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• LETTER TO THE EDITOR •

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Photoperiodic refractoriness in energy balance: a specific pattern in Mongolian gerbils (*Meriones unguiculatus*)

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Dear Editor,

Small mammals inhabiting temperate and arctic zone have evolved seasonal life-history traits, such as seasonal body mass cycle and seasonal reproduction. Photoperiod delivers an unambiguous cue to this seasonal acclimatization in most small mammals. Some species lose body mass, and some others increase body mass in short day (SD) compared to those in long-day (LD) acclimation. The variation in body mass is due to the balance of energy intake and expenditure. Basal or resting metabolic rate (BMR or RMR) and nonshivering thermogenesis (NST) are usually increased in SD condition.

Melatonin, a hormone secreted by the pineal gland, is responsible for the photoperiod-mediated physiological process in energy metabolism. The synthesis and secretion of melatonin follow a circadian rhythm, with high levels at night. SD acclimation prolonged the melatonin synthesis and chronic melatonin injection mimicked the response to SD with decreased body mass, carcass lipid stores and food intake in Siberian hamsters (*Phodopus sungorus*). The release of melatonin is regulated by the photoreceptive system in mammals. Melanopsin (encoded by *OPN4*) is an opsin-like photopigment expressing in the most of intrinsically photosensitive retinal ganglion cells (ipRGCs) (Rollag et al., 2003). Previous studies showed that the ipRGCs in *OPN4*-ablated mice were no longer photosensitive intrinsically. Conversely, over-expression of *OPN4* enhanced the photic response of amphibian melanophores. Thus, the sensitivity of ipRGCs to the light seems to be determined by the melanopsin.

Mongolian gerbils (*Meriones unguiculatus*), a non-hibernating rodent species, inhabit in the semi-arid steppes, desert grasslands and agricultural fields of northern China, Mongolia and Russia. The previous studies showed that both wild-trapped and outdoor-raised gerbils displayed significant seasonal variations in body mass and NST (Li and Wang, 2005; Zhang and Wang, 2007). However, SD acclimation or combined SD and cold acclimation did not induce any changes in body mass and NST (Li and Wang, 2005; Zhao and Wang, 2006). These inconsistent data between seasonal acclimatization and photoperiodic acclimation imply that the laboratory-bred gerbils may become refractory to day length. In the present study, the adult gerbils were acclimated in SD for 10 weeks or first SD for six weeks and then transferred to LD for another four weeks, and subadult individuals were also used to test the photoperiodic response. We predicted that the energy balance of gerbils would not show photoperiodic variations and the levels of melanopsin and melatonin would not change in different day length.

The adult male and female gerbils acclimated to SD for 10

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weeks did not change body mass or food intake. The transfer from SD to LD did not induce any changes in energy balance (Figure S1 in Supporting Information). Serum melatonin levels were also unaffected by photoperiod. Adult males had higher serum melatonin levels than adult females (Figure S2 in Supporting Information). In subadult gerbils, no photoperiodic differences were found in either body mass or dry matter intake per day between two groups (Figure 1A–D). RMR and NST were not affected by photoperiod either (Figure S3 in Supporting Information). Compared with females, males had higher body mass and RMR. No sexual difference was found in either dry matter intake or NST. The content of uncoupling protein 1 (UCP1) in interscapular brown adipose tissue (iBAT) showed no photoperiodic or sexual difference (Figure S4 in Supporting Information). In addition, no any difference was detected in the melanopsin contents in retina or serum melatonin levels (Figure 1E and F).

The photoperiodic response of energy balance in small mammals is usually within six weeks. For example, three weeks of acclimation for Siberian hamster, four weeks for root voles, and six weeks for Brandt's voles are sufficient to trigger photoperiodic changes in energy balance. However, eight to 10 weeks of SD treatment in our experiment did not affect energy balance in Mongolian gerbils. The switch of day length is generally used to stimulate photoperiodic response. But the gerbils still showed refractoriness in energy balance when they were transferred to LD after six weeks of SD acclimation. It is verified that age effect is involved in some photoperiodic response of physiological activities. For example, young white-footed mice (*Peromyscus leucopus*) are more likely to be reproductively suppressed by SD than adults (Broussard et al., 2009). Mongolian gerbils show age-dependent effects on energy metabolism, and the younger individuals seem to be more vulnerable to photoperiod. But no photoperiodic differences were also found in subadult gerbils. These results suggest that Mongolian ger-

