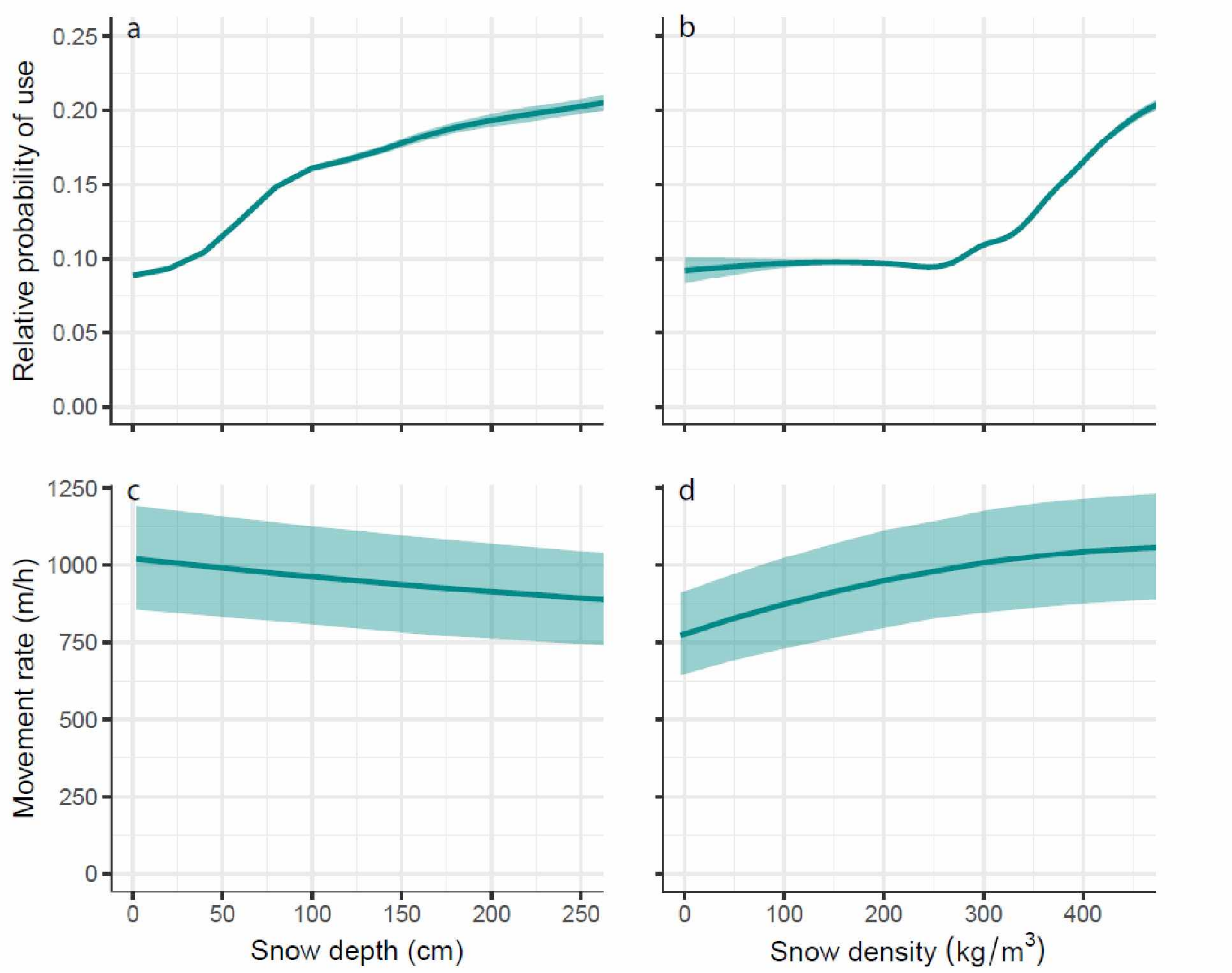

Figure 3.4: Conditional, relative probability of use (a,b) and mean movement rate (c,d) in response to non-melting snow depth (a,c) and snow density (b,d). Relative probability of use is calculated by exponentiating the linear predictors of the step selection function, and can be interpreted by comparing values against one another. For example, a relative probability of use value of 0.2 for snow of depth 250 cm is 2.2 times higher than a relative probability of use value of 0.09 for snow of depth 20 cm. Therefore, wolverines are 2.2 times more likely to select snow of depth 250 cm than snow of depth 20 cm.

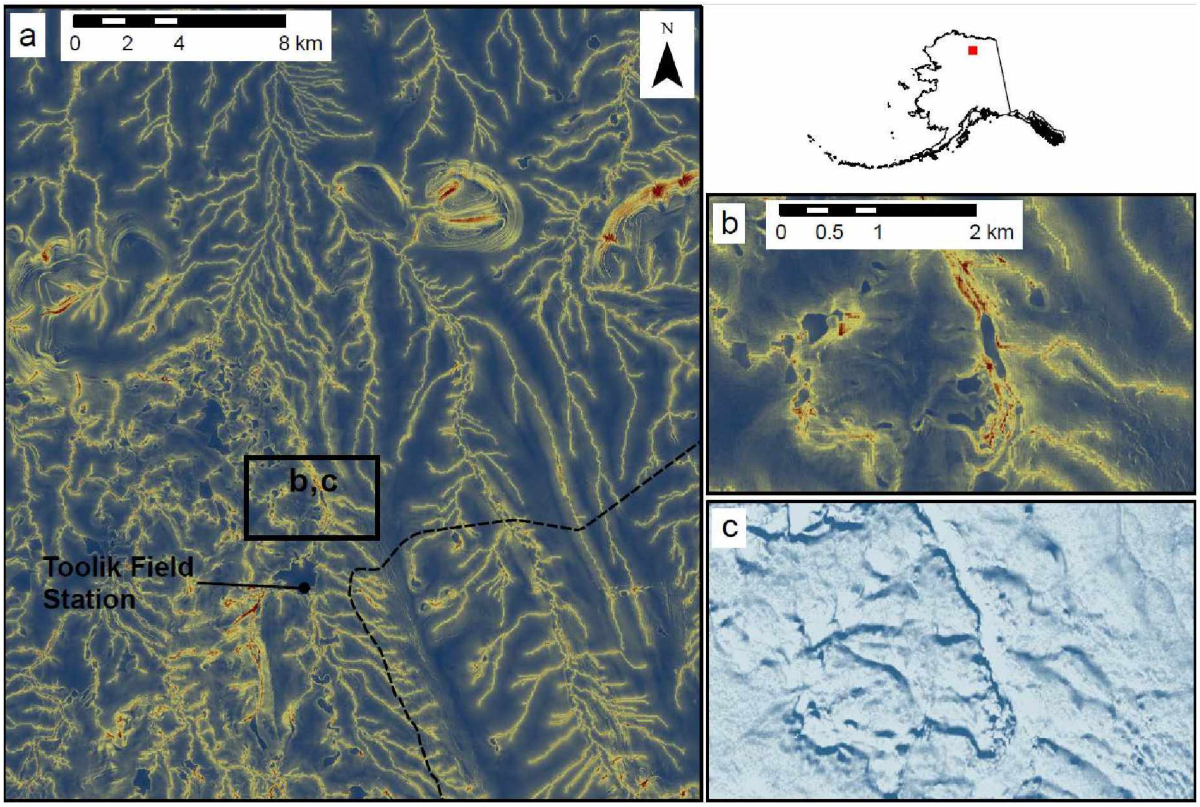

Figure 3.5: Regional (a) and detailed (b) relative probability of use map for wolverines, as well as SnowModel-produced snow depth (c) in the vicinity of Toolik Field Station, Alaska. In (a) and (b), red indicates higher relative probability of use, generally associated with streams and deep, dense snow, and blue indicates lower relative probability of use. Model output based on SnowModel predictions for 18-April-2017. In (c), darker shades represent deeper snow. The broken black line in (a) shows the Dalton Highway.

3.10 Tables

Table 3.1: Summary statistics for environmental covariates used in step selection analysis for non-melting snow. Upper and lower bounds are the 2.5th and 97.5th quantiles, respectively.

	Available				Used			
	Mean	Median	Lower	Upper	Mean	Median	Lower	Upper
Snow Depth (cm)	52.6	30.6	4.3	238.0	57.4	32.6	4.1	265.0
Snow Density (kg/m3)	277.0	278.0	146.0	445.0	283.0	285.0	144.0	449.0
Distance to Stream/River (m)	220.0	147.0	4.0	807.0	189.0	90.9	2.3	811.0
Distance to Lake Edge (m)	2049.0	1411.0	26.3	7268.0	2046.0	1410.0	19.7	7273.0
Terrain Ruggedness Index (unitless)	50.5	32.7	2.1	164.0	54.0	35.3	2.4	165.0

Table 3.2: Akaike weights for candidate "melt" and "no melt" models, as well as the base model. Akaike weights were calculated for each individual and a population-level weight was calculated using a non-parametric bootstrap, weighted by sample size, resulting in weights that do not sum to 1.

	Model	Akaike Weight
No Melt	Density+Depth	0.40
	Depth	0.24
	Density	0.21
	Base	0.14
Melt	Base	0.39
	Density	0.25
	Depth	0.25
	Density+Depth	0.10

Table 3.3: Coefficient estimates for the top performing model fit to wolverine GPS data associated with non-melting snow. All predictor covariates except log-transformed variables were standardized. Estimates and 95% upper and lower confidence bounds were generated by calculating a non-parametric bootstrapped mean of individual coefficient estimates, weighted by inverse variance.

Coefficient	Estimate	Lower	Upper
lnSL	0.027	0.012	0.044
Terrain Ruggedness	0.835	0.687	1.020
Terrain Ruggedness^2	-0.148	-0.228	-0.091
ln(distance to lake edge)	-0.076	-0.131	-0.025
ln(distance to stream/river)	-0.375	-0.422	-0.334
Snow density	-0.011	-0.099	0.070
Snow density^2	0.018	-0.035	0.073
Snow depth	0.128	-0.050	0.319
Snow depth^2	-0.010	-0.025	0.000
lnSL : Snow density	0.016	-0.002	0.043
lnSL : Snow density^2	-0.003	-0.011	0.009
lnSL : Snow depth	-0.017	-0.060	0.015
lnSL: Snow depth^2	0.001	-0.002	0.005

Chapter 4: Accounting for unknown behaviors of free-living animals in accelerometer-based classification models: Demonstration on a wide-ranging mesopredator[3]

4.1 Abstract

Describing the behaviors of free-living animals is broadly useful for ecological and physiological research, but obtaining accurate records for difficult-to-observe species presents a considerable challenge. Tri-axial accelerometers are increasingly used for this purpose by exploiting behavioral observations from accelerometer-carrying animals to predict behaviors of unobserved conspecifics. We developed a modeling approach to predict behaviors of wolverines from collar-mounted accelerometers using Support Vector Machines. By applying a temporal smoothing function and setting a lower threshold for a-posteriori prediction probabilities, we improve the predictive performance of our model and simultaneously create a framework for explicitly accounting for behaviors unknown to the model, a problem that remains largely unaddressed in similar studies. We demonstrate that such an approach can achieve a model-averaged accuracy of 98.3%, with high predictive performance for the behaviors resting, running, scanning, tearing at food, and transferring items with the mouth, a behavior typically associated with caching food among captive wolverines. To illustrate the utility of this approach, we apply this model to a sample of seven free-living wolverines in Arctic Alaska.

4.2 Introduction

Describing the behaviors of free-living animals can provide important insights regarding a wide range of ecological processes. Taken alone, analysis of such behavioral records can be used to investigate temporal patterns in activity, including association among behaviors, yielding insights regarding circadian rhythms in the daily partitioning of behaviors or inter-individual differences in such temporal patterns (Garthe et al., 2003; Yoda and Ropert-coudert, 2007). When coupled with environmental and physiological information, behavioral analyses can address how such extrinsic and intrinsic factors influence behavioral decisions made by animals, including tradeoffs such as

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[3] Glass, T. W., Breed, G. A., Robards, M. D., Williams, C. T., & Kielland, K. (2020). Accounting for unknown behaviors of free-living animals in accelerometer-based classification models: Demonstration on a wide-ranging mesopredator. *Ecological Informatics*, *60*(101152). https://doi.org/10.1016/j.ecoinf.2020.101152

allocating time between foraging and antipredator behavior (Hamel and Côté, 2008; Studd et al., 2019; Switalski, 2003).

However, since documenting behavior has traditionally relied on direct observation, it is often a difficult or impossible task to assemble comprehensive records for remotely tracked free-living animals that have not been directly observed. Species that occupy areas that are remote or logistically difficult for human observers to access, such as under water, under snow, or in trees, present obvious challenges, as do species that range widely, travel quickly, or for which human observation alters behavior.

The rise of accelerometer-derived behavioral records promises to reduce these obstacles (Shepard et al., 2008). This process, whereby free-living animals are tagged with tri-axial accelerometers and the resulting data are used to predict the behaviors of the wearer, has been applied to a variety of marine (Battaile et al., 2015; Viviant et al., 2010; Whitney et al., 2010), and increasingly, terrestrial species (Hammond et al., 2016; McClune et al., 2014; Pagano et al., 2017; Wang et al., 2015). Resulting behavioral records have been used to investigate behaviors important to life history and fitness, including predation and mating events, and foraging strategies.

Using accelerometer data to classify behavior typically begins by building a predictive classification model based on observer-labeled accelerometer data. The labeled data are collected either by directly observing conspecific or surrogate species while wearing accelerometers (Campbell et al., 2013), or with the use of additional biologgers, such as video cameras, affixed to free-living individuals (Nakamura et al., 2015; Pagano et al., 2017; Watanabe and Takahashi, 2012). A classification model, such as a statistical learning classifier (Tatler et al., 2018) or decision tree analysis (Studd et al., 2019) can then be applied to the labeled data to train and evaluate candidate models, after which the final model can be applied to free-living individuals where no direct observations or ancillary data for determining behaviors are available.

Here, we developed and evaluated the first predictive model that can be used to classify behaviors of free-living wolverines (*Gulo gulo*) using collar-mounted tri-axial accelerometers, based on visual observations of captive wolverines wearing similar collar-mounted accelerometers. Further, we used labeled accelerometer data from these captive conspecifics to create a framework by which behaviors not exhibited by the captive wolverines, and therefore unknown to the model, would be classified as "unknown," rather than incorrectly classified to the best fitting known acceleration pattern. By developing such a model, we hoped to broaden the field of possible questions that can be addressed regarding the interactions of the environment, physiology, and ecology of wolverines, and provide a framework that other researchers can employ for other species to address similar questions while explicitly addressing the problem of incorrect attribution for behaviors unknown to the model. Finally, to demonstrate the utility of our modeling approach, we applied several candidate models to a small sample of free-living wolverines and assessed temporal trends of resting, running, vigilance behavior, and behaviors associated with handling food.

4.3 Methods

A schematic outlining the workflow is included in Figure 4.1.

4.3.1 Data Collection

4.3.1.1 Captive Wolverines

We collected accelerometer data and behavioral observations from three captive adult wolverines (two females and one male) at Nordens Ark, Hunnebostrand, Sweden, between March 4 and March 14, 2019. Wolverines were anaesthetized using a combination of ketamine, midazolam, and medetomidine. Collars were mounted with tri-axial accelerometers (AXY-3, 10g, Technosmart Europe Srl., Colle Verde, Italy), GPS units (GIPSY 5, 100g, Technosmart Europe Srl., Colle Verde, Italy), light/temperature loggers (Intigeo-C330, 3.3g, Migrate Technology Ltd., Cambridge, United Kingdom) and timer-activated release mechanisms (TRD-L, 30g, Lotek Wireless Inc., Newmarket, Canada), and weighed less than 3% of the animal's body mass. Accelerometers recorded at a frequency of 10 Hz. Collars were set to automatically release after approximately 10 days.

We conducted behavioral observations of these captive collared wolverines for 4-8 hours per day from a platform and paths adjacent to their enclosures. We assembled an ethogram during the course of observations, creating new behavioral classes to accommodate behaviors as they were observed. We defined behaviors according to distinct motions and/or postures, which we expected to register differently in the accelerometer data (Appendix C). We opportunistically recorded behaviors exhibited by wolverines, along with associated timestamps from a watch that was synchronized with the accelerometers. Upon retrieving the accelerometers, we recorded the time each device was turned off, for use later in assessing temporal drift.

All animal handling and observation was consistent with Nordens Ark's own permitting and University of Alaska Fairbanks Institutional animal Care and Use Committee (UAF IACUC) protocol #1373175.

4.3.1.2 Free-Living Wolverines

We collected accelerometer data from seven free-living adult wolverines (three females and four males) in the vicinity of Toolik Field Station, Alaska (68° 38' N, 149° 36' W) during spring and summer 2018. Captures took place between February 25 and April 18, and accelerometer data were collected between February 25 and July 27. Wolverines were captured using baited lumber box traps (modified from Lofroth *et al.*, 2008), and anaesthetized using Telazol™ (175 mg, Golden et al., 2002). We used Lotek Iridium Litetrack 250 collars (~250g, Lotek Wireless, Newmarket, Canada), to which we attached tri-axial accelerometers (AXY-3, 10g, Technosmart Europe Srl., Colle Verde, Italy), using a combination of epoxy and steel cable ties. Accelerometers recorded at a frequency of 10 Hz. Collars weighed less than 3% of the animal's body mass, and were equipped with both mechanical release mechanisms and rot-away strips to ensure release from the animal. All capture and handling of free-living wolverines was conducted under UAF IACUC protocol #847738, and Alaska Department of Fish and Game scientific permit 18-085.

We opportunistically collected a single instance of labeled accelerometer data from a free-living collared wolverine. To do so, we followed fresh tracks in the snow at a site used <24 hours prior by the collared wolverine. We followed the tracks for approximately 1 km, during which time the individual maintained an unfaltering 3x3 lope characteristic of a running wolverine. Upon retrieving the accelerometer, we examined the data associated with this time period and extracted the portions having high-amplitude periodic motion, which we labeled as running. We included these data in our labeled full training dataset.

4.3.2 Data Processing

Prior to processing data collected from captive wolverines, we first corrected for temporal drift in accelerometers by comparing the "power off" time recorded by the accelerometer with that displayed by the watch (which were synchronized at accelerometer deployment). Drift rates ranged between 0.3 and 1.5 seconds per day, depending on accelerometer, during the 10 days deployed. To account for this, we assumed a constant rate of drift and applied an accelerometer-specific linear correction to the timestamps associated with observations. In addition, we subtracted one second from the end of every behavioral observation to account for recorder error, reflecting the difference between the actual end of the activity and the moment the observer looked at their watch.

Since the accelerometers we deployed on free-living wolverines were not oriented in the same direction with respect to the animal's body, and we suspected that collars rotated around the animal's neck during deployment, we were unable to confidently delineate the surge, sway, and heave axes traditionally used in tri-axial accelerometer analysis for all individuals. To mitigate this problem, we converted the tri-axial measurements taken by the accelerometers into a vertical and horizontal component based on (Mizell, 2003). This required first estimating the magnitude of gravity along each axis, $g = (g_x, g_y, g_z)$, by applying a running mean over a 2 second window to the raw accelerometer data (the result is referred to as the static acceleration). We then subtracted this from the raw acceleration to estimate dynamic acceleration $d = (a_x - g_x, a_y - g_y, a_z - g_z)$ where (a_x, a_y, a_z) is the vector representing the raw acceleration data for any given time. We then computed the projection v of d on the vertical axis g using vector dot products, as

$$v = \left(\frac{d \cdot g}{g \cdot g}\right) g$$

This computation yields the vector $v = (v_x, v_y, v_z)$, which represents the vertical component of dynamic acceleration along each axis of the accelerometer. The horizontal component can then be calculated for each axis using the Pythagorean theorem, wherein

$$h = \sqrt{d^2 - v^2}$$

resulting in a horizontal value for each axis, representing the directionless magnitude of acceleration in the horizontal plane. We summed v_x, v_y, and v_z to find the total acceleraton in the vertical direction which we term "vertical acceleration" (analogous to the heave axis), and we summed h_x, h_y, and h_z as a representation of the total acceleration in the horizontal plane, which we term "horizontal acceleration" (analogous to the sum of the absolute values of the sway and surge axes). In addition, we calculated the overall dynamic body acceleration (ODBA, Gleiss et al., 2011) by summing the absolute dynamic acceleration values across the all three axes, and the vectorial dynamic body acceleration (veDBA, Gleiss et al., 2011) as

$$veDBA = \sqrt{d_x^2 + d_y^2 + d_z^2}$$

4.3.3 Summary Statistic Calculation

To generate predictor variables for behavioral classification, we partitioned the vertical and horizontal acceleration data, ODBA, and veDBA into 10 second segments, each segment termed an "observation," and calculated summary statistics for each (complete list in Table 4.1, distributions of summary statistics in Appendix C). We calculated dominant power spectrum (DPS) and frequency at DPS using a Fast Fourier Transform (Brigham and Morrow, 1967). We discarded any observations less than 10 seconds in duration, only retained behavioral classes with at least 20 observations, and termed the resulting dataset the "full training" dataset. We excluded 13 observations for which the horizontal or vertical acceleration was zero for the duration of the observation, since kurtosis and skewness could not be calculated. We assumed, and verified, that all such observations belonged to the behavioral class Rest, and employed this assumption in making predictions for the data of free-living wolverines (see *Application to free-living wolverines*). This resulted in nine behavioral classes ultimately included in our analysis (Table 4.2). All observations belonging to classes with fewer than 20 observations were termed the "withheld" dataset and were used later in evaluating performance (see *Modeling*).

