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A Field Test of the Activity Budget Hypothesis: The Case of Blue Sheep in Helan Mountains of Ningxia, China

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LT and ZL conceived and designed the experiments. HG performed the experiments. MZ analyzed the data. JD and HG wrote the article.

Key words
Blue sheep (*Pseudois nayaur*), Sexual segregation, Activity budget hypothesis, Helan Mountains.

ABSTRACT

Blue sheep (*Pseudois nayaur*) is a sexually dimorphic ungulate. In general, males are larger than females and the two sexes live in separate groups outside the breeding season. We studied the seasonal activity of blue sheep from May 2010 through August 2012 to test the activity budget hypothesis, which predicts that females spend more time on feeding and that the activity synchronization of same-sex groups is higher than for mixed-sex groups. Our results support the hypothesis. Both males and females spent most of their time on feeding and moving. Feeding behavior differed significantly by sex but moving behavior did not. Activity synchronization indices of same-sex groups were higher than for mixed-groups and were highest for male groups. The activity budget hypothesis of sexual segregation was supported by blue sheep behavior in the Helan Mountains.

INTRODUCTION

Blue sheep (*Pseudois nayaur*) inhabits alpine valleys with bare rock or grass at elevations of 2 500-5 500 m above sea level (Liu *et al*., 2005). Blue sheep has highly economic, medicinal (Du *et al*., 2001), ornamental and recreational values (Hu, 1994). Blue sheep is classified as a Category II Protected Wildlife under the Wildlife Protection Law in China (Wang *et al*., 1998). This species is distributed in the Tibetan Plateau and the surrounding mountain areas. Helan Mountain region is one of the central distribution areas of blue sheep (Wang and Schaller, 1996). Males and females sheep have different external attribute and body size, and they live in separate groups outside the breeding season. Studies on the home range and activity rhythms of blue sheep in Helan Mountain region found sexual segregation between male and female (Cui, 2007), and more investigations should be carried out to make further understanding of the sexual segregation mechanism in blue sheep.

Sexual segregation exists in many ungulates (Ruckstuhl and Kokko, 2002; Ruckstuhl and Neuhaus, 2002). It may occur at various ecological scales and within different 'aggregation units', which means the social group, the habitat type, or merely the space occupied (Pérez-Barbería and Gordon, 1998). Hence, it is difficult to define sexual segregation (Mooring *et al*., 2003). Sexual segregation has an important implication on population dynamics, conservation and management of ungulate populations (Singh *et al*., 2010). Ruckstuhl and Neuhaus (2000) proposed the activity budget hypothesis to explain sexual segregation. The activity budget hypothesis has two key assumptions (Yearsley and Pérez-Barbería, 2005): (1) females digest forage less efficiently than males, because females are smaller than males in body size, mouth, and stomach, which may lead to lower metabolic rates (Demment, 1982; Robbins, 1993; Xu *et al*., 2008); (2) differences in activity budgets may lead to increased costs of synchrony for males and females to maintain group cohesion, so they could hardly stay in mixed-sex groups (Ruckstuhl and Neuhaus, 2002). On the one hand, males may feed forage of lower quality with more efficient digestion, which would reduce time on searching food and increase time on chewing, ruminating, and digesting. On the other hand, females may be more dependent on higher quality food resources. They would spend more time on foraging and moving in search of higher quality forage and less time on chewing, rumination, and digesting

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(Ruckstuhl, 1999; Conradt and Roper, 2000; Ruckstuhl and Neuhaus, 2002; Yearsley and Pérez-Barbería, 2005). The activity budget hypothesis predicts (1) Females spent more time on feeding than males; (2) In order to maintain the behavioral synchrony of group activities, the same sex ungulate tend to coalesce into single-sex groups (Ruckstuhl, 2007). We will verify these predictions for blue sheep, which is the most abundant ungulate in this area. This study will be a significant implication for understanding the sexual segregation and the evolution of sociality in this species, which was important for effective management of blue sheep populations.

