Sexual segregation in Tibetan gazelle: a test of the activity budget hypothesis

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Abstract

Tibetan gazelle *Procapra picticaudata*, a threatened endemic species on the Qinghai-Tibet Plateau, is a sexually dimorphic ungulate. Males are larger than females and both sexes live in different groups, except during the rutting season. In order to test the activity budget hypothesis, which was proposed to explain social segregation in ungulates, we studied the activity budget of male and female Tibetan gazelles during the summers of 2005 and 2006. The activity budget hypothesis predicts that females spend more time feeding and group members synchronize their activities more in the same-sex groups than in the mixed-sex groups. We found that females and males of Tibetan gazelle had different activity budgets; females spent significantly longer time feeding and comparably less time on other activities. Activity synchronization indexes between female groups and male groups were similar (female groups: 0.81 ± 0.17, male groups: 0.80 ± 0.19), whereas both of them were significantly higher than that of mixed-sex groups (0.58 ± 0.29). These results suggest that although sexual segregation might be caused by multiple mechanisms, the activity budget hypothesis about sexual segregation is supported by our studies of Tibetan gazelle on the Qinghai-Tibet Plateau.

Introduction

Sexual segregation has been commonly observed in many ungulates outside the rutting season (Ruckstuhl & Neuhaus, 2005). Many hypotheses have been proposed to explain sexual segregation. These hypotheses are classified into four principle categories: reproductive strategy (predation risk) hypothesis, forage selection (sexual dimorphism-body size) hypothesis, social affinity hypothesis and activity budget hypothesis (Main, Weckerly & Bleich, 1996; Ruckstuhl & Neuhaus, 2000).

The reproductive strategy hypothesis and the forage selection hypothesis are trying to explain habitat segregation between the sexes, while the social affinity hypothesis and the activity budget hypothesis center on social segregation (Ruckstuhl, 2007). The former two hypotheses consider sexual differences in body size leading to either sexual differences in predation risk and reproductive strategies or in digestive abilities and forage selection, ultimately causing habitat segregation. These two hypotheses have been testified in some ungulates (Main et al., 1996; Jiang et al., 2000). However, habitat segregation cannot fully explain the cause of sexual segregation, because social segregation is also observed within the same habitat. Social segregation focuses on sexual differences in social preferences or in activity budgets, which are generated not only between males and females but also between different age groups of the same sex (Yearsley & Pérez-Barbería, 2005). Therefore, social segregation may be universal to explain the sexual segregation of ungulates.

Based on social segregation, the activity budget hypothesis is proposed firstly by Ruckstuhl (1998), and has received special attention in recent years (Ruckstuhl, 1999; Ruckstuhl & Kokko, 2002; Yearsley & Pérez-Barbería, 2005; Michelena et al., 2006; Ruckstuhl et al., 2006). Based on the allometry of metabolic rate, body size and mouth size between sexes, the hypothesis states that females, which are considered less efficient at digesting food, should spend more time feeding and less time bedding or engaged in other behaviors than males (Ruckstuhl, 1998). Another prediction of the activity budget hypothesis is that females and males would separate to aggregate in the same-sex groups, respectively, because of behavioral asynchrony (Ruckstuhl, 1999). Some studies lend support to the activity budget hypothesis (Conradt 1998; Ruckstuhl & Neuhaus, 2002) while others do not (Mooring et al., 2003; Michelena et al., 2006).

Similar activity budget and activity synchronization are the key factors of the activity budget hypothesis (Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2002). In this paper, we used the Tibetan gazelle *Procapra picticaudata*, an endemic

ungulate to the Qinghai-Tibet Plateau, as a study animal to test this hypothesis. The study area, Upper Buha River valley, is mostly covered by the homogeneous alpine meadows, and we found no obvious habitat segregation between sexes. We collected the behavioral data of both sexes of the Tibetan gazelle with the behavioral scan sampling method during the summers of 2005 and 2006, and then calculated the activity budgets to test whether smaller females spend more time feeding and less time in other activities. The behavioral synchronization index was calculated to compare the activity synchronization between same-sex groups and mixed-sex groups.