4.3.4 Modeling

We used the machine learning technique support vector machines (SVM) to classify behaviors from accelerometer data, implemented in R package *e1071* (Meyer et al., 2018; "R Core Team," 2018). Our choice of SVM reflects this method's high predictive performance in behavior-recognition tasks (Campbell et al., 2013; Grünewälder et al., 2012; Tatler et al., 2018), and our desire to employ a probabilistic modeling framework, since probabilities associated with predictions are integral to our evaluation of unknown behaviors. SVM assign data to user-defined classes by constructing a hyperplane between binary classes. The number of observations allowed to violate the hyperplane is controlled by a user-defined cost parameter, and a margin surrounding the hyperplane is maximized. The hyperplane is chosen as that which allows the largest separation between classes, *i.e.,* the widest margin surrounding the hyperplane. Hyperplanes are defined by the observations that either fall within the separating margin, or that violate the separating hyperplane, and these observations are termed "support vectors." Hyperplanes can take nonlinear forms by applying a kernel function to the inner product of the support vectors (Aizerman et al., 1964). We chose to use a radial kernel for maximal flexibility in hyperplane definition. To generalize this binary classifier to a multiclass response, we used a "one-versus-one" approach, in which observations are classified for every possible pair of classes and the class most commonly selected is the predicted value. A-posteriori class probabilities can be computed by fitting a logistic distribution to the decision values of all binary classifiers and extracting class probabilities using quadratic optimization. In addition to the cost parameter, support vector machines with a radial kernel can be tuned using a gamma parameter, which weights support vectors in the definition of the hyperplane. We used 5-fold cross validation on the full training dataset and calculated accuracy (see *Model evaluation*) as an indication of model performance across all combinations of gamma = (0.001, 0.01, 0.1, 1, 2, 4) and cost = (0.1, 1, 10, 100, 250, 500, 750, 1000, 10,000), selecting the parameters that yielded the best performing model for all further analyses (parameters chosen per recommendations in Hsu, Chang and Lin, 2010). A more detailed, accessible description of SVMs can be found in (James et al., 2017).

Since our behavioral classes were unbalanced, we included class weights in the SVMs, calculated as

$$w_{ik} = \frac{N_k}{n_{ik}}$$

where w_{ik} is the weight of class i for the k^{th} iteration of cross validation, N_k is the total number of observations in the full training data for the k^{th} iteration of cross validation, and n_{ik} is the number of observations in class i for the k^{th} iteration of cross validation.

We were interested in building a modeling framework that explicitly incorporated unknown behaviors (*i.e.,* behaviors within the ethogram of a free-living wolverine that we did not observe among those in captivity), such that these unknown behaviors would be identified as Unknown by the model. To do this, we set a threshold level for a-posteriori class probabilities associated with predicted behaviors, below which predictions were assigned to the category Unknown. To evaluate how well the model correctly classified such unknown behaviors, we fit a model to the full training dataset and made predictions for all observations in the "withheld" dataset, using these as proxies for behaviors that we didn't observe among wolverines in captivity. Since these withheld observations (observations that belonged to behavioral classes observed at low frequency among captive wolverines) were all known to belong to behaviors other than those in the full training dataset, the "perfect" model would categorize them all as Unknown, and this result is approached as the threshold probability value increases to one. However, increasing the threshold probability comes at the cost of incorrectly categorizing some known observations as Unknown, so we selected the optimum threshold probability as that which maximized both the proportion of withheld observations that were correctly classified as Unknown and the model's accuracy in classifying known observations correctly, referenced to the entire dataset (termed "full accuracy", see *Model evaluation*). We evaluated threshold probabilities ranging from 0 to 0.95 by increments of 0.05, and bootstrapped the procedure 300 times, resampling the full training dataset with replacement, to generate confidence intervals.

We were also interested in examining the effect of applying a smoothing function to predicted behavioral classes (Cao et al., 2012; Chimienti et al., 2016; Grünewälder et al., 2012). We therefore made predictions for the 10 second observations immediately following and preceding the observation of interest, and the predicted behavior of the observation of interest became the class that occurred most commonly within this 30 second window. If the three predicted classes within the window were all different, the observation of interest retained its original class. We performed this in tandem with applying threshold probabilities, such that predictions were subject to reclassification as Unknown according to the threshold probability before being subject to the smoothing function.

We defined the "base model" as that which was subject to neither a smoothing function nor a threshold probability, the "base + smoothing" model as that which was subject to a smoothing function but no threshold probability, and the "threshold model" as either the smoothing model or the non-smoothing model that had the highest accuracy at the optimal threshold probability.

4.3.5 Model Evaluation

To evaluate the performance of our model, we relied on metrics derived from tallies of True Positives (T+), True Negatives (T-), False Positives (F+), and False Negatives (F-). These groups are tallied for each behavioral class in a single model independently. Specifically, for a given behavior, observations whose predicted class and true class both match the given behavior are considered T+, observations whose predicted class and true class neither match the given behavior are T-, observations whose predicted class matches the given behavior but whose true class does not are F+, and observations whose true class matches the given behavior but whose predicted class does not are F-. These terms are straightforwardly depicted using a confusion matrix (Figure 4.2). We used 300 bootstrapped samples, with a new random 70/30 draw of training/testing data drawn from the full training dataset, stratified by behavior, for each iteration, to generate tallies of T+, T-, F+, and F-, and to calculate associated confidence intervals. The training/testing split mentioned here, used only during this bootstrapping process, should not be confused with the full training dataset defined above. The bootstrap method allows explicit estimation of confidence intervals for performance metrics, unlike the more traditional k-fold cross validation (Champagne et al., 2014).

Once these values are calculated for each behavior, a variety of metrics can be derived to evaluate the performance of the model. We chose to calculate accuracy, precision, and recall (sometimes called sensitivity), as these are relatively common among accelerometer-based behavioral classifiers and enable comparison across studies. Accuracy is defined as the proportion of the observations that are classified correctly, calculated as:

$$\frac{(T+) + (T-)}{(T+) + (T-) + (F+) + (F-)}$$

When calculating accuracy for the purpose of selecting a threshold probability (see *Modeling*), we replaced the denominator with the total number of observations (*i.e.,* including those which fell below the threshold probability and were classified as Unknown), thereby providing a metric that assessed the cost of increasing the threshold probability, and termed the result "full accuracy."

Precision is defined as the proportion of predicted observations for a given behavior that actually belong to that behavior, calculated as:

$$\frac{(T+)}{(T+) + (F+)}$$

Recall is defined as the proportion of true observations for a given behavior that were predicted to belong to that behavior, calculated as:

$$\frac{(T+)}{(T+) + (F-)}$$

To assess overall model performance, each metric can be either micro-averaged, whereby the values for T+, T-, F+, and F- are summed across behaviors and the overall metric is calculated on the summed values, or macro-averaged, whereby the metric is calculated for each behavior independently and subsequently averaged (Sokolova and Lapalme, 2009). Since micro-averaging favors larger groups in an unbalanced model, we macro-averaged accuracy to reduce such bias. Since precision and recall can be undefined for a given behavior, we did not average these values and instead evaluated them at the level of individual behaviors only.

We were also interested in evaluating the relative importance of each variable in the predictive performance of the model. To do this, we iteratively left one variable at a time out of the model and calculated the decrease in accuracy from the full model. We found that model predictive accuracy was reduced by <0.1% regardless of the variable dropped, suggesting high redundancy across variables.

4.3.6 Application to Free-Living Wolverines

To illustrate the efficacy of this model, we made predictions of the behaviors exhibited by the seven free-living wolverines. To do this, we processed the data of free-living wolverines and extracted summary statistics as described above, and used all three candidate models, fit to the full training dataset (see *Summary statistic calculation*), to make predictions for the free-living observations. Since kurtosis and skewness for observations with horizontal or vertical acceleration values of zero could not be calculated, we did not use the models to make predictions for such observations, instead assigning them to Rest, a classification that was supported by the data of the captive wolverines (see *Summary statistic calculation*). We chose to retain only predictions associated with behaviors whose lower confidence level of precision was greater than 0.6 for all three models, since low precision values indicate a low probability that the prediction is correct. For each model's predictions, we calculated the proportion of each hour of the day each animal spent engaged in each behavior, averaged across a season. We defined the seasons spring and summer as between February 25-May 10 and May 11-July 27 respectively, roughly corresponding to the many ecological and physiographic changes that take place in the Arctic around May 10, including rapid snow ripening and melt (Macander et al., 2015), disappearance of river and lake ice (Arp et al., 2013), caribou and bird migration (Tape and Gustine, 2014), and grizzly bear and ground squirrel emergence (Buck and Barnes, 1999; McLoughlin et al., 2002). Since the purpose of this study was to develop a modeling framework for making such predictions, and not to make inference on the behaviors of free-living wolverines *per se*, we chose to simply visualize these predictions by plotting the mean proportions of time spent in each behavior by hour of day, averaged across individuals.

Since the purpose of this study was to develop and evaluate a modeling framework for making behavioral predictions of free-living animals, we also used the predictions made for free-living wolverines to compare broad-scale differences of predictions made by the three models.

4.4 Results

4.4.1 Model Development and Evaluation

Model tuning yielded optimum values of gamma = 0.01 and cost = 10. The base model had an overall predictive accuracy of 94.6% (95% CI: 93.2-95.8%) and correctly classified 326 (95% CI: 288-360) of the 433 observations in the 30% portion of the full training dataset used for testing (75.4%, 95% CI: 66.5-83.1%). Performance for individual behaviors ranged from a precision of 0 to 0.98, and recall ranged from 0 to 0.97 (Table 4.3). The "base + smoothing" model had an overall accuracy of 95.8% (95% CI: 94.4-96.8%), and correctly classified 349 (95% CI: 311-379) of the 433 observations in the testing dataset (80.6%, 95% CI: 71.8-87.5%). The optimum threshold probability for the non-smoothed model was 0.65, and for the smoothed model was 0.625 (Figure 4.3). At the optimum threshold probability of each, the smoothed model and non-smoothed model correctly classified 55.4% (95% CI: 41.7-70.9%) and 51.2% (95% CI: 40.5-64.3%) of observations in the withheld dataset as Unknown, respectively. The full accuracy at the optimum threshold probability for the smoothed model was 57.5% (95% CI: 52.3-62.4%), which was higher than that of the non-smoothed model (53.4%, 95% CI: 49.0-57.7%). Therefore, the "threshold" model was selected as the smoothed model with a threshold probability of 0.625. The "threshold" model incorrectly classified 179 (95% CI: 157-202) observations as unknown, and had an overall accuracy of 98.3% (95% CI: 96.6-99.5%), correctly predicting 92.2% (95% CI: 88.5-95.4%) of the remaining observations (Figure 4.4).

4.4.2 Application to Free-Living Wolverines

At a gross level, the "base" and "base+smoothing" models yielded similar predictions for free-living wolverines, while the "threshold" model classified 32.4% of observations as Unknown (Figure 4.5). Of the observations classified as Unknown by the "threshold" model, the "base" model classified 13.8% as Run, 4.3% as Scan, 8.5% as Rest, 12.0% as Transfer, and 50.8% as Tear, while the "base+smoothing" model classified 13.4% as Run, 3.7% as Scan, 8.3% as Rest, 10.4% as Transfer, and 55.4% as Tear. The remaining observations that were classified as Unknown by the "threshold" model were predicted by the other two models to belong to behavioral classes with low precision values. All three models predicted Rest as the most commonly occurring behavior at 47.3%, 48.1%, and 45.4% of all observations for the "base," "base+smoothing," and "threshold" models respectively. All three models revealed that the seven wolverines generally spent more time resting between approximately 14:00 and 00:00 local time during summer, and had peak resting times around 17:00 and 02:00 during spring (Figure 4.5).

4.5 Discussion

Classifying behaviors from accelerometer data is an increasingly popular technique for addressing questions relating to the ecology and physiology of free-living animals. Considerable progress has been made in the field, particularly in evaluating the performance of different classification models (Nathan et al., 2012; Tatler et al., 2018) and the integration of multiple data sources, such as GPS and acoustic recorders, with acceleration to predict behavior (Shamoun-Baranes et al., 2012; Studd et al., 2019). Despite many such studies relying on predictive models built from direct observation of captive conspecifics, to our knowledge only one has explicitly addressed the problem of behaviors exhibited by free-living animals but not their captive counterparts (Rast et al., 2019), and that did so without a formal evaluation of efficacy.

Therefore, the purpose of this study was to create and evaluate a modeling framework that maximized predictive performance of behaviors from accelerometer data while simultaneously minimizing the incorrect classification of behaviors that are unknown to the model. Our results indicate that this process can yield a high-performing model, with macro-averaged accuracy of over 98%, using a modeling framework that is conceptually straightforward and computationally efficient. Moreover, the explicit allowance for behaviors unknown to the model improves its generalizability to accelerometer data gathered on free-living animals, since it is likely that the range of behaviors exhibited by captive animals is different from those of wild animals.

Additionally, our results indicate that predictive performance can be improved by applying a temporal smoothing function to predictions (Table 4.3, Figure 4.4), exploiting the apparently high degree of temporal correlation among behaviors exhibited by captive wolverines over a 30 second period. Previous studies have employed similar approaches (Cao et al., 2012; Chimienti et al., 2016; Grünewälder et al., 2012), although formal evaluation of the effect on model performance has been limited. A notable exception is (Cao et al., 2012), who evaluated the effect of applying such a smoothing function across a range of window lengths, and allowing such windows to vary by behavioral class. It is important to note that increasing the window length for both the smoothing function and the initial computation of summary statistics will reduce predictive performance for behaviors that typically occur at intervals shorter than the chosen window.

The practice of applying a threshold probability to behavioral predictions from accelerometer data has been employed before (Bellsolá, 2019; Bidder et al., 2014; Rast et al., 2019; Ware et al., 2015), including as an explicit means of reducing the incorrect classification of unknown behaviors (Rast et al., 2019). However, as noted above, previous studies have not formally evaluated the efficacy of this approach. By including observations from behaviors unknown to the model in our approach, we have developed a method of achieving such explicit evaluation. Our model selection process settled on 0.6 as the optimum threshold probability for maximizing model performance, but this value will undoubtedly vary by species, training dataset, and classification model used. Importantly, the model selection process developed here, whereby we evaluate the predictive performance of the model simultaneously for behaviors both known and unknown to the model across a range of threshold probabilities, can be used with any probabilistic classification model (or any classification model for which a-priori class probabilities can be calculated), not just SVM.

While the process of explicitly accounting for unknown behaviors improves the precision of the classifier, it does not yield a complete activity budget for a free-living animal and therefore excludes or introduces uncertainty into some biological questions, including those addressing temporal niche partitioning or rhythms of specific behaviors. We argue that this trade-off is necessary, since investigating such questions using a classifier that fails to account for such unknown behaviors would be based on the likely incorrect assumption that all behaviors are known to the model.

Although our "threshold" model had a macro-averaged accuracy of 98.3%, this metric risks overstating the performance of the model. Since model performance can be somewhat subjectively determined by whichever metric is most important for a given study, it is important to inspect the behavior-specific precision and recall values as well. A high precision value indicates that most of the observations classified as a given behavior actually belong to that behavior, and a high recall value indicates that most of the observations that belonged to a given behavior were actually classified as that behavior. Since our interest was in making predictions for out-of-sample observations of free-living wolverines, model performance is best reflected by precision (Bidder et al., 2014). Our "threshold" model had very poor precision and recall for certain behaviors, but quite high values for others. Specifically, it failed to classify any observations, or classified only two observations, into four of the nine categories (Eat, Gnaw, Groom, and Walk), instead incorrectly classifying many of these observations as either Unknown or Tear. As a result, the model had lower precision for Tear, and low recall for Eat, Gnaw, Groom, and Walk. Each of these behaviors are medium activity (Table 4.2), with little to no periodicity, so this result is unsurprising. The behaviors most frequently misclassified as Tear were all associated with food handling, so for out-of-sample predictions this category could be considered a catch-all "food-handling" class. The relatively high precision values for Rest, Scan, Run, and Transfer suggest that the most reliable biological inference will be made about these behaviors.

In applying the model to data from free-living wolverines, we aimed to demonstrate its utility and provide a proof-of-concept that could be used by other researchers to evaluate the applicability of the model to their specific questions. The behavioral predictions we obtained show considerable variation by hour-of-day and season. Previous research of circadian rhythms in wolverines at high latitudes found a drop in activity around midday during spring and summer (Thiel et al., 2019), consistent with the generally higher frequency of resting that we observed during that period among the animals in our study, although the seven animals in our study also exhibited more resting around 02:00 during spring (Figure 4.5). These results cannot be generalized without a larger sample.

Behavioral classification from accelerometer data is a promising area of active research, with the potential to greatly improve our understanding of the behavior of free-living animals. Coupled with other biologged data, such as location, body temperature, and heart-rate, accelerometry can shed light on the wide range of ecological and physiological processes governing behavioral decisions (Wilmers et al., 2015), including species' response to climate change (Chmura et al., 2018). However, developing accurate predictive models to extract behavior from accelerometer data remains challenging, and each model will be characterized by relative strengths and weaknesses. Formal evaluation of such characteristics, through consistently defined metrics such as accuracy, precision, and recall, is crucial to the advance of the field and comparison of different modeling approaches. Here, we have presented a novel high-performance modeling approach for classifying accelerometer data into discrete behaviors, which can be readily exploited by other researchers with accelerometer data from wolverines, or adapted to other species.

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4.8 Author Contributions

Thomas Glass: conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing – original draft preparation, writing – review and editing, visualization, project administration, funding acquisition; Greg Breed: writing – review and editing, visualization, supervision; Martin Robards: resources, writing – review and editing, visualization, supervision, funding acquisition; Cory Williams: resources, writing – review and editing, visualization, supervision, funding acquisition; Knut Kielland: writing – review and editing, visualization, supervision, funding acquisition.

4.9 Competing interests

The authors declare no competing interests.

4.10 References

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4.11 Figures

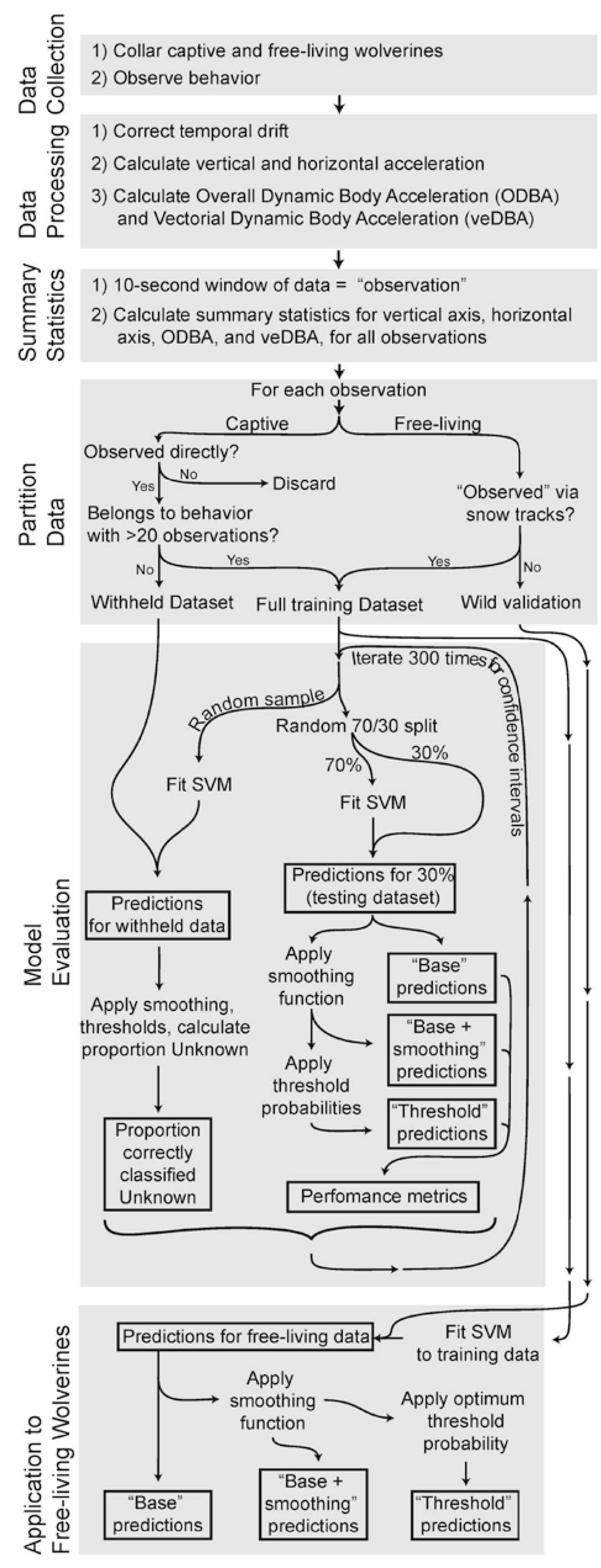


Figure 4.1: Methodological workflow of the study. A combination of accelerometer data from captive and free-living wolverines was used to train, evaluate, and validate the use of Support Vector Machines (SVM) for behavior classification. The "full training" dataset refers to all accelerometer data for which we observed the animal's behavior, and which belongs to a behavior with >20 observations. This dataset was randomly split into two (70% and 30% for training and testing, respectively) to evaluate the performance of the model, and this process was iterated 300 times to generate confidence intervals. The smoothing function reclassifies SVM predictions for each observation based on the nearest temporal neighbors, and the threshold probabilities reclassify observations as Unknown if the probability associated with the SVM prediction falls below the designated threshold.

