

Adaptive evolution of flaky thumb claw and elongated compulsory arousal duration in the subterranean rodent plateau zokor

G. LIN¹, W. LI¹, E. NEVO², J. SU¹ and T. ZHANG^{1,3}

¹*Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China*

²*Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel*

Received 5 April 2010, accepted 2 June 2010

The opportunities and challenges that life underground poses have led to remarkable examples of adaptive evolution in subterranean species. Here, we report two amazing specialised adaptations in a typical subterranean species, plateau zokor (*Eospalax baileyi*): (1) the flaky thumb claw, which facilitates the holding and cleaning of vegetation roots in the dark; and (2) largely elongated compulsory arousal duration from deep sleep, which may affect its safety in the subterranean niche. To our knowledge this is the first report of these adaptations relevant to specialisations of underground species. We propose that these findings will provide valuable information for further understanding of the developmental mechanisms involved in patterning distal limb appendages as well as sleep physiology.

KEY WORDS: subterranean rodent, plateau zokor, thumb claw, compulsory arousal duration, adaptive evolution.

INTRODUCTION

Subterranean rodents are a widely distributed group of taxa that live primarily underground and are highly adapted to their environment (NEVO & REIG 1990; NEVO 1999; LACEY et al. 2000; BEGALL et al. 2007). The subterranean niche, on the one hand, protects the subterranean rodents from predators and from environmental fluctuations or extreme conditions predominating above ground. Protection is particularly important in periods of enhanced vulnerability: during resting, sleeping, or breeding. On the other hand, however, the subterranean niche is highly specialised and challenging. Burrow inhabitants live under dark stress and are deprived of most sensory cues available above ground, face low food supply, expend high amounts of energy in digging (BEGALL et al. 2007), and are exposed to high pathogenicity (NEVO 1999). The opportunities and

³ Corresponding author: Tongzuo Zhang, Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China (E-mail: zhangtz@nwipb.ac.cn; nwipb@hotmail.com).

challenges that life underground poses have led to remarkable examples of convergent and/or divergent adaptive evolution in ecology, genetics, morphology, physiology, and behaviour in subterranean species across the globe (NEVO 1999).

Plateau zokor (*Eospalax baileyi*) (WILSON & REEDER 2005) is a typical subterranean rodent species that uses its extremities to excavate underground tunnels and to acquire food. The biology and ecology of this species have been widely studied by Y. Zhang and his Chinese colleagues (ZHANG 2007). In our daily observations, we observed two more amazing specialisations related to morphology and behaviour. One is the flaky shape of the thumb claw and the other is largely elongated compulsory arousal duration. Here we report on the two adaptive specialisations and will also discuss the significance of their adaptation.

MATERIALS AND METHODS

Twenty adult zokors (12 males and 8 females) were captured in the field in Datong County (altitude 2800 m a.s.l.) in the eastern Qinghai Province and housed individually in rat cages under normal laboratory conditions (temperature 20 ± 1 °C, length of day 14 hr). Normal rat feed consisted of water (in a drink bottle, to which zokors adapt well, although they obtain water only from food in the field) and carrots, which were provided as the daily diet.

For the observation of food handling (by means of claws), dandelion (*Taraxacum* sp.) roots, which are common food resources of zokors in the field, and threads of carrot, which mimic the shape of dandelion roots, were given to the zokors ($n = 20$). The way the zokors held and ate the two food items was recorded with a camcorder DCR-HC96E (Sony Inc.) for detailed analysis.

Two very distinct behaviours of the zokor were observed during the hours they were awake compared to deep sleep. During waking hours zokors will react immediately when people try to turn their bodies; however, when they are sleeping, they can be handled and even loud noises can be made without disturbing them (e.g. traffic noises, loud flapping, etc.). In order to be consistent, for the compulsory arousal duration analyses in this study, we turned over the bodies of zokors that fell asleep and at the same time recorded the duration using a stopwatch until they awakened and immediately got up by themselves.

RESULTS AND DISCUSSION

Flaky thumb claw

All individuals have a flaky thumb claw with a gap in the apex (Fig. 1). They place the dandelion roots and carrot threads in this gap when holding and eating them. When eating the dandelion roots, zokors slice their thumb claws to shave off any unwanted debris.

The subterranean niche forces the subterranean rodent to have efficient adaptations to hold and deal with food in the dark (BURDA et al. 1999). Plateau zokors possess stocky and strong forelimbs and claws for digging (ZHANG 2007). However, the severely elongated claws may reduce the flexibility for holding their food (mostly stick-shaped vegetation roots), while the flaky thumb claw will thus remedy this deficiency. Moreover, this kind of specialisation on the thumb claw also largely aids zokors in cleaning the dirt from the surface of roots. We also surveyed the claws of other zokor species, as well as other above-ground (Scuridae, etc.) and subterranean (Geomyidae, etc.) rodent species in the Specimen Museum for Biota in Qinghai-Tibetan Plateau. All other zokor species (including *E. fontanierii*, *E. rothschildi*, *E. smithi*, *E. rufescens*, *E. baileyi* and *Myospalax psilurus*), in contrast to other rodent species, have this kind of specialisation, indicating that this might be the result of unique adaptive evolution for the extant subfamily Myospalacinae.



