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Research Article

Temperature Trade-Offs in High-Altitude Himalayan Marmot Burrowing: Balancing Predator Avoidance and Energy Expenditure

Herbert H.T. Prins[1*], Tsewang Namgail[2], Ashok Subedi[3], Yorick Liefting[4]

[1] *Animal Sciences Group, Wageningen University, the Netherlands*

[2] *Snow Leopard Conservancy India Trust, Changspa Sheldan, Leh, Ladakh, India*

[3] *National Trust for Nature Conservation, Khumaltar, Lalitpur, Nepal*

[4] *Wildlife Ecology & Conservation Group, Wageningen University, the Netherlands*

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ABSTRACT

The Himalayan marmot (*Marmota himalayana*) inhabits short steppic grasslands in Tibet and the Trans-Himalaya regions of Nepal and India, at altitudes ranging from around 3000 meters to 5500 meters in the subnival zone. Their family life is centred on burrows, which may go down 2-10 m deep. Marmots are primarily preyed upon by the Golden eagle, Brown bear, Snow leopard and feral dogs. Consequently, marmots depend on safe burrows not only for hibernation but also for refuge when they sense danger. In order to gain deeper insights into the burrowing behaviour of marmots, we performed soil temperature measurements across various depths (ranging from 10 cm to 120 cm) and altitudes (ranging from approximately 3700 meters to 4750 meters), considering different slope orientations, in the sandy and gravelly soil where marmots create their burrows. Measurements were taken between late May which is when the marmots emerge from hibernation and mid-July. While surface temperatures can be high during the day, which benefits the marmots by reducing their energy expenditure, burrow temperatures at night are warmer than those at the surface. However, it is clear that if the marmots have to spend too much time underground due to disturbances, such as predators or humans, they face a trade-off due to low burrow temperatures during the day. Burrow temperature may also affect infectiousness of fleas carrying *Yersinia pestis*.

*CORRESPONDING AUTHOR

Herbert H.T. Prins;Animal Sciences Group, Wageningen University, the Netherlands ; Email: herbert.prins@wur.nl

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1. Introduction

Most members of the Marmota prefer open grasslands, but some live in wooded areas. For example, the Long-tailed marmot (*Marmota caudata*) inhabits lightly wooded areas in the Himalayan region [1]; but they can also live in open arid areas [2], while the Groundhog (*M. monax*) primarily lives in forested areas of North America [3]. This paper focuses on the Himalayan marmot (*M. himalayana*), which inhabits alpine grasslands in the Himalaya and Tibet, similar to nearly all other marmot species [4,5]. Himalayan marmots are the least studied and least known among all marmot species [6,7]. In the Central Himalayas, *M. himalayana* can be found between the tree line and the snow line, at elevations ranging from 3000 to 5500 m, living in the subalpine and alpine mountain belts. Unlike other marmots, their lower distribution limit never descends below 3000 m [6]. They hibernate for about six to seven months, usually from October to April [6,8]. During the active summer months, they may collect grass and store it [7]. Their range is very vast stretching from north-west India, all the way to north of 42° N in China, comprising about four million km^2 (see map in [9]). In north-west China, they utilize three different types of dens: sleeping dens, breeding dens, and temporarily used dens [8]. However, it remains unknown whether they have the same den types in the (Trans)-Himalayan region. In China, the depth of their dens ranges from 60 to 240 cm from the ground surface to the deepest point of the first tunnel (although burrows may go even deeper) [8]. In the Trans-Himalayas, their activity area is typically concentrated within 2 to 40 m from the entrance of their burrows (personal observation).

Himalayan marmots exhibit vigilant behaviour while foraging, frequently scanning their surroundings. When alarmed, they may whistle and quickly retreat to a den entrance to seek shelter underground (pers. obs.). Throughout the warm season, they usually remain active outside their burrows, unless faced with severe weather conditions such as heavy rain and/or snow ([8]; personal observation). A study conducted near Mount Manaslu in Nepal, situated at an altitude of approximately 3500 m above sea level, showed that the air temperature never reaches the critical value of 22–25°C, which could lead to heat stress in other marmot species and result in a significant decrease in their activity level [6]. However, in our study area in Ladakh, located in north-west India at higher elevations, the daytime temperature often exceeds this critical value (as demonstrated in the Results).

