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# Investigation on Oxygen and Carbon Dioxide Fluctuations in *Lasiopodomys mandarinus* Burrows

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**ZLW, HS and YFZ designed the experiments. HS, BSW and YWL performed the experiments. HS, WBX and RNM analysed the data. HS wrote the paper.**

**Key words**
**Mandarin vole, Oxygen, Carbon dioxide, Temperature, Humidity.**

## ABSTRACT

The mandarin voles (*Lasiopodomys mandarinus*) is a subterranean rodent that spends its entire life underground in burrow systems, having to endure a hypoxic environment. In this study, we used the embedded artificial tunnel method in a natural burrow system to measure oxygen ($O_2$) and carbon dioxide ($CO_2$) concentrations and the temperature and humidity in the underground burrows of mandarin voles in Xinzheng, Henan Province, China during the spring and summer of 2015. Our results show that 1) the depth and complexity of the burrow were higher during summer than during spring; 2) maximal $CO_2$ levels (2.55%) and minimal $O_2$ levels (16.04%) were recorded in the underground burrows during summer; and 3) the temperature and humidity in the underground burrows were relatively stable during spring and summer. In conclusion, mandarin voles face hypoxic/hypercapnic stress predominantly during summer. The humidity and temperature of the burrows were relatively stable and were not affected by seasonal variation. The burrow system of mandarin voles was more complex and deeper during the rainy summer season. Our study provides a basis for further investigations regarding the evolutionary, physiological, and molecular basis of hypoxia-hypercapnia in mandarin voles.

## INTRODUCTION

Subterranean rodents are rodents that live in an underground burrow ecotope throughout their life (Jike, 2002; Lacey *et al*., 2010; Davies and Jarvis, 2015). Subterranean rodents can be classified into 25 genera, five families, three subfamilies and approximately 160 species (Schleich and Antenucci, 2009). They are widely distributed in Asia, Africa, America, and Europe. The habitats of subterranean rodents are tropical grasslands, grasslands, mountains, arid and semi-arid areas, dense thickets, and forests. The specific climate, soil type, and vegetation pattern in a habitat determine the morphological traits and microclimate of burrows (Burda *et al*., 2007).

All subterranean rodents utilise a unique tunnel system (Begall *et al*., 2007; Wei *et al*., 2007), which affords them several favourable conditions such as relatively stable temperatures, humidity and protection from many predators in the sealed burrows (Antenucci and Busch, 1992; Schleich and Antenucci, 2009). However, subterranean rodents are exposed to multiple stresses including low $O_2$ levels (hypoxia), high $CO_2$ levels, darkness and energy costs of digging (Maina *et al*., 2010). Hypoxic/hypercapnic conditions and darkness are the most stressful challenges all subterranean rodents face in the burrow environment (Arieli and Nevo, 1991; Shams *et al*., 2004; Avivi *et al*., 2010; Maina *et al*., 2010; Park *et al*., 2017). Previous reports have shown that *Spalax carmeli* inhabiting heavy clay soil can survive under minimal $O_2$ levels (7.2%) and maximal $CO_2$ levels (6.1%) (Shams *et al*., 2005); the extreme gas concentration values in golden hamsters reach 10.0% $O_2$ and 10.8% $CO_2$ (Kuhnen, 1986); and *Heterocephalus glaber* (naked mole-rat) can tolerate hours of extreme hypoxia and survive 18 min of total oxygen deprivation (anoxia) without any apparent injury (Park *et al*., 2017). Previous research has demonstrated that subterranean mammals have evolved complex adaptive mechanisms that allow them to cope with severe hypoxia including physiological strategies, molecular biological mechanisms and adaptive evolution (Ar, 1987;

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Shams *et al*., 2004; Wei *et al*., 2007; Listed, 2009; Fang *et al*., 2015). These include improved oxygen delivery and high blood haemoglobin and haematocrit concentrations (Shams *et al*., 2005; Listed, 2009; Avivi *et al*., 2010). The naked mole-rat has even evolved the ability to use fructose to fuel vital organs, such as the heart and brain, during anoxia (Maina *et al*., 2010; Park *et al*., 2017).