Fig. 1. — A zokor holding a piece of dandelion root: note the lateral image of its flaky thumb claw in the lower right corner.

Modern mammals exhibit the morphology of their distal limb integumentary appendages, which are mainly divided into three types: short, stout hooves (e.g. ungulates), thin, flat nails (e.g. monkeys and humans) and long, keeled, curved claws. Research in developmental biology, utilising the limb as a model system for understanding embryonic patterning of the vertebrate body plan, has generated new insights into the processes underlying the evolution of mammalian limb morphology. Very little was known, however, about the developmental mechanisms involved in patterning distal limb appendages until recently (see the review by HAMRICK 2001). Our findings on the amazing adaptive specialisation of the thumb claw in zokors might improve our understanding of the evolution of limb appendages.

Arousal from deep sleep

In our experiments, zokors occasionally fell into deep sleep, which might have had something to do with the animals feeling uncomfortable in a man-made environment. A total of 15 individuals (9 males and 6 females) fell into deep sleep. Three to five periods of compulsory arousal duration data for each individual were successfully recorded. The average duration for each individual was 61.20–176.82 sec, with a large variation among individuals. No significant variation was found between the two sexes (Mann–Whitney U test, $n = 64$, $P = 0.571$). Further, the durations of different recording times within an individual varied; i.e., the duration maximum could be 5 times the minimum value, which might reflect different depths of sleep. The average of the maximum durations was 129.69 ± 53.82 sec, while the analogous minimum value was 53.96 ± 23.19 sec.

Although there were obvious variations both among and within individuals, our results found largely elongated compulsory arousal duration of this species. Moreover, the sleep was so deep that frequent and strong artificial disturbances did not influence their arousal processes. In contrast, the plateau pika (*Ochotona curzoniae*), which is a fossorial species, inhabits the same area and hardly sleeps in the laboratory. This kind of specialisation in plateau zokors might be due to the feeling of safety in a subterranean niche, i.e. zokors need not respond as quickly as the corresponding above-ground animals do. Another subterranean rodent species, the *Spalax ehrenbergi* superspecies (Y. MAROM pers. comm.) in Israel, seems to have a similar characteristic, in that they also keep sleeping even though they might be disturbed during their sleep. Arousal from sleep is associated with substantial cardiovascular activation and the most notable effects are increases in heart rate, blood pressure, and peripheral vasoconstriction (TRINDER et al. 2003). Elongated compulsory arousal duration will provide sufficient time for data collection in terms of research. We suggest that our findings on the elongated compulsory arousal duration from deep sleep in the plateau zokor will provide useful information for a further understanding of the adaptive evolution and physiology of deep sleep.

ACKNOWLEDGEMENTS

This study was supported by the Training Qualified People Plan "Hope of Western China" of The Chinese Academy of Sciences and the Ministry of Personnel of China (No. O954021211) and General Programs of the National Natural Science Foundation of China (No. 30970366). We also thank Yamit Marom of Tel Aviv University, Israel, who provided analogous information on *Spalax ehrenbergi* superspecies.

REFERENCES

- BEGALL S., BURDA H. & SCHLEICH C.E. 2007. Subterranean rodents: news from underground. *Heidelberg: Springer Verlag*.
- BURDA H., BEGALL S., GRUTJEN O., SCHARFF A., NEVO E., BEILES A., CERVENY J. & PRUCHA K. 1999. How to eat a carrot? Convergence in the feeding behavior of subterranean rodents. *Naturwissenschaften* 86: 325–327.
- HAMRICK M.W. 2001. Development and evolution of the mammalian limb: adaptive diversification of nails, hooves, and claws. *Evolution and Development* 3 (5): 355–363.
- LACEY E.A., PATTON J.L. & CAMERON G.N. 2000. Life underground: the biology of subterranean rodents. *Chicago: University of Chicago Press*.
- NEVO E. 1999. Mosaic evolution of subterranean mammals: regression, progression and global convergence. *Oxford: Oxford University Press*.
- NEVO E. & REIG O.A. 1990. Evolution of subterranean mammals at the organismal and molecular levels: Proceedings of the Fifth International Theriological Congress held in Rome (Progress in Clinical and Biological Research). *Delaware: Wiley-Liss Inc*.
- TRINDER J., ALLEN N., KLEIMAN J., KRALEVSKI V., KLEVERLAAN D., ANSON K. & KIM Y. 2003. On the nature of cardiovascular activation at an arousal from sleep. *Sleep* 26 (5): 543–551.
- WILSON D.E. & REEDER D.M. 2005. Mammal species of the world: a taxonomic and geographic reference (3rd ed.). *Maryland: Johns Hopkins University Press*.
- ZHANG Y.M. 2007. The biology and ecology of plateau zokors (*Eospalax fontanierii*), pp. 237–250. In: Begall S. et al., Eds. Subterranean rodents: news from underground. *Heidelberg: Springer Verlag*.