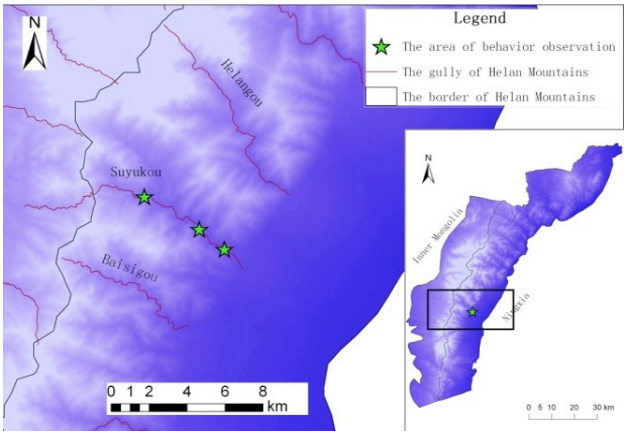

Fig. 1. The study area of behavior observation of blue sheep in the Helan Mountains, China.

MATERIALS AND METHODS

Study area

This study was conducted in the Suyukou National Forest Park in the Helan Mountain National Nature Reserve of Ningxia, China 38°21′ 39°22′N, 105°44′ 106°42′E (Fig. 1). Helan Mountains supports core populations of blue sheep and is the northern range limit of blue sheep in China (Wang and Schaller, 1996), which are located at the boundary between temperate grassland and desert. Elevations used by blue sheep generally range from 2000 to 3000 m above sea level, and the terrain is rocky and rough. Average annual rainfall ranges from 200 to 400 mm, with most rainfall occurring at summer. Extreme maximum temperature is 35.2°C and extreme minimum temperature is -32.6°C. Vegetation in this areas is typical temperate arid and semi-arid upland vegetation types. The vertical distribution of vegetation from low to high altitude is mountain grassland, mountain woodland steppe, mountain conifer forest, and sub-alpine shrubland and meadow. Blue sheep in Helan Mountain region mainly inhabit mountain woodland steppe (Di, 1986; Liu *et al.*, 2004, 2005, 2009).

Behavioral observations

We observed blue sheep from May 2010 through August 2012. Because blue sheep are inactive at night, we established three daylight observation periods during four seasons: 08:00 to 18:00 in spring and autumn, 08:00 to 17:00 in winter, and 08:00 to 19:00 in summer. Observation was conducted from the 21th to 26th days every month, a total of 180 observation days including 36 days in spring (from April 11 to June 20), 36 days in summer (from June 21 to August 10), 30 days in autumn (from August 11 to October 10) and 78 days in winter (from October 11 to April 10). Observation distances were generally from 20 to 200 meters to avoid disturbing blue sheep. We used binoculars (8 x 42) and a telescope (40–60 x 63) to observe randomly selected groups. The groups were classified as male groups, female groups, or mixed-sex groups. The group size of the observed groups ranged from 2 to 46 individuals. Male groups consisted of at least two adult or subadult males. Female groups consisted of at least two adult or subadult females. Mixed-sex groups consisted of at least one adult male and one adult female (Li and Jiang, 2008). Following Xu *et al.* (2012) and Shi *et al.* (2003) and the field observation of blue sheep, we classified sheep activities into five categories: Feeding (biting, chewing, browsing, grazing or swallowing food), standing (feet in contact with the ground, and supporting the body in a stationary state), moving (walking and running), resting (abdomen, back or side of the body in contact with the ground, eyes closed or opened) and others (not mentioned above, such as drinking, grooming, lactating, defecating *etc.*).