Methods

Study areas and subjects

This study was conducted in the Upper Buha River valley, Tianjun County, Qinghai Province, China (36°53′30″–48°39′12″N, 96°49′42″–99°41′48″E), which is located in the north-west part of the Qinghai Lake watershed area and south of the Qilian Mountains. Elevations range from 2850 to 5826 m above sea level, with an average elevation of 3800 m. The local climate is characterized by dry, cold and long winters, strong winds, high levels of solar radiation and a short frost-free period. The mean annual temperature is −1.5 °C, and the lowest recorded temperature was −40 °C. Annual precipitation varies from 330 to 412 mm and most rain falls between June and September. Alpine meadow, dominated by *Kobresia* spp. and *Stipa* spp., is the main vegetation in the study area. Shrubs of *Hippophae rhamnoides* only distribute along the Buha River valley, which is the largest river flowing into the Qinghai Lake. The four seasons are not clearly distinguished in the study area; however, the period from June to September is the plant-growing period while the period from October to next May is the plant-withering period.

Our study subject was the Tibetan gazelle, a threatened and endemic species to the Qinghai-Tibet Plateau (Jiang, 2004). The populations of Tibetan gazelle are decreasing sharply while their ranges are fragmented and rapidly shrinking (Yin & Liu, 1993; Schaller, 1998; Zhang & Jiang, 2006). Accordingly, it is now classified as a Category II Protected Wild Animal Species under the Wild Animal Protection Law in China and is listed as 'Low Risk' in the IUCN Red List of Threatened Species (Zhang & Jiang, 2006). Tibetan gazelle are sexually dimorphic (Yin & Liu, 1993). The body length of the gazelle is short than 1 m; body weights range from 44 to 77 lb (Macdonald, 1984; Zheng, 1994). Males are longer and heavier than females. The mixed-sex groups are mainly found during the rutting season from late December to early January and after then they separate and aggregate in same-sex groups (Lian *et al.*, 2004). The lambing period in Tibetan gazelles lasts about 2 weeks, from late July to early August (Li & Jiang, 2006). Tibetan gazelle is a common wild ungulate along the Buha River. The focal population at the south of Buha River consists of about 100 individuals. The gazelles spend most of their time on the alpine meadows, except going to the river valley for drinks.

Behavioral observation

The behaviors of Tibetan gazelle were observed with the group scan sampling method (Martin & Bateson, 1993) during the plant-growing periods from June to September 2005, and from June to July 2006. As Tibetan gazelle were inactive during the night (Zheng, 1994), observations were conducted during the daytime between 07:00 and 20:00 h. Because it was difficult to identify the individuals in the wild, we observed randomly selected groups with a binocular (8×42) and a (20–60×63) telescope. We classified the groups into three categories (1) female group, included individuals of one or more adult or subadult females, with or without lambs; (2) male group, composed of one or more adult or subadult males; and (3) mixed-sex group, included individuals of at least one adult female and one adult male (Li & Jiang, 2006). The activities (feeding, bedding, moving, standing and others) of all the group individuals were instantaneously recorded by scan sampling at 5-min intervals. One behavioral sample was defined as an observation started when a group of Tibetan gazelle was found until the group size changed or the group ran out of sight. The observation time ranged from 20 to 275 min, with a median of 70 min. We attempted to observe the gazelle evenly over all daylight hours and to sample equally between both sexes. The group size of the observed groups ranged from 1 to 20 individuals.

Behaviors were classified into five categories: feeding and searching ('feeding' in the following text), bedding and ruminating ('bedding' in the following text), moving, standing and other behaviors. Feeding was defined as grazing on the pasture or moving during a grazing bout with the head below the vertebral column. Bedding referred to lying on the ground for rest and ruminating. Moving consisted in walking or running with its head above its vertebral column. Standing referred to a standing gazelle scanning its surroundings or being motionless with its head erect, and sometimes regurgitating and masticating a cud. Other behaviors included grooming, defecating and lactating. Behavioral samples, that were shorter than 30 min were discarded. All behaviors were observed by the same person. A total of 155 behavioral samples were observed, of them, 73 (5, 085 min) on female groups, 74 (4, 980 min) on male groups and eight (375 min) on mixed-sex groups.

