



Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore

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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.

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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 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; McPeck, 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

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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, Santee, & Erskine, 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, Pellikka, & Travis, 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.

METHODS

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 be 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.

Study Area

We conducted this study in a roughly 20 000 km² region surrounding Toolik Field Station, Alaska, U.S.A. (68.63°N, 149.60°W; Fig. 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: 700–2700 m) dominates the southern portion, transitioning to foothills (elevation: 60–1000 m) in the north. The Brooks Range is characterized by tall peaks, steep scree slopes and river valleys, while the terrain of the

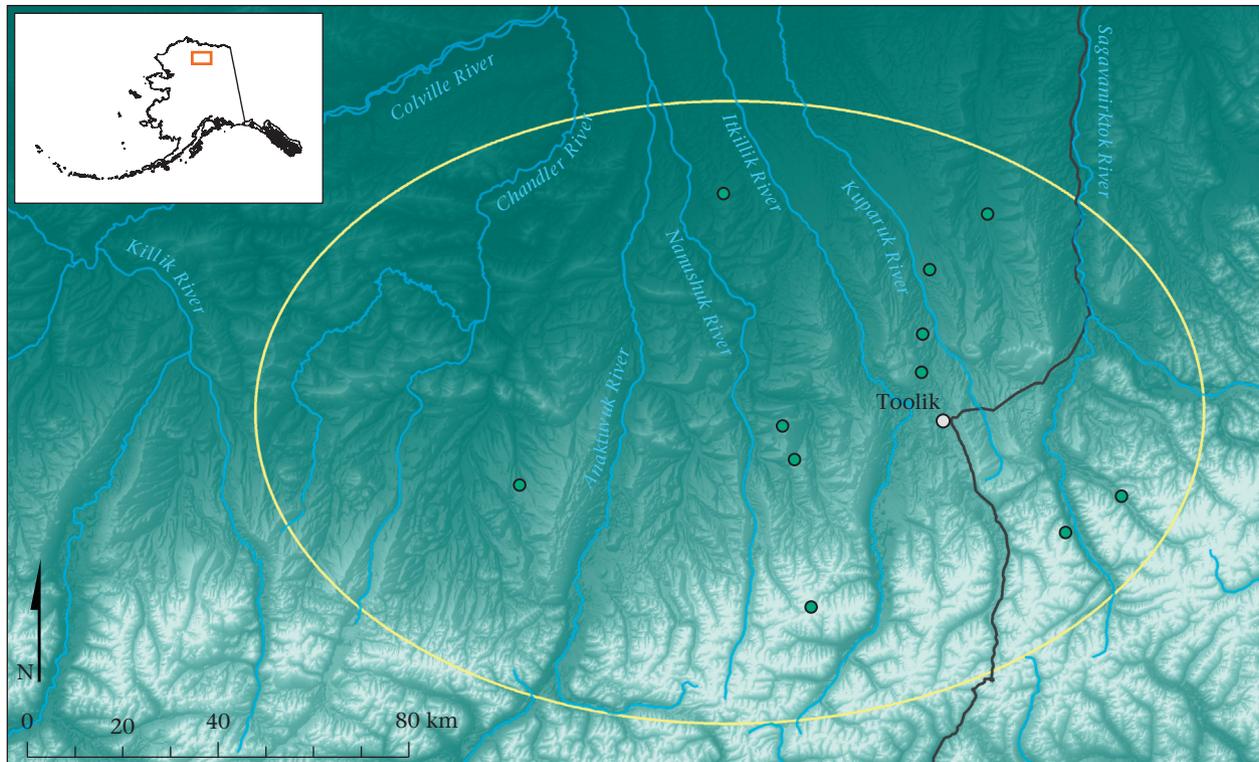


Figure 1. Study area (yellow oval) in northern Alaska. Points indicate centroids of resting locations for each wolverine, and the grey line shows the Dalton Highway.

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: ‘vener’ 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/m²), but begins increasing in February until peaking at summer solstice (~350 W/m²; 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 grey 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. 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).

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, Klafki, Krebs, & Lewis,



Figure 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.

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, Shults, & Kunkel, 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. 3). Here, we provide a summary of this approach, with full details and validation metrics in the Appendix. 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 3240 resting periods across 11 animals.

Data Analysis

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) 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 1207 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).