We recorded behaviors by focal sampling and group scan sampling methods. Focal sampling was used for identifiable small groups: observers selected focal animals, observed them for a certain amount of time, and recorded the transition time from one behavior to another (Ruckstuhl, 1998). Scan sampling was used for large groups and those not easily observed, by observing each individual in turn at regular intervals until the group ran out of sight (Altmann, 1974). We recorded gender and behavioral state of blue sheep every ten minutes by using a SJ-1 electronic event recorder (Jiang, 1999; Karadas *et al.*, 2017) (Institute of Zoology, Chinese Academy of Sciences). All observations were recorded by the same person. The total sampling time was 264 h, and we observed 115 groups in spring, 72 groups in summer, 96 groups in spring and 260 groups in winter.

Data analysis

We calculated the percentage of each behavioral category (feeding, standing, moving, resting, others). We

used Kruskal-Wallis tests to determine sexual differences in each behavioral category (Zar, 1999). We used a behavior synchronization index to analyze blue sheep behavior by gender group. A synchronization factor (S_f) was calculated for each group for which more than 50% of individuals were engaged in the same activity, When $S_f=1$, group behaviors were highly synchronized. When $S_f=0$, group behaviors were not synchronized. We used $S_t=\sum(S_f)/n$ and $S=\sum(S_t)/k$ to calculate the behavior synchronization index. The mean synchronization S_t for the behavioral observation sample was $S_t=\sum(S_f)/n$, where n is the number of scans. The mean group synchronization index, S, was $S=\sum(S_t)/k$, where k is the number of observed groups. S varied from 0 to 1, and high S values indicated high behavioral synchronization. To avoid the effect of group size, we only calculated S when group size was >5 (Ruckstuhl, 1999). Data were analyzed with SPSS 19.0 (IBM, Armonk, New York, 2010).

RESULTS

Both male and female sheep spent most time on feeding (Figs. 2, 3). Females spent over 50% of time on feeding in all seasons, while males spent over 40%. Feeding as a proportion of total time was followed in decreasing order by moving, standing, resting and other behaviors.

Male and female blue sheep showed significant differences in feeding behavior ($P<0.01$). The proportions of foraging behavior for females were higher than males among four seasons. Proportions of moving behavior were similar for males and females. Proportions of standing behavior were similar for males and females in spring and summer, but males stood more than females during autumn and winter ($P<0.01$). Proportions of resting behavior were similar for males and females during summer and winter, but males rested more than females during spring and autumn ($P<0.01$). Proportions of other behaviors were greater for males than for females during spring, summer and autumn, and much greater in winter ($P<0.01$, Table I).

Behavior synchronization varied by seasons. Behavior synchronization of mixed groups peaked during the winter breeding season and was lowest in summer. Female and male groups showed the opposite trend (Fig. 4).

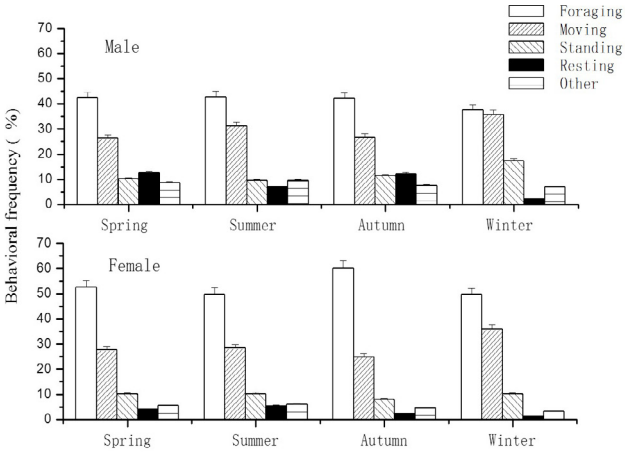

Fig. 2. Proportional allocation of behaviors of male and female blue sheep by season in the Helan Mountains, China.