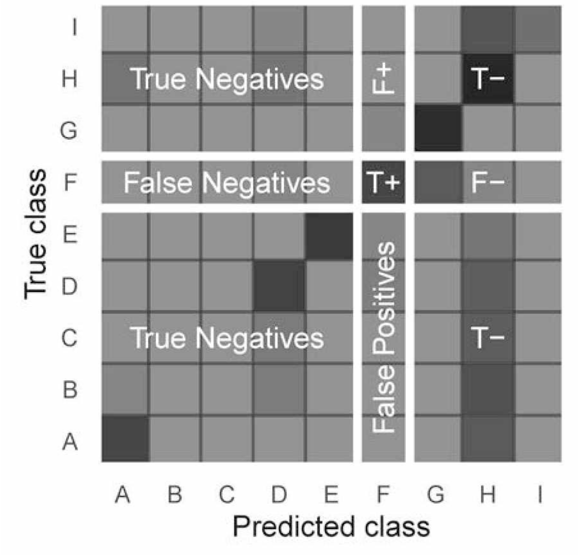


Figure 4.2: Example confusion matrix for behavioral classes A-F depicting the calculation of True Positive (T+), True Negative (T-), False Positive (F+), and False Negative (F-) values. Each metric is tallied for each class independently; the figure depicts these values for behavioral class F. This figure does not represent actual data, and is included only to demonstrate how performance metrics are calculated.

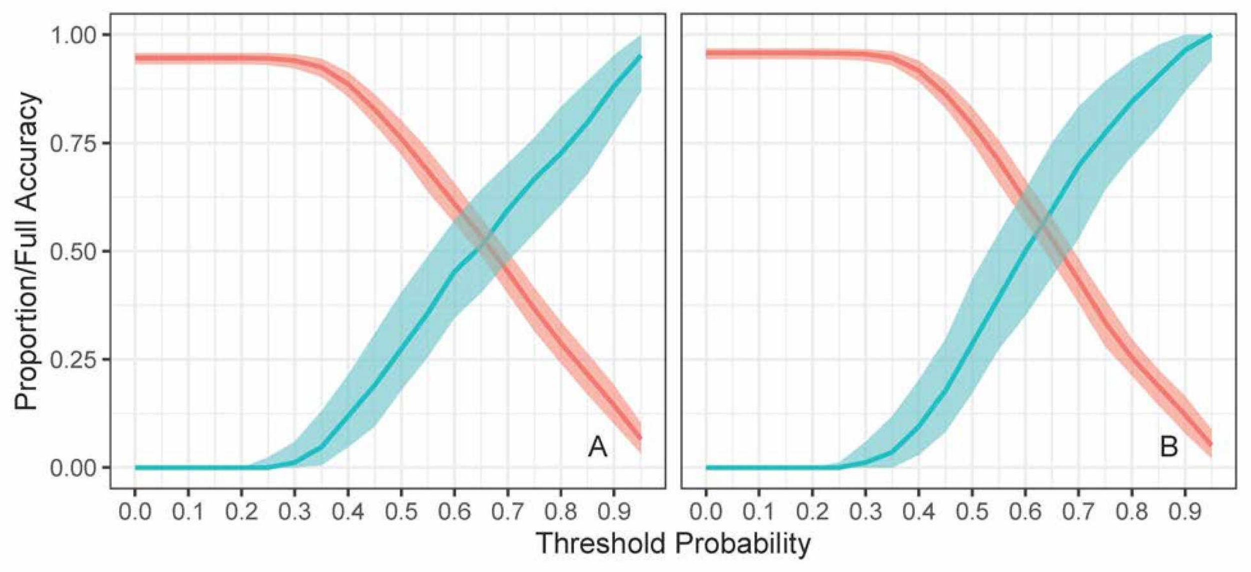
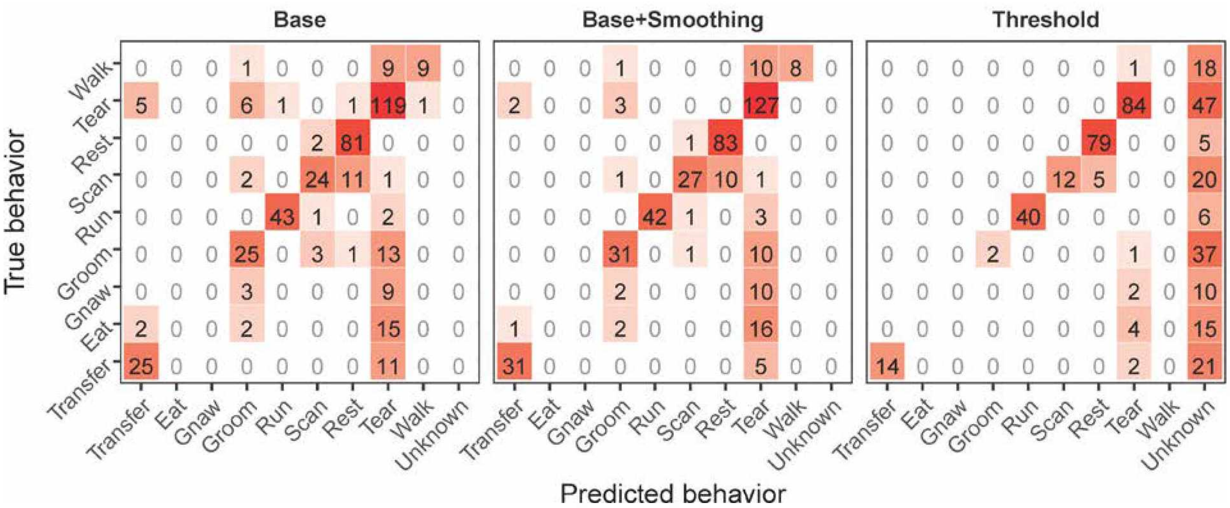


Figure 4.3: Full accuracy (red) and proportion of withheld observations classified correctly as unknown (blue) across threshold probabilities, without (A) and with (B) a smoothing function. The optimum threshold probability was selected as that which maximized both values (0.625 using the smoothing function, 0.65 without the smoothing function). Confidence bands are 95% quantiles, calculated pointwise using 300 bootstrap iterations.



Base

	Transfer	Eat	Gnaw	Groom	Run	Scan	Rest	Tear	Walk	Unknown
Walk	0	0	0	1	0	0	0	9	9	0
Tear	5	0	0	6	1	0	1	119	1	0
Rest	0	0	0	0	0	2	81	0	0	0
Scan	0	0	0	2	0	24	11	1	0	0
Run	0	0	0	0	43	1	0	2	0	0
Groom	0	0	0	25	0	3	1	13	0	0
Gnaw	0	0	0	3	0	0	0	9	0	0
Eat	2	0	0	2	0	0	0	15	0	0
Transfer	25	0	0	0	0	0	0	11	0	0

Base+Smoothing

	Transfer	Eat	Gnaw	Groom	Run	Scan	Rest	Tear	Walk	Unknown
Walk	0	0	0	1	0	0	0	10	8	0
Tear	2	0	0	3	0	0	0	127	0	0
Rest	0	0	0	0	0	1	83	0	0	0
Scan	0	0	0	1	0	27	10	1	0	0
Run	0	0	0	0	42	1	0	3	0	0
Groom	0	0	0	31	0	1	0	10	0	0
Gnaw	0	0	0	2	0	0	0	10	0	0
Eat	1	0	0	2	0	0	0	16	0	0
Transfer	31	0	0	0	0	0	0	5	0	0

Threshold

	Transfer	Eat	Gnaw	Groom	Run	Scan	Rest	Tear	Walk	Unknown
Walk	0	0	0	0	0	0	0	1	0	18
Tear	0	0	0	0	0	0	0	84	0	47
Rest	0	0	0	0	0	0	79	0	0	5
Scan	0	0	0	0	0	12	5	0	0	20
Run	0	0	0	0	40	0	0	0	0	6
Groom	0	0	0	2	0	0	0	1	0	37
Gnaw	0	0	0	0	0	0	0	2	0	10
Eat	0	0	0	0	0	0	0	4	0	15
Transfer	14	0	0	0	0	0	0	2	0	21

Figure 4.4: Confusion matrices for the base model, base+smoothing model, and threshold model. Values are the median number of observations classified in each category across 300 bootstrap iterations. For the threshold model, the percent classified as correct in the confusion matrix differs from the median value reported in the results since the number of observations classified as Unknown varied across bootstrap iterations.

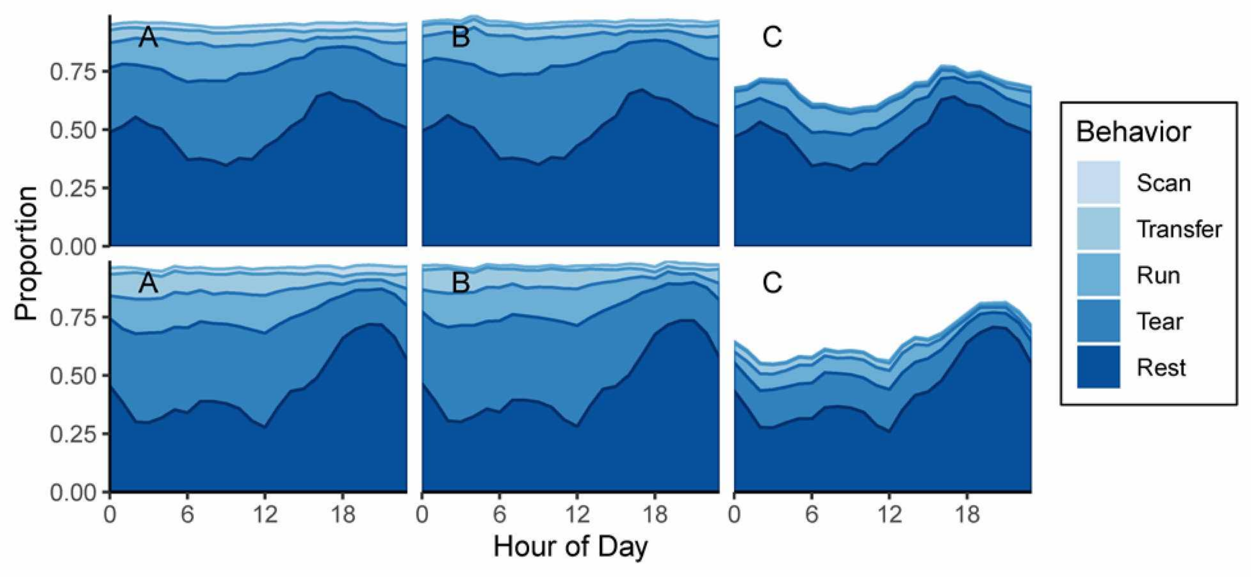


Figure 4.5: Mean proportion of time per hour in each of five predicted behavioral classes for seven wolverines in Arctic Alaska during spring (top) and summer (bottom). Proportions are shown for the base model (A), base+smoothing model (B), and threshold model (C). Mean proportions were first averaged within individual across days, and then across individuals.

4.12 Tables

Table 4.1: Summary statistics calculated for each 10 second partition of accelerometer behavior, used as predictor variables in support vector machine classification models.

Summary statistic	**Label/Predictor**	**Description**
Mean	*meanH, meanV, meanODBA, meanQ*	Mean of the horizontal acceleration, vertical acceleration, ODBA, and veDBA
Max	*maxH, maxV, maxODBA, maxQ*	Maximum of the horizontal acceleration, vertical acceleration, ODBA, and veDBA
Standard deviation	*sdH, sdV, sdODBA, sdQ*	Standard deviation of the horizontal acceleration, vertical acceleration, ODBA, and veDBA
Kurtosis	*kurtH, kurtV, kurtODBA, kurtQ*	Kurtosis of the horizontal acceleration, vertical acceleration, ODBA, and veDBA
Skewness	*skewH, skewV, skewODBA, skewQ*	Skewness of the horizontal acceleration, vertical acceleration, ODBA, and veDBA
Dominant power spectrum	*dpsH, dpsV*	Maximum power spectral density of the horizontal and vertical acceleration
Frequency at the dominant power spectrum	*freqH, freqV*	Frequency at the maximum power spectral density of the horizontal and vertical acceleration

Table 4.2: Description, number of 10 second observations, and number of individuals represented in the full training dataset used in classification model. Observations from all three captive wolverines were included for all behaviors, to which we added observations of the behavior "Run" from a single free-living wolverine.

Intensity	**Behavior**	**Description**	***N* observations**	***N* Ind (m,f)**
Low	**Rest**	Motionless except breathing. Excludes motion during rest, e.g., rolling over.	299	3 (1,2)
	Scan	Survey surroundings by moving head while torso and legs remain stationary.	128	3 (1,2)
Medium	**Walk**	Slow, sometimes meandering, directional movement.	63	3 (1,2)
	Groom	Lick and lightly chew on feet, stomach, and groin.	141	3 (1,2)
	Eat	Chew item in mouth with head raised.	66	3 (1,2)
	Gnaw	Chew on bone, piece of wood, or frozen food by holding it in front (and sometimes hind) paws, usually using one side of the mouth only.	40	3 (1,2)
	Transfer	Pick up items such as sticks and leaves from the ground and move them with a rapid sway of the head to the side. In captivity this behavior was always associated with covering food items.	121	3 (1,2)
	Tear	Remove pieces of meat from carcass by pulling with teeth, can include short bursts of gnawing and eating.	443	3 (1,2)
High	**Run**	Rapid directional movement.	158	4 (1,3)

Table 4.3: Accuracy, precision, and recall for all behaviors for the base, base+smoothing, and threshold models. Bootstrapped 95% confidence intervals are shown in parentheses.

	Base model			**Base + Smoothing**			**Threshold model**		
Behavior	*Accuracy*	*Precision*	*Recall*	*Accuracy*	*Precision*	*Recall*	*Accuracy*	*Precision*	*Recall*
Tear	0.83	0.67	0.90	0.86	0.70	0.96	0.95	0.89	0.99
	(0.80,0.86)	(0.63,0.71)	(0.84,0.95)	(0.83,0.88)	(0.66,0.74)	(0.91,0.99)	(0.92,0.98)	(0.81,0.95)	(0.96,1.00)
Groom	0.93	0.63	0.60	0.96	0.79	0.74	0.99	0.75	0.58
	(0.91,0.94)	(0.52,0.76)	(0.45,0.74)	(0.94,0.97)	(0.66,0.90)	(0.58,0.86)	(0.97,1.00)	(0.00,1.00)	(0.00,1.00)
Transfer	0.96	0.76	0.69	0.98	0.90	0.86	0.99	0.94	0.90
	(0.94,0.97)	(0.63,0.89)	(0.54,0.83)	(0.97,0.99)	(0.80,1.00)	(0.75,0.97)	(0.97,1.00)	(0.80,1.00)	(0.70,1.00)
Scan	0.95	0.78	0.65	0.97	0.88	0.71	0.98	0.94	0.70
	(0.94,0.97)	(0.67,0.91)	(0.50,0.76)	(0.95,0.98)	(0.75,1.00)	(0.55,0.83)	(0.95,0.99)	(0.80,1.00)	(0.47,0.90)
Rest	0.96	0.86	0.97	0.97	0.88	0.99	0.98	0.93	1.00
	(0.94,0.98)	(0.79,0.91)	(0.91,1.00)	(0.96,0.99)	(0.83,0.93)	(0.94,1.00)	(0.96,0.99)	(0.88,0.99)	(0.99,1.00)
Eat	0.95	0	0	0.95	1.00	0	0.98	-	0
	(0.95,0.95)	(0.00,1.00)	(0.00,0.05)	(0.95,0.96)	(0.00,1.00)	(0.00,0.05)	(0.96,0.99)		(0.00,0.00)
Walk	0.97	0.90	0.47	0.97	0.90	0.42	1.00	1.00	0
	(0.96,0.98)	(0.63,1.00)	(0.21,0.68)	(0.96,0.98)	(0.61,1.00)	(0.08,0.68)	(0.99,1.00)	(0.00,1.00)	(0.00,1.00)
Run	0.99	0.98	0.92	0.99	0.98	0.89	1.00	1.00	0.98
	(0.98,1.00)	(0.91,1.00)	(0.84,0.98)	(0.97,1.00)	(0.93,1.00)	(0.79,0.96)	(0.99,1.00)	(0.97,1.00)	(0.92,1.00)
Gnaw	0.97	0	0	0.97	0	0	0.99	-	0
	(0.97,0.97)	(0.00,0.00)	(0.00,0.00)	(0.97,0.97)	(0.00,0.00)	(0.00,0.00)	(0.98,1.00)		(0.00,0.00)

Chapter 5: Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore[4]

5.1 Abstract

Behavioural trade-offs arise when animals must decide to engage in one behaviour at the expense of another, potentially to the animal's detriment. Here, we investigate the existence of such a trade-off by exploring the relative influence of two important behavioural processes, thermoregulation and predation avoidance, on resting behaviour in a cold-adapted mesocarnivore, the wolverine (*Gulo gulo*). Using animal-borne biologgers, we evaluate the hypothesis that wolverine resting behaviour in both subnivean cavities and on surface snow beds is influenced by a combination of ambient weather conditions and predation risk. Specifically, we posit that although resting on the snow surface is more thermally advantageous in certain weather conditions, it is traded off against heightened predation risk. In support of the importance of thermoregulation, we find that wolverines rest almost exclusively in subnivean cavities at very low temperatures and low levels of solar radiation, and rest almost exclusively on the snow surface at higher temperatures and higher levels of solar radiation. In support of the importance of predation avoidance, we find that wolverines select more topographically concealed sites and are more vigilant while resting on the snow surface. We also find that wolverines are more vigilant at topographically exposed resting sites than at concealed sites. Together, these lines of evidence suggest that wolverines trade security from predators for thermal advantage at warmer ambient temperatures and higher solar radiation levels during winter, but that this trade-off is not necessary at lower temperatures when wolverines preferentially use subnivean cavities to simultaneously meet both demands. Parsing such contextually dependent trade-offs is important to understanding species' habitat selection, energy management, and survival.

5.2 Introduction

Animals must partition their time among behaviours to meet the demands associated with growth, reproduction, and survival. In many cases, certain behaviours interfere with others, forcing

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[4] Glass, T. W., Breed, G. A., Robards, M. D., Williams, C. T., & Kielland, K. (2021). Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*, *175*, 163–174. https://doi.org/10.1016/j.anbehav.2021.02.017

animals to make decisions that facilitate the response to one demand at the expense of others (Lima & Dill, 1990; Sih, 1980). Understanding such trade-offs underlying animal behaviour provides insight regarding the relative influence of conflicting demands in shaping the activities of free-living animals and offers a mechanistic foundation for the emergent processes that result, including habitat selection and energy partitioning. Since certain demands (e.g., avoiding predation) can preclude or reduce access to resources such as food, heat, or reproductive habitats, these trade-offs can ultimately impact fitness via differential reproduction, growth, or indirect mortality (Lima, 2009; McPeek, Grace, & Richardson, 2001; Verdolin, 2006).

Thermoregulation is one such demand, the costs of which can be particularly severe for species inhabiting climatically extreme environments. For endotherms, the ambient air temperatures in deserts and polar tundra can be well outside an animal's thermoneutral zone (TNZ), defined as 'the range of ambient temperatures at which temperature regulation is achieved only by control of sensible heat loss, i.e., without regulatory changes in metabolic heat production or evaporative heat loss' (Blix, 2016; IUPS Thermal Commission, 2001, p. 273). This severe difference between TNZ and ambient conditions can induce hyper- or hypothermia, dehydration, frostbite, and myriad other sublethal, and in some cases lethal, effects (du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Liknes, Swanson, Liknes, & Swanson, 1996). To cope with these demands, animals have evolved numerous physiological, morphological, and behavioural adaptations, including metabolic suppression, insulation, countercurrent heat exchange, and selective brain cooling (Blix, 2016; Fuller, Hetem, Maloney, & Mitchell, 2013). Among these, behavioural thermoregulation, for example huddling, posturing, or basking, offers animals considerable flexibility in reducing the energetic demands of maintaining normothermia (Terrien, Perret, & Aujard, 2011). However, these behaviours can be costly as they divert energy and time from engaging in other behaviours and life-history demands, including foraging (Mason, Brivio, Stephens, Apollonio, & Grignolio, 2017), reproduction (Klug & Barclay, 2013) and predation avoidance (Milling, Rachlow, Johnson, Forbey, & Shipley, 2017).

