Effects of human activity on the habitat utilization of Himalayan marmot (Marmota himalayana) in Zoige wetland

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Abstract

Human activity is increasingly and persistently disturbing nature and wild animals. Affected wildlife adopts multiple strategies to deal with different human influences. To explore the effect of human activity on habitat utilization of the Himalayan marmot (Marmota himalayana), habitat utilization patterns of three neighboring marmot populations in habitats affected differently by human activities were recorded and compared. We found that: (1) Distance between reproductive burrows becomes shorter under the influence of human activity, and further, the more disturbance a population suffers, the more burrows were dug as temporary shelter to reduce the distance to those shelters when threatened. More burrows that are closer in the disturbed habitats improve ability to escape from threats. (2) Burrow site selection is determined by the availability of mounds in the habitat. Breeding pairs selectively build burrows on mounds to reproduce, potentially to improve surveillance and the drainage of their burrows. Human activities generally drive breeding pairs away from the road to build their reproductive burrows, likely to reduce disturbance from vehicles. However, even heavy human activity exerts no pressure on the distance of reproductive burrows from the road or the mound volume of the high disturbance population, potentially because mounds are the best burrowing site in the habitat. Marmots deal with nonlethal human disturbance by digging more burrows in the habitat to flee more effectively and building reproductive burrows on mounds to gain better vigilance and drainage efficiency.

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Abstract

Human activity is increasingly and persistently disturbing nature and wild animals. Affected wildlife adopts multiple strategies to deal with different human influences. To explore the effect of human activity on habitat utilization of the Himalayan marmot (*Marmota himalayana*), habitat utilization patterns of three neighboring marmot populations in habitats affected differently by human activities were recorded and compared. We found that: (1) Distance between reproductive burrows becomes shorter under the influence of human activity, and further, the more disturbance a population suffers, the more burrows were dug as temporary shelter to reduce the distance to those shelters when threatened. More burrows that are closer in the disturbed habitats improve ability to escape from threats. (2) Burrow site selection is determined by the availability of mounds in the habitat. Breeding pairs selectively build burrows on mounds to reproduce, potentially to improve surveillance and the drainage of their burrows. Human activities generally drive breeding pairs away from the road to build their reproductive burrows, likely to reduce disturbance from vehicles. However, even heavy human activity exerts no pressure on the distance of reproductive burrows from the road or the mound volume of the high disturbance population, potentially because mounds are the best burrowing site in the habitat. Marmots deal with nonlethal human disturbance by digging more burrows in the habitat to flee more effectively and building reproductive burrows on mounds to gain better vigilance and drainage efficiency.

KEYWORDS

Habitat utilization; Himalayan marmot; Human activities; Burrow feature; Burrow site selection

1 INTRODUCTION

Nature is increasingly affected by human disturbances around the world. With the human population growing, more than 80% of global land surfaces are affected by human activities (Sanderson et al., 2002). Besides affecting environments on a macro level, human activities also affect aspects of wildlife interaction with those environments such as distribution, population dynamics, and ability to survive in changing conditions (Trombulak & Frissell, 2000; UNEP, 2001; Gül et al., 2013). This has a further influence on the regional community dynamic (Hebblewhite et al., 2005; Gehr et al., 2017).

Generally, human activities exert direct and indirect negative effects on animals. Direct and fatal disturbances include poaching (Ménard et al., 2014), road killing by vehicles (Richini-Pereira et al. , 2008) and local extinction due to habitat removal (Griffin et al., 2007; Imperio et al., 2013). Indirect and less fatal effects include habitat degradation (Primack, 2008), reduced reproductive output (Safina & Burger, 1983; French et al. , 2011; Webber et al., 2013) and decline in body condition (Hellgren & Polnaszek, 2011). To deal with human influence, animals have adopted multiple survival strategies such as adjusting time budgets (Poudel et al., 2015a), allocating more time to vigilance (Griffin et al., 2007; Poudel et al., 2015b), or using habitats farther away from human activity (Paudel & Kindlmann, 2011; Macedo et al., 2018; Pita et al., 2020). Furthermore, species that accompany humans, such as domestic dogs (*Canis lupus familiaris*), also negatively impact the survival of wild animals (Mainini et al., 1993; Mori, 2017). Affected animals typically avoid dogs, adjusting their habits to minimize spatiotemporal overlap with dogs (Silva-Rodríguez et al., 2010; Poudel et al., 2015a). On the other hand, some animals benefit from human activity. For instance, some prey species experience reduced mortality because humans drive their predators and/or competitors away from human-dominated habitats (Hebblewhite et al., 2005; Muhly et al., 2011; Lambe, 2016). Some species have improved feeding efficiency due to human activities (Xiang et al., 2011; Marty et al., 2019) or gain reproductive success due to better nesting conditions in areas with human activity (O'Donnell & Denicola, 2006).