Many marmot species live in areas with permafrost. This permafrost partly explains the absence of trees in alpine grasslands because the combined effects of frozen soil and harsh environmental conditions make tree establishment and survival difficult. Evidence suggests a relationship between permafrost and tree cover in Tibet and the Himalayas, with permafrost limiting tree growth and density in these regions [10,11]. Consequently, many Himalayan marmots inhabit grasslands where permafrost is likely to occur. Although the depth of marmot burrows may be limited where an ice-rich permafrost layer is present, permafrost in the Trans-Himalaya and Tibet is typically not a hard, ice-rich layer because the soil remains relatively dry owing to the extremely low precipitation [12-14]. Instead of encountering solid ice, marmots living in areas with permafrost are more likely to encounter soil layers with temperatures close to 0°C at some depth below the surface. In this study, alpine permafrost refers to ground with a mean annual soil temperature below 0°C [15]. In doing so, we follow the temperature-based definition commonly used in Europe and North America rather than the Soviet tradition, which places greater emphasis on the presence of subsurface ground ice [16]. In Tibet, which to quite some extent is similar to the Trans -Himalayan region of Ladakh and Nepal, permafrost has developed some 800 m to 1100 m lower than the present snow line [17]. The snowline between 36° N (the northernmost part of the Ladakh Range) and 28° N (the southern part of the Greater Himalayan Range in Nepal) lies on average at about 5300 m above sea level, with the highest snowline around 6200 m a.s.l., and the lowest at about 4400 m a.s.l. [18]. In other words, permafrost may be expected to start around 4200 m a.s.l. and this is the altitude above which we often encountered cryoturbation in the

Trans-Himalaya of Ladakh (pers. obs.). The depth of the upper side of the permafrost is shallow [10,19,20]. In contrast to many other places, the temperature of the deep soil in the geographic range of the Himalayan marmot is thus not equal to the average annual temperature but is lower where permafrost occurs.

Himalayan marmots can be preyed upon by a range of carnivores, including wolves, foxes, coyotes, bears, eagles, and hawks. Snow leopards (*Uncia uncia*), Lynxes (*Lynx lynx*) Golden eagles (*Aquila chrysaetos*), Grey wolves (*Canis lupus*), Red foxes (*Vulpes vulpes*) and Brown bears (*Ursus arctos*) are the main natural predators in the Trans-Himalaya [5,21,22]. Elsewhere in their range, Himalayan marmots are also hunted by Eagle owls (*Bubo bubo*) and the large Upland buzzard (*Buteo hemilasius*) [8]. Increasingly, feral dogs prey on marmots too here and in Tibet. Although marmots are not known for their speed and are not considered fast runners, they can run at high speeds for short distances to escape predators. The Yellow-bellied marmot (*Marmota flaviventris*) has been estimated to run at a maximum speed of 11 kilometres per hour [23], and our own observation of the Himalayan marmot show that they can reach approximately the same maximum speed. Himalayan marmots use their burrows as bolt holes to hide from predators, and their flight distance is shorter when further from a shelter such as a burrow [24]. Snow leopards, Brown bears, and Grey wolves are known to hunt marmots as part of their diet; Red foxes seldom venture into the range of the Himalayan marmot and our maximum altitude sightings were 4200 m a.s.l. (pers. obs.). Marmots provide a high-calorie meal that is rich in fat, making them an important food source for these predators. Snow leopards are particularly adept at hunting marmots on rocky terrain, using their agility to chase and ambush their prey; they do not dig. Himalayan Grey wolves, also prey on marmots in high-altitude areas, although there is no conclusive evidence that they dig them out from their burrows. Grey wolves in general are not particularly good at digging, and even for their own dens often use Badger (*Meles meles*) or Red fox holes [25]. However, the speed of these predators is quite extraordinary, with Brown bears reaching maximally about 48 $km.h^{-1}$, and wolves even 64 $km.h^{-1}$ [26]. The maximum speed reported for Golden eagle in an attack dive is 240 $km.h^{-1}$ and perhaps even faster (320 $km.h^{-1}$ [27] thus all predators outstrip the marmots with a wide margin. This makes sociality, vigilance, and warning calls for kin, of very high importance for their survival. In general, it may be assumed that if a (Himalayan) marmot reaches its burrow and dives into it, it is safe from predation from foxes, jackals, dogs, wolves, snow leopards and eagles.

However, Brown bears have been seen digging up marmots from their burrows to feed on them, and marmots are an important part of the Brown bear's diet in some areas [28]. Brown bears have a keen sense of smell and can easily find marmot burrows. Once they find a burrow, they use their powerful claws and muscles to dig in and catch the marmots. Studies in the Tian Shan Mountains of Central Asia and the Tibetan Plateau, which includes parts of the Himalayas, suggest for example that marmots are indeed an important part of the Brown bear's diet in certain regions, and bear can delve deeply to get at their chosen food [29,30]. The depth of their dens is in the order of 3 m [31]. Even though Himalayan Brown bears are nowadays rare, we have seen them digging and turning over large rocks, and there is no doubt they could delve deep. As a result, marmots may be facing a situation where its burrow is limited in depth by the permafrost and the low soil temperature while still being in reach of predators that can dig deep.