The mandarin voles (*Lasiopodomys mandarinus*) is a typical subterranean rodent species found in central China, the southern and central Korean Peninsula, north and central Mongolia and the adjacent areas of Siberia south of Lake Baikal in the Russian Federation (Shouqin, 1981; Antenucci and Busch, 1992; Tian and Wang, 2001; Begall *et al*., 2007; Marcy *et al*., 2013). Mandarin voles are wild, territorial and solitary rodents and are one of the main rodents causing damage to fields in central China (Shouqin, 1981; Tian and Wang, 2001).

Similar to other subterranean rodents, the most stressful challenges faced by mandarin voles are hypoxic/hypercapnic conditions in their underground environment. Mandarin voles have developed unique physiological and molecular mechanisms to deal with hypoxic stress not present in other above-ground rodents (Shams *et al*., 2004; Listed, 2009; Shang, 2016). An increase in haemoglobin concentration can enhance oxygen delivery in mandarin voles, and their platelet number is significantly lower than in mice (Liu *et al*., 2010). Furthermore, the expression of hypoxic related genes, such as *HIF-1α*, vascular endothelial growth factor (*VEGF*) (Ema *et al*., 1997), period circadian clock 3 (*PER3*), thrombospondin 1 (*THBS1*), and hexokinase 1 (*HK1*), is enhanced under hypoxia. Transcription data has shown that following exposure to hypoxic conditions; genes that control functions such as oxygen transportation, angiogenesis, anti-angiogenesis, DNA repair, apoptosis and autophagy were up-regulated in the brains of mandarin voles (Li, 2017).

The habitat of mandarin voles in China is situated in temperate monsoon areas with a highly seasonal rainfall distribution (Qian *et al*., 2002), the dry season includes winter and spring, and the rainy season occurs during summer and autumn (Huang *et al*., 2009; Jiang *et al*., 2013). This persistent seasonal rainfall constitutes an important stress for this subterranean species, the water-logged soil becomes airtight, resulting in high $CO_2$ and low $O_2$ concentrations in the burrow. In this study, we measured the $O_2$ and $CO_2$ fluctuations and temperature and humidity in burrows during spring and rainy summer, and examined the stress of rain on subterranean rodents. The findings of this study further elucidate the natural basis of the physiological and molecular adaptations of mandarin voles enabling hypoxia-hypercapnia tolerance.

## MATERIALS AND METHODS

### *Excavation of burrow systems*

Measurements were carried out during spring (April-May) and summer (June-August) (Zheng, 2007) of 2015 in farmland (113.73°E, 34.40°N) in Xinzheng, Henan province, China. Burrow systems were excavated manually with a spade to expose the entire tunnel system (Shouqin, 1981; Shams *et al*., 2005). Tunnel length and burrow depth were measured using a tape measure. The measurement dates were presented as average value and SEM. Nests were defined as areas filled with nesting material such as dry grass, the granary was defined as the area in the tunnel system containing large amounts of food resources such as peanuts, wheat, and geophyte, and the blind-ended tunnel packed with faeces was regarded as the toilet (Thomas *et al*., 2016).

### *Measurement of gases, temperature, and humidity*

The burrow systems of mandarin voles were identified by the presence of fresh mounds on the surface, and the tunnels were then excavated (Kuhnen, 1986; Shams *et al*., 2005; Anyan *et al*., 2011). If the tunnel became blocked in a short time, we judged that it was being used by mandarin voles. The location of underground tunnels or chambers was determined by piercing the soil with a 10 mm (diameter) steel rod. Once a tunnel was located, a hard PVC pipe was immediately and correctly inserted into the tunnel. To obtain gas samples, a plastic tube, with a length greater than 50cm, was attached to the underground PVC pipe wall. The other end of the plastic tube was attached to a clip and exposed to the air.

$O_2$ and $CO_2$ concentrations were measured using a pump suction $O_2$ detector and pump suction $CO_2$ detector (ADKS, Electromechanical Instruments, Slater, Qingdao, China) with sensitivity ranging from 0-50 000 ppm ± 3% F.S. for $CO_2$ and 0-30% ± 3% F.S. for $O_2$. Soil volumetric water content (volume of liquid water per volume of soil, %) was measured using a soil moisture measuring apparatus (Tsingtao Toky Instruments, China) with a 40 cm probe. The humidity in the tunnel was measured using a hygrometer with a 20 cm probe. Burrow and air temperature were measured using a high precision digital thermometer (-50–300 °C ± 0.1).