One of the primary means by which animals behaviourally thermoregulate is the selection of microhabitats with operative temperatures (the temperature experienced by the animal, incorporating conductive, convective, and radiative heat transfer, as well as the morphology and absorptivity of the animal; Bakken et al., 1985) nearer the animal's TNZ than the macroclimate. However, since shuttling between microhabitats to thermoregulate necessitates that the animal occupy a specific habitat, the net fitness benefit depends on the extent to which that habitat supports other important processes as well. For example, alpine ibex (*Capra ibex*) thermoregulate by moving to higher altitudes, but this reduces their access to high-quality forage (Mason et al., 2017). Conversely, pygmy rabbits (*Brachylagus idahoensis*) select shady, concealed locations during summer, simultaneously reducing the physiological demands of thermoregulation and predation risk (Milling et al., 2017). The former example demonstrates potential for poor overlap between thermoregulatory habitats and those habitats needed and used for other critical behaviours (i.e., energy intake), resulting in a trade-off; the latter example shows a coupling of thermoregulation with antipredator behaviour, precluding a trade-off. Since the specific microhabitat offering thermoregulatory advantage changes seasonally and with ambient weather conditions (e.g., a burrow provides thermal refuge on hot summer days whereas a sunny slope is superior on cold spring days), the extent to which thermoregulatory microhabitats support or conflict with competing demands can also reflect this shift.

Avoiding predation is a crucial behavioural demand that can conflict with behavioural thermoregulation (Kusler, Elbroch, Quigley, & Grigione, 2017). Antipredator behaviour enables prey species to mediate predation risk, and generally the risk of direct mortality is expected to decrease as prey species exhibit more antipredator behaviour. However, this reduction comes at the cost of increased trait-mediated or 'risk' effects, including reduced reproductive output, survival, and growth (Creel & Christianson, 2008). In some cases, these risk effects can have greater population level impacts than direct predation mortality (Creel & Christianson, 2008). Therefore, antipredator behaviour can be an important indicator of the indirect influence of predation pressure on prey species. Selection for smaller viewsheds (the area from which a given location can be viewed and thus exposed to visual detection by predators; Aben et al., 2018), heightened vigilance behaviour, and the use of subnivean cavities are examples of antipredator behaviour; each of these behaviours likely varies in the extent to which it reduces predation risk versus increases indirect risk effects.

Generally, prey species are expected to exploit habitats that minimize predation risk while maximizing competing demands (Lima & Bednekoff, 1999), but in many cases no habitat can meet all demands simultaneously, and animals must trade predation avoidance for other activities. Since structural protection and visual concealment are strongly associated with reduced predation risk (Mabille & Berteaux, 2014), the degree to which microhabitats can provide both concealment and thermal advantage determines the extent to which prey species must trade antipredator behaviour for thermoregulation (Marchand et al., 2017; Milling et al., 2017).

Here, we examined a potential trade-off between behavioural thermoregulation and predation avoidance associated with specific microhabitats in a cold-adapted mesocarnivore, the wolverine (*Gulo gulo*), which is vulnerable to predation by larger carnivores such as grey wolves (*Canis lupus*; Krebs, Lofroth, Copeland, Banci, & Cooley, 2004). Specifically, we investigated the extent to which the use of subnivean cavities versus surface beds for resting sites is driven by thermoregulatory demands versus intraguild predation avoidance. Since our study area is treeless, supranivean concealment is mostly afforded by topographic features, such as stream cutbanks and cliffs, whereas subnivean resting sites offer considerable visual and olfactory concealment, in addition to structural protection and insulation. We exploited these differences to test the hypotheses that wolverines select sites that confer both thermoregulatory benefits and predation avoidance, but that subnivean resting sites are more effective in reducing predation risk than surface bed sites. We assumed that increased vigilance behaviour, in which wolverines scanned their surroundings, corresponded to increases in real or perceived predation risk, with potentially larger impacts of risk effects (e.g., energy and time diverted from other behaviours), and refer to these effects as 'predation risk' for simplicity.

5.3 Methods

5.3.1 Conceptual Approach

We developed three predictions to evaluate our hypotheses regarding wolverine resting site selection, and tested each with a specific statistical model (see Data analysis). For Prediction 1, we expected that wolverines would rest in subnivean cavities when air temperature and solar radiation were lower and rest on the snow surface when air temperature and solar radiation were higher. Support for this prediction would be consistent with our hypothesis that the thermoregulatory benefits of subnivean cavities and surface beds, which vary depending on environmental conditions, influence which resting site type wolverines choose. For Prediction 2, we expected that wolverines would select more topographically concealed sites to reduce predation risk and that this selection would be particularly strong at surface beds. Support for this prediction would by consistent with our hypothesis that predation risk influences which resting site type wolverines use. For Prediction 3, we expected that wolverines would be more vigilant at surface beds than subnivean sites, with the degree of vigilance proportionate to topographic concealment. Support for this prediction would be consistent with our hypothesis that subnivean resting sites are more effective at reducing predation risk than surface beds, even when wolverines use topographic concealment to mitigate predation risk at surface beds.

5.3.2 Study Area

We conducted this study in a roughly 20,000 km^2 region surrounding Toolik Field Station, Alaska, U.S.A. (68.63°N, 149.60°W; Fig. 5.1) between late February and mid-May of 2017 and 2018. The study area is treeless, although tall shrubs occur along river corridors. The rugged Brooks Range (elevation: 700–2,700 m) dominates the southern portion, transitioning to foothills (elevation: 60–1,000 m) in the north. The Brooks Range is characterized by tall peaks, steep scree slopes, and river valleys, while the terrain of the foothills region is gentler, with topographic variability primarily arising from erosional features such as incised streams, cutbanks at lake edges, and permafrost thawing, as well as cliffs associated with larger foothills.

The snowpack in the study area is dominated by two functional types: 'veneer' and 'snowdrift' (Benson & Sturm, 1993), created by wind-driven redistribution of snow (Colbeck, 1982). Wind transports snow across the landscape, scouring it from open, gentle tundra and depositing it in topographic depressions and around taller vegetation, forming high-density snowdrifts. These drifts, up to several metres deep, comprise approximately 5% of the surface area of the tundra, while the thin veneer layer (generally <50 cm) accounts for the remaining 95% (Sturm, Liston, Benson, & Holmgren, 2001). Snow acts as an insulator, so mean wintertime temperatures at the ground are around 8 °C higher than air temperatures in our study area, although this difference lessens as spring progresses and air temperatures increase (Taras, Sturm, & Liston, 2002). For animals, solar radiation during late spring likely results in higher operative temperatures on the surface of the snow than under the snow. Snowmelt initiates in late April or early May and proceeds rapidly as air temperatures warm (Liston & Hiemstra, 2011).

Climate in the study area is strongly seasonal. Mean daily solar radiation is negligible between mid-November and January (~5 W/m^2), but begins increasing in February until peaking at summer solstice (~350 W/m^2; Cherry et al., 2014). Between 2009 and 2020, mean monthly air temperatures at Toolik Field Station for February, March, April, and May were -19.6 °C, -18.7 °C, -12.0 °C, and -1 °C, respectively (Toolik Field Station, 2020). Temperatures are generally less variable as spring progresses; mean monthly standard deviation in air temperature for the same period was 9.3 °C, 7.7 °C, 7.4 °C, and 6.4 °C (Toolik Field Station, 2020). The temporal and spatial design of our study exploits natural gradients in weather and concealment opportunities across the seasonal landscape.

On tundra, wolverines excavate and occupy subnivean cavities for resting, reproduction, and to cache food (Magoun, 1985; Magoun & Copeland, 1998). Wolverines select deep, dense snow during spring, suggesting that the hardness conferred by high-density snow is important for structural protection, whereas the thermal insulation conferred by depth may be important for thermoregulation (Glass et al., 2021). Across their global range, wolverines are killed by wolves, mountain lions (*Puma concolor*), bears (*Ursus americanus* and *Ursus arctos horribilis*), conspecifics, and humans (Inman, Inman, Mccue, & Packila, 2007; Krebs et al., 2004; T.W. Glass, personal observations); of these, wolves, conspecifics, and humans occur within our study area during winter and spring. Over the course of our study, wolves killed one tagged wolverine and were observed investigating wolverine-occupied snow cavities on several occasions (Fig. 5.2). Wolves are known to use vision, scent, and snow tracking to locate prey; of these, vision and scent are likely of similar importance (Gable & Gable, 2019; Peterson, 1977), and vision may be more important in sparsely vegetated areas such as tundra (Conover, 2007). Humans harvested at least two of 24 tagged wolverines in this study area (this figure includes captures from field seasons not included in this study). Wolverines can be legally trapped or shot between 1 November and 15 April (Alaska Department of Fish and Game, 2019).

5.3.3 Data Collection and Processing

We captured 19 individual wolverines during 3 March – 28 April 2017 and 25 February – 18 April 2018 using portable baited wooden box traps (modified from Lofroth et al., 2008). We monitored traps using satellite transmitters, which sent immediate e-mail notification upon being triggered, and we checked traps manually every 3 days to ensure proper functioning. Upon capture, we anaesthetized animals using 175 mg of Telazol (Golden et al., 2002) administered via syringe pole and monitored heart rate, respiratory rate and body temperature at 5 min intervals continuously during anaesthesia (Arnemo & Evans, 2017). We fitted wolverines with GPS collars (~250 g, Followit Tellus Ultra Light, Followit Sweden AB, Lindesberg, Sweden or Lotek LiteTrack 250 Iridium GPS, Lotek Wireless, Newmarket, Canada), to which we attached tri-axial accelerometers (AXY-3, 10 g, Technosmart Europe Srl., Colle Verde, Italy) and light/temperature (LT) loggers (Intigeo-C330, 3.3 g, Migrate Technology Ltd, Cambridge, U.K.). Cumulatively, collars weighed on average 2% (range 2–3%) of the animal's body weight. We monitored animals until they had fully recovered from anaesthesia. To ensure that the collars released from the animal after approximately 20 weeks, we used timer- or user-activated mechanisms as well as canvas rot-away strips. GPS collars recorded the animal's position every 40 min, accelerometers recorded data at 1 Hz during 2017 and at 10 Hz during 2018, and LT loggers recorded ambient light levels every minute and ambient temperature every 5 min. All animal capture and handling was approved by University of Alaska Fairbanks Institutional animal Care and Use Committee protocol 847738 and Alaska Department of Fish and Game scientific permits 17-085 and 18-085. We recovered 11 collars that retained both the LT logger and the accelerometer; analyses are restricted to these individuals. Since snowmelt prevents the use of subnivean cavities and increases nontopographic concealment from shrubs, we restricted all analyses to collar data collected before 10 May, and, by virtue of collar deployment timing, after 25 February.

We used accelerometer data to identify resting periods and LT loggers to determine whether they occurred in snow cavities or surface beds (Fig. 5.3). Here, we provide a summary of this approach, with full details and validation metrics in Appendix D. The predictive model used *k*-means clustering (Likas, Vlassis, & Verbeek, 2003) to identify resting periods and exploited the low light levels and relatively high temperatures in snow cavities to predict whether each resting period occurred in a snow cavity or surface bed. We trained and validated the model by visiting resting sites in the field to ground truth the use of snow cavities and surface beds. In total, this approach identified and classified 3,240 resting periods across 11 animals.

5.3.4 Data analysis

5.3.4.1 Prediction 1: Effect of Weather on Selection for Snow Cavities versus Surface Beds

To test our prediction that wolverine use of snow cavities versus surface beds is influenced by weather, consistent with behavioural thermoregulation, we extracted air temperature and solar radiation data during resting periods from a meteorological tower centrally located within our study area (Toolik Field Station, 2020). The data are available at 5 min intervals; we interpolated between observations using a cubic spline to obtain 1 min frequency. Since the *k*-means classifier used to identify resting periods (Appendix D) yielded many predictions separated by short periods, thereby introducing nonindependence of associated weather variables, we grouped resting periods that occurred within 10 min of one another and belonged to the same individual and response variable (surface bed versus snow cavity) and calculated the median radiation and air temperature values for each of these grouped resting periods. We then fitted a mixed logistic regression (generalized linear mixed model with binomial error distribution) with cavity/surface bed as the response and the interaction between air temperature and radiation, as well as the main effects for each, as the predictors, reflecting the interactive effects of these variables on operative temperature (Chappell, 1980), particularly for dark-coated animals like the wolverine. To ensure that any observed response was not driven by snowmelt, we compared the parameter estimates of a model that excluded resting periods that occurred above 0 °C (N = 101), with those of the full data set, proceeding with the full data set if the estimates were similar. We included individual as a random intercept. We standardized the predictors before fitting the model and evaluated all predictor variables for multicollinearity. The data used for this analysis included 1,207 resting periods across 11 individual wolverines. We conducted analyses in R v.3.6.3 using the package lme4 (Bates, Mächler, Bolker, & Walker, 2015; R Core Team, 2018).

5.3.4.2 Prediction 2: Effect of Viewshed on Snow Cavity and Surface Bed Site Selection

To test our prediction that wolverines select well-concealed locations for resting sites and that this selection is stronger at surface beds, we performed a case-control resource selection function (RSF, Manly et al., 2002), with the interaction between resting site type (surface bed/snow cavity) and viewshed size, as well as the main effect of resting site type, as predictors (Aben et al., 2018). To do this, we first extracted the location of each resting period using GPS data from collars, excluding resting periods for which a GPS fix did not occur during the resting period. If multiple GPS fixes were taken during a resting period, we calculated the resting coordinates as the medians of the projected x and y coordinates. We then generated two 'available' control sites for each resting period by randomly drawing two distances from a uniform (50, 300) metre distribution and two bearings from a uniform circular distribution (Thurfjell, Ciuti, & Boyce, 2014). We calculated viewshed for each resting site and available site within a 50 m radius of the site (Fig. 5.4). The viewshed is the area surrounding the resting site from which the site can be seen (Aben et al., 2018), so large values indicate high visual exposure to the surroundings (e.g., the bottom of a valley or a concave hillslope) while small values indicate low visual exposure to the surroundings (e.g., the bottom of an incised creek bed or the base of a cliff). We performed this using a 5 m resolution digital elevation model (DEM; Carswell, 2013) in the Environmental Systems Research Institute's (ESRI) Viewshed tool (Arcmap 10.3.1, ESRI, Redlands, CA, U.S.A.), thereby capturing the fine-scale topographic features capable of concealing a wolverine. For each resting site, this tool evaluates all pixels of the DEM within 50 m and determines whether each is obstructed from view by an intervening pixel; if not, it is considered part of the viewshed. Although vegetation is sufficiently tall in some places in the study area to obscure wolverines, particularly along major rivers, we lacked the high-resolution vegetation height data necessary to incorporate such information and instead focused solely on topographic concealment. We chose a 50 m radius to reflect the low visual acuity of canids, wolverines' primary predator, which typically must be three to four times closer to an object to distinguish its features than an average human (Miller & Murphy, 1995). Before fitting the model, we evaluated viewshed at resting sites for spatial autocorrelation using a variogram in R package geoR. We identified 20 m as the minimum acceptable distance between resting sites to ensure independence among observations, and therefore iteratively removed the resting site nearest the most other resting sites, stratified by individual and resting site type, until no resting sites were closer than 20 m apart. We fitted the RSF as a Poisson regression, stratified by resting site, with strata-specific fixed intercepts in R package glmmTMB. This modelling framework provides a computationally efficient option for including random effects in a conditional RSF (Muff, Signer, & Fieberg, 2020), and we therefore included individual as a random slope. We expected that wolverines would select microhabitats with smaller viewsheds, and therefore higher concealment, and that this selection would be stronger when resting on the snow surface. The data used for this analysis included 388 snow cavities and 504 surface beds across 11 individual wolverines.

5.3.4.3 Prediction 3: Effect of Snow Cavity Use and Viewshed on Vigilance Behaviour

To test our prediction that snow cavities and topographic concealment reduce predation risk for resting wolverines, we first extracted the duration of vigilance behaviour immediately following and preceding each resting period. We determined vigilance behaviour associated with resting periods by applying the behavioural classification model developed by Glass, Breed, Robards, Williams, and Kielland (2020) to the 5 min period immediately preceding and following each resting cluster. This model uses a supervised learning classifier to generate behavioural predictions from 10 Hz accelerometer data across 10 s windows, based on direct behavioural observations of captive collared wolverines. Since this method only classifies behaviours that are exhibited continuously for at least 10 s, grouping behaviours that occur at shorter time intervals as 'unknown', estimates for total time exhibiting any given behaviour are biased low. Nevertheless, the model performs quite well at predicting 10 s bouts of vigilance behaviour (94% precision, termed 'scanning' in Glass et al., 2020, p. 4), defined as 'surveying [the] surroundings by moving [the] head while torso and legs remain stationary'. Therefore, we applied this model to the seven wolverines from whom 10 Hz accelerometer data were collected and calculated the number of 10 s periods spent vigilant in the 5 min preceding and following each resting period (hereafter 'vigilance'). If resting periods were separated by less than 10 min, we randomly removed one of the pair to avoid double-counting vigilance behaviour.

We then evaluated whether vigilance was influenced by viewshed size and whether this influence differed between surface beds and snow cavities, using a zero-inflated negative binomial (ZINB) regression with the interaction between viewshed and resting site type (surface bed or snow cavity), and the main effect of resting site type, as predictors, performed in R package countreg (Zeileis & Kleiber, 2016). A ZINB regression assumes that the response of each observation arises from one of two processes, determined by a Bernoulli trial (Lambert, 1992). The first process results solely in zeros, which are termed 'structural zeros', while the second process results in an integer count value drawn from a negative binomial distribution, which can include zeros (termed 'sampling zeros'). Covariates can be supplied to the zero-inflation (i.e., Bernoulli) and count (i.e., negative binomial) models separately. For our purposes, we interpreted structural zeros as products of the behavioural prediction process, possibly resulting from an animal exhibiting vigilance behaviour for periods shorter than 10 s, or from an animal exhibiting vigilance behaviour from a different posture than was included in the training data set. We did not expect structural zeros to vary systematically across our data set; therefore, we included viewshed and resting site type as covariates in the count model and did not supply any covariates to the zero-inflation model. We used a rootogram (Kleiber & Zeileis, 2016) and *Q–Q* plot of the quantile residuals to assess goodness of fit and check for overdispersion. We standardized viewshed before fitting the model. The data used in this analysis consisted of 245 snow cavity and 384 surface bed resting periods distributed among seven individuals. We expected that wolverines would spend more time vigilant at surface beds than at snow cavities and that viewshed size would positively influence vigilance behaviour. We performed all analyses in R v.3.6.3 (R Core Team, 2018).

5.4 Results

We identified 3,240 resting periods from 11 individual wolverines. Wolverines occupied snow cavities for 51% of these (*N* = 1,657) and used surface beds for the remaining 49% (*N* = 1,583). Mean resting period duration was 81 min in surface beds and 85 min in snow cavities. Wolverines rested an average of 8.5 times per day.

5.4.1 Effect of Weather on Selection for Snow Cavities versus Surface Beds

We found that the probability of resting on the snow surface was positively influenced by both air temperature ($z = 6.34$, $P < 0.001$) and solar radiation ($z = 7.77$, $P < 0.001$). Solar radiation interacted significantly with air temperature ($z = -3.03$, $P < 0.003$), such that high solar radiation at low air temperatures increased the probability of resting on the surface, whereas variation in radiation had little effect at high air temperatures (Fig. 5.5). The influence of air temperature was particularly strong; model predictions showed that wolverines rested almost exclusively on the snow surface at ≥ 5 °C regardless of solar radiation, and conversely rested almost exclusively in subnivean cavities at -40 °C with no incoming solar radiation (Fig. 5.5). Fitting the model with and without resting periods above 0 °C yielded nearly identical parameter estimates, indicating no evidence that snowmelt drives the weather-related selection for subnivean versus surface sites across temperatures. Air temperature and solar radiation were only weakly correlated (Pearson's product-moment correlation coefficient = 0.35 [95% confidence interval: 0.30–0.40], $N = 1{,}207$), reflecting the seasonal decoupling of the two variables during winter when most of our data were collected.

5.4.2 Effect of Viewshed on Snow Cavity and Surface Bed Site Selection

Wolverines selected smaller viewsheds when resting in both surface beds ($z = -6.06$, $P < 0.001$) and snow cavities ($z = -6.96$, $P < 0.001$; Fig. 5.6). Specifically, wolverines were approximately two times more likely to select a surface resting site with a 1,500 m^2 viewshed than one with a 6,000 m^2 viewshed (Fig. 5.6). Contrary to our prediction, there was not a significant difference between viewshed size selection at surface beds versus snow cavities ($z = -1.68$, $P = 0.09$); viewshed was similarly important in driving resting site selection regardless of resting site type.