One may reason that the best strategy for marmots in the Himalayas and Central Asia would be to detect aerial predators or Golden eagles and Upland buzzards early, run fast to a burrow and hide. This strategy would work for most predators but Brown bears. Where the latter predator is involved, natural selection would favour marmots that burrow very deep. However, deeper burrows closer to the permafrost come at the cost of facing lower temperatures, increasing energy expenditure. In this study we aimed to quantify the temperatures marmots face in their burrows, by measuring the temperatures of soil layers at different depths in the western Himalayan region of Ladakh. In the discussion, we will thus speculate on a possible trade-off between delving deep to avoid burrowing predators and the costs of facing lower burrow temperatures due to the associated higher expenses of thermoregulation, as digging deeper brings marmots closer to the below-ground permafrost. As a serendipitous outcome of our investigation into the burrow temperatures of Central-Asian marmots, we place our findings in the light of One Health. Since burrow temperatures have a direct effect on the questing behaviour of fleas, and these fleas are occasionally carriers of *Yersinia pestis* (a microbe that can potentially infect humans with bubonic plague) our study on marmot burrow temperature may acquire societal significance in understanding and addressing potential public health implications.

2. Materials and Methods

In Ladakh, an autonomous region in north-western India, we chose several locations in the Trans-Himalayan mountain ranges near the border with China where marmots were reported to live. We then selected areas used by marmots for burrowing at various altitudes and with diverse exposures to the south and southwest. We collected data near the village of Ulley (34.33º N, 77.13º E; between 3700 and 4750 m a.s.l. facing SE, S, and SE) and near the village of Mangyu (34.23º N, 77.05º E; between 3800 and 4400 m, facing NE and NW) in western Ladakh. The sites near Ulley all had marmot colonies within 50 m, but there were no marmots on the N-facing slopes of Mangyu. The Ulley-slope was gentle, with about a ten degrees slope while at Mangyu it was generally twenty degrees. Both slopes were grassy. At different depths, we installed standard type-K thermocouples, which were connected periodically to a handheld digital thermometer. The accuracy of measurements was ±0.3% with a resolution of 0.1 °C. The depths of measurements were in cm: 10, 20, 40, 60, 80, 100, 120 and at some places 140. Using the same type of thermocouples, we also measured at the surface and 10 cm above the surface. Measurements were done between 04:30 hrs and 20:30 hrs local time at two hourly intervals. They started on 30th May 2018 and continued till 19th July 2018, so at the time of the year that marmots were active. Every measurement comprised the arithmetic mean of three readings taken within a few minutes of one another. The total number of measurements per site and sampling date ranged from 432 to 468 because repeat measurement series were occasionally required when sensors had been disturbed by animals or village children. Soils were gravelly to sandy. Per depth, we calculated the average temperature over the entire day per sensor, and then we calculated the average of these two sensors. We did not calculate a confidence interval or an error estimate because the data were not spread around a mean but followed a part of a sine-function over the day thus violating the central limit theorem.

Because no official weather station existed at elevations comparable to our study sites (3700-4800 m a.s.l.), we relied on our own measurements. The highest Government of India weather station was installed only in 2020 at Leh (Ladakh) only at 3500 m a.s.l..

We calculated the change of the temperature of the different soil layers at the different altitudes, slope aspects (N vs. S) over time. Because the soils are variable mixtures of sand and gravel, and because the soil moisture changed over time and with depth, we only calculated arithmetic means without error estimates or confidence intervals simply because statistical homogeneity requirements were violated by nature. Thermal conductivity and thermal diffusivity vary wildly with soil type, gravel type and water content [32,33].

Although we did not collect weather data at these sites, we did so in a location in Nepal located further to the East. There, in the Nar Valley (28.71° N, 84.16° E), we installed a series of weather stations on a south-facing slope of approximately 30 degrees and on a north-facing slope of approximately 30 degrees on the opposite side of the same valley. We positioned our pairs of weather stations at 3500, 4000, 4500 and 5200 m a.s.l. Our weather stations recorded ambient air temperature (in degrees Celsius), windspeed (in kilometre per hour), wind direction (in degrees), incoming radiation at zenith (in Watts.m^{-2}) and reflected radiation from the ground (in Watts.m^{-2}). Measurements were recorded in a 10-minute interval, 24/7, year-round to a memory card on the central data logger

(Logic energy LeNetMobile). Air temperature, wind direction and radiation were logged as instantaneous values while wind speed was logged as a 10-minute average. We refrained from utilizing these data to make statements about the weather in our study area in Ladakh due to the limited correlation in daily weather patterns over such a distance (895 km great circle distance) [34]. Instead, we employed them to estimate the lapse rate of the decreasing temperature with altitude in these types of mountain, a crucial factor for determining the altitude of the permafrost line.