Data analysis

Data were analyzed with SPSS 13.0 statistical package. The percentages of each behavioral category (feeding, bedding, moving, standing and other behaviors) were calculated for each behavioral sample, and then they were arcsine square-root transformed in order to achieve the normal distribution for parametric tests. An independent t-test was used to test sexual differences in 'feeding' and 'standing.' The transformation of 'bedding,' 'moving' and 'other behaviors' did not

result in normality, and hence we applied Kruskal–Wallis tests.

The degree of activity synchronization was measured with the behavior synchronization index (S) proposed by Ruckstuhl (1999). At each scan, a synchronization factor (S_f) was calculated for each group: $S_f = 1$ when more than 50% of individuals in the group were engaged in the same activity; otherwise, $S_f = 0$. The mean synchronization S_i for the ith behavioral observation sample was calculated as $S_i = \sum (S_f)/n$, with n being the number of scans. The mean group synchronization index S was calculated as $S = \sum (S_i)/k$, with k being the number of the observed groups. The group S varies from 0 to 1, meaning from asynchrony to complete synchrony. We only analyzed groups that included at least five gazelles to control the effect of group size on vigilance and feeding behavior (Ruckstuhl, 1999). After taking out the groups of less than five individuals, there were 43 behavioral samples of female groups, 36 samples of male groups and eight samples of mixed-sex groups. Synchronization indexes were arcsine square root transformed, but they were still not normally distributed. We used non-parametric tests to compare the sexual differences in synchronization index. Group size did not affect the synchronization index (Kruskal–Wallis test: $\chi^2 = 19.704$, d.f. = 14, $P = 0.140$); we did not correct the index by dividing it by group size. The length of observations has no significant effect on the synchronization index either (Kruskal–Wallis test: $\chi^2 = 16.438$, d.f. = 20, $P = 0.689$). All significant levels were set at $P = 0.05$.

Result

Both sexes spent most of their time feeding and bedding (Fig. 1); however, female gazelles spent significantly more time feeding than male gazelles (t-test, $t_{145} = 2.635$, $P = 0.009$). Comparably, less time was spent by females on standing ($t_{145} = -2.193$, $P = 0.030$). There were no significant sexual differences in bedding (Kruskal–Wallis test: $\chi^2 = 0.326$, d.f. = 1, $P = 0.568$), moving (Kruskal–Wallis test: $\chi^2 = 2.731$, d.f. = 1, $P = 0.098$) and other behaviors (Kruskal–Wallis test: $\chi^2 = 0.166$, d.f. = 1, $P = 0.683$).
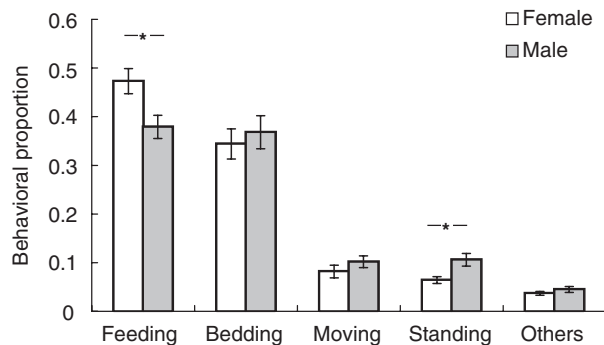

Figure 1 Activity time budgets (mean ± SE) in male and female Tibetan gazelles *Procapra picticaudata* in Upper Buha River, Qinghai-Tibet Plateau. *Significant difference between sexes at $P = 0.05$.

Table 1 Synchronization indexes S for different group types of Tibetan gazelle *Procapra picticaudata*

Group type	S_{mean}	SD	K
Female groups	0.81	0.17	43
Male groups	0.80	0.19	36
Mixed-sex groups	0.58	0.29	8
Total	0.78	0.20	87

The group synchronization differed according to group type. Group synchronization was the highest in female groups, followed by male groups and mixed-sex groups (Table 1). However, the difference was not significant (Kruskal–Wallis test: $\chi^2 = 5.571$, d.f. = 2, $P = 0.062$). There was no difference in synchronization indexes between male groups and female groups (Mann–Whitney U-test: $Z = -0.065$, $P = 0.949$), while there were significant differences between male groups and mixed-sex groups (Mann–Whitney U-test: $Z = -2.252$, $P = 0.024$), and between female groups and mixed-sex groups (Mann–Whitney U-test: $Z = -2.239$, $P = 0.025$).