5.4.3 Effect of Snow Cavity Use and Viewshed on Vigilance Behaviour

Wolverines were more vigilant at surface beds than at snow cavities ($z = 3.09$, $P = 0.002$; Fig. 5.7) and more vigilant as viewshed size increased when resting at snow cavities ($z = 2.91$, $P < 0.004$; Fig. 5.7). Viewshed size did not significantly influence vigilance at surface beds ($z = 1.52$, $P = 0.12$); wolverines showed similarly high levels of vigilance at surface beds across viewshed size (Fig. 5.7). At small viewsheds, wolverines were more vigilant at surface beds than at snow cavities, but at large viewsheds wolverines were highly vigilant at both (Fig. 5.7). On average, wolverines spent four more seconds (i.e., 0.4 more 10 s periods) vigilant at surface beds than at snow cavities during the 10 min window surrounding the resting period and spent two more seconds (0.2 more 10 s periods) vigilant for every 1000 m^2 increase in viewshed size at snow cavities. We reiterate that the method for classifying vigilance behaviour only detects bouts that last at least 10 s in duration, so total amount of time spent vigilant, and the above effect sizes, are likely underestimates.

5.5 Discussion

We found support for our hypotheses that resting behaviour in wolverines during winter and spring is influenced by the need to meet thermoregulatory requirements and reduce predation risk, but that microhabitats vary in how well they support each. Using animal-borne biologgers, we found evidence that wolverines sacrifice the perceived security of snow cavities when surface beds confer higher thermoregulatory advantage. Wolverines used snow cavities almost exclusively at lower air temperatures and when there was less solar radiation and used surface beds almost exclusively at higher air temperatures and when there was more solar radiation. Additionally, wolverines were more vigilant at surface beds, suggesting greater real or perceived predation risk, despite mitigating this by selecting surface bed sites with smaller viewsheds. Wolverines resting on the surface in small viewsheds still showed elevated levels of vigilance, suggesting that resting in subnivean cavities was most effective in reducing the energy and time required to monitor the surroundings for predators.

Several aspects of this study must be highlighted when considering the extent to which the behavioural dynamics we evaluated constitute a trade-off. First, we have defined a behavioural trade-off as any situation requiring that animals choose between conflicting behaviours, under the assumption that sacrificing either behaviour will negatively impact the individual. However, the possible costs of occupying less thermally favourable microhabitats or engaging in vigilance behaviour (and thereby diverting time from other activities such as eating, grooming, sleeping) are unclear in this system. We did not measure the possible negative consequences of sacrificing these behaviours directly, and it is possible both that the antipredator behaviour we observed was solely compensatory (i.e., it successfully reduced predation risk with no or minimal accompanying negative impacts), and that the physiological costs of thermoregulation in suboptimal habitat are negligible. These potential negative impacts would need to be measured directly to determine the magnitude and biological importance of a trade-off. Second, the effects of viewshed size and resting site type on vigilance behaviour were sufficiently small to make their biological significance uncertain. Although we believe that these effect sizes are likely underestimates (since accelerometers only detected vigilance behaviour exhibited in continuous 10 s bouts), the impact of these variables on vigilance behaviour (as well as other possible risk effects, including physiological responses) ought to be investigated using more robust methodologies to confirm this finding. If future work confirms this small effect, the limited influence of viewshed and resting site type on vigilance behaviour and site selection suggests that thermoregulatory demands may outweigh predation risk in influencing resting behaviour.

These caveats notwithstanding, we think that the lines of evidence presented here support our hypothesis that wolverines trade reduced predation risk off against thermal energy conservation, but the extent of this trade-off varies by ambient weather conditions. These findings contribute to our understanding of the importance of behavioural thermoregulation as an adaptation to cold environments, the risk effects of intraguild predation among mesocarnivores, and how these two processes can give rise to a trade-off between competing behavioural demands.

5.5.1 Behavioural Thermoregulation in Cold-Adapted Species

Our finding that Arctic wolverine behaviour during winter reflects thermoregulation to minimize heat loss is somewhat novel in the context of mid- to large-size Arctic mammals. Polar species have evolved remarkable physiological and morphological strategies to cope with severe cold during winter, including torpor, countercurrent peripheral heat exchange, and highly insulative fur and plumage, and these adaptations are well documented (reviewed in Blix, 2016). By comparison, the behavioural strategies used by such species have received little attention, particularly among larger mammals for whom a lower surface area-to-volume ratio reduces heat loss. Although many large Arctic terrestrial mammals use burrows or dens for reproduction (Chesemore, 1969; Harington, 1968; Klaczek, Johnson, & Cluff, 2015; Magoun & Copeland, 1998), and many species have been documented using subnivean dens during winter apart from reproduction (Gray, 1993; Jonkel, Kolenosky, Robertson, & Russell, 1972; Prestrud, 1991), the importance of these structures for their role in thermoregulation remains largely unaddressed. Our findings suggest that such subnivean sites are likely an important source of thermal protection for these species, particularly at very low air temperatures. Indeed, although large mammals that are active through the Arctic winter may have lower critical temperatures of -40 °C or below (Scholander, Hock, Walters, & Johnson, 1950), our findings point to thermal preference well above this threshold for wolverines, at least while resting (Terrien et al., 2011). This is supported by the finding that warm microclimates promote sleep quality, since peripheral vasodilation and consequent warming coupled with core cooling are integral to mammalian sleep induction (Harding, Franks, & Wisden, 2020). Here, we provide evidence indicating that despite considerable physiological and morphological adaptations to cold, wolverines still modify their behaviour to minimize heat loss while at rest. Since sun basking and the use of subnivean cavities, behaviours that occur across the range of air temperatures included in this study, both provide thermal advantages in accordance with the operative temperature of the given resting site, our findings suggest that wolverines behaviourally thermoregulate across a range of winter and springtime temperatures, not only during extreme cold.

5.5.2 Risk Effects of Intraguild Predation

The support for our hypothesis that perceived predation risk from wolves influences resting behaviour in a mesopredator, the wolverine, fits well in the theoretical and empirical literature of intraguild predation. Intraguild predation risk influences bed site selection among cougars persecuted by wolves (Kusler et al., 2017), shifts habitat selection among intermediate predators temporally and spatially in favour of higher concealment (Michel, Jiménez-Franco, Naef-Daenzer, & Grüebler, 2016; Mukherjee, Zelcer, & Kotler, 2009), and modifies vigilance and foraging behaviour (Wikenros, Ståhlberg, & Sand, 2014). These behavioural modifications constitute risk effects induced by intraguild predation, a field of study that remains nascent despite receiving more attention among traditional predator–prey relationships (Creel & Christianson, 2008). Theoretical work suggests that the use of spatial refugia and increased vigilance by mesopredators are important mechanisms by which intraguild population dynamics can attain stability (Heithaus, 2001; Rosenheim, 2004). To our knowledge, no other study has investigated vigilance behaviour among mesopredators at resting sites, a type of question that for many wide-ranging or cryptic species is only possible with advancing biologging technology.

Since wolverines compete with wolves for prey and also scavenge the remains of wolf-killed ungulates (Magoun et al., 2018; Van Dijk et al., 2008), the intraguild dynamics in this particular system balance direct competition with facilitation. Wolverines must behave in such a way that permits them to maximize food acquisition from wolves, while minimizing predation risk. Indeed, wolverines have been found to broadly associate with wolf presence (Koskela et al., 2013) but reduce foraging time at carcasses used intensively by wolves (Nordli & Rogstad, 2016). The fact that the predation of our study animal by wolves took place at a wolf-killed caribou carcass provides further anecdotal support for this point. Although wolves also detect prey by scent and snow tracking (Peterson, 1977), mechanisms that we do not account for in our study, our findings suggest that visual detection plays a non-negligible role in this system and affects the behaviour of wolverines accordingly. Vigilance behaviour and the selection of small viewsheds or subnivean cavities for resting are therefore likely important to wolverines' ability to coexist with wolves.

5.5.3 Trade-off Between Behavioural Thermoregulation and Predation Avoidance

Trade-offs between microhabitat-based behavioural thermoregulation and competing behavioural demands arise when no habitat is able to maximize both simultaneously (Milling et al., 2017). Since the specific microhabitat meeting thermal requirements changes according to ambient conditions, and since the extent to which different microhabitats support competing behavioural demands also varies, the presence and magnitude of trade-offs are highly contextual. Here, we have described one pathway by which a trade-off can arise. Specifically, in a species that rests in both concealed cavities and exposed surface beds during winter and spring, the thermoregulatory advantage conferred by sunny, warm surface beds must be traded off against increased predation risk. To minimize the magnitude of this trade-off, we found evidence that wolverines seek topographic concealment, but this concealment appears insufficient to achieve the same low level of predation risk conferred by snow cavities, as evidenced by elevated vigilance at surface beds. Conversely, our findings suggest that the coupling of concealment and thermal protection in subnivean cavities at lower ambient temperatures and when there is less solar radiation removes the need for such a trade-off. In this way, we have found evidence that snow cavities better meet both the thermoregulatory and predation avoidance needs of wolverines in this environment.

Thermoregulatory demands and predation avoidance are important predictors of resting site selection among both pygmy rabbits and mountain lions (Kusler et al., 2017; Milling et al., 2017). However, in both cases, these animals are capable of simultaneously maximizing predation avoidance and thermal advantage across seasons, likely due to the availability of vegetation for concealment. More vegetated landscapes may similarly afford wolverines a reduced trade-off in more southerly portions of their range. However, in regions across the species' range where above-snow operative temperatures drop to 5–10 degrees below zero, we would still expect wolverines to seek insulative structures for resting (Fig. 5.5).

This trade-off between behavioural thermoregulation and antipredator behaviour has implications for other species that rest in both protected cavities and surface beds in landscapes lacking tall vegetation. Species including Arctic hare (*Lepus arcticus*), Arctic fox (*Vulpes lagopus*), and ringed seal (*Phoca hispida*) rest both on the snow surface and in subnivean cavities during winter

(Gray, 1993; Kelly & Quakenbush, 1990; Prestrud, 1991); for such species the decision to rest on the snow surface is likely also weighed against increased predation risk.

5.6 Conclusions

This study explores the seasonally variable trade-offs demanded by behavioural thermoregulation and provides an example of one such trade-off in which animals choose to increase predation risk in order to minimize heat loss. Using information provided by animal-borne biologgers, we illustrate the behavioural responses to these demands and the ways in which wolverines seek to reduce this trade-off. We highlight that this study was conducted exclusively using biologgers to infer fine-scale behaviours, exemplifying the increasingly complex types of behavioural questions that can be addressed among cryptic and wide-ranging animals using this technology (Chmura, Glass, & Williams, 2018). Documenting these behavioural and energetic trade-offs, particularly among species for whom direct observation has limited such studies in the past, is an important component of understanding species habitat selection, energy management, and survival.

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5.8 References

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5.9 Figures

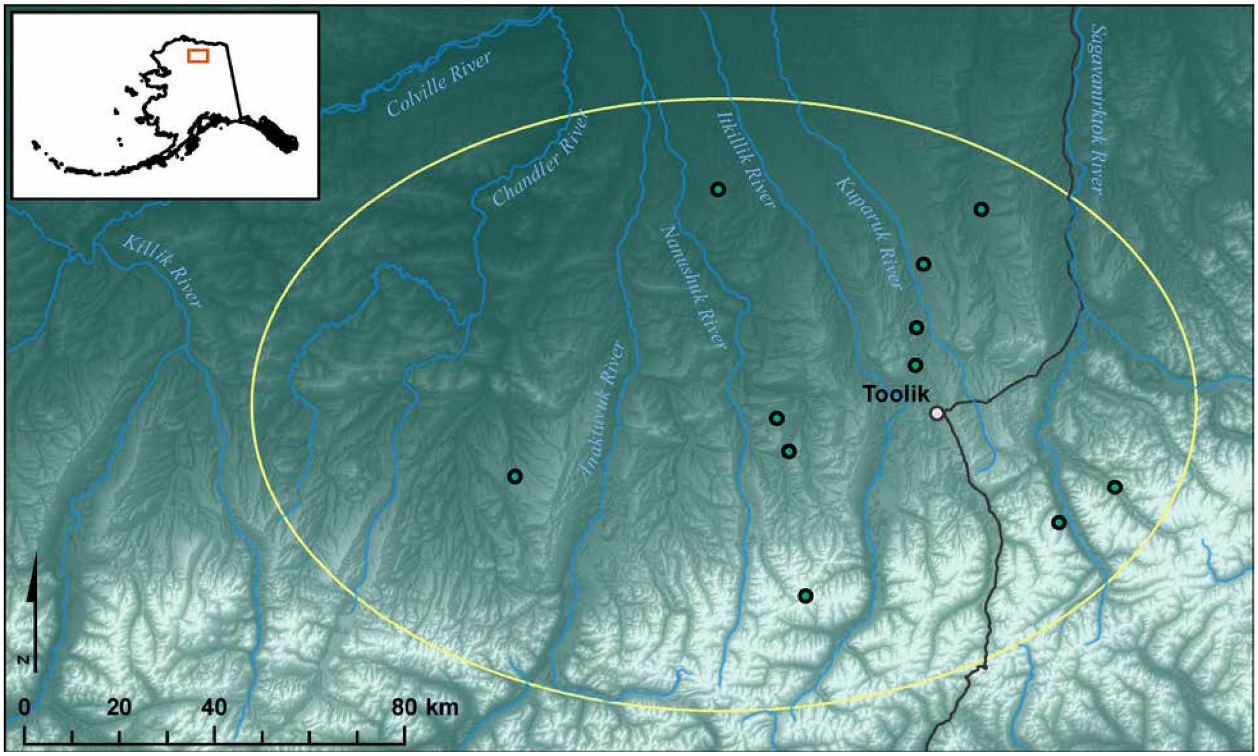

Figure 5.1: Study area (yellow oval) in northern Alaska. Points indicate centroids of resting locations for each wolverine, and the grey line shows the Dalton Highway.

Figure 5.2: A wolverine visits the entrance to a snow cavity, followed by a wolf the next day. Wolves visited wolverine snow cavities on several occasions.

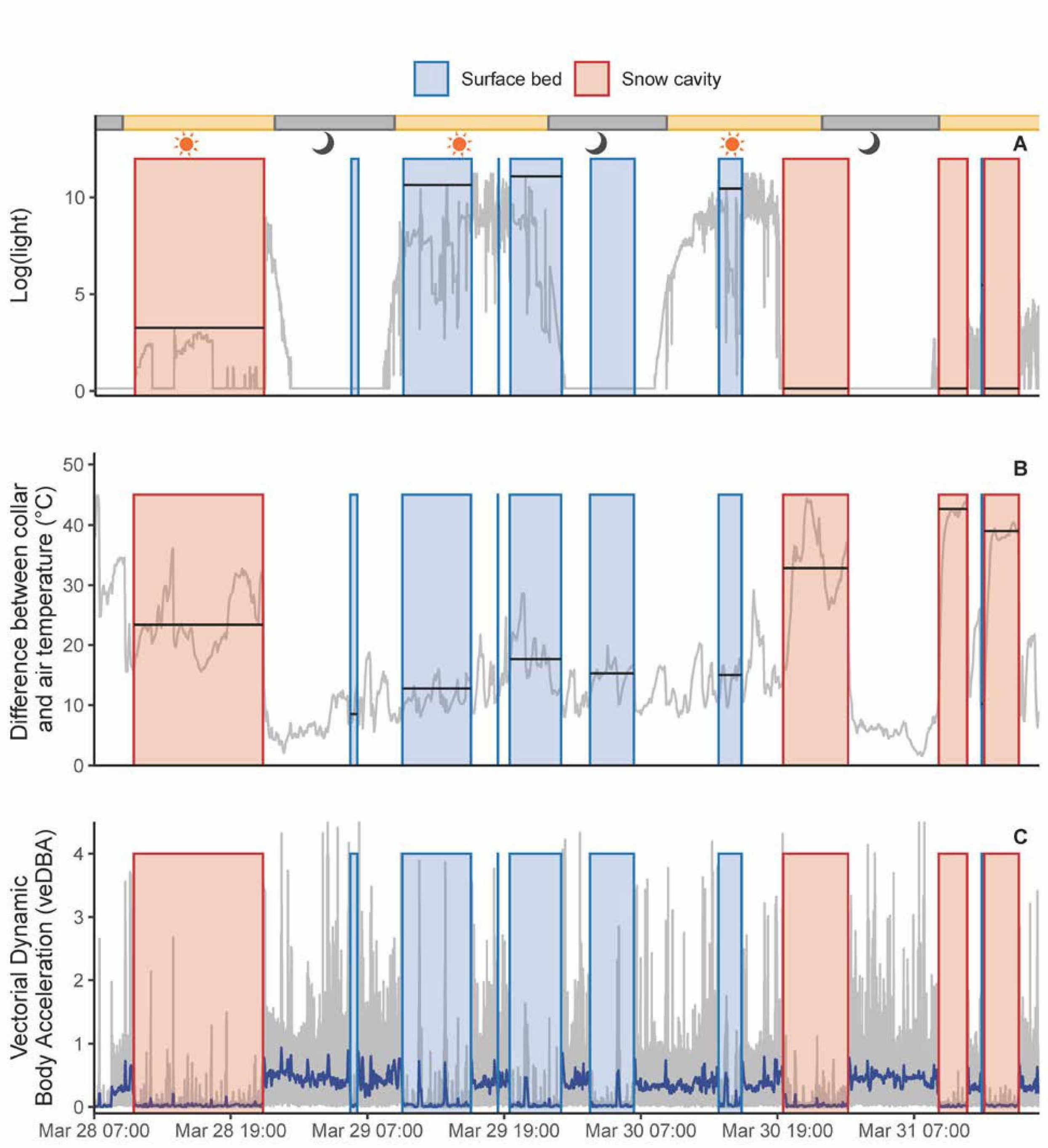

Figure 5.3: Example 80 h period showing data from collar-mounted biologgers used to identify resting periods and classify them as occurring in a surface bed or snow cavity. In (a) and (b), horizontal black lines depict the maximum log(light) value and median temperature difference value for each resting period, respectively; these values were used to predict whether the resting period occurred in a snow cavity or surface bed (see Appendix D). Only light values measured during daytime were used. In (c), the grey line shows the vectorial dynamic body acceleration (veDBA) and

Figure 5.3 continued:

blue shows the 5 min running mean of veDBA used to identify resting periods (Appendix D). Resting periods, shown in shaded boxes, depict those used in the weather analysis, and therefore have been clustered temporally to address autocorrelation.

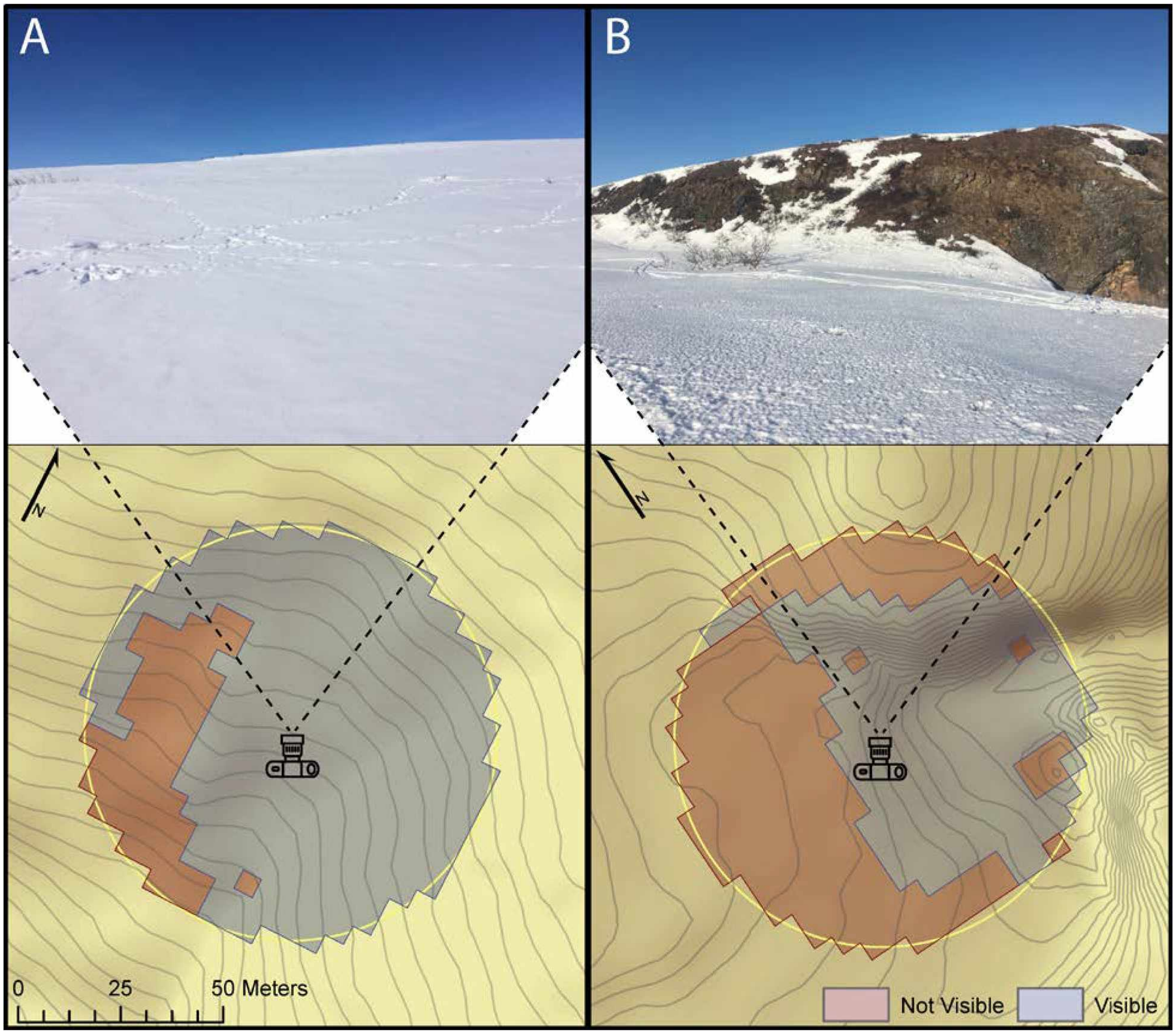

Figure 5.4: Example viewsheds for (a) relatively open and (b) relatively concealed wolverine resting locations. The camera icon indicates the resting site location, which is also the location from which the respective photographs were taken (photograph field of view indicated by broken black lines). For each site, the viewshed (grey shaded pixels on map) was calculated as the total area within 50 m (yellow circle) of the resting site that was not obscured by intervening topography. For example, the rocky slope in (b) obscured the terrain beyond the slope, so these pixels were excluded from the viewshed (brown shaded pixels).