In our results and their interpretation, we reference the thermoneutral zone of our study animal, the Himalayan marmot, as ranging between 15°C and 20°C. It's important to note that the thermoneutral zone for our specific study animal has not been established. Therefore, we adopted the thermoneutral zone established for the Yellow-bellied marmot *M. flaviventris* [35,36], and similarly, for the Alpine marmot *M. marmota* [37].

3. Results

Our results show that as the season progresses, the temperature of the soil increases. The data support the idea that there is permafrost at an altitude of 4400 m a.s.l. at the N-facing slopes of Mangyu and at 4750 m at the S-facing slopes of Ulley (Table 1). While the season progresses, the sub-soil (10 to 50 cm deep) warms up and reaches a temperature high enough for marmots that would sit in shallow burrows to be thermoneutral (15 ºC – 20 ºC). This happens at the beginning of June but only for sites at 3700 m and 4200 m; at sites at 4400 m or 4750 m the soil stays too cold whether the slope is facing S or N (Table 1).

Changes in soil temperature (mainly warming up, but also sometimes a bit of cooling) were different for the different terrains. Generally, South-facing slopes (i.e., the sites near Ulley) warmed up faster (on average about 1.2 ºC per 10-day decade) than those facing North (the sites near Mangyu, which on average warmed up at a rate of 0.6 ºC per decade) (Table 1). There is no indication that this was caused by warmer air temperatures at these S-facing slopes, but can be explained much better by solar radiation differences (Table 2). Our observations on the weather from Nar Valley (Table 2) support the idea that the permafrost must hover around 4500 meter above sea level at the latitude of the western Himalayan ranges.

Table 1. Soil temperature profiles at two slopes in Ladakh, namely, at Ulley (where Himalayan marmots occur) and close-by Mangyu (where there are no marmots). Data have been collected at different altitudes during the summer. Temperatures in dark blue are far below the thermoneutral zone of marmots and in light blue still below that zone. Temperatures in green are within the thermoneutral zone of marmots. Until far in the summer, for marmots to be deep enough in the soil to be out of reach of Brown bears is only possible if the marmots accept conditions that cost energy to stay warm. At Ulley, data could be collected at a higher altitude than at Mangyu.

S-facing 3700 m 31 May		N-facing 3700 m 6 June		S-facing 3700 m 16 June		N-facing 3700 m 24 June		S-facing 3700 m 4 July		N-facing 3700 m 15 July	
D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)
10	17.8	10	23.7	10	18.9	10	18.4	10	15.9	10	25.0
0	14.1	0	20.4	0	16.6	0	17.7	0	15.4	0	20.9
-10	12.6	-10	16.8	-10	16.2	-10	16.5	-10	15.6	-10	18.8
-20	11.4	-20	14.6	-20	15.6	-20	15.4	-20	15.6	-20	16.6
-40	10.8	-40	12.8	-40	14.8	-40	14.3	-40	15.1	-40	14.8
-60	10.0	-60	11.7	-60	13.7	-60	13.7	-60	14.5	-60	14.6
-80	9.2	-80	10.6	-80	12.7	-80	12.8	-80	13.9	-80	13.9
-100	8.4	-100	9.4	-100	11.7	-100	12.0	-100	13.3	-100	13.3
S-facing 4200 m		N-facing 4100 m		S-facing 4200 m		N-facing 4100 m		S-facing 4200 m		N-facing 4100 m	

1 June		8 June		17 June		25 June		5 July		16 July	
D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)
10	12.0	10	21.4	10	16.1	10	18.0	10	13.9	10	22.0
0	12.1	0	19.0	0	16.4	0	16.4	0	14.2	0	21.3
-10	11.9	-10	20.0	-10	15.8	-10	16.1	-10	13.6	-10	20.5
-20	11.3	-20	15.8	-20	15.5	-20	15.5	-20	14.1	-20	18.8
-40	10.8	-40	14.0	-40	14.6	-40	14.5	-40	14.2	-40	16.6
-60	9.9	-60	11.8	-60	13.6	-60	13.2	-60	13.7	-60	14.6
-80	9.3	-80	10.5	-80	12.6	-80	12.4	-80	13.1	-80	13.3
-100	8.6	-100	9.8	-100	11.6	-100	11.6	-100	12.5	-100	12.4