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, McDonald, Thomas, McDonald, & Erickson, 2002), with the interaction between resting site type (surface

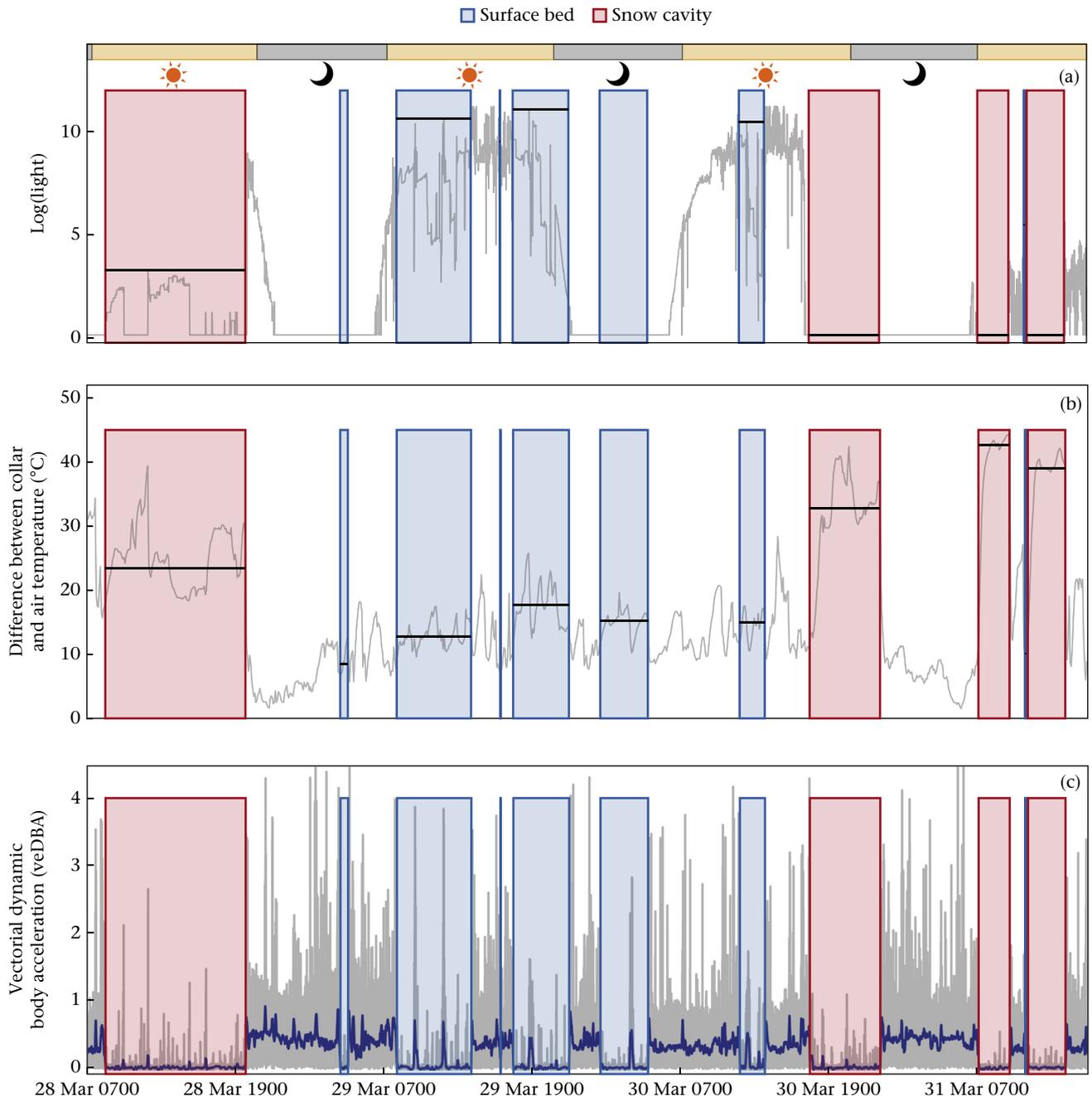


Figure 3. Example 80 h period showing data from collar-mounted biologgers used to identify resting periods and classify them as occurring in a surface bed or snow cavity. In (a) and (b), horizontal black lines depict the maximum log (light) value and median temperature difference value for each resting period, respectively; these values were used to predict whether the resting period occurred in a snow cavity or surface bed (see [Appendix](#)). Only light values measured during daytime were used. In (c), the grey line shows the vectorial dynamic body acceleration (veDBA) and blue shows the 5 min running mean of veDBA used to identify resting periods ([Appendix](#)). Resting periods, shown in shaded boxes, depict those used in the weather analysis, and therefore have been clustered temporally to address autocorrelation.