Anthropogenic landscape alterations like deforestation, agricultural development, and commercial exploitation are considered a threat to natural habitats and animals (Bryant, 1996; Primack, 2008). Consequently, animals confronted with human disturbance of their habitats will either fail to adapt and perish or become accustomed to the changed environment, actively or passively. For example, highly mobile species like certain birds and ungulates may survive by exploring new habitats away from the disturbed areas (Safina & Burger, 1983; Paudel & Kindlmann, 2011; Scholten et al., 2018). However, for residential species such as some large carnivores or amphibians who cannot avoid human disturbances in the form of roads or logging through migration, their populations decline, and local extinctions are common (Hebblewhite et al., 2005; Fei et al., 2006; Griffin et al., 2007; Klaassen & Broekhuis, 2018). Nevertheless, certain other residential species, like rodents and small carnivores, are better able to adapt and survive in human-dominated habitats (Lambe, 2016; Harris & Munshi-South, 2017). In terms of the effect of human activities on habitat utilization for animals that can survive disturbances which are not directly fatal, human activities may promote the density of the regional population, as in rodents (Lehrer et al., 2012; Pipoly et al., 2019). Such animals may build additional burrows for shelter when threatened (Blumstein et al. , 2001), construct their burrows away from roads (Sahlen et al., 2011; Yuan et al., 2017) or select regions with large stones to allow better vigilance (Borgo, 2003).

Marmots (*Marmota* spp.) are large, ground-dwelling and burrowing squirrels with relatively weak ability to disperse and high philopatry (Griffin et al.. , 2007; Armitage et al., 2011), forcing them to continue exploiting habitats disturbed by humans (Neuhaus & Mainini, 1998). Previous studies illustrated that Himalayan marmots (*M.himalayana*) deal with grazing disturbances by adjusting their daily time budget (Poudel et al., 2015a) and changing the time allocated to feeding and vigilance behavior (Poudel et al., 2015b). In comparison, yellow-bellied marmots (*M. flaviventris*) also adjust time spent on feeding and vigilance and adjust their flush initiation distance when disturbed by different human activities (Li et al., 2011), while alpine marmots (*M. marmota*) and Olympic marmots (*M. olympus*) have learned to tolerate hikers that pass by (Mainini et al., 1992; Griffin et al. , 2007).

Himalayan marmots are mainly distributed across the Qinghai-Tibetan Plateau (Shrestha, 2016). Some regional populations suffer persistent disturbance from human activities such as extermination campaigns to prevent disease, which subsequently has caused them to increase their reproductive rate in the years following these population reductions (Huang et al., 1986). Other populations are indirectly disturbed by domesticated yaks and goats, resulting in changes to time spent feeding and greater feeding efficiency (Poudel et al., 2015a; Poudel et al., 2015b).

The effects of persistent, but not fatal, human disturbances on the Himalayan marmot requires further investigation. For example, the impact of motor vehicle activity on their habitat utilization, population dynamics and behavioral plasticity is still underexplored (Kitchen et al., 1999; Klaassen & Broekhuis, 2018; Edwards et al., 2019); Whittington et al., 2019). In the present study, we recorded and compared the patterns of habitat utilization of three Himalayan marmot populations sharing the same habitat type, but suffering different levels of anthropogenic disturbance, to explore the effects of human activity on this species' behavior and discover changes that might improve their survival. We predict that: (1) the distance between burrows of each breeding pair will decrease with increasing human activity; (2) more temporal burrow will be dug and consequently, the distance between burrows will become shorter with increasing human activity; (3) the distance from reproductive burrows to the nearest road will become longer with increasing human activity; and (4) due to the absence of large rocks in the region, marmots impacted by human disturbance will preferentially build reproductive burrows on sites that allow for better surveillance of the area, such as big mounds occurring on the grasslands.

2 MATERIALS AND METHODS

2.1 Study site and animals

This study was conducted around Duoma (103.01°E, 33.5°N), a village approximately 8.5 km southwest of the town of Ruoergai County in the Zoige wetland, the biggest plateau peat bog in the world (Zhang et al., 2005). The Zoige wetland is located in the eastern Qinghai–Tibet Plateau, southwestern China. The study site is a mosaic of grasslands, ground frost heaves, rivers and wet and dry wetland patches. Marmots residing in the area prefer dry, flat patches with short grass and few frost heaves (Guo et al., 2020).

The study group consists of marmots living around the village of Duoma (Fig. 1A). This population has been the subject of ongoing behavioral ecology study since 2017, and we had no direct interaction with them during data collection for the present study. Three populations live in different regions with the same types of habitat, but suffer different degrees of anthropogenic disturbances. These groups were compared to determine what effect human activity has had on the habitat utilization strategies of Himalayan marmots and how the marmots cope with these influences. The marmots living in front of the village, hereafter the high disturbance habitat (HDH), are persistently disturbed by the daily activities of local residents including passing motor vehicles and stray dogs. This interference does not directly kill marmots and does not change their preferred habitat type (Guo et al., 2020). Marmots living behind the village in the low disturbance habitat (LDH) endure relatively fewer disturbances than those living in front of the village. A third population living to the west of the village lives in a minimally-disturbed natural habitat (NH) and serves as a control group (Figure 1).

2.2 Sampling method and statistical analyses

During the marmots' active period (not in hibernation) in 2019, we classified the intensity of human disturbance of each habitat based on the degree of pressure from human activity on the different groups recorded during behavioral observations in 2018. The three study groups were designated as living in the high disturbance habitat (HDH), the low disturbance habitat (LDH), and the natural habitat (NH). To quantify the amount of human activity in the area, we recorded how many automobiles, motorcycles and stray dogs passed by the marmot habitat every 15 days from April 20 to October 5, 2019.