All measurements were carried out from 08:00–18:00, at 8:00, 12:00, 14:00 and 18:00, and measurements were conducted at least for a week.

### *Statistical analysis*

Statistical analysis was performed using SPSS for Windows (version 13.0). The mean or maximal and minimal absolute values of the daily measurements were used for subsequent comparative analysis. Comparisons between data sets were performed using a mixed model, with $P < 0.05$ as the criterion of significance.

## RESULTS

*The burrow systems*

The burrow systems of the mandarin voles contained nest chambers, toilet, granary, and tunnels (Fig. 1). Central tunnels were connected to the nest area, toilet, and granary, and secondary tunnels, including a number of shallow tunnels, were used to obtain food and for courtship. Shallow tunnels generally led off from the main deeper tunnels. Burrow systems were generally comprised of tunnels at different depths. Main central tunnels had a depth of 35–68 cm, whereas shallow tunnels had a depth of 10-30 cm. The main nest used in summer (56 ±0.33 cm, n = 6) was deeper than that used in spring (47.66 ±0.19 cm, n = 5). The average tunnel depth in spring and summer was 21.33 ±0.84 cm and 24.66 ±0.84 cm, respectively (n = 12). The length of the burrows system in summer was relatively longer than in spring. Three to five fresh mounds were produced per burrow system.