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. 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,

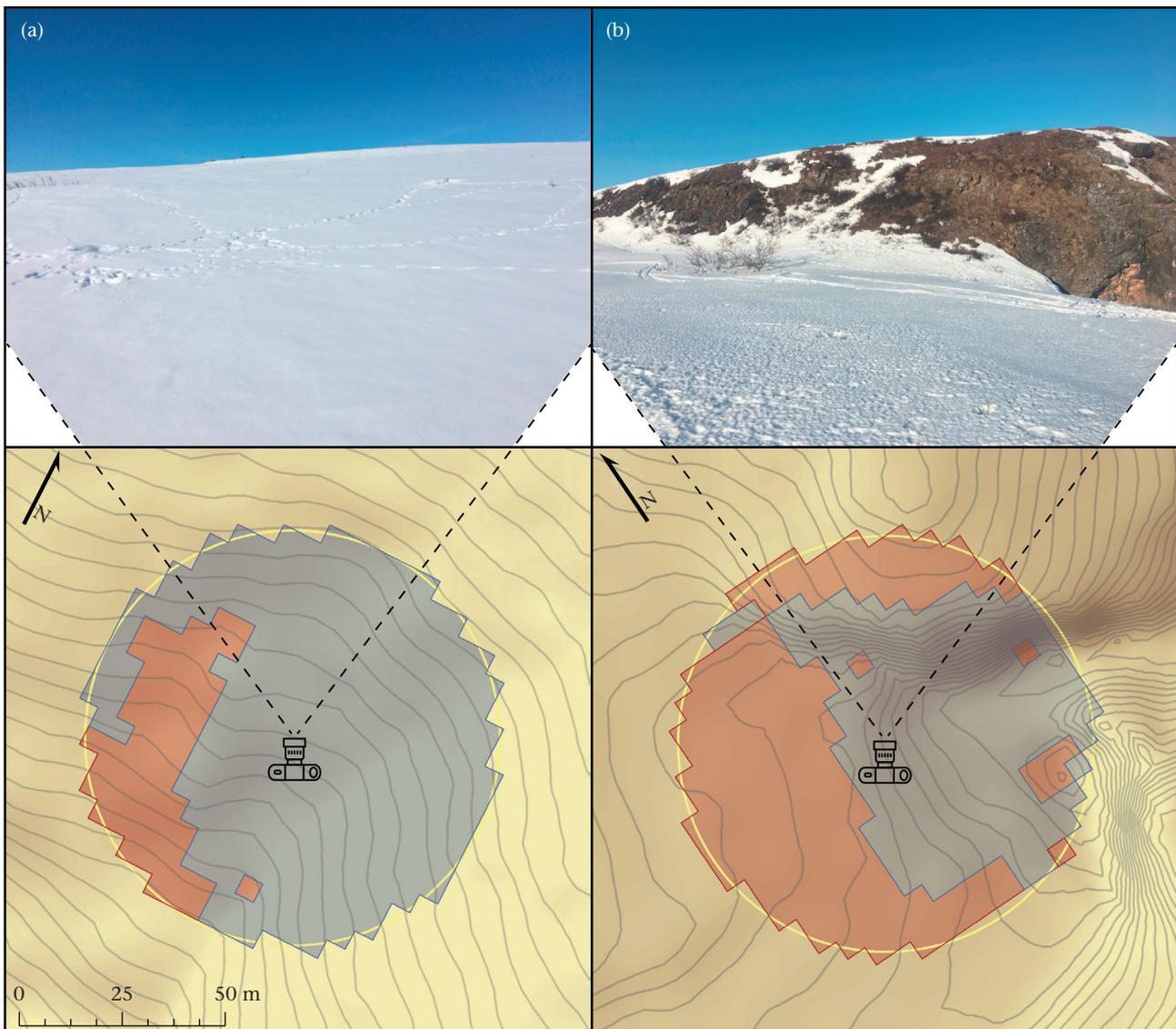


Figure 4. Example viewsheds for (a) relatively open and (b) relatively concealed wolverine resting locations. The camera icon indicates the resting site location, which is also the location from which the respective photographs were taken (photograph field of view indicated by broken black lines). For 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 (red shaded pixels).