In each of the three habitat areas, we recorded the GPS coordinates of reproductive burrows (the most extensively used burrows) and temporary burrows (used only occasionally for shelter) of every breeding pair, as well as the physical parameters of each reproductive burrow and the natural feature where it occurred (e.g. hummock/mound or flat ground). The locations of all burrows were mapped in Google Earth, which was then used to find the distance between each (adjacent) reproductive burrow (only burrows with geographical connectivity were included, and finally result in 51, 47 and 31 inter reproductive burrow distances for HDH, LDH and NH); the distance between all burrows (50 distances were randomly selected in each habitat); and the distance from some reproductive burrows to the nearest road (for detail please see Supporting Information figure S1 to S4 and table S1). We measured habitat utilization by linking the outermost burrows recorded to form a perimeter and calculating the density of breeding pairs and burrows inside. The same procedure was applied to all three populations, but because there is no disturbance from motor vehicles in the natural habitat, the distance from the outermost reproductive burrow to the nearest road was used as the standard distance to the road for all burrows in the natural habitat.

A chi-square test was used to determine whether there was seasonal variation in human activity and corresponding diversification of burrow density and breeding pair density. A t-test was used to determine whether the intensity of human activity was significantly different among the three habitats and whether differences in parameters such as the number of reproductive burrows and total burrows, the distance between burrows, the distance between reproductive burrows and the road, and burrow site measurements were significantly different by population. All statistic were conducted in SPSS 20.0.

3 RESULTS

3.1 Differences in intensity of human disturbance

In the high disturbance habitat, within an area of 0.51 km^2, there were 37 marmot breeding pairs; in the low disturbance habitat, within an area of 0.62 km^2, there were 31 breeding pairs; and in the natural habitat, within an area of 0.31 km^2, there were 17 breeding pairs (Figures 1B, 1C, 1D; Table 1). There were no lethal encounters between marmots and either humans or stray dogs observed during the sampling period. The intensity of different human activities differed significantly among the three study habitats (Figure 2). No seasonal variation in the intensity of those human activities was detected for either the high disturbance or low disturbance habitats, but there is seasonal fluctuation in the frequency of automobile and stray dog incursion into the natural habitat (Table 2).

3.2 Differences in habitat utilization

The density of breeding pairs was 72 pairs per km^2 in the high disturbance habitat, 50 pairs per km^2 in the low disturbance habitat, and 55 pairs per km^2 in the natural habitat, although none of the differences detected among the three habitats are statistically significant. However, inter-group differences emerged in measurements related to the burrows themselves, with a significant negative correlation between the intensity of human activity and the number of burrows per breeding pair: the more human activities, the more burrows were dug in the habitat (Figure 2; Figure 3A). Consequently, burrow density in the high disturbance habitat was significantly greater than either of the natural habitat (χ^2 = 143.35, p = 0.000) and low disturbance habitat (χ^2= 130.5, p = 0.000), though no significant difference was found between the low disturbance habitat and the natural habitat (χ^2 = 0.3, p = 0.60) (Figure 3B).

Furthermore, average distance between burrows derived from burrow density also differs between different habitats: inter-burrow distance of reproductive burrows in the high disturbance habitat is less than that of the other two habitats (t = -3.22, p = 0.002 relative to natural habitat and t = -2.95, p = 0.004 relative to low disturbance habitat), although no significant difference was found between the low disturbance and natural habitats (t = -0.18, p = 0.86) (Figure 4). As for the distances between all burrows in the habitat, relative to the natural habitat, human activities led to the same decline in the inter-burrow distance in two disturbed habitats (Figure 2; Figure 4).

Similarly, the characteristics of sites selected for the digging of reproductive burrows also differed depending on human activity levels. Relative to pairs in the low disturbance population, both reproductive pairs in the high disturbance population (χ^2= 7.28, p = 0.007) and the natural population (χ^2 = 5.89 p = 0.015) preferentially constructed their reproductive burrows on mounds raised above the level of the surrounding ground (Figure 5A). The volume of those mounds also differed between sites, with mounds used for reproductive burrows in the high disturbance population being significantly smaller than mounds in the natural habitat (t = -3.66, p = 0.001), and both of those habitats' mounds being much smaller than the mounds selected by pairs in the low disturbance population (Figure 5B; Figure 6). Finally, mean distance from reproductive burrows to the nearest road in the high disturbance habitat is significantly shorter than in the low disturbance habitat (t = -6.17, p = 0.000) (Figure 5C).

4 DISCUSSION

We found that breeding pairs in the high disturbance habitat tended to dig more burrows, resulting in greater burrow density and a consequent decrease in inter-burrow distance. Marmots in the region generally prefer to construct reproductive burrow on mounds in all three habitats. However, the mound size and distance to the corresponding nearest roads varied. Similarly, breeding pairs in the low disturbance habitat also dug more burrows than in the natural habitat, resulting in shorter inter-burrow distance but no difference in burrow density or inter-burrow distance for reproductive burrows only between the two habitats. Relative to reproductive burrow site selection of pairs in the HDH, breeding pairs in the LDH on average dug their burrows farther away from roads but did not show an increased tendency to build burrows on mounds.