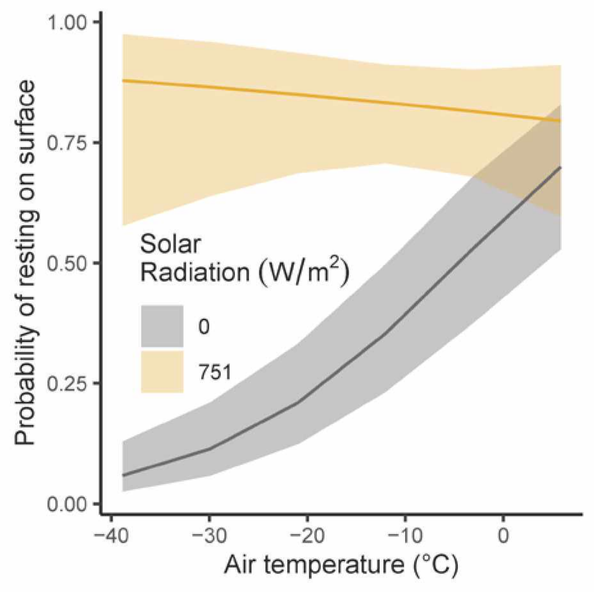

Figure 5.5. Marginal effects of air temperature and solar radiation on the probability that a wolverine rests on the snow surface versus a subnivean cavity. Solar radiation values of 0 and 751 W/m^2 were the minimum and maximum measured during resting periods.

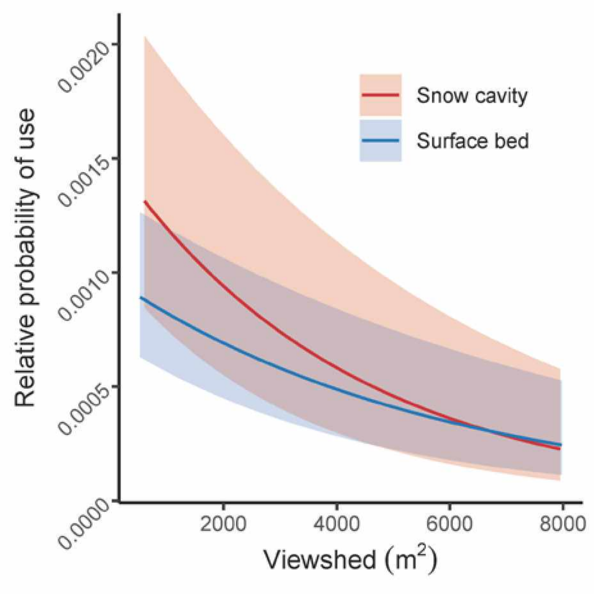

Figure 5.6: Relative probability of use for resting sites predicted by the viewshed within 50 m, compared to randomly selected 'available' resting sites in the nearby area. Relative probability of use can be interpreted by comparing values with one another. For example, a relative probability of 0.0008 at a surface bed with a viewshed of approximately 1500 m^2 is two times higher than a relative probability of 0.0004 for a viewshed of 6000 m^2; therefore, a wolverine is approximately two times more likely to select the former.

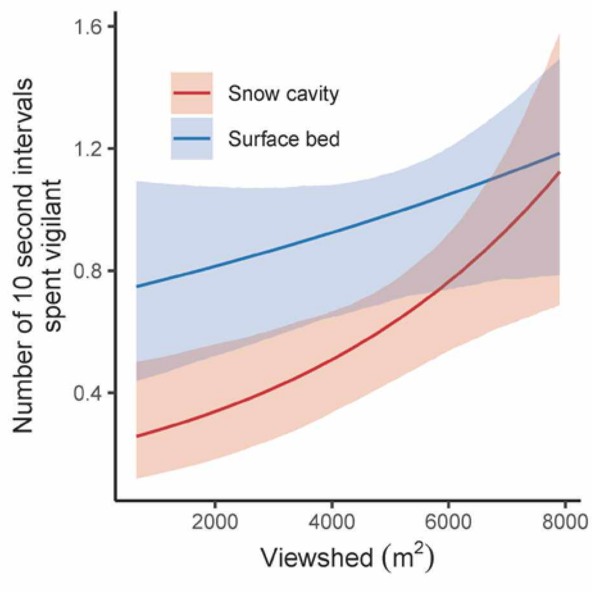

Figure 5.7: Number of 10 s intervals spent vigilant during the 5 min preceding and following resting periods, by resting site type and viewshed size. Bands represent 95% bootstrapped confidence intervals.

Chapter 6: Conclusion

In this dissertation, I investigated wolverines' (*Gulo gulo*) use of snow for structural habitat in the Arctic, focusing on behavioral processes facilitated by snow and snow properties important to wolverines. Specifically, I (1) described terrain features and architecture of snow burrows used for resting sites and reproductive dens, (2) evaluated the influence of snow depth, density, and melt timing on wolverine habitat selection and movement, (3) developed a novel modeling approach capable of classifying wolverine behaviors from accelerometer data, and (4) used this modeling approach to investigate the importance of snow burrows for behavioral thermoregulation and avoiding predators.

This dissertation demonstrates the value of combining different scientific disciplines (animal behavior and snow science) to understand the complexities of wintertime animal ecology (Boelman et al. 2019). I found that Arctic wolverine behavior is influenced by dynamically-changing snow depth, density, and melt status at 10-m resolution. I worked directly with snow scientists to identify these properties, leveraging interdisciplinary expertise to link ecological and physical processes and design a robust workflow for incorporating snow information into my analyses. Such direct collaboration between ecologists and snow scientists will be critical for continuing to advance our understanding of snow ecology, since snow is a complex and continually changing substrate and dozens of snow properties (e.g., compressive strength, tensile strength, density of basal layer, thermal resistance) may influence a given species or behavior (Reinking et al. *In press*). Snow is often represented using just a few properties (e.g., depth and disappearance date) in wildlife research, typically due to logistical limitations. This dissertation demonstrates a methodology for expanding the candidate set of snow properties used in ecological analyses, and the complex type of inference that can result. Just as wildlife research incorporates complex aspects of other habitat features (e.g., vertical versus horizontal cover, microclimate, latitude-adjusted elevation), the field must continue to incorporate snowpack complexity as well, particularly as modeling and remote sensing tools increasingly permit this approach.

The importance of understanding relationships between animals and snow will continue to grow as climate-induced snowpack changes accelerate. Globally, snow depth, extent, and seasonal duration have declined in recent decades, a trend that is particularly pronounced at high latitudes and altitudes (Callaghan et al. 2011; IPCC 2019). Animals relying on snow for habitat are forced to contend with these changes, and predicting population-level impacts relies on accurately understanding behaviors associated with snow (Berteaux et al. 2017). By describing and investigating how Arctic wolverines use snow not solely for reproductive dens but also for resting sites, this dissertation identifies additional behavioral processes susceptible to climate change impacts.

It remains unknown whether wolverines in this environment will exploit novel forms of structural habitat as snow availability decreases, although observations of wolverines using permafrost ice caves for reproductive dens and resting sites suggest some degree of flexibility (Glass et al. 2021). Snow loss will likely coincide with increases in air temperature, and thus reduce the importance of burrows for thermoregulation. Nonetheless, avoiding predators will probably remain important in this environment, so snowpack loss could expose wolverines to increased predation risk. Disentangling population-level consequences of snowpack loss via these distinct behavioral mechanisms is a priority for effective conservation and management of Arctic wolverines.

The findings that Arctic wolverines use snow burrows for resting sites and that these burrows facilitate both thermoregulation and avoiding predators fit well among observations of other Arctic animals. Arctic hares (*Lepus arcticus*), arctic fox (*Vulpes lagopus*), ringed seals (*Phoca hispida*), and polar bears (*Ursus maritimus*) have been documented excavating snow burrows for resting, and there is evidence for most of these species that this a behavioral response to the requirements of thermoregulation and/or avoiding predators (Harington 1968; Kelly and Quakenbush 1990; Prestrud 1991; Gray 1993). However, relatively little attention has been devoted to use of snow for resting sites compared with reproductive denning. This omission has important conservation implications, since climate-related loss of snowpack used for resting sites could compound any population-level effects of losing reproductive den sites. Effective conservation and management of these species will benefit from additional research regarding the full range of behaviors supported by snow, and the possible impacts of snowpack loss that may result.

Wolverines' relationship with snow has received considerable attention in the Contiguous U.S. during recent decades, prompting the species to be considered for listing under the Endangered Species Act due to concerns over climate change-induced snowpack loss (U.S. Fish and Wildlife Service 2020). Although the U.S. Fish and Wildlife Service recently withdrew its proposed rule, ongoing litigation suggests that policy is not resolved (Bishop and Mellgren 2020). This study does not address the heart of the listing debate, since Arctic tundra differs in important ways from the montane environment inhabited by the wolverines considered for listing. Nonetheless, several findings from this dissertation are relevant for evaluating wolverines' vulnerability to climate change in more southerly regions. First, this study identifies a previously unrecognized mechanism linking wolverines to snow: resting in snow burrows. To my knowledge, no study has yet investigated this behavior among wolverines in the Contiguous U.S. or the possible climate change implications for this facet of the species' ecology (but see Copeland 1996). Addressing this knowledge gap would aid wildlife managers in evaluating the cumulative climate change impacts to the species in this region (i.e., beyond impacts to reproductive dens). Second, this study highlights the importance of considering diverse high-resolution snow properties when evaluating the role of snow in animal ecology. Most investigations of montane wolverines' relationship with snow focus on limited properties (i.e., snow disappearance date and sometimes depth) at relatively coarse (>250 m) spatial resolutions, and these studies have yielded divergent projections of habitat loss resulting from climate change, confounding management decisions (McKelvey et al. 2011; Barsugli et al. 2020). This dissertation demonstrates the importance of considering the full suite of snow properties to identify those with ecological relevance, and incorporating such properties at resolutions that are appropriate for the behavioral process of interest. Although logistical limitations have generally complicated incorporating such snow information in the past, emerging technologies such as those used here make such an approach increasingly viable.

To investigate the relationship between wolverines and snow in the Arctic, I relied on detailed behavioral information of free-living wolverines, which I generated in part using models trained on observations of captive wolverines. Behavior of wide-ranging animals is challenging to study since direct observations are typically infeasible. To evaluate wolverine behavior associated with snow, I therefore used animal-borne biologgers. Each biologger provided distinct behavioral information; GPS collars yielded movement metrics and habitat associations, light/temperature loggers described when wolverines occupied snow burrows, and tri-axial accelerometers classified a suite of behaviors including vigilance, resting, running, and food handling. Collectively, these tools allowed me to determine both that snow is important to Arctic wolverines (i.e., certain snow properties are selected), and why snow is important (i.e., for behavioral thermoregulation and avoiding predators). Using a suite of tools in this way facilitates complex inference regarding behavioral processes and improves our ability to understand and predict the consequences of habitat change (Chmura et al. 2018).

Technology for studying ecological dynamics is advancing at a remarkable pace, enhancing our ability to describe and predict complex, often interdisciplinary, ecosystem processes. Snow science and behavioral ecology are two such processes, and evaluating either is perennially complicated by logistical hurdles. In this dissertation, I aimed to demonstrate the inference possible in coupled snow-wildlife systems by leveraging emerging technology (e.g., biologgers) and computational environments (e.g., numerical snow simulation modeling). Such technologies are continually improving and highly applicable to other study systems as well. I hope that this work may serve as a template for improving our understanding of snow ecology across taxa.

6.1 References

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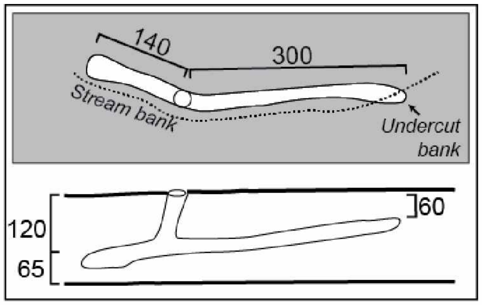
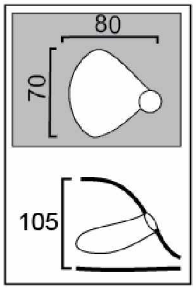
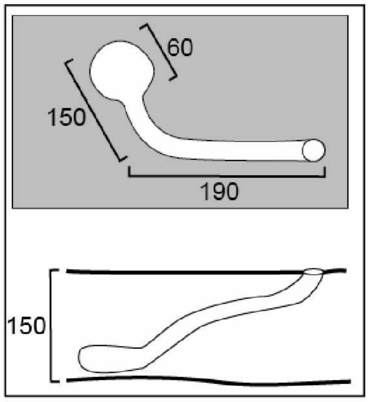
Appendices

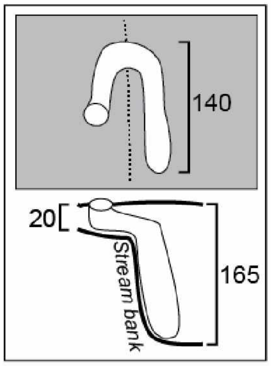
Appendix A: Chapter 2 Supplemental Figures

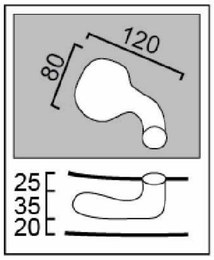
Diagrams of excavated burrows: Below are diagrams of excavated resting burrows and reproductive dens, excluding thermokarst caves which are described by Glass et al. (2021a). Each burrow is depicted both from a top-down perspective (grey background) and a side-view perspective (white background). The single reproductive den excavation, marked with ***, has two side-views, rotated 90 degrees from one another. Dashed lines at tunnel ends indicate incomplete excavation. Caribou antlers indicate a complete or nearly complete caribou carcass. All distances are in centimeters.