S-facing 4400 m		N-facing 4400 m		S-facing 4400 m		N-facing 4400 m		S-facing 4400 m		N-facing 4400 m	
2 June		9 June		19 June		24 June		13 July		16 July	
D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)
10	11.3	10	14.5	10	11.9	10	11.3	10	19.7	10	17.3
0	6.9	0	15.5	0	11.2	0	15.3	0	14.8	0	15.5
-10	7.7	-10	12.6	-10	10.7	-10	14.9	-10	14.0	-10	14.0
-20	7.1	-20	11.1	-20	10.2	-20	9.3	-20	13.1	-20	13.2
-40	6.9	-40	9.1	-40	9.6	-40	7.9	-40	12.2	-40	11.7
-60	6.7	-60	7.5	-60	9.2	-60	6.5	-60	11.5	-60	10.3
-80	6.2	-80	5.8	-80	8.6	-80	5.1	-80	10.7	-80	8.6
-100	6.0	-100	3.9	-100	7.8	-100	3.9	-100	10.1	-100	6.8
-120	5.7										

S-facing 4750 m		S-facing 4750 m		S-facing 4750 m	
2 June		20 June		14 July	
D (cm)	T (ºC)	D (cm)	T (ºC)	D (cm)	T (ºC)
10	15.6	10	12.6	10	14.5
0	10.3	0	12.9	0	13.5
-10	6.5	-10	8.8	-10	12.7
-20	4.9	-20	7.7	-20	11.3
-40	3.4	-40	6.5	-40	9.8
-60	2.2	-60	5.2	-60	8.1
-80	0.9	-80	4.9	-80	6.7
-100	0.7	-100	2.8	-100	5.3
-120	0.7	-120	1.5	-120	4.2

Our results show that Himalayan marmots when reacting to a disturbance from a predator incur temperatures around 13.8 ºC if they are about 0.4 m underground in the transition from woodland to grassland at 3700 m, and 11.4 oC when 1.0 m below the surface (Table 1). Higher up, where grasslands peter out in the alpine zone, at 4400 m, these values are only 9.6 ºC and 6.4 ºC, respectively. Note, however, that during cold cloudy days the temperature above ground can be colder than below ground while at night it is above ground nearly always colder (Table S1, Table S2). Even during the day, the air temperature reaches the thermal neutral zone of marmots only at low altitudes except for peak moments during the day (Table S3). In other words, to forage, Himalayan marmots must live above the (current) tree line to be able to forage but by doing so incur the cost for staying warm because the air temperature is nearly always lower than their thermal neutral zone except around noon. Radiative heating reduces this cost. Peak solar radiation is exceedingly high in the Himalayas and Trans-Himalaya (Table 2), nearly twice as high as in temperate latitudes.

Table 2. Average air temperature between 2020 and 2023 (three years of continuous measurements) in Nar Valley (Nepal) in relation to altitude (m above sea level) and maximum solar radiation (Watt/m^2). On average, the air is slightly warmer over south-facing slopes (0.7 ^oC). The effect of altitude is strong with an average lapse rate of 0.58 ^oC/100 m. By interpolation, the long-term frost line is estimated to be at 4500 m.

	North		South		
Altitude (m)	Air temperature (^oC)	Maximum radiation (W.m^{-2})	Air temperature (^oC)	Maximum radiation (W.m^{-2})	Average temperature (^oC)
3600	6.1	800	5.4	900	5.8
4200	0.1	865	2.5	910	1.3
4600	-0.6	830	-0.1	930	-0.3
5200	-3.9	no data	-3.2	925	-3.5

4. Discussion

On the Himalayans grasslands, the optimal habitat for Himalayan marmots is open grasslands. These grasslands are limited at the lower side by forest and scrub-lands. The natural tree line at the south-facing side of the Himalayas generally lies between 3500 to 4500 meters above sea level, while on the north-facing side, specifically the Trans-Himalaya region, the tree line is generally lower and ranges between 3000 to 4000 meters above sea level due to the drier climate and the rain-shadow effect caused by the mountains. The upper limit of the sub-alpine zone on the south-facing slope of the Himalayas is generally around 4000 to 4500 meters a.s.l., while on the north-facing slopes, this limit is lower, ranging between 3500 and 4000 meters. Above this elevation, alpine meadows and rock outcroppings are more common than grass-lands, and the upper limit of alpine vegetation is typically around 4500 to 5000 meters on the south-facing side, and 4000 to 4500 m at the north-facing slopes. These grass-lands, and their productivity depend on slope steepness, slope aspect and altitude within this vegetation zone [38]. These are the areas where the Himalayan marmots live (pers. obs.). Higher up, rock outcroppings, and snowfields are common; marmots are rare there.