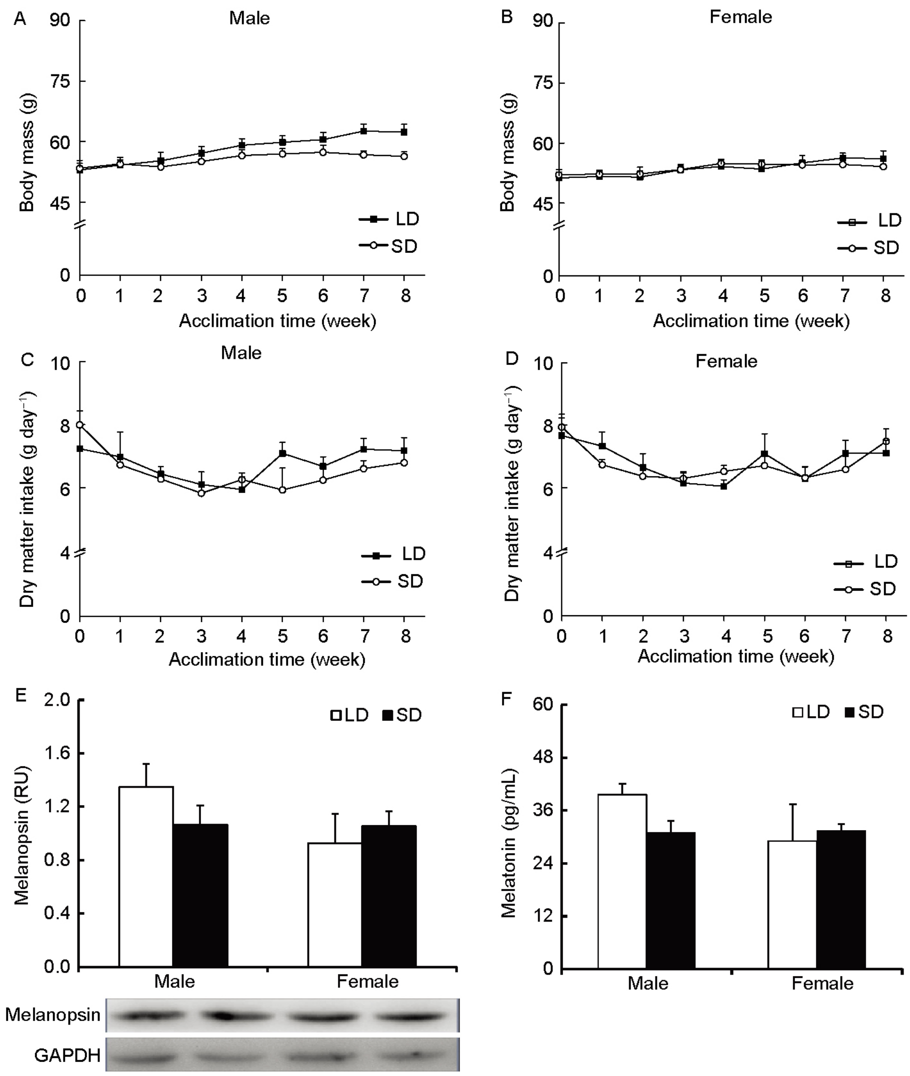

Figure 1 The effects of photoperiod on body mass (A and B), dry matter intake (C and D), melanopsin contents in the retina (E) and serum melatonin levels (F) in subadult gerbils. LD, long day (16L:8D); SD, short day (8L:16D). Results are mean±SE.

bils exhibit a species-specific photoperiodic refractoriness, which is uncommon in seasonal mammals. This photoperiodic refractoriness in gerbils may contribute to the physiological adaptation to the wide distribution along a more than 1,500 km distance from the Hulunbuir Grasslands to the edge of the Tengger Desert in northern China. Nevertheless, gerbils displayed seasonal fluctuation in energy balance with the lowest body mass and NST values peak in winter (Li and Wang, 2005). Seven days of water deprivation led to an obvious decrease in body mass, RMR and NST, and a combined effect of SD and cold treatment on NST and dry matter intake was also found (Li and Wang, 2005). Therefore, comprehensive effects of cold, water and other factors rather than photoperiod alone trigger seasonal adaptation in Mongolian gerbils. This disagreement in photoperiod response relative to combination of photoperiod and temperature may imply that gerbils are animal models that can handle environmental threat at most of time of a year, except in some condition of extreme environment.

Melanopsin and melatonin are two key parts of the photoneuroendocrine pathway controlling body mass and food intake. Melanopsin may mediate circadian responses to light and regulate the release of melatonin. Studies in rats reveal that the daily profile of melanopsin transcripts depends on the seasonal photoperiod. The circadian responses to light in melanopsin knock-out mice become disordered. But in the present study, the subadult gerbils acclimated to different photoperiod showed similar content of melanopsin in retina. In both adults and subadults, no differences were found in serum melatonin levels. The previous studies showing that eight weeks of subcutaneous melatonin implants had no effects on body mass of gerbils support our result. We also found that male gerbils had higher levels of melatonin than females. This sexual dimorphism in the basal level of melatonin may be associated with different sensitivity to exogenous melatonin. For example, the previous studies indicated that the reproductive system was inhibited in females, but not in males by melatonin implants. All these data suggest that the stable melatonin associated with the unchanged melanopsin is the possible mechanism for the absence of photoperiodic responses in energy balance variables of the gerbils.

This study suggests that single photoperiodic cue could not trigger any changes in energy balance in Mongolian gerbils. This refractoriness may be associated with the invariable melanopsin and melatonin in different day length. The physiological mechanisms and evolutional importance for the gerbils to be insensitive to photoperiod are worth further studying.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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SUPPORTING INFORMATION

Figure S1 The effects of photoperiod on the body mass (A and B) and dry matter intake (C and D) of adult gerbils.

Figure S2 Serum melatonin levels of adult gerbils acclimated in different photoperiod.

Figure S3 Changes of RMR (A and B) and NST (C and D) in subadult male and female gerbils during eight weeks of acclimation.

Figure S4 The contents of UCP1 in iBAT of subadult gerbils treated with different photoperiod.

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