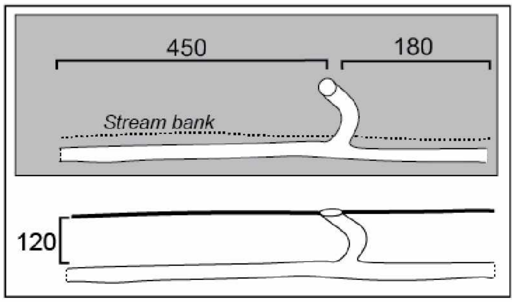


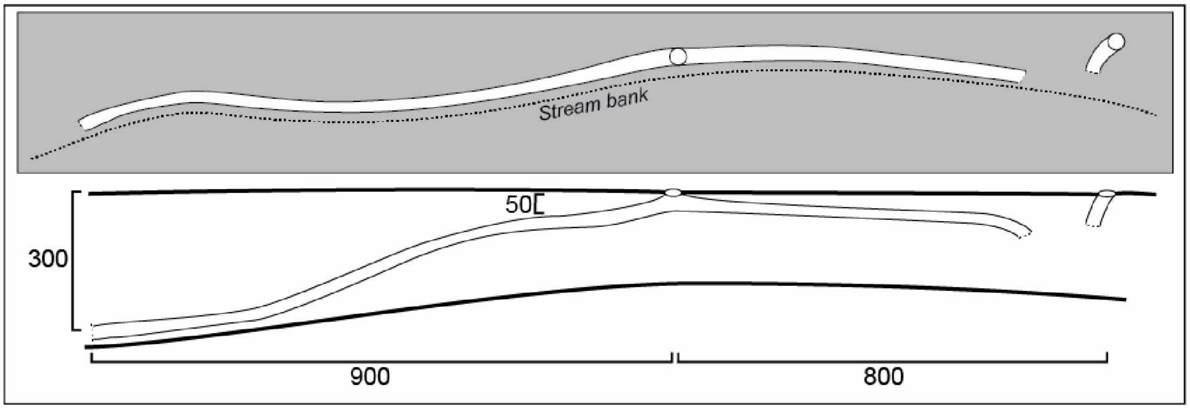


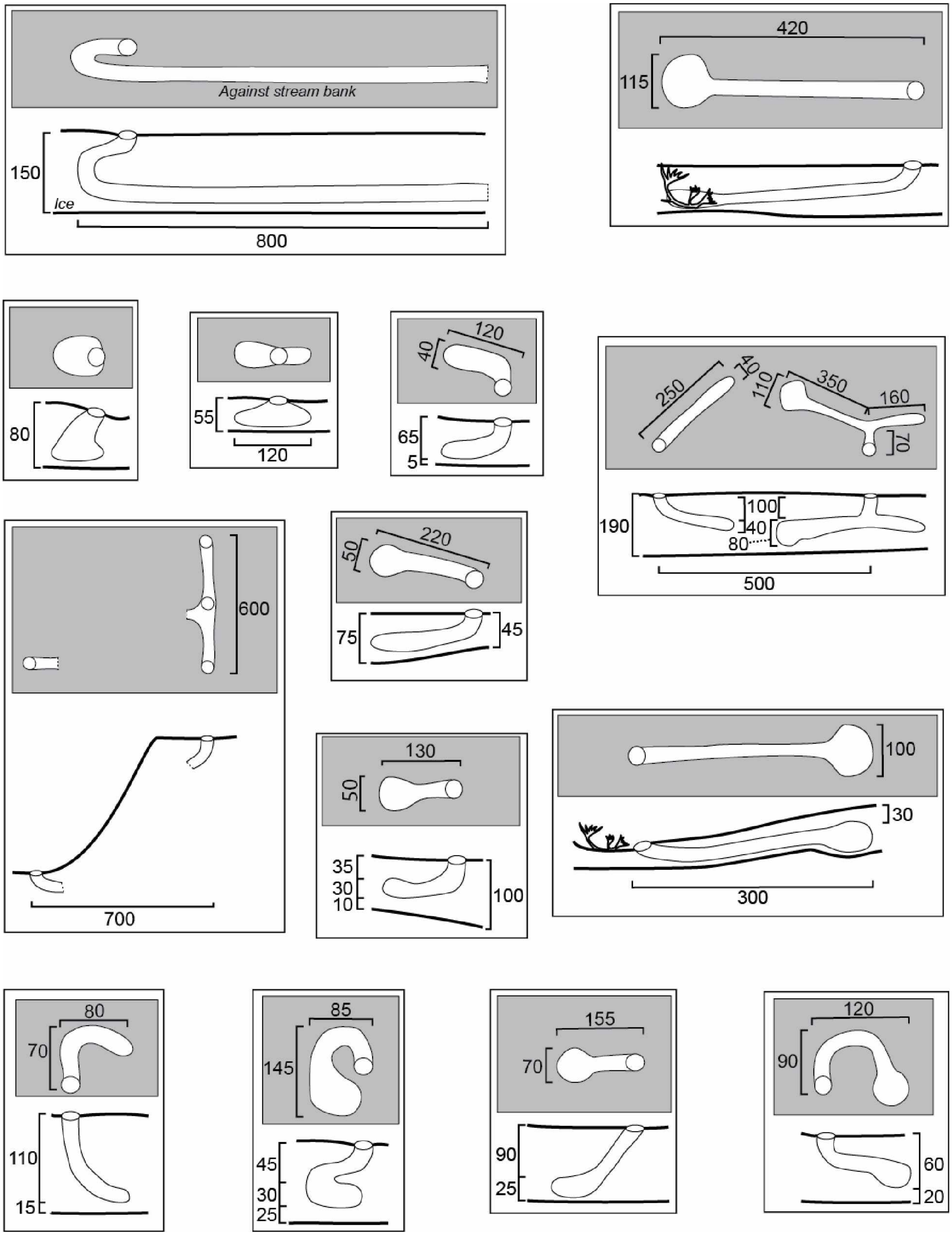








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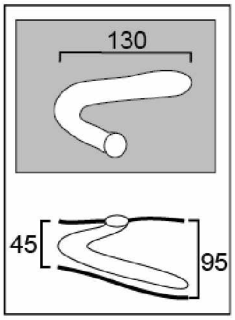
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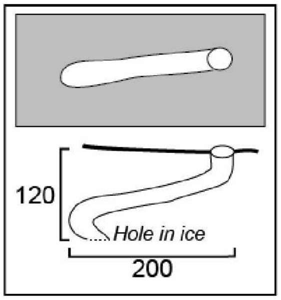
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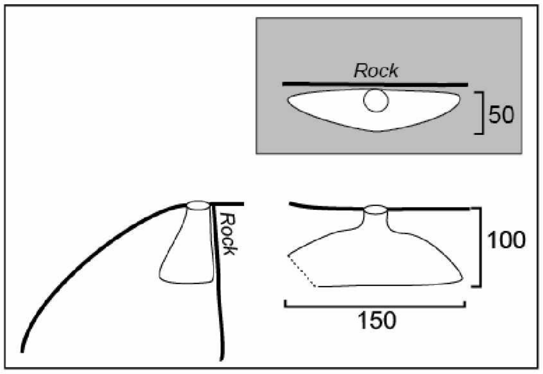
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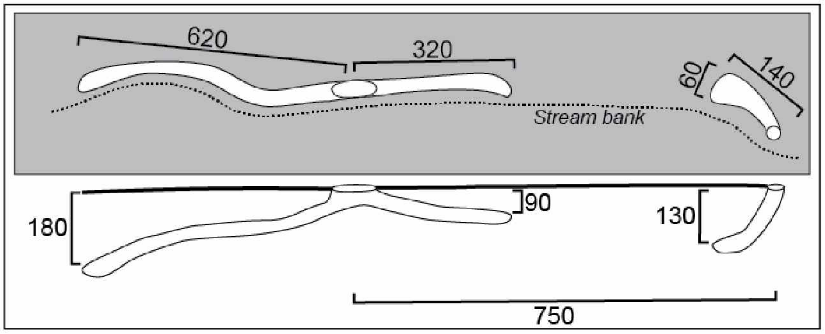
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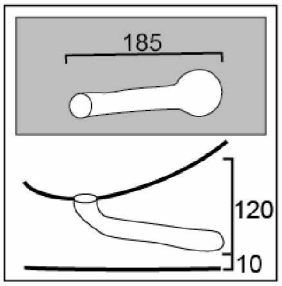
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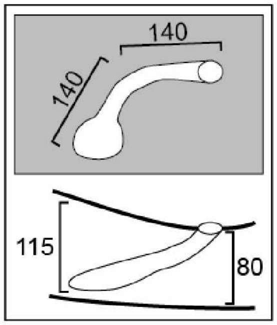
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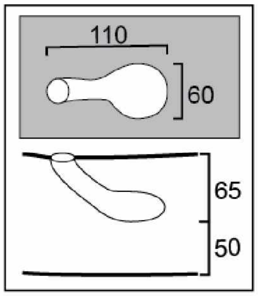
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60
65
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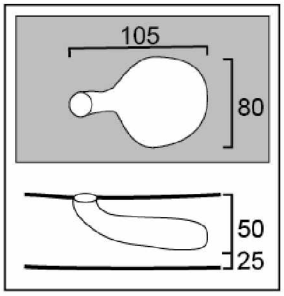
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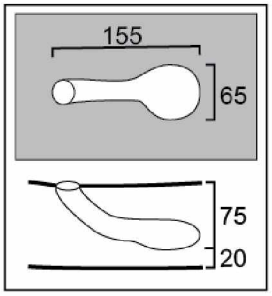
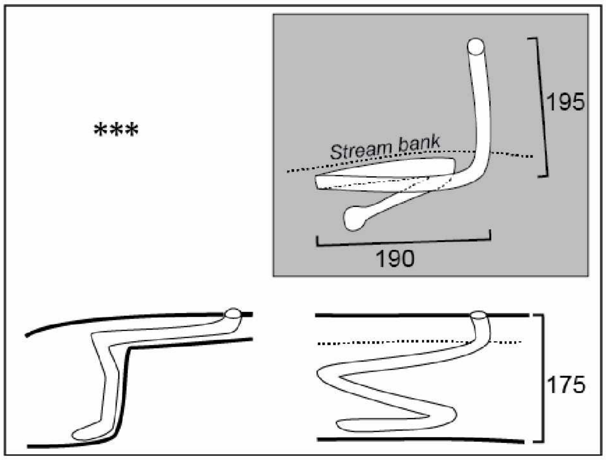

155
65
75
20


***
195
Stream bank
190
175

Appendix B: Chapter 3 Supplemental Tables

Table B.1: Akaike weights for candidate base models. Akaike weights were calculated for each wolverine separately and a population-level weight was calculated using a non-parametric bootstrap, weighted by sample size.

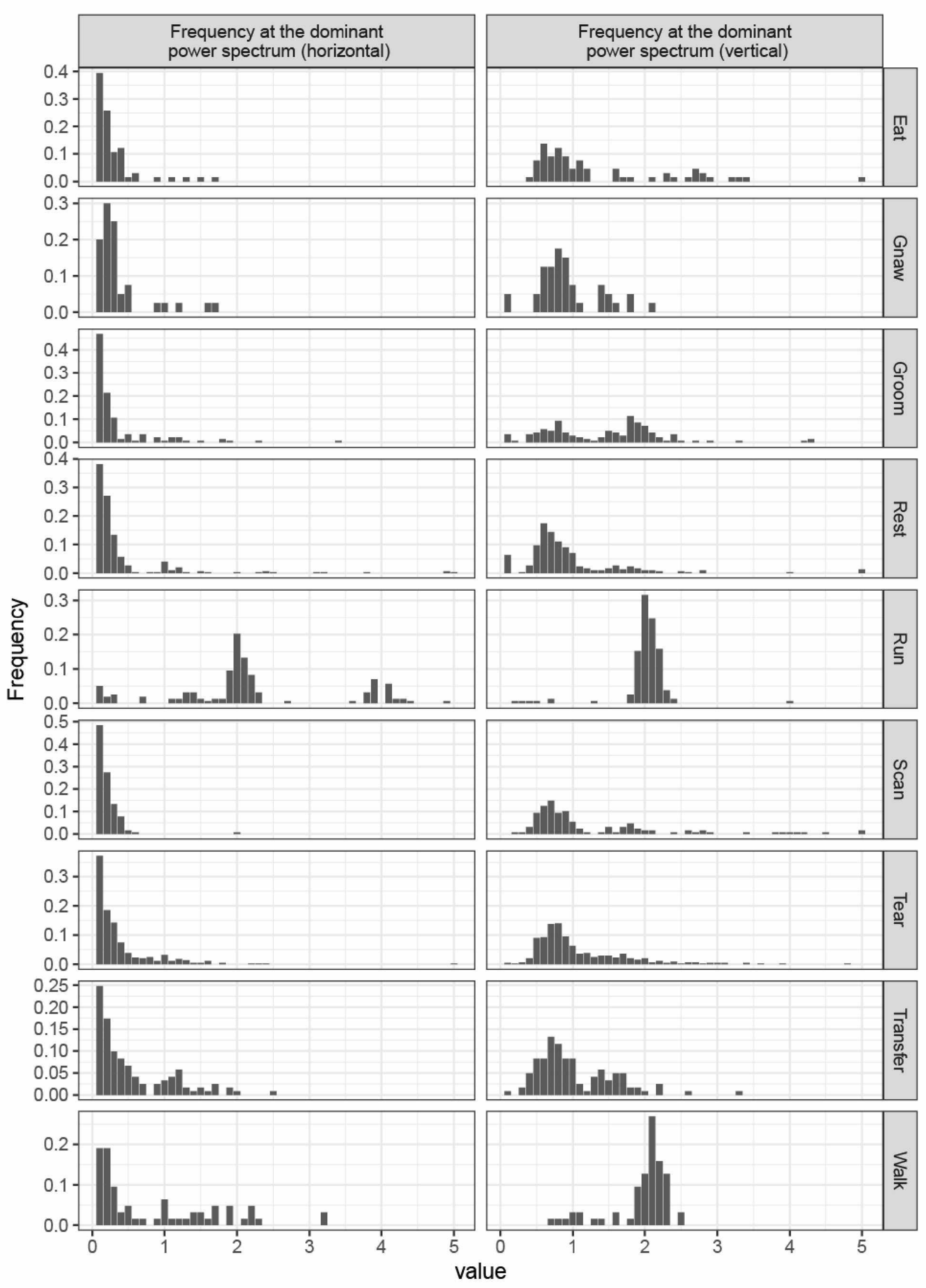
Environmental Covariates in Model			
Terrain Ruggeness	Distance to Streams/Rivers	Distance to Lake Edge	Akaike Weight
X	X	X	0.50
X	X		0.48
	X		0.01
X			0
	X	X	0
		X	0
X		X	0
	NULL MODEL		0

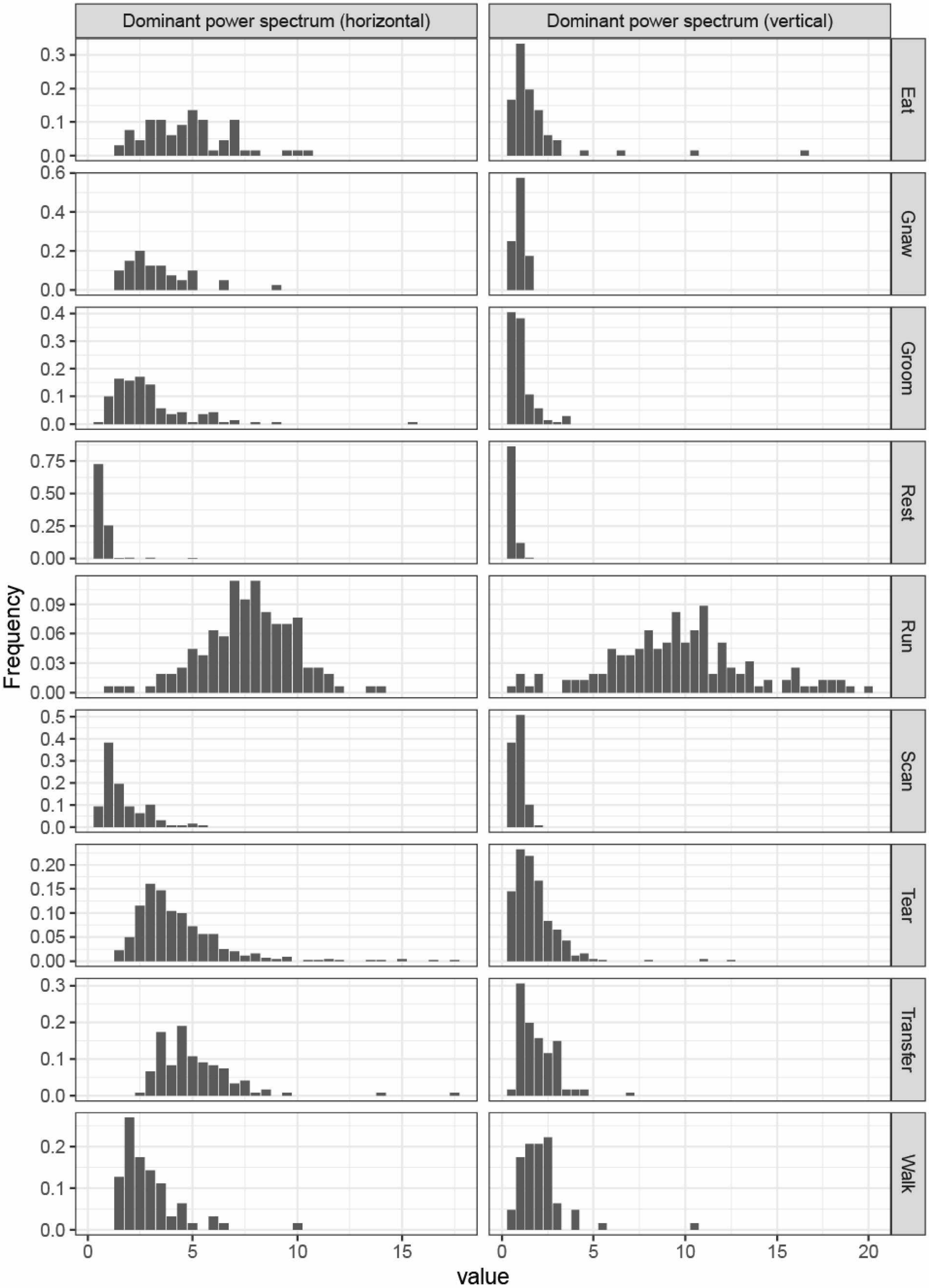
Table B.2: Population-level coefficient estimates for the base model. Terrain ruggedness was standardized prior to fitting the model. Estimates and 95% confidence bounds were generated by calculating a non-parametric bootstrapped mean of individual estimates, weighted by inverse variance.

Coefficient	Estimate	Lower	Upper
ln(distance to lake edge)	-0.076	-0.125	-0.020
ln(distance to stream/river)	-0.373	-0.425	-0.326
lnSL	0.023	0.010	0.044
Terrain Ruggedness	0.841	0.693	1.030
Terrain Ruggedness^2	-0.139	-0.217	-0.091

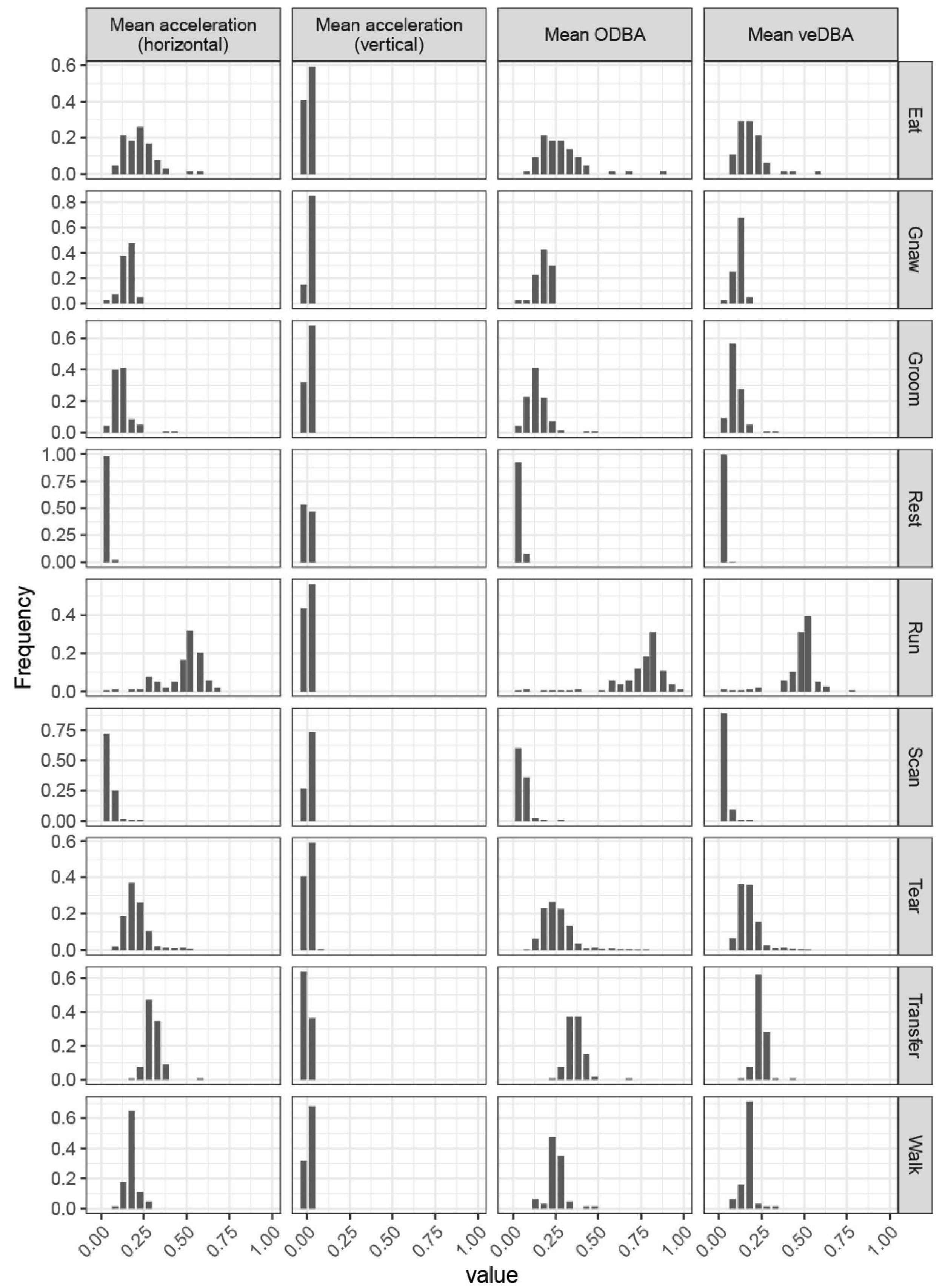
Appendix C: Chapter 4 Supplemental Figures

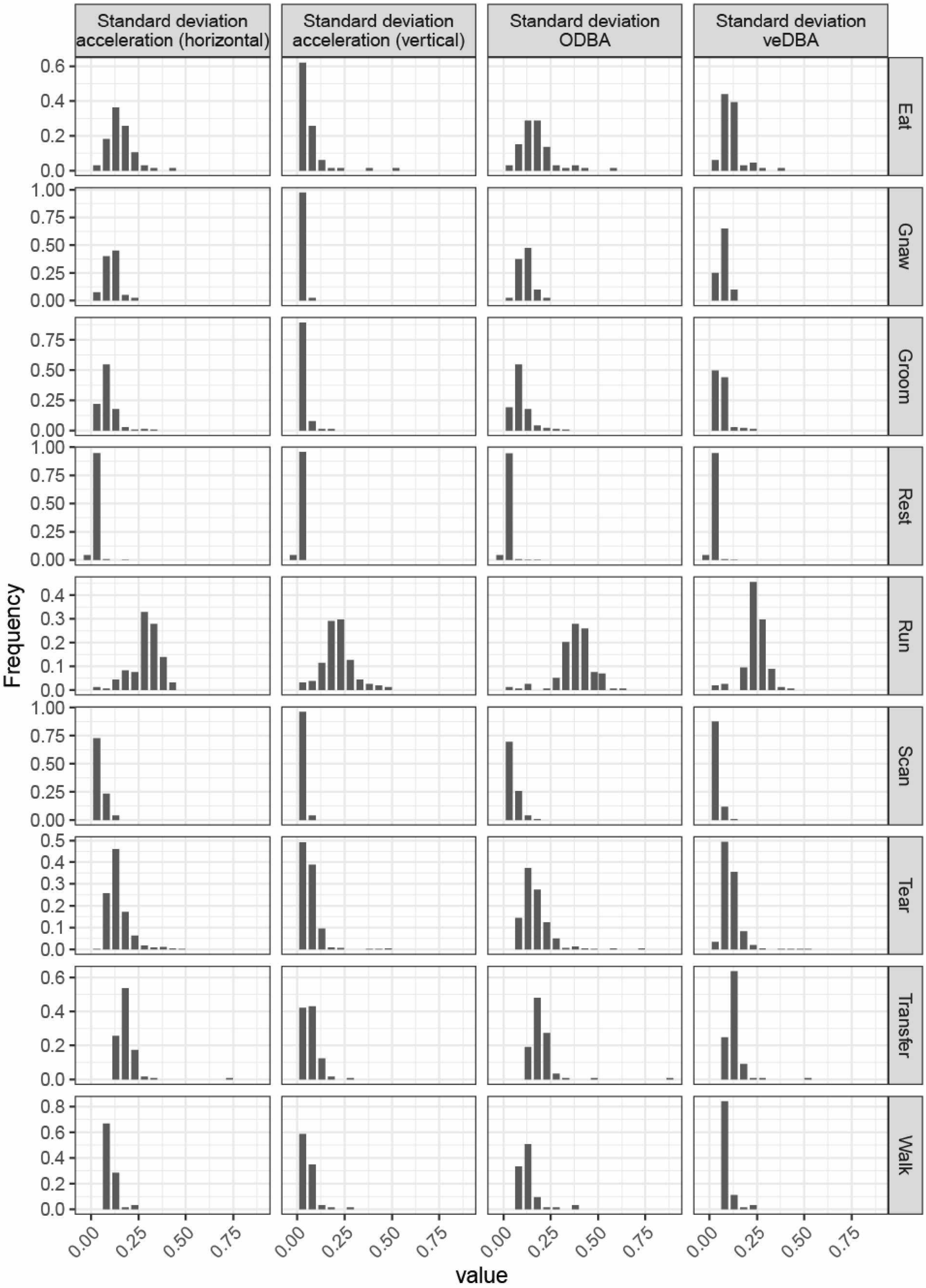
Distribution of predictor variables by behavior: The following pages contain histograms showing the distributions of all predictor variables by behavior, based on the full training dataset used in the classification model. These distributions demonstrate the quantitative differences in acceleration among behavioral classes.