Marmots are known to prefer burrowing on south-east and south-facing slopes compared to north-facing slopes, probably due to increased warmth from sunshine but not from higher air temperature (Table 2) as well better foraging opportunities. This choice for south-facing slopes has been observed in Himalayan marmots in the western Himalayas of India, as well as in the Alpine marmots in the French Alps [39], and this is corroborated by our results. On the Tibetan plateau, Himalayan marmots may also select flat areas in wetlands given that these places are best for burrowing there [40].

The body temperature of marmots is high: of the related Yellow-bellied marmot it is known that their night body temperature is 36.6 ^oC and their daytime body temper-ature even 39.8 ^oC [35] and we assume the former is about the same for the Himalayan marmot. The thermal neutral zone for the Yellow-bellied marmot is between 15 ^oC and 20 ^oC [35,36] as it is for the Alpine marmot [37]. Assuming that Himalayan marmots have a similar thermal neutral zone, this implies that spending time in a deep burrow where the temperature is lower than 15 ^oC incurs a cost. Of course, this is not the case when they are hibernating in winter and early spring.

Soil possesses a significant thermal mass, leading to a gradual adjustment to temperature changes occurring at its surface. This results in a reduction of the intensity of temperature fluctuations as the depth increases, eventually reaching a state of relative stability [41]. At a depth of 10 to 15 m, the soil temperature is equal to the annual average air temperature [40]. Our results show that it is probable that permafrost occurs around 4400 m and the evidence is even stronger at 4750 m: with a linear interpolation from our soil temperature data, we estimate that permafrost occurs at about 2 to 3 m depth around 4500 m (inferred from Table 1). Air temperature data show that above 4500 m a.s.l., the average annual temperature is below zero ºC (Table 2) thus corroborating the idea of permafrost above that level. Digging to below the sub-soil frostline, as reported for American marmot species, is thus impossible for these Himalayan marmots at an altitude where grass productivity peaks [38]. Note that even though recent climate change may result in degradation of the permafrost layer [43] this would result only in the lowering of the transition from icy conditions to non-icy conditions at the top side of the permafrost with a few centimetres per ten years-period. Indeed, this was observed [43] and can be explained by the fact that the phase-change from ice to water demands much more energy than the increase in temperature of ice [44] underpinning the importance of the legacy effect of the Little Ice Age which ended in the Himalayas around 1600 CE [45]. Yet, [20] show that in Nepal the lower elevation of the permafrost may have crept up at a rate of about 0.3 $m.yr^{-1}$ in the last decades. Anyhow, we do not see benefit of digging out extremely deep hibernation burrows as deep as ten meter as reported by [46]. Even though hibernation brings the body temperature to a few degrees above the ambient only [47], their metabolism does not come to a halt. This may have led to genetic adaptations in, e.g., the fatty acid metabolism [48]. This is to be expected if poly-unsaturated fatty acids play a role in cold adaptation in vertebrates [49]. Because diet choice affects metabolic rates during hibernation in Yellow-bellied marmots [50], we recommend diet studies of Himalayan marmots along a climate gradient. Of course, macronutrients are of significant importance [51] but we expect significant insights if the dietary studies would include fatty acid composition.

Our study is relevant from a One Health perspective. Human plague caused by *Yersinia pestis* was first reported in Nepal in 1967, during an outbreak in the western part of the country [52]. However, it had been previously reported in 1823 in the northern region of India's Himalayan ranges, specifically in Garhwal and Kumaon (now in the state of Uttarakhand), which border Nepal and Tibet. This evidence was reviewed in [52]. The 1967 Nepal case was transmitted through human ectoparasites, mainly fleas, as well as through coughing. However, it is suspected that the outbreak might have originated from rodents. Another possible source of the plague outbreak could be traced back to dogs that scavenged and hunted freely, leading to their contact with local wildlife. These outbreaks in Nepal marked the most southern occurrences of the Central Asian bubonic plague [52]. It is noteworthy that there is a significant genetic similarity between *Y. pestis* strains from Nepal and those from Tibet. Both types fall within the Medieval genotype cluster [53].

