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Permafrost ice caves: an unrecognized microhabitat for Arctic wildlife

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The Arctic is changing rapidly, introducing new challenges and opportunities for animals. Rising air temperatures are driving dramatic shifts in habitat quality and availability, including increased shrub abundance, reduced pond area, and reduced springtime snow cover (Hinzman et al. 2005). In some cases, these changes have net positive effects for particular species, as exemplified by northward range expansions of moose and beavers following shrubification (Tape et al. 2016, 2018). In other cases, these changes reduce the quality or availability of habitat required for crucial life history processes, such as loss of waterfowl breeding habitat or reduced access to forage (Berteaux et al. 2017). Cataloguing such habitat changes and studying their mechanistic links to animal fitness is an important part of understanding species' response to climate change.

We had the opportunity to document one such form of climate change–driven habitat creation while studying wolverines (*Gulo gulo*) in the Brooks Range foothills of Arctic Alaska. This tundra landscape, devoid of trees and other forms of structural protection, hosts many animals that use snow structures for insulation and protection during winter, including cricetid rodents, ermines (*Mustela erminea*), ptarmigan (*Lagopus spp.*), arctic fox (*Vulpes lagopus*), and polar bears (*Ursus maritimus*). Snow is particularly important for wolverines, who excavate resting burrows, food caches, and reproductive dens in snowdrifts (Magoun 1985, Glass et al., *in review*). Across their global range, wolverines use a variety of structures for reproductive dens and resting sites, including large boulders, fallen trees, root wads, and abandoned beaver lodges, typically beneath snow (Magoun and Copeland 1998, Scrafford and Boyce 2015, Jokinen et al. 2019). Through GPS-collaring efforts and aerial track surveys in April of 2017 and 2018, we found three subterranean ice caves, presumably formed by eroding permafrost, that had been exploited by wolverines (Fig. 1).

The three sites were used by at least five wolverines (four of these were a family: a mother, father, and two kits). The first site (Cave A) was used once (April 5) by a single wolverine for 12 h, and the second site (Cave B, 37 km from Cave A) was used twice (April 15 and May 3) by the same wolverine for 1–3 h during each visit. The third site (Cave C, 125 km from the nearest known other cave) was used by the family of wolverines continuously for at least 39 d (10 April –18 May) as a reproductive den.

Of the three sites, we excavated and investigated Caves A and B within 2 d of their use by the wolverine. We visited and did not excavate Cave C during winter to minimize impact to the denning wolverines, but placed a motion-activated camera at the entrance and returned after snowmelt to document subnivean structure and activity. All three caves were located on relatively flat tundra with no obvious topographic features visible in the immediate snow-covered landscape (Fig. 1b). At Caves A and B, the wolverine had dug a tunnel through ~1 m of snow and entered the cave via eroded tunnels in the soil (Fig. 1e). Cave A was roughly round, approximately 12 m^2 with a 60-cm ceiling at the highest point, and had hundreds of icicles stretching from floor to ceiling, including one 50 cm in diameter. Wolverine scat littered the ice floor, and snow had drifted in through the entrance, partially filling the cave. Cave B had a floor plan the shape of a four-pointed star, each arm stretching at least 10 m from the center, the ceiling becoming lower and eventually meeting the floor at each point of the star. Like the first, the floor and ceiling were both ice, with some soil present at the edges, and snow had drifted in through the entrance used by the wolverine, on which the wolverine had made a bed. This bed was located under a gap in the ice ceiling, such that the resting wolverine was in a section of the cave where both the floor and ceiling