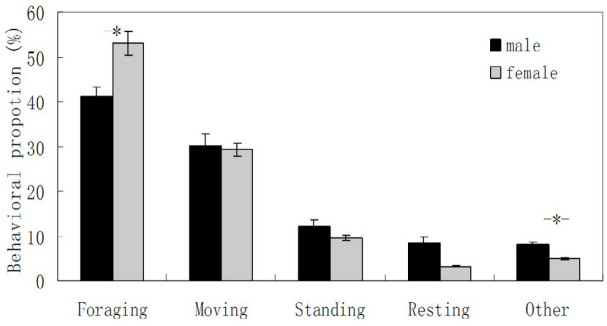

Fig. 3. Activity time budgets (mean±SE) in male and female blue sheep in the Helan Mountains, China. *indicates significant difference between sexes.

The behavior synchronization of mixed group was obviously different from that of male group ($P<0.01$), and the female group ($P<0.01$). And a significant difference was also tested between the behavior synchronizations of male groups and females ($P<0.01$). The behavior synchronization of mixed groups was mostly different from that of male groups.

Table I.- Seasonal daytime behaviors of blue sheep in the Helan mountains.

	Feeding		Moving		Standing		Resting		Others	
	Z	*P*	*Z*	*P*	*Z*	*P*	*Z*	*P*	*Z*	*P*
Spring	-4.155	0.000	-0.193	0.847	-0.045	0.964	-3.643	0.000	-2.134	0.033
Summer	-3.173	0.002	-1.803	0.071	-0.744	0.457	-1.540	0.124	-2.085	0.037
Autumn	-6.704	0.000	-1.233	0.218	-3.542	0.000	-4.928	0.000	-2.518	0.012
Winter	-3.311	0.001	-0.129	0.897	-5.011	0.000	-0.031	0.976	-3.725	0.000

Z, indicates the statistic; *P*, indicates the significance.

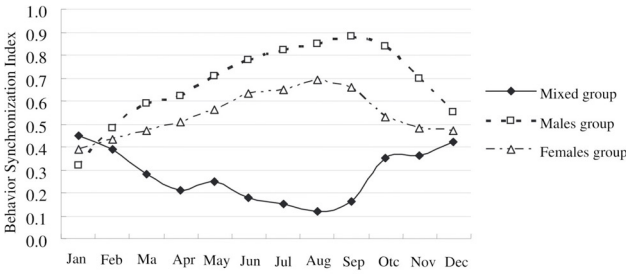

Fig. 4. Behavioral synchronization index of different blue sheep groups in the Helan Mountains, China.

DISCUSSION

A variety of hypotheses have been proposed to explain sexual segregation, such as same-sex peer preference (Bon and Campan, 1996), differences in habitat preferences between males and femals (Mysterud, 2000), sexual differences in predation risks (Jakimchuk *et al*., 1987; Corti and Shackleton, 2002), or different activity budgets (Ruckstuhl, 1998). The activity budget hypothesis has received special attention (Conradt, 1998; Ruckstuhl, 1999; Ruckstuhl and Neuhaus, 2000, 2001, 2002; Neuhaus and Ruckstuhl, 2002; Michelena *et al*., 2004; Li and Jiang, 2008). A prediction of the activity budget hypothesis is that males and females separate and form same-sex groups because of their behavioral asynchrony in mixed-sex groups (Ruckstuhl and Neuhaus, 2002). Ruckstuhl and Kokko (2002) suggested body size dimorphism is a driving factor leading to the sexual differences in activity budget, and an increasing of the sexual dimorphism triggers greater differences in the activity between males and females. But the activity budget hypothesis is still debatable. Some authors found no differences between the sexes in the time spent foraging, moving, resting or ruminating (Mooring *et al*., 2003), and no perceptible sexual segregation and a high synchronization between the activities of males and females (Michelena *et al*., 2004). Females are thought to be less efficient than males at digesting fiber because females are generally smaller than males, but Yearsley and Pérez-Barbería (2005) considered this assumption was based on the species' body masses span three orders of magnitude (Robbins, 1993), while the maximum male to female body mass ratio was 2.6 (Pe´rez-Barberı´a and Gordon, 2000), so the sexual difference in the digestion efficiency of fiber should be very small. However, Ruckstuhl (1998) proposed that energy requirements and foraging behaviour were affected by body size, and females should have a higher metabolic rate and higher nutritional need per unit body mass than males, and they found sexual dimorphism in body size would lead to different movement patterns and time budgets through studying bighorn sheep, *Ovis canadensi*, and adult bighorn rams are about 50% heavier than females. Whether and how the difference of body size between female and male would lead to sexual differences in activity budget still needs more evidence for further investigation.