Recent cases of plague in Mongolia [54,55] and Kyrgyzstan [56] as well as in Russia [57] have been linked to marmots, although several other mammal species have also been identified as potential hosts [54,58]. For an outbreak to occur, several environmental factors must coincide, including (i) higher altitudes, (ii) locations in arid or semiarid zones with low precipitation, (iii) locations in or around saline soil, (iv) the presence of at least two hosts/vectors and one species of flea, and (v) an enzootic epidemiology seemingly regulated by a subtle interplay between resistant hosts (resulting from selection pressure) and susceptible hosts [58]. The study in the Tien Shan Mountains is particularly interesting because it involves not only a marmot (the Grey marmot [*M. baibacina*]) but also other cohabiting rodents [59]. It is noteworthy that *Y. pestis* can survive for extended periods in saline soil and even within amoebas and blue-green algae present in soil [58]. Asian marmots show a low susceptibility to *Y. pestis* and can even exhibit resistance, leading to low levels of bacteria in their blood, which are insufficient to infect fleas [60]. Dogs seem to be a primary suspect for carrying infected fleas to humans [58]. For instance, there have been cases where bubonic plague was transmitted to humans through dogs that had consumed infected Himalayan marmots in China [61]. Additionally, infected sheep can also serve as a direct source of bubonic plague in Tibet when consumed or skinned [62]. These sheep might have acquired the bacteria from marmots [63] or possibly from the soil surrounding the marmot burrows. Notably, sheep graze on the lawns created by marmots in the Trans-Himalayan mountain systems (pers. obs.). In this regard, village dogs and feral dogs may pose a great threat, not only by directly attacking people or sheep but also through hunting and burrowing for marmots, where they can acquire infected fleas.

Temperature plays an unexpected role in the transmission of *Y. pestis* by fleas. The early transmission phase, when a flea ingests *Y. pestis* from an infected source during a meal and subsequently bites an animal, seems to be negatively impacted by lower temperatures, potentially halting below 10 °C [64]. Note that in our study, burrow temperatures often fell below this threshold. However, after a flea becomes infected, a biofilm develops in its gut, preventing ingested blood from reaching the digestive channel. As a result, the flea becomes hungry, quests for more hosts, and bites more frequently. At lower temperatures, this blockage appears to be less well developed, leading to a complex interaction between flea living conditions, including temperature, and infectiousness [58].

Feral dogs not only pose a threat to wildlife and livestock through hunting [65-69] but also have an impact on people in other ways. They can hunt marmots and dig their burrows, which puts them at risk of acquiring fleas that may carry a disease deadly to people. This situation highlights the need for further research into the complex interactions between marmot burrow temperatures, dogs, sheep, and marmots, as well as the ecology of Y. pestis under real-world conditions.

5. Conclusions

1. Disturbances from predators affect the energy expenditure of Himalayan marmots: When marmots are disturbed by predators during the summer, they seek refuge in their burrows, which are below their assumed thermal neutral zone. At a depth of 0.4 meters, the temperature inside the burrows is around 13.8 °C, and at a depth of 1.0 meter, it further decreases to 11.4 °C. These temperature decreases are more significant at higher altitudes, with temperatures as low as 9.6 °C and 6.4 °C at 4400 meters.
2. Marmots face challenges in maintaining their energy balance: The air temperature in the marmots' habitat is generally colder than their thermal neutral zone, except for brief periods during the day. Living above the tree line is necessary for marmots to access grass for foraging, but it exposes them to lower temperatures. To cope with this, marmots utilize radiative heating to reduce the energy required to stay warm.
3. Permafrost is likely present at around 4400 meters and the chance for it becomes more pronounced at 4750 meters in the Himalayan region. Soil's significant thermal mass leads to gradual temperature adjustments with increasing depth. At a depth of 10 to 15 meters, the soil temperature aligns with the annual average air temperature which above 4500 meters is below freezing. This supports the presence of permafrost at higher elevations within burrowing distance at the upper edge of the marmots' distribution range.

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Author's Contributions

Conceptualization, HP, TN.; methodology, HP, YL.; field supervision, TN; software, YL.; validation, HP, YL, TN.; formal analysis, YL, HP; investigation, YL, HP, TN, AS.; resources, YL, HP, NT, AS..; data curation, YL; writing—original draft preparation, HP; writing—review and editing, HP, YL, S, TN.; project administratio

Data Availability

Due the large volume, the measurements underlying the data presented in this study are available on request from the corresponding author.
n, YL.; funding acquisition, HP, YL. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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Table S1. Average daily maximum temperature in the months that Himalayan marmots are not hibernating (May – September) between 2020 and 2023 (three years of continuous measurements) in Nar Valley (Nepal) in relation to altitude (meter above sea level). Cables of the N-facing station at 4200 meters had been chewed by Himalayan pikas (Ochotona himalayana) resulting in loss of data. Lower than about 4000 meters, the maximum temperature is on average thermally neutral for marmots.