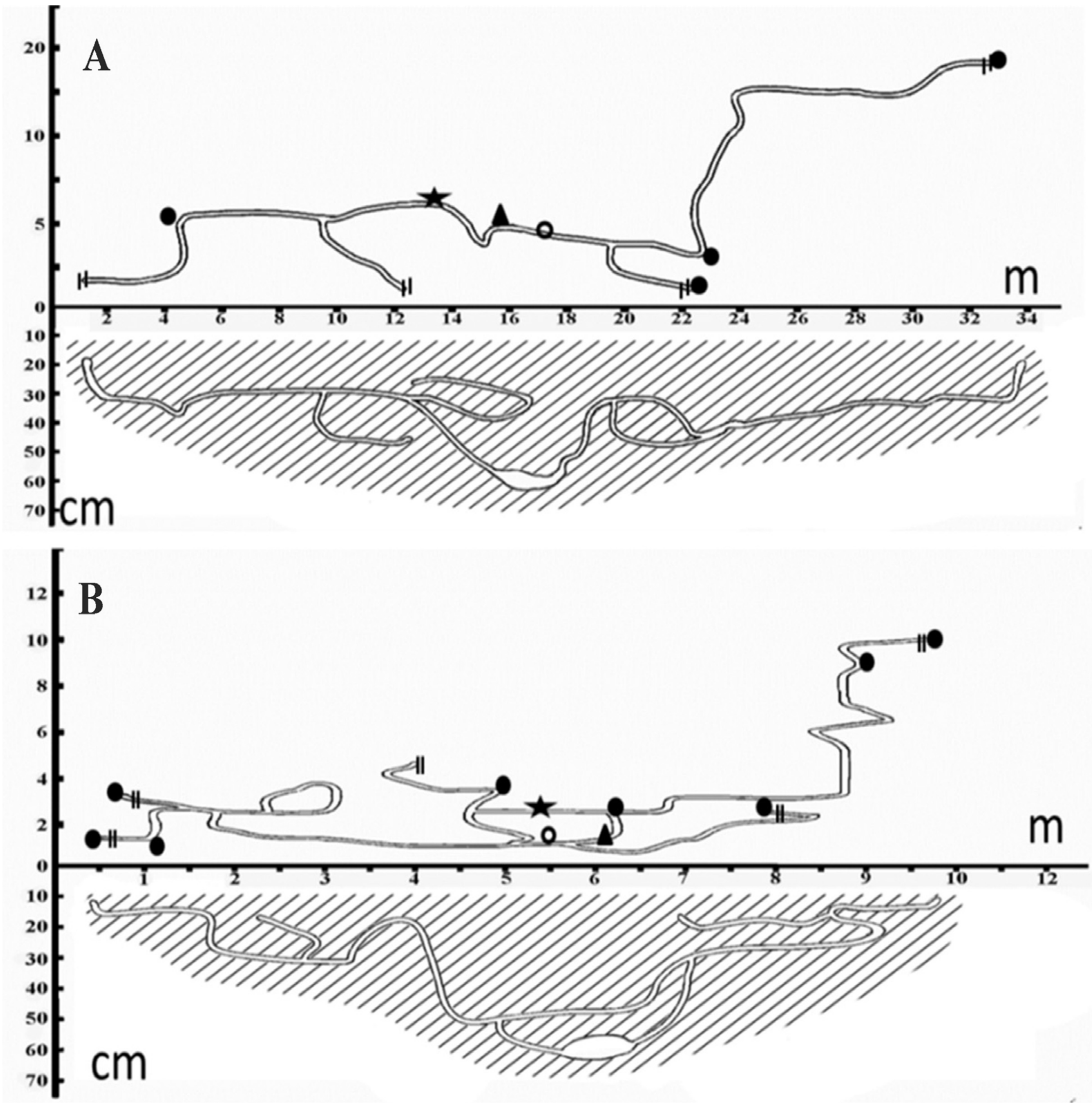


Fig. 1. Mandarin vole burrow systems in spring (A) and summer (B). Black slashes represent the soil, black circles indicate mounds, lines indicate the ending of the tunnel, a triangle indicates a nest, circles indicate the granary and the star indicates the toilet.

*Temperature and humidity in the burrow system and soil moisture content*

The temperature in the underground burrows was relatively stable and lower than the corresponding air temperature both in spring and summer (F = 96.676, df = 85, $P < 0.01$; Fig. 2). However, the temperature in the burrows during summer was higher than that during spring (F = 96.676, df = 85, $P < 0.01$). There was no significant difference in burrow temperature during summer for the four measurement time points (F = 1.132, df = 196, $P > 0.05$); however, there was a significant change in burrow temperature between the four measurement time points in spring (F = 20.007, df = 16, $P < 0.01$).

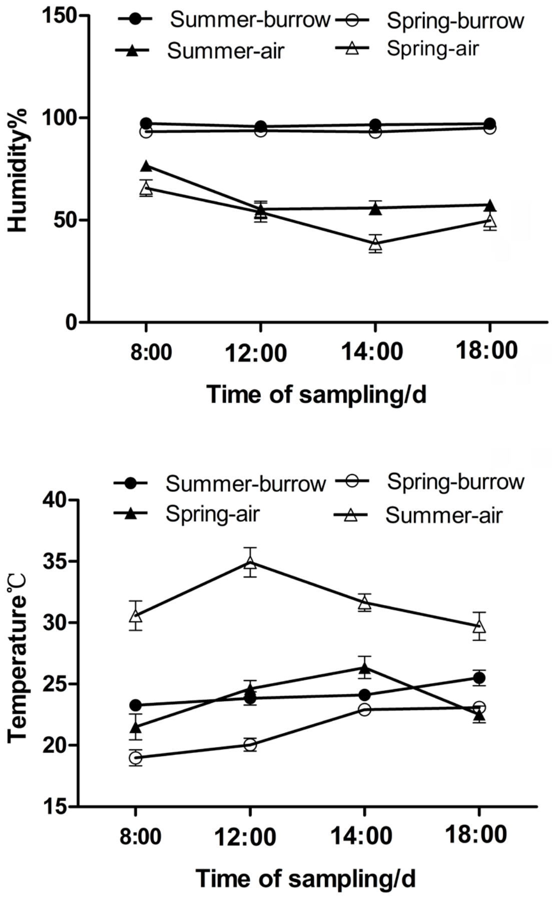


Fig. 2. Temperature and humidity variation in burrows and corresponding air during spring and summer.

No significant difference was observed between burrow humidity in spring and summer (F = 171.285, df = 95, $P > 0.05$), and the humidity in the burrows was maintained at a stable level. However, the humidity in the burrows was significantly higher than in the air (F = 171.285, df = 95, $P < 0.01$). Soil moisture at a depth of 40 cm was significantly higher in summer than in spring (F = 92.199, df = 47, $P < 0.01$; Fig. 3).