The activity budget hypothesis predicts that females spend more time grazing than males, and that activity synchrony is higher within single-sex than mixed-sex groups (Ruckstuhl, 1998, 1999). Mooring *et al*. (2003) found that bighorn sheep, *Ovis canadensis mexicana*, had no difference in time budget between the sexes. A study by Weckerly (1993) on the black-tailed deer (*Odocoileus hemionus*) achieved the similar conclution. In contrast, our study found that there was a huge difference in the activity budget between female and male blue sheep, and the same-sex groups had a higher behavior synchronization index than mixed-sex groups (Fig. 4). Besides, females had a longer feeding time than males (Fig. 3). These results gave support to the activity budget hypothesis. Similar results have been reported in the sutdy of Tibetan gazelle *Procapra picticaudata* (Li and Jiang, 2008). Studies on Alpine ibex *Capra ibex ibex* showed that females and males were more synchronized in activities when they were in the same-sex groups than in mixed-sex groups (Ruckstuhl and Neuhaus, 2001). Ruckstuhl (1998) found that the female of bighorn sheep *Ovis canadensis* had longer foraging time, and considered it was difficult for males and females to stay in the same group for their difference in movement patterns and time budgets.

The weight of male blue sheep is 1.52 times over the female blue sheep in the Helan Mountains. The differential of size is more than 50%. Throughout our study, there is a huge difference in the activity budget between females and males. Like other temperate region ungulates, blue sheep are active during the daytime and rest at night (Sayre and Seabloom, 1994), they devote a lot of time to feeding (Liu *et al*., 2005). Blue sheep spent most daylight hours feeding. Ungulate females spend more time than males on feeding (Ruckstuhl, 1998; Xu *et al*., 2012). This phenomenon could be supported by the fact that females have low digestive efficiency, and on the other hand they have a higher nutritional need for pregnancy and lactation, females must rely on feeding high-quality food resources to satisfy their nutritional needs (van Soest, 1994). In the Helan Mountains, the dry climate and low rainfall lead to relatively resource-poor vegetation. This is compounded by complex geological and geomorphological conditions, and low quality and uneven distribution of Gramineae species. Females need higher quality nutrition to gestate and feed their offspring, therefore females need more time for feeding and moving to different types of forage. In contrast, males have a high digestive efficiency and are able to feed on low-quality food resources that are widely distributed. Thus, instead of feeding, males spend more time in resting and rumination.

We recorded significant differences in behavior synchronization between same-sex and mixed-sex groups, and between male and female groups. Behavior synchronization of mixed-sex groups varied seasonally. Mixed-sex groups had a high behavior synchronization in autumn and winter due to breeding. In the non-breeding season, mixed-group behavior synchronization was very low. Behavior synchronization of male groups was lowest during the winter breeding season, even lower than for mixed-sex groups, possibly due to the fact that male groups compete for breeding rights in winter. In the non-breeding season, behavior synchronization of male groups was the highest of the three groups.

CONCLUSION

In conclusion, our research supported the two predictions of the activity budget hypothesis. Even though there are several reasons for sexual segregation, the activity budget hypothesis could explain the sexual segregation mechanism in blue sheep, whether other hypothesis could account for this phenomenon of blue sheep in Helan Mountains or not still need further investigation.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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