Different animals have greater or lesser chances to survive in the face of human disturbance (Richini-Pereira et al., 2008; Fei et al., 2006; Ménard et al., 2012; Imperio et al., 2013) depending upon the type and degree of human activities (Griffin et al., 2007; Ménard et al., 2012) as well as the species' ability to adapt to disturbance (Griffin et al., 2007; Muhly et al., 2011; Webber et al., 2013; Yang et al., 2019). Possible outcomes for these populations include either coexistence with humans or active avoidance of humans (Magle et al., 2005; Griffin et al., 2007), or local extinction (Fei et al., 2006; Imperio et al., 2013). Large-bodied animals tend to avoid habitats impacted by humans regardless of whether humans actively kill them (Macedo et al., 2018; Klaassen & Broekhuis 2018; Pita et al., 2020). In rare cases populations forced to share habitats with humans, such as leopards (*Panthera pardus*) in Mumbai, India, develop particular strategies like adjusting their daily time budget and prey selection to survive (Braczkowski et al., 2018). Other, small-bodied species may survive more easily in areas of intense human activity than bigger species and even benefit from the altered landscape. For example, red foxes (*Vulpes vulpes*) occur at higher densities in the city than in rural areas because of the absence of coyotes (*Canis latrans*), and some urban-living macaques (*Macaca* spp.) obtain better food relative to rural populations animals (Lambe, 2016, Marty et al., 2019). Highly residential species with limited migration ability and low phenotypic plasticity are at the greatest risk of going locally extinct due to human disturbance (Fei et al., 2006; Imperio et al., 2013). However, species that are able will cope with human disturbance through changes in demographic dynamics (Edwards et al., 2019), habitat utilization (Kumar et al., 2017; Klaassen & Broekhuis 2018), and social structure and mating systems (Pipoly et al., 2019) not observed in populations of the same species unaffected by humans.

As a residential species, the three Himalayan marmot populations in the present study suffer varying levels of disturbance from different human activities, leading to different patterns of habitat utilization. While the local residents never kill marmots due to their religious faith, their daily activities are a persistent disturbance for the animals, and the level of disturbance differs between the habitats due to different road locations and number of motor vehicles passing through. Stray dogs are a deadly threat to marmots (Poudel et al., 2015a), but although they are more abundant in the HDH and LDH, several garbage dumps in the area are capable of supplying enough food for those dogs (Figure 1B). Dogs around the village do not go out of their way to hunt marmots within their range (Altmann & Muruth, 1988), and no stray dog predation on marmots was observed during our field work. The main human influence on the marmot populations comes from motor vehicles that pass through the habitat. Seasonal fluctuation in the intensity of human disturbance in the natural habitat occurs due to local residents driving by with their dogs during the annual seasonal rotation of pasture, while daily trips between the village and pastures are done by motorcycles.

We found that marmots in the HDH and the LDH dug more burrows for shelter than breeding pairs in the NH, similar to Vancouver Island marmots (*M. vancouverensis*) (Blumstein et al., 2001). All marmot breeding pairs dig a reproductive burrow for regular use to reproduce and rest, but they also dig temporary burrows, which are occupied less frequently, throughout the home range to use as a refuge when threatened (Blumstein et al., 2001; Zhang et al., 2019). To deal with potential danger from vehicles that pass by daily and occasionally stray dogs, breeding pairs in the HDH showed a greater tendency to dig more temporary burrows. We also found a positive relationship between intensity of human activity and the number of burrows per breeding pair as well as burrow density and a negative relationship with inter-burrow distance for both reproductive burrows only and all burrows. Shorter inter-burrow distances resulting from higher burrow density enable marmots to reach a refuge more quickly when threatened, increasing the likelihood of survival. Based on observations recorded from 2017 to 2019, no new temporary burrows were dug during those years. It is possible that more burrows were dug in the HDH during initial human settlement of the area, but marmots that had grown accustomed to humans' daily activities no longer saw a benefit to digging new burrows (Schell et al., 2018), which is energetically expensive. Similarly, though to a lesser degree than in the HDH, burrow density in the LDH is also higher than in the NH and reduces the inter-burrow distance, allowing the same reduction in time required to reach a safe place.

Though less than pairs in HDH, breeding pairs living in the LDH also dug more burrows than those in the NH and subsequently enjoyed the same shorter inter-burrow distances like what is seen in the HDH. No differentiation emerges on inter all burrow distance between two disturbed habitats probably due to marmots will dig more new temporary burrows however the intensity of human activities, but they may selectively dig new burrow in certain locations and consequently a certain inter burrow distance to meet the requirements of flee efficiency and spend as little energy as possible on digging extra burrows simultaneously. The another fact that no significant differences in inter-burrow distance between reproductive burrows only or total burrow density were detected between the LDH and the NH suggests the human-mediated disturbances were not intense enough to exert pressure on the distance between reproductive burrows (Griffin et al., 2007).