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 viewsheds 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.

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).

RESULTS

We identified 3240 resting periods from 11 individual wolverines. Wolverines occupied snow cavities for 51% of these ($N = 1657$) and used surface beds for the remaining 49% ($N = 1583$). 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.

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). The influence of air temperature was particularly strong; model predictions showed that wolverines rested almost exclusively on the snow surface at $\geq 5^\circ\text{C}$ regardless of solar radiation, and conversely rested almost exclusively in subnivean cavities at -40°C with no incoming solar radiation (Fig. 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], $N = 1207$), reflecting the seasonal decoupling of the two variables during winter when most of our data were collected.

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. 6). Specifically, wolverines were approximately two times more likely to select a surface resting site with a 1500 m^2 viewshed than one with a 6000 m^2 viewshed (Fig. 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.

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. 7) and more vigilant as viewshed size increased when resting at snow cavities ($z = 2.91$, $P < 0.004$; Fig. 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. 7). At

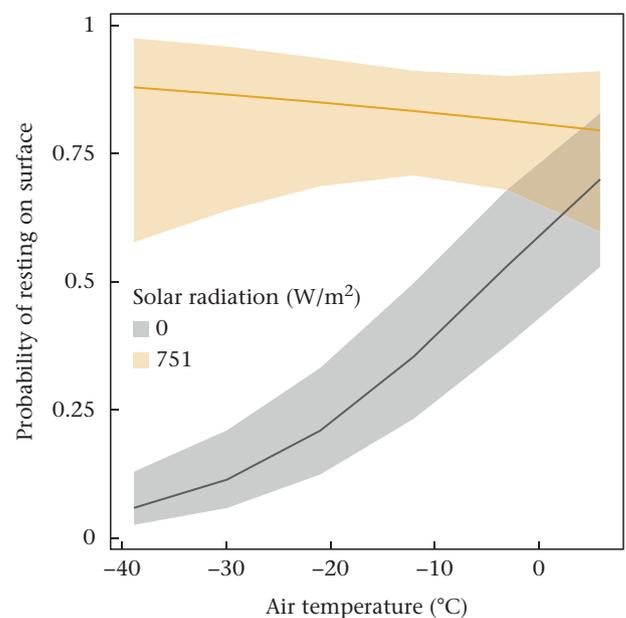


Figure 5. Marginal effects of air temperature and solar radiation on the probability that a wolverine rests on the snow surface versus in a subnivean cavity. Solar radiation values of 0 and 751 W/m^2 were the minimum and maximum measured during resting periods.

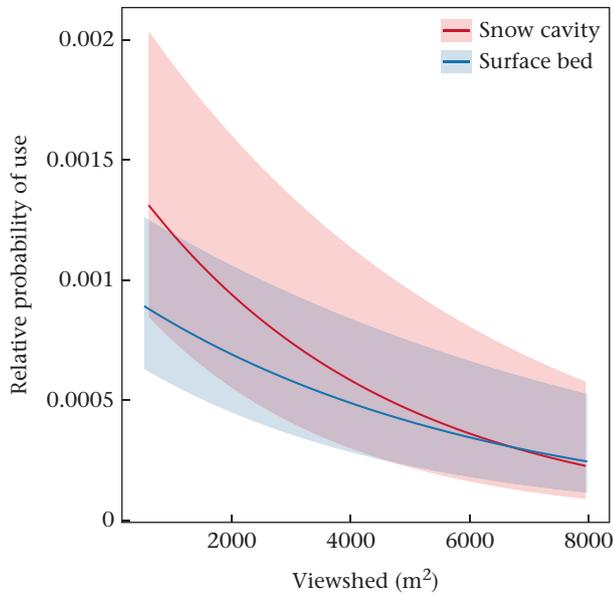


Figure 6. Relative probability of use for resting sites predicted by the viewshed within 50 m, compared to randomly selected ‘available’ resting sites in the nearby area. Relative probability of use can be interpreted by comparing values with one another. For example, a relative probability of 0.0008 at a surface bed with a viewshed of approximately 1500 m² is two times higher than a relative probability of 0.0004 for a viewshed of 6000 m²; therefore, a wolverine is approximately twice as likely to select the former.