Discussion

Our objective was to test the two predictions of the activity budget hypothesis: whether females have a longer feeding time, and whether the gazelles of different sexes synchronize their behaviors. We found: (1) female and male gazelles showed significantly different activity budgets; (2) females and males were more synchronized in activities when they are in the same-sex groups than in mixed-sex groups. These results gave support to the activity budget hypothesis.

The activity budget hypothesis points out that different energy requirements due to sexual dimorphism lead to differences in activity budget, even when males and females graze on the same forages in the same habitat (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000). One prediction of the activity budget hypothesis is that smaller females would compensate for their lower digestive efficiency by foraging longer; selecting tender forages thus leads to slower ingesting rates whereas larger males, being less selective in forages and having a higher intake rate, would spend more time in bedding/ruminating and other behaviors (Ruckstuhl, 1998). Females of Tibetan gazelle spent significantly more time foraging, whereas males spent longer time on other behaviors, which supported the prediction of the activity budget hypothesis. Similar results have been reported in many ungulates (gerenuk *Litocranius walleri*: Leuthold & Leuthold, 1978; red deer *Cervus elaphus*: Clutton-Brock *et al.*, 1982; bighorn sheep *Ovis canadensis*: Ruckstuhl, 1998), showing that extending foraging time is an effective method to increase food intake for females.

Behavioral synchronization could entail energy costs for individuals that differ in activity budget (Conradt, 1998; Ruckstuhl, 1998). Thus, another prediction of the activity budget hypothesis is that males and females would separate and form the same-sex groups because of their behavioral asynchrony in mixed-sex groups (Ruckstuhl, 1999;

Ruckstuhl & Neuhaus, 2002). In our study, there were significant differences in the behavior synchronization index between same-sex groups and mixed-sex groups, although no difference occurred in the synchronization index between male groups and female groups. Studies on the social patterns of Tibetan gazelle showed that the mixed-sex groups only contributed to <4% of the total groups during the plant-growing period (June–September) on the plateau (Li & Jiang, 2006), implying that the formation of mixed-sex groups might be highly related to the behavioral synchronization. Similar results were also found in Alpine ibex *Capra ibex ibex* (Ruckstuhl & Neuhaus, 2001).

Additionally, movement pattern was also an important factor influencing sexual segregation (Ruckstuhl, 1998). Differences in time spent moving, stride rates and movement might directly result in behavioral asynchrony and therefore dissolution of the group (Ruckstuhl & Neuhaus, 2001). Male Tibetan gazelles tended to spend more time moving, although the difference was not significant (Fig. 1). This means it might be difficult for males to keep behavioral congruency with females.

In conclusion, many studies have reported that multiple mechanisms cause the sexual segregation in dimorphic ungulates (Ruckstuhl & Neuhaus, 2002; Calhim, Shi & Dunbar, 2006; Loe *et al.*, 2006). However, the activity budget hypothesis could explain the sexual segregation mechanism in Tibetan gazelle.

Acknowledgement

References

Calhim, S., Shi, J. & Dunbar, R.I.M. (2006). Sexual segregation among feral goats: testing between alternative hypotheses. *Anim. Behav.* **72**, 31–41.

Clutton-Brock, T.H., Iason, G.R., Albon, S.D. & Guinnes, F.E. (1982). The effects of lactation on feeding behaviour and habitat use of wild red deer hinds. *J. Zool. (Lond.)* **198**, 227–236.

Conradt, L. (1998). Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc. Roy. Soc. Lond. Ser. B* **265**, 1359–1363.

Jiang, Z. (2004). Status of antelopes and gazelles in China. In *Przewalski's gazelle* pp. 66–72. Jiang, Z. (Ed.). Beijing: Chinese Forestry Press. [In Chinese].