It is also worth noting that the HDH in front of the village has been fully explored and exploited by marmot breeding pairs; the regions surrounding the HDH are uninhabitable due to improper soil and vegetation characteristics or direct human occupation (Guo et al., 2020; Figure 1). The situation is comparable to a fenced-in population of brown hyena (*Parahyaena brunnea*), which has the highest population density observed in the species due to better access to food and the exclusion of other species that pose threats (Edwards et al., 2019). As the HDH is isolated from other habitat due to the village and predators have been excluded by humans, the total marmot population and consequently the number of breeding pairs can grow faster than it would otherwise (Muhly et al., 2011; Lambe, 2016). This could also contribute to the smaller distance between reproductive burrows, and while it was not statistically significant, there was a trend that the HDH had a higher breeding pair density than the other two habitats. In contrast, the LDH is an open area conducive to free dispersal, more like the NH. This might explain why the inter-burrow distance for reproductive burrows in the LDH was no different than that observed in the NH. It is possible that marmots in the LDH have the freedom to actively avoid human influences as many ungulates and big carnivores do, a strategy that is superior to passive adaptation to human influence in some cases (Paudel & Kindlmann, 2011; Macedo et al., 2018). The average inter-burrow distances observed in these two habitats may reflect more typical distancing between marmot pairs, reducing resource competition while maintaining regular contact between pairs. A trend that burrows were arranged more densely in the LDH as opposed to the NH was observed, although it was not statistically significant. Such a trend may arise because human activities affect marmots in the LDH but less so than in the HDH, leading individuals in the LDH to dig only enough burrows to avoid predators. Marmots in the NH dig burrows in response to natural predation pressure, and the marmots in the LDH may be experiencing conditions intermediate to those in the NH and the LDH. More available shelter can provide a survival advantage when confronted with greater anthropogenic disturbance. Compared with HDP, the reactions of LDP individuals may be the most normal outcomes (dig more extra burrows to avoid potential dangers but also appropriate inter "family" distance) when Himalayan marmot affected by persistent, but non fatal disturbances from humans.

The characteristics of the sites marmots selected to dig their burrows also differed among the habitats. The majority of breeding pairs in the NH constructed their reproductive burrows on mounds, indicating marmots in the Zoige wetlands selectively construct burrows on higher ground even in the absence of human interference. Similarly, breeding pairs in the HDH also preferred to dig their reproductive burrows on mounds, even when those mounds were relatively close to a road and smaller than the typical mounds used by pairs living in the NH. Marmots use their reproductive burrows more extensively than other burrows, giving birth to their offspring there and spending a lot of time resting and basking in the sun near the entrance to the reproductive burrow. Resting on high ground provides better vision of the surrounding areas, improving their chances of detecting predators (Borgo, 2003). Burrows built on mounds also have better drainage relative to burrows dug on flat ground (Szor et al., 2008). Alpine marmots also select habitats that allow them to watch for predators more effectively, preferentially remaining near large stones that they climb to engage in surveillance (Borgo, 2003). There are no large stones in the habitats at our study site. Mounds serve the same purpose for the Himalayan marmots near Duoma that stones serve for the alpine marmots, allowing them to see further, while also providing the added advantage of good drainage for burrows.

Most animals choose to locate reproductive dens at sites where they can conceal themselves from humans or avoid them entirely to better protect themselves and their offspring (Ross et al., 2010; May et al., 2012; Sazatornil et al., 2016; Lai et al., 2020). Based on this, we predicted that breeding pairs would stay as far from the roads as possible, but in the HDH the marmots still preferentially built their reproductive burrows on the mounds near roads despite the increased frequency of disturbance from motor vehicle, which can be harmful (Whittington et al., 2019). This surprising result suggests that the availability of mounds is one of the primary determinants of site selection for reproductive burrows in Himalayan marmots. In Zoige wetland, mounds on the dry flat ground could be the limiting resource (Guo et al., 2020), as marmots always built burrows in the mounds that were present regardless of their size or distance from the road. For example, one occupied mound (HDH11) in the HDH was only 2.2 meters from the road (Supporting Information figure S2), and the average size of the occupied mounds in the HDH is smaller than the average size of occupied mounds in the NH (Figures 6A, 6B), indicating that marmots will use all the mounds they can find in an area, even smaller ones. There were no unoccupied mounds left in the HDH, and some breeding pairs that could not find a natural mound to dig their reproductive burrows built their own very small mounds around the entrance of their burrows (Figures 6C, 6D). There are no natural hiding places for marmots in the Zoige wetland (Zhang, 2019), and unlike predators, disturbances caused by daily human activities are not fatal. Consequently, sites that allowed for vigilance while resting were the only suitable choices for reproductive burrows, even if they were frequently disturbed by motor vehicles. Den site selection of American black bears (*Ursus americanus*) and American badger (*Taxidea taxus*), as well as the habitat utilization of Barbary macaques (*Macaca sylvanus*) were also found to be unaffected by the distance to roads (Waller et al., 2013; Sunga et al., 2017; Waterman et al., 2019), suggesting that many species will tolerate persistent but non-life-threatening human disturbance to retain access to otherwise favorable habitat. The importance to the marmots of the vigilance and good drainage of mound-built burrows (Szor et al., 2008) outweighed any disadvantage to digging reproductive burrows close to a road. Furthermore, dig their reproductive burrows near road may also arise because relative to other species sensitive to human disturbance (i.e. *Charadrius nivosus* , *Hypselotriton wolterstorffi*) (Fei et al., 2006; Webber et al., 2013), marmots species are more able to endure not fatal human disturbances (Neuhaus & Mainini, 1998; Griffin et al., 2007). Himalayan marmots disturbed in HDH for generations are highly accustomed to humans' daily activities and disturbances form human activities are no longer selective pressures on the den site selection of the marmots in the habitat (Schell et al., 2018).