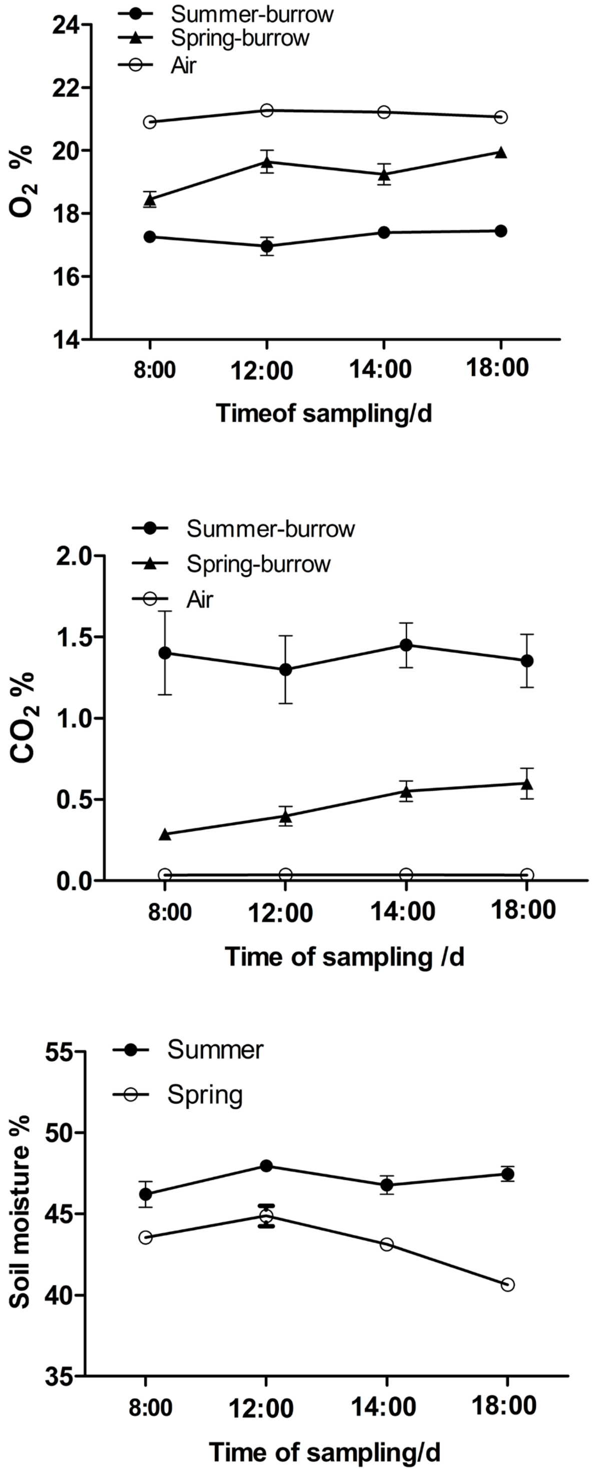


Fig. 3. Gas composition ($O_2$ and $CO_2$) and soil water content in spring and summer.

*Fluctuations in $O_2$ and $CO_2$*

The burrow systems of mandarin voles exhibited fluctuations in gas composition. Minimal $O_2$ levels (16.04%) were measured during the heavy rainy summer (Fig. 3). Rain had a significant influence on $O_2$ concentration in the burrows of mandarin voles (F = 216.370, df = 66, $P < 0.01$). Overall, measurement time had no significant influence on $O_2$ concentration (Wald Z = 0.909, $P > 0.05$); however, the $O_2$ concentration at 8:00 was lower than at 12:00 and 18:00 during spring ($P < 0.05$).

Maximal $CO_2$ levels (2.55%) were also measured during the heavy rainy summer. The $CO_2$ concentration in the burrows was significantly higher than in the air (F = 89.027, df = 61, $P < 0.01$) (Fig. 3). However, time of measurement had no effect on $CO_2$ concentration (F = 0.516, df = 61, $P > 0.05$). Tunnel and air $CO_2$ concentration did not markedly change during rainy summer ($P > 0.05$). However, the $CO_2$ concentration at 8:00 was lower than that at 12:00 and 18:00 during spring ($P < 0.01$).