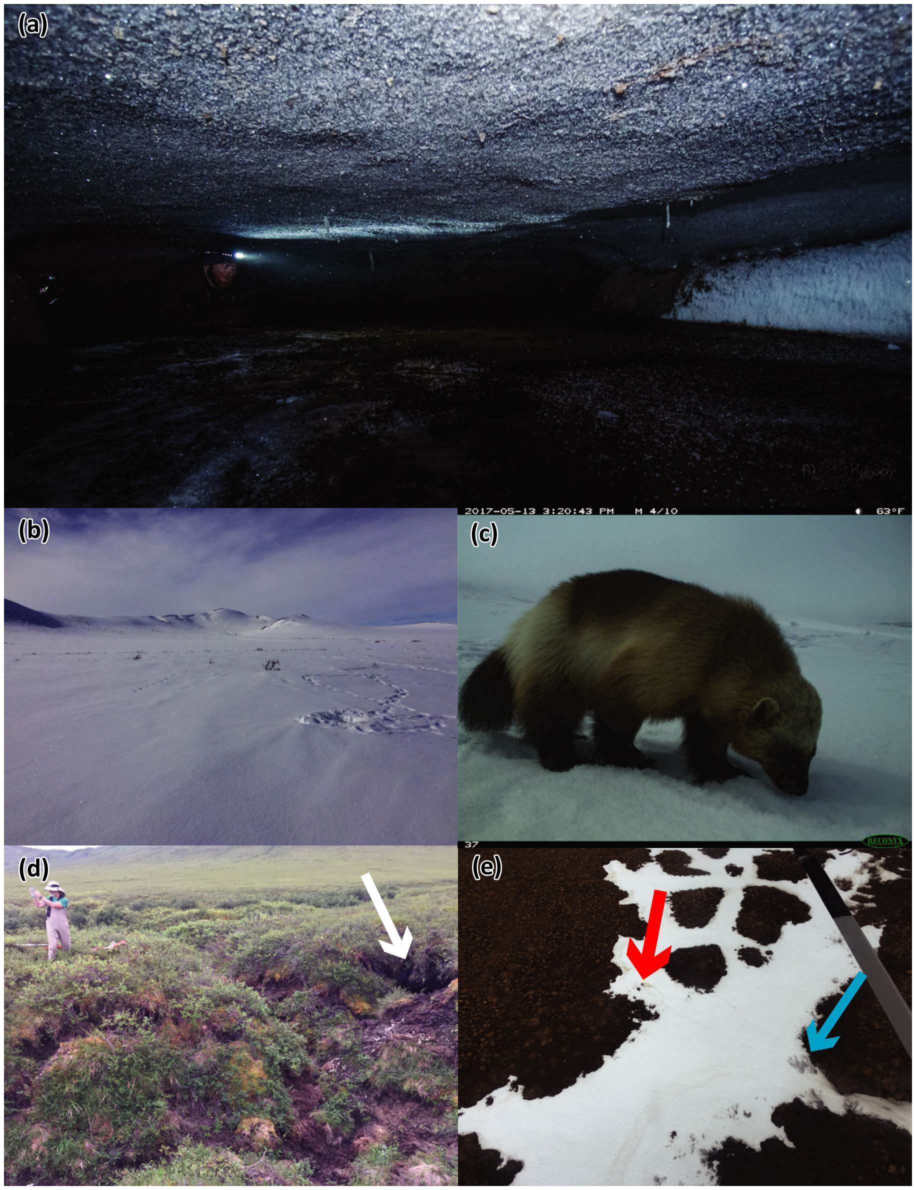

FIG. 1. Thermokarst caves in Arctic Alaska. (a) shows the inside of Cave B, used by a wolverine twice for resting, and panels (b)–(e) show the outside of Cave C, used for a reproductive den. In (b), the main den entrance, located within a few meters of the thermokarst cave, can be seen on the right side of the photograph, also indicated by the red arrow in (e). A wolverine investigates the entrance in (c). The entrance to the cave (white arrow) and thermokarst trenches can be seen in (d). A secondary entrance to the den, 20 m from the first, is shown with the blue arrow in (e). Photographs courtesy of T. Laird and A. Magoun.

were snow. At the center, the cave was 45 cm in height. At Caves A and B, abundant hoar frost along the entrance tunnels indicated warm and moist conditions inside the cave relative to ambient air, which could have aided olfactory detection by the wolverine.