Site selection for reproductive burrows in the LDH showed a different profile relative to the other two habitat conditions, with burrows almost equally likely to be located on the mounds or on flat ground. Moreover, the average volume of the mounds selected for reproductive burrows in the LDH is significantly larger than the mounds used in the HDH and the NH. This discrepancy might result from the radically different topography of the area. Aside from having many large mounds, the LDH is sloped, with some areas of flat ground allowing for surveillance equal to the tops of mounds in the other two habitats (Figures 6E, 6F). As a result, breeding pairs in the LDH are no longer limited by the availability of mounds. This is consistent with the greater average distances from reproductive burrows to the road in the LDH as opposed to the HDH. Unlike the marmots living in the HDH, who are forced to prioritize vigilance and drainage, marmots living in the LDH have greater flexibility in where they can build reproductive burrows and so tend to avoid the roads.

Unlike reproductive burrows, temporary burrows were common on flat ground in all three habitats because they were used only to evade immediate threats. Good vision and drainage are not important for temporary burrows (Borgo, 2003; Szor et al., 2008). As a result, Himalayan marmots dig temporary burrows in any location as needed and reserve their reproductive burrows for mounds when possible. This demonstrates the use of multiple habitat utilization strategies at once to cope with human disturbance and natural dangers.

In this study we found different patterns of habitat utilization in response to different intensity of human disturbance in the Himalayan marmot. Correspondingly, some behavioural features also diversity under different pressures (e.g. shorter flee distance, faster running speed in HDH: Guo Cheng unpublished data), furthermore, it is also possible that other aspects of this species' ecology, such as their time budget, demographic dynamics, or mating system, may also change in response to human activity to improve survival, as has been observed in other animals (Huang et al., 1986; Wright et al., 2009; Poudel et al., 2015b; Yang et al., 2019). Generally, Himalayan marmot has high behavioural plasticity and able to cope with non lethal disturbances from human activities. Further investigation is required to fully explore the effect of anthropogenic disturbance on these marmots and the strategies they develop in response.

Additional, though Himalayan marmot is not a threatened species and requires no special protection (Shrestha, 2016), the present study provides some ideas for protecting other threatened marmot species, for example, the reestablishment of wild Vancouver Island marmot population. To enhance the reintroduction efficiency of the species, besides the stepping-stone approach (Lloyd et al., 2019), to establish a semi-wild population like the HDP in the present study may also helpful, furthermore, artificially build some mounds and dig some burrows in the territory may help to promote the growth of breeding pair, and consequently the growth of wild population.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTION

Cheng Guo: Conceptualization (lead); Project Administration (equal); Supervision (equal); Writing - Original Draft Preparation (equal). **Shuailing Zhou:** Data Curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization equal (equal); Writing - Original Draft Preparation (equal). **Ali Krzton:** Writing - Review & Editing (equal). **Shuai Gao:** Data Curation (supporting); Visualization equal (equal). **Zuofu Xiang:** Funding Acquisition (lead); Project Administration (equal); Resources (lead); Supervision (equal); Writing - Review & Editing (equal).

DATA AVAIL ABILIT Y S TATEMENT

The datasets supporting this article are provided as Table S1.

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TABLE 1 The number and density of breeding pair and burrows in three habitats

	Area (km^2)	Number of breeding pair*	Density of breeding pair**	Number of all burrow	Density of all burrow
HDH	0.51	37	72	694	1361
LDH	0.62	32	50	350	565
NH	0.31	17	55	167	539

*the same as number of breeding burrow

**the same as density of breeding burrow

TABLE 2 Seasonal variation in the intensity of human activities (measured in the number of daily different human activities) in different habitats

	Automobile	Motorcycle	Stray dog
HDH	0.83	0.83	1.33

LDH	0.83	0	2.00
NH	11.33**	1.33	16.00**

*p<0.05, **p<0.01

Figure legend

FIGURE 1 Map of the study site and location of the three study populations. Blue lines represent roads. (A) The region circled in red represents high disturbance habitat, the region circled in yellow represents low disturbance habitat, and the region circled in green represents minimally-disturbed natural habitat. (B) Area of the high disturbance habitat. Black rectangles represent garbage dumps. Green pushpins represent the location of reproductive burrows. (C) Area of the habitat with minimal disturbance (natural habitat). Pink pushpins represent the location of reproductive burrows. White line in the figure is a makeshift road in the wetland and generally abandoned by local residents, and they prefer the road marked with blue line. (D) Area of the low disturbance habitat. Blue pushpins represent the location of reproductive burrows.