## DISCUSSION

*The underground ecotope*

Many studies investigating the burrow characteristics of subterranean rodents have examined differences between seasons, burrow size and complexity appear to be correlated with colony size (Thomas *et al*., 2016). The Chinese zokor (*Myospalax fontanieri*) digs most frequently during the spring breeding season, thus, the tunnel is longer in spring (Shouqin, 1981). The burrow structure of the eusocial Damaraland mole-rat (*Fukomys damarensis*) and naked mole-rat is affected by larger colony sizes, this is part of a foraging strategy aimed at expanding their food resources. The mandarin vole is a type of subterranean rodent, which spends its entire life in closed underground burrow systems several metres in length (Arieli, 1979). The burrow systems of mandarin voles are influenced by the season; the burrow systems are relatively longer in spring because this is the mating and reproduction season of mandarin voles, and they need to keep digging the burrows to seek their partners (Zhang *et al*., 1984). In addition, hoarded foodstuffs are consumed in winter, and so mandarin voles may need to search for germinating plant roots. However, the nest appears deeper and more complex (with additional branches) in rainy summer than in spring; this may be caused by the rain collapsing shallow tunnels and the higher air temperature during rainy summer. Another reason may be related to tunnel humidity, the high air temperature in the rainy season leads to soil desiccation, and so deeper nests may be important for maintaining suitable humidity. Thus, mandarin voles require deeper and more complex burrows to avoid the heavy rain and high temperature environment.

*Temperature and humidity in the burrow system and soil moisture content*

The temperature in the burrow depends on soil type, depth, and above ground temperature (Burda *et al*., 2007). The temperature in mandarin vole burrows remains relatively stable and lower than the air temperature. However, the temperature in the burrow changes in correlation with the outside temperature and soil moisture content. Although increased water content reduces breathability, no significant differences in burrow temperature were observed throughout the day in the rainy season. In contrast, in spring, the soil has high breathability and the temperature undergoes significant changes during the day. Subterranean rodents do not drink water in the field, individuals require an intake of exogenous water to maintain their homeostasis, and the body temperature of subterranean rodents increases especially while digging and when low-water content food resources are consumed (Fanjul *et al*., 2006; Baldo *et al*., 2015). Thus, the humidity in the burrow system of subterranean rodents is maintained at a high and stable level. The humidity in the burrows of mandarin voles was also significantly higher than in the air, and the humidity in burrows was not affected by soil moisture. High humidity in the burrow microenvironment contributes to maintaining the water balance, moreover, subterranean mammals can reduce water usage by minimizing evaporative cooling from the lung surface and can satisfy their water requirements from food (Burda *et al*., 2007; Baldo *et al*., 2016). This result demonstrates that burrows constitute an underground, relatively closed system (Ar, 1987; Antenucci and Busch, 1992). In addition, we conclude that mandarin voles are afforded with some favourable conditions by living under relatively stable temperatures, humidity, and shelter protection, similar to other subterranean rodents.

*Fluctuations in $O_2$ and $CO_2$.*

Tolerating low $O_2$ (hypoxia) and high $CO_2$ (hypercapnia) in the burrows is the most stressful challenge facing subterranean rodents (Nevo, 2013). As subterranean rodents, mandarin voles experience an atmosphere that is different from the atmosphere above-ground. The burrows exhibited lower $O_2$ and higher $CO_2$ concentrations than those in the air during both seasons. $O_2$ and $CO_2$ concentrations were simultaneously lower at 8:00 during spring, and we hypothesise that this phenomenon may be related to gas flux in soil (Liu *et al*., 2013). The day and night temperatures in spring differed greatly, and the low temperature at 08:00 in spring reduced the oxygen and carbon dioxide flux in soil, while the relatively high temperature during the day increased gas emissions from the soil. In contrast, the day and night temperature in summer differed only slightly.

The $O_2$ concentration was lower and the $CO_2$ concentration was higher during rainy summer than during spring. The maximal measured concentration of $CO_2$ in mandarin vole burrows was 2.55% at a depth of 40–50 cm, and, simultaneously, 16.04% $O_2$ was measured in high water content soil. Gas exchange between these two atmospheres depends on diffusion related to soil water content and burrow depth. The heavy rains in summer cause the soil to retain more water and thus, the soil has less air space for gas diffusion. During the rainy summer season, the burrows were sometimes flooded and collapsed, the digging activity and animal metabolism of the mandarin voles increased, leading to a rise in $O_2$ consumption and $CO_2$ production. It has been suggested that lower $O_2$ and higher $CO_2$ in burrows are associated with high soil water content and flourishing soil flora during the rainy, high temperature season (Zhang, 2016).