Cave C was broadly similar, underlying 1.5 m of soil and ice (Fig. 1d). The entrance to this cave was located in a 3–3.5-m-deep polygonal trench network in the tundra, presumably formed during the erosion of ground ice along an ice wedge network (Fortier et al. 2007). Although the cave was partially flooded during the summer visit, it was at least 15 m^2 with a low ceiling (~30 cm). Abundant wolverine scat was present in the vicinity of the cave entrance, including in the trench, suggesting that the wolverines used both the cave and the snowdrifts formed in the trench for their den.

To our knowledge, the existence of these caves as an accessible form of structural habitat for wildlife is undocumented, although their existence as ephemeral and inaccessible subterranean permafrost structures is known from permafrost cores (Jorgenson et al. 2015), and their existence as accessible caves during winter is implied from summertime observations of ground ice degradation (Fortier et al. 2007). Caves such as these form during the erosion of ice wedges, a type of ground ice that occurs in permafrost regions by repeated infiltration and freezing of water in the seasonally cracked frozen ground. Ice wedges can be several meters deep and over 5 m wide (Kanevskiy et al. 2017). Across the landscape, these wedges often form in a regular, polygonal pattern, responsible for the polygonal patterned ground characteristic of the Arctic, and consistent with our observations at caves of polygonal trenches and a star-shaped cave layout (Fig. 1).

Ice wedges are more common and larger in areas that remained unglaciated during recent glaciations, which on the North Slope of Alaska generally occur at higher latitudes (Kaufman and Manley 2004). The northern extent of our study area coincided roughly with the maximum glaciation extent of the Pleistocene, north of which the occurrence of cave-forming ice wedges increases. All three of the caves used by wolverines—which we term "thermokarst caves" to reflect their presumed formation resulting from permafrost thaw (Kanevskiy et al. 2017)—were located near this boundary, suggesting that our discovery of only three caves may reflect search extent rather than wolverine behavior.

During warmer climate periods, including contemporary anthropogenic warming, ice wedges thaw more rapidly (Kanevskiy et al. 2017). When they do, deep trenches are left in the space formerly occupied by the wedge, still in the polygonal pattern (Fig. 1e). Meltwater flowing through these trenches and underground tunnels can further erode the ice wedges, leading to caves (Fortier et al. 2007). In some cases, the caves refill with water and subsequently freeze, leading to unique ice signatures detectable as thermokarst-cave ice in permafrost cores and outcrops (Douglas et al. 2011).

Ice wedges in Arctic Alaska began degrading abruptly and rapidly in the late 1980s with climate warming (Jorgenson et al. 2015), so thermokarst cave availability may have been considerably lower in the only other studies to excavate wolverine reproductive dens and resting sites on tundra (Serebryakov 1983, Magoun 1985). Although the increased degradation of ice wedges per se is well documented, the exact conditions that lead to the formation of accessible caves during winter are not. Surveys using high-resolution digital elevation models, wintertime visits, and ground-penetrating radar would help shed light on these questions and improve our understanding of the spatiotemporal trends and drivers associated with the formation of accessible caves.

The abrupt increase in availability of this form of structural habitat establishes an interesting opportunity to study microhabitat use and behavioral flexibility among Arctic wildlife. For instance, are these caves better able to provide for life history requirements (e.g., thermoregulation and predation avoidance) than snow burrows and other structures? As animals must cope with climate change, does an individual's ability to exploit relatively novel microhabitat structures like this flexibly confer a fitness advantage?

It is also important to consider these caves and their implications in an ecosystem-wide context. Permafrost degradation, including the erosion of ice wedges, broadly alters summertime wildlife habitat, and is particularly detrimental for species that rely on water bodies supported by the frozen ground, such as waterfowl and fish (Berteaux et al. 2017). Therefore, although these caves may offer structural habitat to some tundra species, their formation degrades habitat for others. Continuing to parse such complex and nuanced changes in Arctic habitat availability is an important component of understanding and predicting how ecosystems may respond to the changing climate.

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