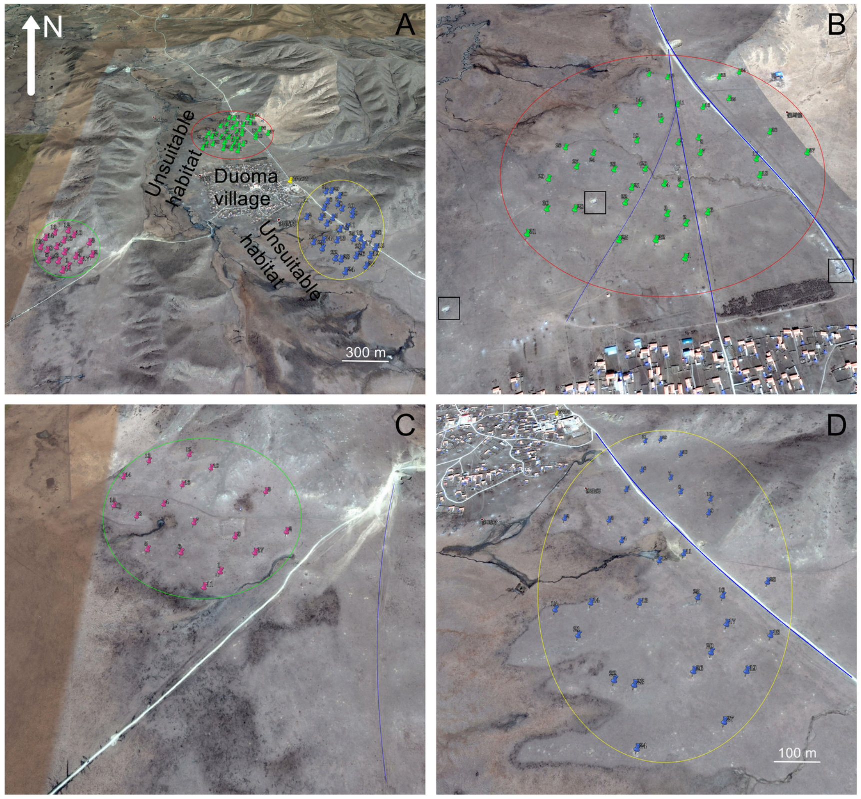
FIGURE 2 Intensity of different human activities within each habitat (the number of automobiles, motorcycles and stray dogs were counted and compared directly to illustrate the intensity of human activities in three habitats).

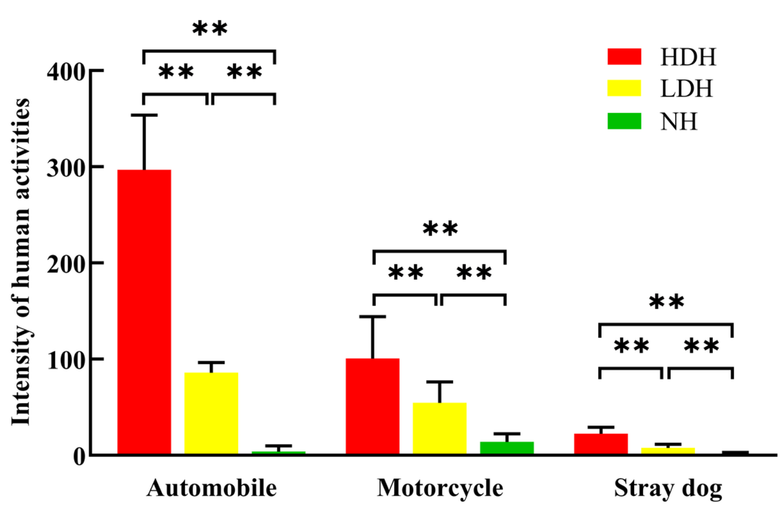
FIGURE 3 Statistics on burrow count by habitat condition. (A) Number of burrows per breeding pair in the three habitats. (B) Burrow density of different habitats.

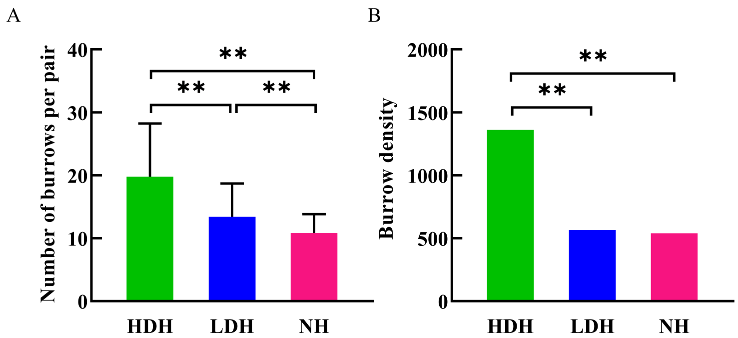
FIGURE 4 Distance between adjacent reproductive burrows and distance between all burrows in the three habitat conditions.

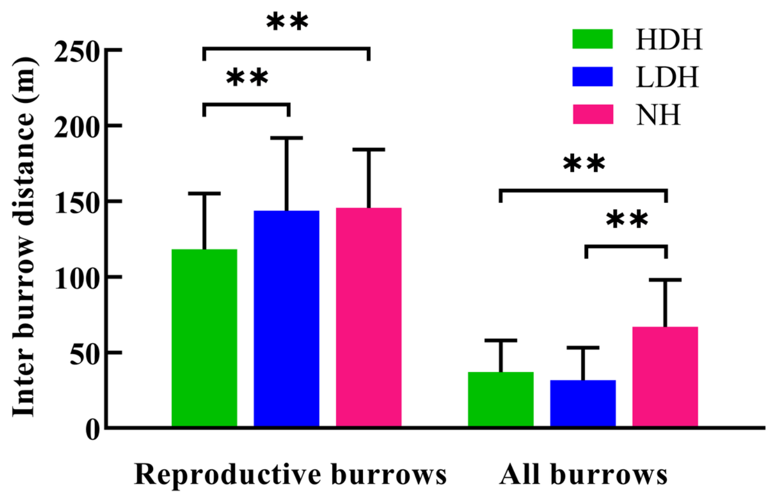
FIGURE 5 Burrow site selection of breeding pairs in the three habitats. (A) The location and number of reproductive burrows by habitat. (B) Volume of mounds selected as reproductive burrow sites by habitat. (C) Distance of reproductive burrow to the nearest road by habitat.