	North				South			
	3600 m	4200 m	4600 m	5200 m	3600 m	4200 m	4600 m	5200 m
May	11.9	9.9	6.0	1.4	10.9	8.6	6.9	2.1
June	14.2	12.2	9.2	4.0	13.1	11.0	8.9	4.8
July	15.0	12.5	10.4	5.1	13.8	11.7	10.1	5.5
August	15.4	13.1	10.2	5.2	14.5	12.0	10.0	5.9
September	13.6	no data	9.0	4.1	13.0	10.4	9.3	4.6

Table S2. Average minimum night temperature in the months that Himalayan marmots are not hibernating (May – September) between 2020 and 2023 (three years of continuous measurements) in Nar Valley (Nepal) in relation to altitude (meter above sea level). Cables of the N-facing station at 4200 meters had been chewed by Himalayan pikas resulting in loss of data. All night temperatures are below the thermoneutral zone of marmots.

	North				South			
	3600 m	4200 m	4600 m	5200 m	3600 m	4200 m	4600 m	5200 m
May	5.3	0.9	-0.4	-4.7	4.8	1.3	-0.7	-4.3
June	8.6	5.2	4.1	-0.7	8.1	5.3	3.9	-0.2
July	10.3	7.2	6.0	1.9	9.8	7.2	5.9	2.2

August	10.3	7.9	6.0	1.7	9.8	7.1	5.8	2.1
September	9.1	no data	4.3	-0.1	8.4	5.6	4.1	0.3

Table S3. Summarizing characteristics of the soil and air at two slopes in Ladakh, namely, at Ulley (where Himalayan marmots occur) and close-by Mangyu (where there are no marmots). Data have been collected at different altitudes during the summer. In blue, inconducive to marmot thermal demands and in red favourable thermal conditions. When we write 'warming up is possible', it means that during the day of the soil temperature readings the maximum air temperature was as indicated in the Table.

Ulley, South-facing grassy slope (with marmots)			Mangyu , North-facing grassy slope (no marmots)		
3700 m; 31 May No permafrost All soil below thermoneutral Warming up possible: maximum of 25 °C	3700 m; 16 June No permafrost Shallow soil above thermoneutral Warming up possible: maximum of 25 °C	3700 m; 4 July No permafrost Soil above thermoneutral Warming hardly possible: maximum of 18 °C	3700 m; 6 June No permafrost Deeper soil below thermoneutral Warming up possible: maximum of 31 °C	3700 m; 24 June No permafrost Shallow soil above thermoneutral Warming up possible: maximum of 24 °C	3700 m; 15 July No permafrost Soil nearly thermoneutral Warming very well possible: maximum 33 °C
4200 m; 1 June No permafrost All soil below thermoneutral Warming up possible: maximum of 19 °C	4200 m; 17 June No permafrost Deep soil below thermoneutral Warming up possible: maximum of 26 °C	4200 m; 5 July No permafrost Soil close to thermoneutral Warming up possible: maximum of 23 °C	4100 m; 8 June No permafrost Deeper soil below thermoneutral Warming up possible: maximum of 26 °C	4100 m; 25 June No permafrost Shallow soil above thermoneutral Warming up possible: maximum of 25 °C	4100 m; 16 July No permafrost Deep soil lower than thermoneutral Warming very well possible: maximum of 27 °C
4400 m; 2 June No permafrost All soil below thermoneutral Warming up possible: maximum of 23 °C	4400 m; 19 June No permafrost Deep soil below thermoneutral Warming up possible: maximum of 21 °C	4400 m; 13 July No permafrost Topsoil close to thermoneutral Warming up possible: maximum of 27 °C	4400 m; 9 June Possibly permafrost All soil below thermoneutral Warming up possible: maximum of 20 °C	4400 m; 24 June Possibly permafrost Most soil above thermoneutral Warming up impossible: maximum of 14 °C	4400 m; 16 July Possibly permafrost All soil below thermoneutral Warming very well possible: maximum of 22 °C
4750 m; 2 June Probably permafrost All soil below thermoneutral	4750 m; 20 June Probably permafrost All soil below thermoneutral	4750 m; 14 July Possibly permafrost All soil below thermoneutral			

Warming up possible: maximum of 23 °C	Warming up possible: maximum of 20 °C	Warming possible: maximum of 21 °C	

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