We hypothesise that the gas concentrations measured in this study are far from the actual extreme values that exist in the burrows. This may be because the pipe was inserted into the tunnels at a depth of 40–50 cm, and deeper burrows may have lower $O_2$ and higher $CO_2$; however, our equipment would have destroyed the nest structures at these depths. An additional reason may be that the soil is covered by snow in winter, causing the soil to harden and subsequently leading to a food shortage. These phenomena limit the activities of mandarin voles and increase oxygen consumption in the tunnel; therefore, gas concentrations could reach much higher values than those reported here. The dynamic changes in $O_2$ and $CO_2$ concentrations observed in the burrows of mandarin voles were similar to those reported for *Spalax* living in light soil (Shams *et al*., 2005). Furthermore, laboratory experiments have shown that *L. mandarinus* maintain good physical condition under 15% $O_2$ (unpublished).

In this study, we examined a subspecies found in China; mandarin voles inhabiting north central Mongolia and the Russian Federation experience extremely low temperatures in winter, and the large amount of snow in these regions results in extensively frozen soil. We hypothesise that these conditions will result in lower $O_2$ and higher $CO_2$ concentrations.

*Adaptive hypoxia-tolerance in mandarin voles*

This study presents new data regarding the tunnel parameters of mandarin voles in their natural environment; the most stressful challenges mandarin voles face are low levels of $O_2$ (hypoxia) and high levels of $CO_2$. The hypoxic–hypercapnic adaptation mechanisms of other subterranean rodents have been studied previously (Ar, 1987; Widmer *et al*., 1997; Shams *et al*., 2005; Caballero *et al*., 2006; Liu *et al*., 2010). Mandarin voles also possess strategies for hypoxia tolerance. These include physiological mechanisms, such as decreased red blood cell volume, increased haemoglobin concentration and erythropoietin (EPO) level and decreased platelet counts compared with *Mus musculus* (Liu *et al*., 2010). In addition, the haematocrit (HCT), mean corpuscular volume (MCV) and mean corpuscular haemoglobin (MCHC) are all significantly higher in mandarin voles than in mice. These adaptive changes in mandarin voles would result in viscosity and blood circulation resistance. At the molecular level, the expression of hypoxia-related genes, such as *HIF-1α* and *VEGF*, is significantly enhanced in response to hypoxia stress. *HIF-1α* mRNA can promote the development of the $O_2$ delivery system, and regulates the gene expression of *VEGF*, which may be involved in vasculogenesis and angiogenesis for the maintenance of existing blood vessels. The enhanced expression of *HIF-1α* simultaneously promotes the transcription of the downstream *P53* gene, which eventually improves hypoxia adaptation abilities (Shang, 2016). Transcription data has revealed that Period circadian clock 3 (*PER3*), Thrombospondin1 (*THBS1*), Hexokinase-1 (*HK1*), Metalloproteinase inhibitor 3 (*TIMP3*), Early growth response protein 1 (*EGR*-1) and Serine Protease Inhibitor (*SEPRIN*) gene expression is up-regulated under hypoxia compared with normoxia conditions. These gene functions are involved in oxygen transportation, angiogenesis, anti-angiogenesis, DNA repair, apoptosis, and autophagy (Li, 2017).

Taken together, these results indicate that mandarin voles can survive under hypoxic and hypercapnic stress and possess positive hypoxia adaption strategies. Therefore, mandarin voles constitute a suitable model for further investigations into the physiological, molecular, and evolutionary basis of hypoxia-hypercapnia tolerance.

## CONCLUSIONS

As strict and widespread subterranean rodents, mandarin voles face hypoxic/hypercapnic stress in their underground burrows. Our results indicate that the characteristics of these burrow systems are affected by the seasons, however, additional studies examining other conditions, such as cold snowy winters, are required to complement our findings. Our study lays the foundation for further investigations into the evolution, physiology, and molecular basis of the tolerance of mandarin voles to hypoxia-hypercapnia and darkness.

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*Statement of conflict of interest*

These authors contributed equally to this work.

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