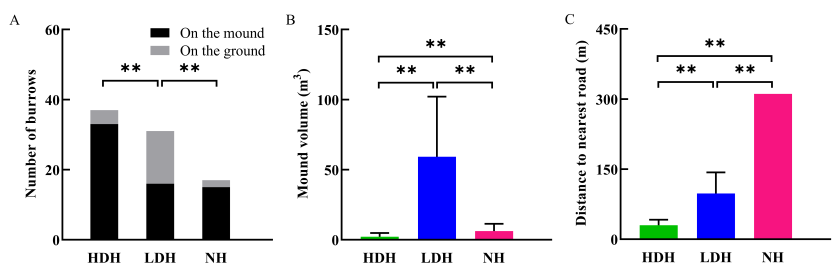
FIGURE 6 The shape and size of mound selected as den site in different habitats. (A) natural mound in natural habitat. (B) natural mound in high disturbed habitat. (C) constructed mound in natural habitat. (D) constructed mound in high disturbed habitat. (E,F) hill in low disturbed habitat. The white arrows in the pictures illustrate the cage (80 cm in height) as the reference and black arrow in figure B is the road next to a reproductive burrow (HDH 13: Supporting Information FIGURE S2).

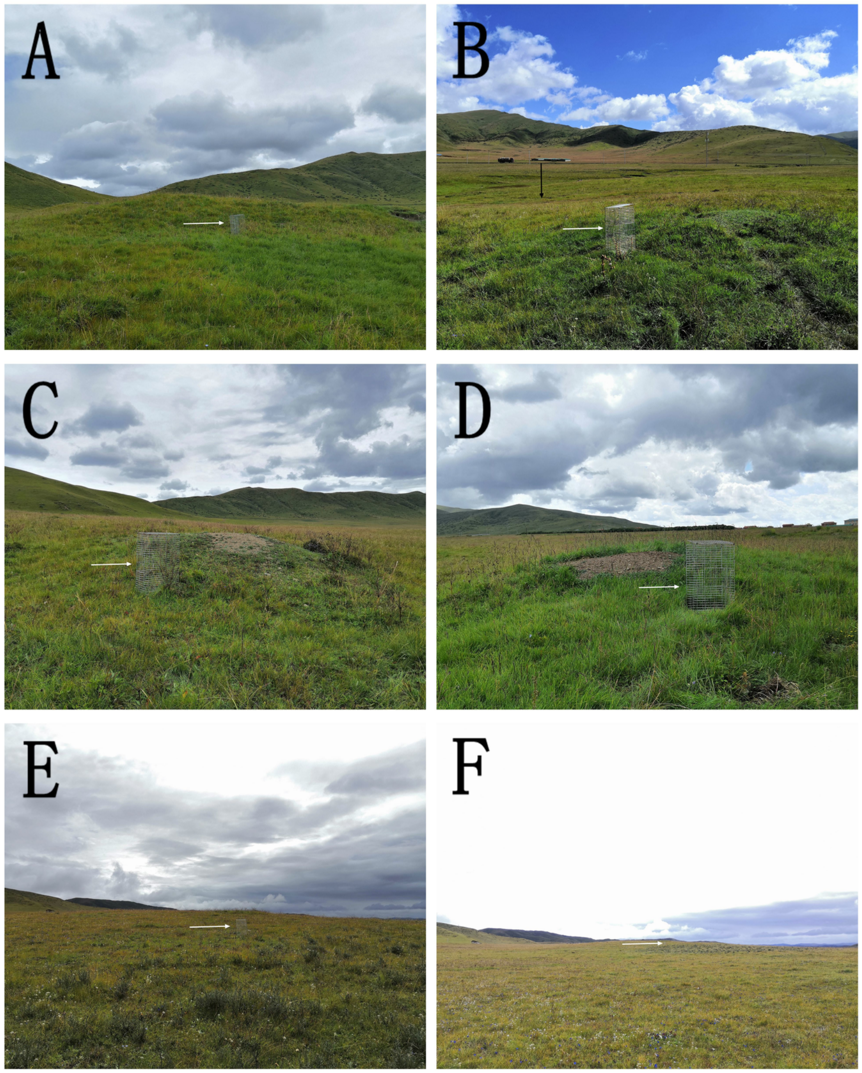

N
A
Unsuitable habitat
Duoma village
Unsuitable habitat
300 m
B
C
D
100 m


Intensity of human activities
400
300
200
100
0
Automobile
Motorcycle
Stray dog
HDH
LDH
NH
**


A
Number of burrows per pair
0
10
20
30
40
**
**
**
HDH
LDH
NH
B
Burrow density
0
500
1000
1500
2000
**
**
HDH
LDH
NH


Inter burrow distance (m)
0
50
100
150
200
250
**
**
**
**
HDH
LDH
NH
Reproductive burrows
All burrows


A
Number of burrows
0
20
40
60
On the mound
On the ground
**
**
HDH
LDH
NH
B
Mound volume (m3)
0
50
100
150
**
**
**
HDH
LDH
NH
C
Distance to nearest road (m)
0
150
300
450
**
**
**
HDH
LDH
NH


A
B
C
D
E
F