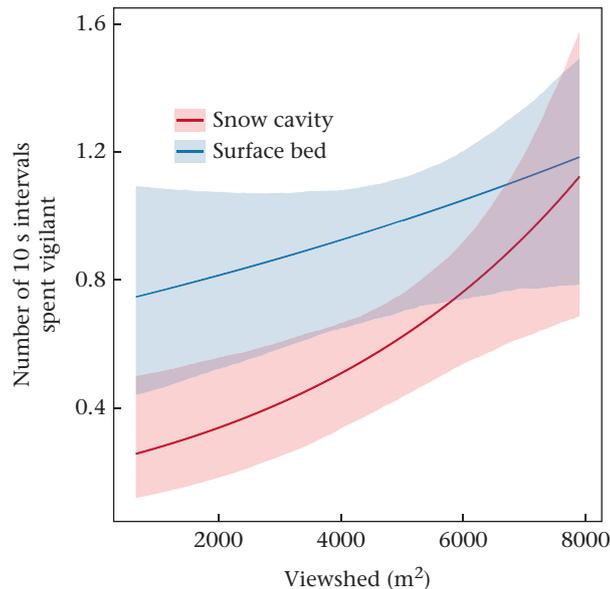


Figure 7. Number of 10 s intervals spent vigilant during the 5 min preceding and following resting periods, by resting site type and viewshed size. Bands represent 95% bootstrapped confidence intervals.

small viewsheds, wolverines were more vigilant at surface beds than at snow cavities, but at large viewsheds wolverines were highly vigilant at both (Fig. 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 m² 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.

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 across levels of 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 meso-carnivores and how these two processes can give rise to a trade-off between competing behavioural demands.

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.

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, & Gruebler, 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.

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).

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.

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 biologists, 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 using biologists 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 which 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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Appendix

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, McNairn, Daneshfar, & Shang, 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%).

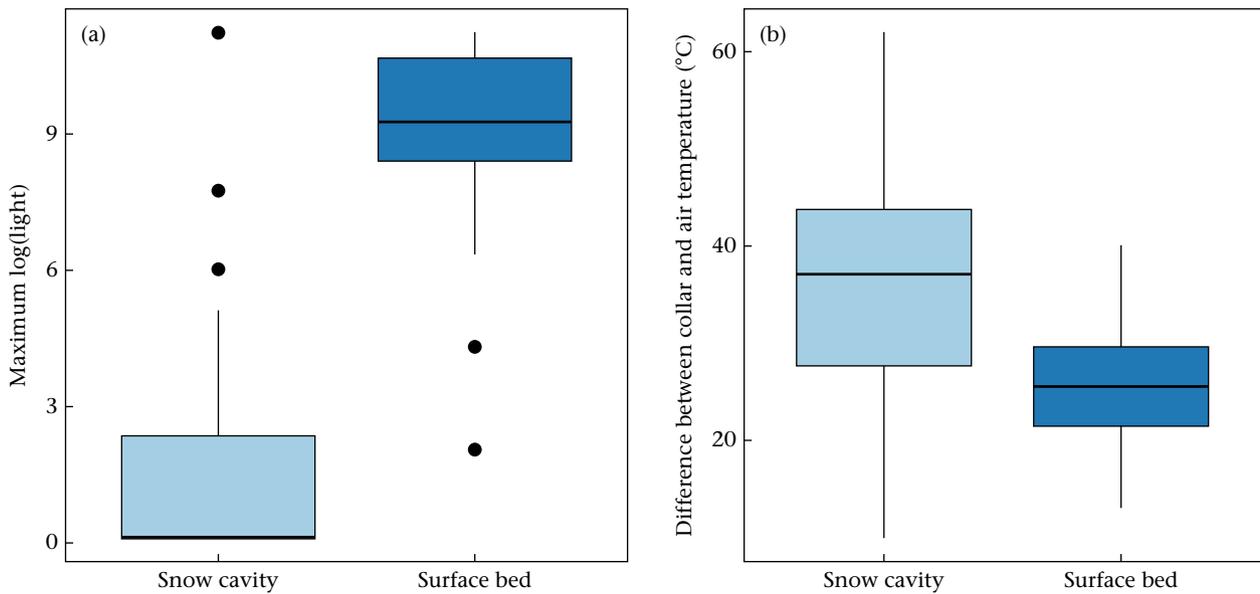


Figure A1. (a) Maximum log(light) values (*l.max*) and (b) the difference between median ambient air temperature and median collar temperature (*t.diff*) during resting periods in snow cavities and surface beds.