Jiang, Z., Liu, B., Zeng, Y., Hang, G. & Hu, H. (2000). Attracted by the same sex, or repelled by the opposite sex? – sexual segregation in Pere David's deer. *Chinese Sci. Bull.* **45**, 485–491.

Leuthold, B. & Leuthold, W.L. (1978). Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* **16**, 231–243.

Li, Z. & Jiang, Z. (2006). Group patterns of sympatric Przewalski's gazelle and the Tibetan gazelle during the green grass period in Upper Buha River, Tianjun County, Qinghai Province. *Zool. Res.* **27**, 396–402. [In Chinese with English Abstract].

Lian, X., Su, J., Zhang, T. & Cao, Y. (2004). Grouping behavior of the Tibetan gazelle (*Procapra picticaudata*) in Hoh Xil region, China. *Biodivers. Sci.* **12**, 488–493. [In Chinese with English Abstract].

Loe, L.E., Irvine, R.J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S.D., Mysterud, A. & Stenseth, N.C. (2006). Testing five hypotheses of sexual segregation in an arctic ungulate. *J. Anim. Ecol.* **75**, 485–496.

Macdonald, D. (1984). *Hoofed animals*. New York: Torstar Books Inc.

Main, M.B., Weckerly, F.W. & Bleich, V.C. (1996). Sexual segregation in ungulates: new directions for research. *J. Mammal.* **77**, 449–461.

Martin, P. & Bateson, P. (1993). *Measuring behaviour: an introductory guide*. 2nd edn. Cambridge: Cambridge University Press.

Michelena, P., Noël, S., Gautrais, J., Gerard, J.F., Deneubourg, J.L. & Bon, R. (2006). Sexual dimorphism, activity budget and synchrony in groups of sheep. *Oecologia* **148**, 170–180.

Mooring, M.S., Fitzpatrick, T.A., Benjamin, J.E., Fraser, I.C., Nishihira, T.T., Reisig, D.D. & Rominger, E.M. (2003). Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). *Behaviour* **140**, 183–207.

Ruckstuhl, K.E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav.* **56**, 99–106.

Ruckstuhl, K.E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour* **136**, 805–818.

Ruckstuhl, K.E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes. *Integ. Comp. Biol.* **47**, 245–257.

Ruckstuhl, K.E. & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Anim. Behav.* **64**, 909–914.

Ruckstuhl, K.E., Manica, A., MacColl, A.D.C., Pilkington, J.G. & Clutton-Brock, T.H. (2006). The effects of castration, sex ratio and population density on social segregation and habitat use in Soay sheep. *Behav. Ecol. Sociobiol.* **59**, 694–703.

Ruckstuhl, K.E. & Neuhaus, P. (2000). Sexual segregation in ungulates: a new approach. *Behaviour* **137**, 361–377.

Ruckstuhl, K.E. & Neuhaus, P. (2001). Behavioural synchrony in ibex groups: effects of age, sex and habitat. *Behaviour* **138**, 1033–1046.

Ruckstuhl, K.E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biol. Rev.* **77**, 77–96.

Ruckstuhl, K.E. & Neuhaus, P. (2005). *Sexual segregation in vertebrates*. Cambridge: Cambridge University Press.

Schaller, G.B. (1998). *Wildlife of the Tibetan steppe*. Chicago: The University of Chicago Press.

Yearsley, J.M. & Pérez-Barbería, F.J. (2005). Does the activity budget hypothesis explain sexual segregation in ungulates? *Anim. Behav.* **69**, 257–267.

Yin, B. & Liu, W. (1993). *Wildlife protection in Tibet*. Beijing: Chinese Forestry Press. [In Chinese].

Zhang, F. & Jiang, Z. (2006). Mitochondrial phylogeography and genetic diversity of Tibetan gazelle (*Procapra picticaudata*): implications for conservation. *Mol. Phylogenet. Evol.* **41**, 313–321.

Zheng, S. (1994). *Fauna of rare and endangered species of vertebrates in Northwestern China*. Beijing: China Forestry Press.