Frequency at the dominant power spectrum (horizontal)
Frequency at the dominant power spectrum (vertical)
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0
1
2
3
4
5



Dominant power spectrum (horizontal)
Dominant power spectrum (vertical)
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0
5
10
15
20
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.00
0.25
0.50
0.75
0.03
0.06
0.09
0.05
0.10
0.15
0.20


Mean acceleration (horizontal)
Mean acceleration (vertical)
Mean ODBA
Mean veDBA
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0.00
0.25
0.50
0.75
1.00
0.0
0.2
0.4
0.6
0.8


Standard deviation acceleration (horizontal)
Standard deviation acceleration (vertical)
Standard deviation ODBA
Standard deviation veDBA
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0.00
0.25
0.50
0.75
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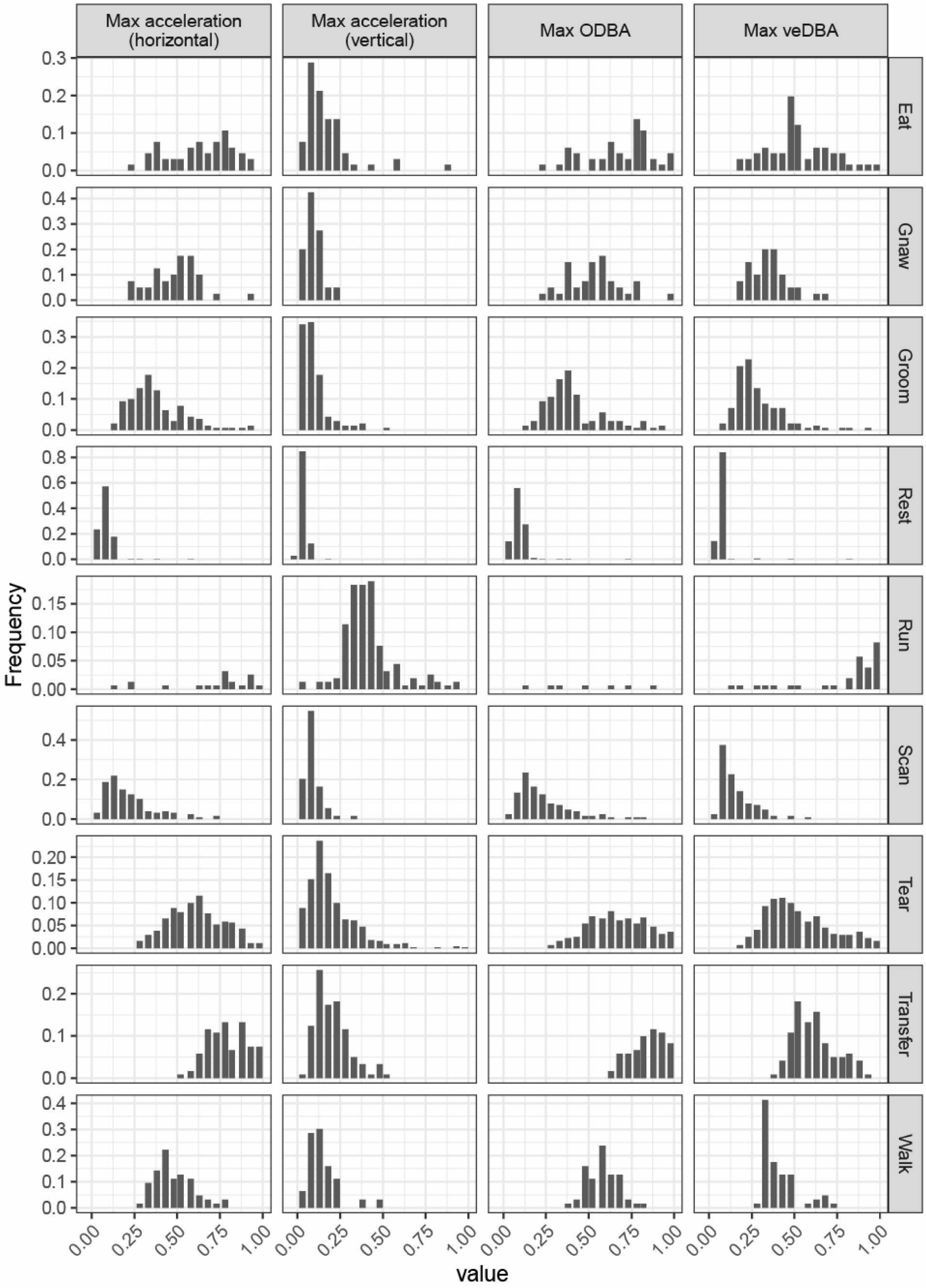
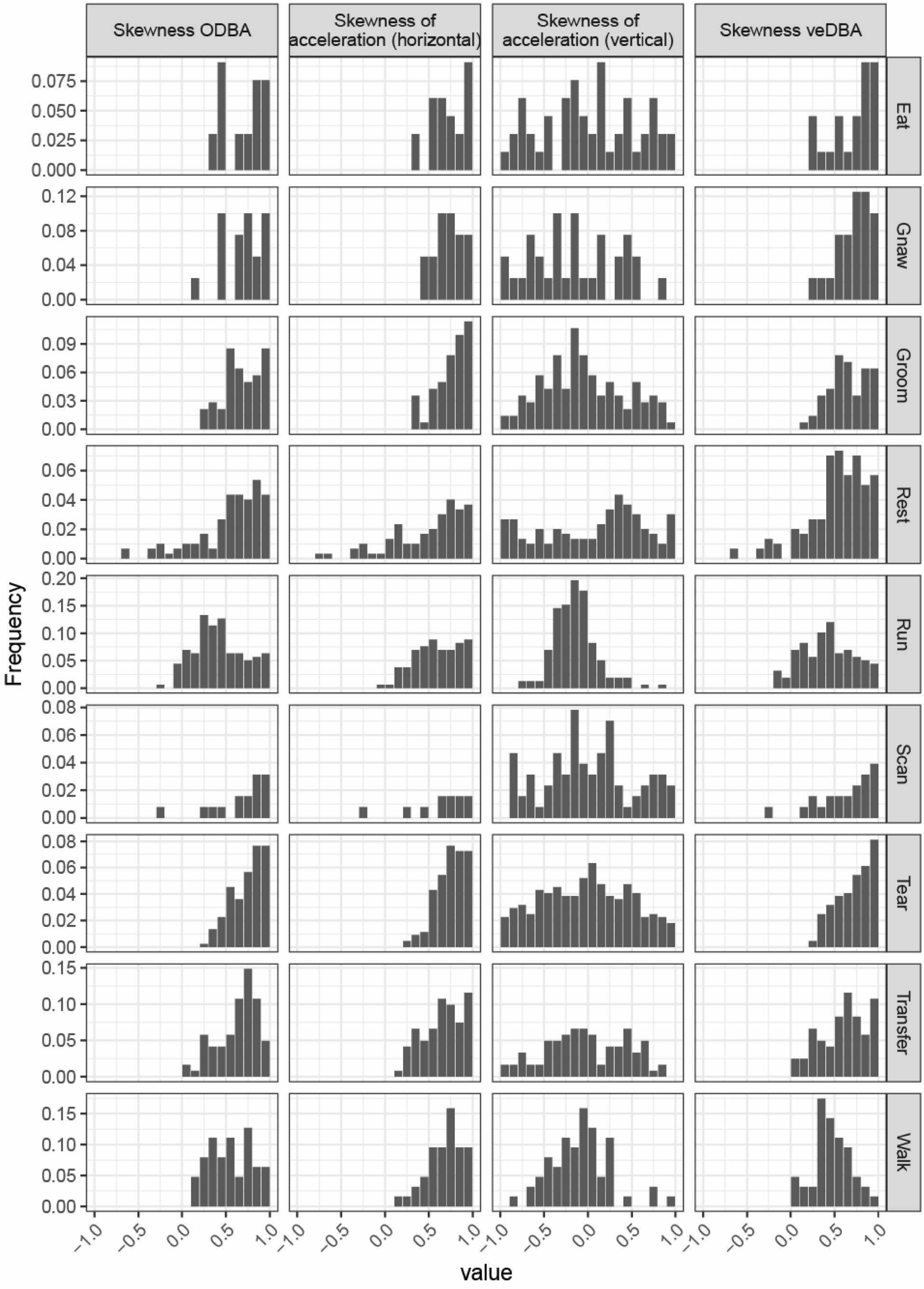
0.2
0.4
0.6
1.00
0.1
0.3
0.5
0.8



Max acceleration (horizontal)
Max acceleration (vertical)
Max ODBA
Max veDBA
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0.00
0.25
0.50
0.75
1.00


Skewness ODBA
Skewness of acceleration (horizontal)
Skewness of acceleration (vertical)
Skewness veDBA
Eat
Gnaw
Groom
Rest
Run
Scan
Tear
Transfer
Walk
Frequency
value
0.000
0.025
0.050
0.075
0.00
0.04
0.08
0.12
0.00
0.03
0.06
0.09
0.00
0.02
0.04
0.06
0.00
0.05
0.10
0.15
0.20
0.00
0.02
0.04
0.06
0.08
0.00
0.02
0.04
0.06
0.08
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
-1.0
-0.5
0.0
0.5
1.0

Appendix D: Chapter 5 Supplemental Information

Resting Period Identification and Classification as Snow Cavity or Surface Bed

To identify resting periods using accelerometer data, we first subsampled 10 Hz accelerometer data to 1 Hz to standardize the sampling frequency across individuals. We then calculated the vectorial dynamic body acceleration (veDBA, Wilson et al., 2020), as a measure of total animal movement, and applied a 5 min running mean to this value. This running mean smoothed the data, thereby excluding short periods of inactivity from being categorized as 'resting'. We classified the running mean using *k*-means clustering with three centres and labelled the cluster with the smallest mean 'resting' (Likas et al., 2003). We then grouped all consecutive resting observations and termed each group a resting period.

To determine whether resting periods occurred in snow cavities or surface beds, we built a predictive model based on field visits to resting sites and data from collar-borne light/temperature (LT) loggers. To visit resting sites in the field, we identified GPS clusters by inspecting recent GPS data (transmitted ~twice daily via the Iridium network) for two or more consecutive locations located within ~20 m of each other. During cluster visits, we recorded the presence of snow cavities and surface beds. We only included snow cavities deep enough to obscure the animal from direct sunlight in our predictive model. We identified surface beds as hardened, icy depressions in the snow containing wolverine fur encased in the ice, indicating that the wolverine had occupied the site for long enough to partially melt the snow underneath. We discarded GPS clusters lacking either a surface bed or snow cavity, as well as those containing both, from our predictive model, resulting in 73 total visited clusters.

To build the snow cavity/surface bed predictive model, we exploited the low light levels and relatively high temperatures inside snow cavities. Specifically, we extracted the maximum log-transformed light level (l.max) and the median temperature recorded by the LT logger, as well as the median air temperature recorded by a meteorological tower within our study area during each resting period. We calculated t.diff for each resting period as the difference between median ambient air temperature and the median LT-recorded temperature, thereby reflecting the extent to which the animal was buffered from ambient temperatures. The variables l.max and t.diff were available in different combinations for each resting cluster. To this end, we excluded light levels recorded between sunset and sunrise, since these would not differ between cavities and surface beds.

Additionally, the meteorological tower had missing temperature observations during our study period, thereby precluding the calculation of t.diff for some resting periods, and some resting periods were too short for a concurrent light level and/or temperature level measurement from the LT logger. Therefore, we built three separate models, each applied to a different subset of resting periods depending on the available data, to predict snow cavity use. Specifically, resting periods occurring during daylight hours for which air temperature data were available were subject to a model including both l.max and t.diff as predictors (model 1), resting periods occurring during daylight hours but missing air temperature data were subject to a model using only l.max as a predictor (model 2), and resting periods occurring at night were subject to a model using only t.diff as a predictor (model 3). Resting periods lacking both predictors were excluded.

We identified 443 resting periods using accelerometer data that occurred during the 73 visited GPS clusters; these observations constituted our full training data set. Of these, 218 were included in model 1, 237 in model 2 and 320 in model 3. We used logistic regression, with cavity/surface bed as the response, and evaluated model performance using a bootstrapped cross-validation approach for each of the three models separately (Champagne et al., 2014). To do this, we randomly split the data set for each model along a 70/30 training/testing split, fitted the model to the training portion, and calculated the accuracy of predictions for the testing portion. We then iterated this process 500 times to obtain confidence intervals associated with classification accuracy for each model. We made predictions for unvisited resting periods using models fitted to the full training data set associated with each model.

Among the training data set, both the variables l.max and t.diff predicted snow cavity use well, with l.max almost perfectly distinguishing surface beds from snow cavities (Fig. A1a). All three models performed well in predicting the use of snow cavities versus surface beds. Model 1, using both l.max and t.diff as predictors, had a median accuracy of 96.9% (95% confidence interval: 93.8–100%). Model 2, using only l.max as a predictor, had a median accuracy of 97.2% (95% C.I.: 94.4.8–100%). Model 3, using only t.diff as a predictor, had a median accuracy of 81.2% (95% C.I.: 74.0–87.5%).

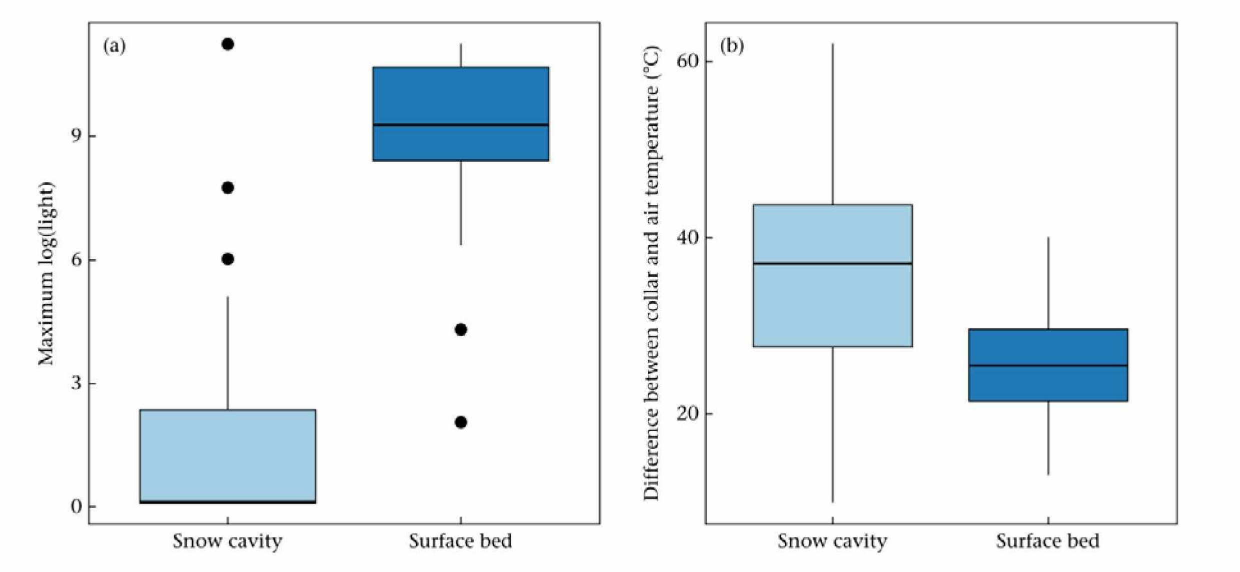


Figure D.1: (a) Maximum log(light) values (l.max) and (b) the difference between median collar temperature and median ambient air temperature (t.diff) during resting periods in snow cavities and surface beds.

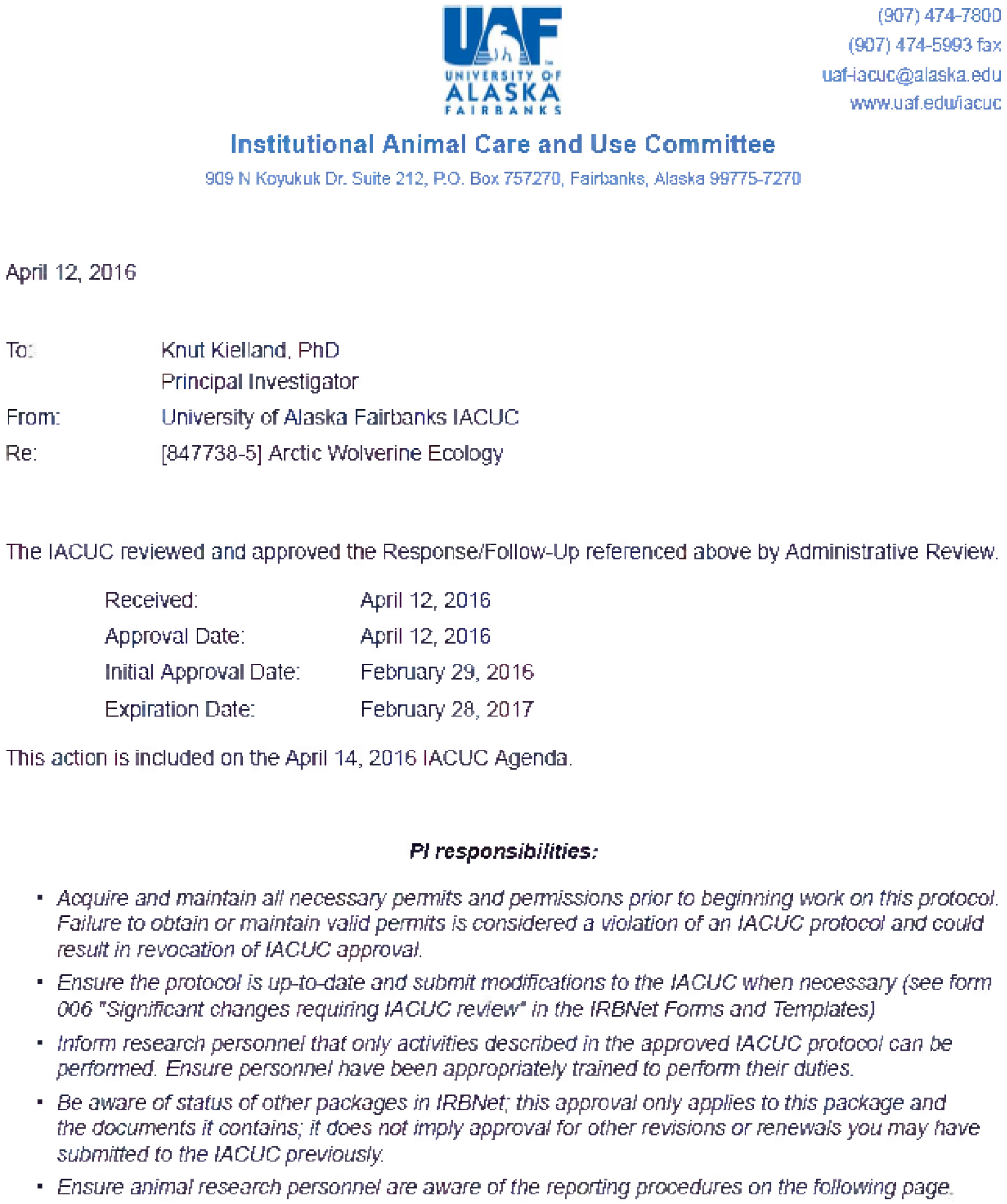
Appendix D References

Champagne, C., H. McNairn, B. Daneshfar, and J. Shang. 2014. A bootstrap method for assessing classification accuracy and confidence for agricultural land use mapping in Canada. *International Journal of Applied Earth Observation and Geoinformation* 29:44–52.

Likas, A., N. Vlassis, and J. J. Verbeek. 2003. The global k-means clustering algorithm. *Pattern Recognition* 36:451–461.

Wilson, R. P., L. Börger, M. D. Holton, D. M. Scantlebury, A. Gómez-Laich, F. Quintana, F. Rosell, P. M. Graf, H. Williams, R. Gunner, L. Hopkins, N. Marks, N. R. Geraldi, C. M. Duarte, R. Scott, M. S. Strano, H. Robotka, C. Eizaguirre, A. Fahlman, and E. L. C. Shepard. 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* 89:161–172.

Appendix E: IACUC Approval Letters



(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 12, 2016

To:	Knut Kielland, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[847738-5] Arctic Wolverine Ecology

The IACUC reviewed and approved the Response/Follow-Up referenced above by Administrative Review.

Received:	April 12, 2016
Approval Date:	April 12, 2016
Initial Approval Date:	February 29, 2016
Expiration Date:	February 28, 2017

This action is included on the April 14, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

UAF
UNIVERSITY OF
ALASKA
FAIRBANKS

(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

March 1, 2019

To: Knut Kielland, PhD
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [1373175-3] Behavioral observations of captive wolverines to validate inferences from accelerometer data

The IACUC reviewed and approved the Protocol referenced above by Designated Member Review.

Received:	February 28, 2019
Approval Date:	March 1, 2019
Initial Approval Date:	March 1, 2019
Expiration Date:	March 1, 2020

This action is included on the March 7, 2019 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
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- *Ensure animal research personnel are aware of the reporting procedures on the following page.*