Sex-Age Related Rumination Behavior of Père David’s Deer under Constraints of Feeding Habitat and Rainfall

Zhongqiu Li*

The State Key Laboratory of Pharmaceutical Biotechnology, School of Life Sciences, Nanjing University, Nanjing, China

Abstract

Extensive studies have been conducted on the rumination behavior of domestic herbivores. However, studies on wild animals are limited, particularly wild animals with specific ruminating parameters. In this study, Père David’s deer, a previously extirpated species, was observed to analyze the effects of sex-age, feeding habitat, and rainfall on rumination behavior in the Dafeng Nature Reserve, China. Rumination behavior was investigated based on four parameters: proportion of bedding time spent chewing, bolus processing time (s/bolus), chewing frequency (chews/bolus), and chewing rate (chews/s). Results showed that all three factors affect rumination behavior. The extent of their effects varied based on the four rumination parameters. Chewing rate and frequency decreased based on sex-age levels, i.e., from fawns to juvenile female, juvenile male, adult female, stag, and harem holder. Therefore, body size played a major role in shaping rumination behavior. Deer found in grasslands could chew faster compared with deer found in woodlands. This result might be caused by the effects of dietary composition and sunlight intensity. A deer spends a longer time ruminating while bedding during rainy days compared with rainless days to maximize energy and nutrition intake and compensate for the loss of feeding time during rainy days. Therefore, rumination behavior is plastic and is shaped by intrinsic and extrinsic factors.

Introduction

Rumination behavior is important for food utilization because ruminants mechanically process and reduce forages into small particles by repeated chewing [1,2]. The comminution of forages increases the surface area of the food available to the bacteria, thereby increasing fiber degradation and utilization in the rumen.

Rumination is sometimes considered a plastic behavior because several intrinsic and extrinsic factors influence chewing parameters [2–5]. Body size, which is closely related to sex and age, is the most important factor among all intrinsic factors [2,6]. The Jarman–Bell principle states that larger animals can feed on poor diets because of their low metabolic requirement to gut capacity ratio. Metabolic requirements are allometrically related to body size, whereas gut capacity or rumen size is isometrically related to body size [7–9]. Therefore, larger animals can extract more nutrients than smaller animals because they can keep food in the rumen longer. Compared with larger animals, smaller animals are at a disadvantage when extracting nutrients from low quality diets (i.e. high fiber content). Consequently, animals from different sex-age classes are expected to use different ruminating or chewing strategies to maximize energy and nutrition intake.

Animals exhibit different ruminating patterns depending on the different forages available in habitat [1,10]. Several characteristics of forage affect the intake of ruminants, particularly the content of vegetable fiber such as cellulose and lignin [11–13]. Cellulose is accessible to enzymes that normally digest carbohydrates, whereas lignin has high chemical-degradation resistance. Thus, lignin cannot be easily digested by ruminants [1]. Animals may change their chewing behavior such as increasing bolus processing time or slowing down chewing rates to increase chewing efficiency when feeding in areas with rough forages or digesting lignified and high fibrous roughages.

Environmental factors, including temperature, wind, and precipitation, can also affect rumination [2,5]. Animals may find difficulty in searching for food under bad weather conditions, such as the presence of low temperatures, strong winds, or heavy precipitation [5]. Bad weather causes animals to change their rumination behavior such as maintaining bedding time and increasing ruminating proportion to compensate for fluctuations in environmental conditions.

Given the importance of rumination behavior, a number of specific chewing parameters, such as time spent chewing while bedding, bolus processing time, number of chews per bolus, and number of chews per min, have been proposed in the study of herbivore rumination [2]. However, considering the difficulty of tracking and observing free-ranging or even semi free-ranging animals [4], most studies were conducted only on domestic ruminants. The goal of this study is to investigate the effects of sex-age, feeding habitat, and rainfall on the abovementioned rumination parameters of semi free-ranging Père David’s deer. The focus of this study is as follows.
(1) Effects of Body-size Related Characteristics (i.e., Sex-age and Reproductive Status) on Rumination Behavior

According to the Jarman–Bell principle, smaller individuals have higher chewing rates than larger individuals to increase chewing efficiency [7,8,14]. Hence, chewing rates should decrease in the following order: fawn, juvenile, adult.

(2) Effect of Feeding Habitat

Rumination usually occurs shortly after feeding, approximately 10 min for Père David’s deer [15]. Hence, the majority of rumination observations collected from deer in grasslands can be regarded as deer completely feeding on grass. A possibility exists that a deer feeds in woodlands and then rests in grasslands; however, these observations should be rare. Deer ruminating in woodlands are expected to chew slower than deer ruminating in grasslands because a woody diet contains more vegetable fibers, particularly lignin, which is indigestible [1].

(3) Effect of Rainfall

Bedding is beneficial for saving energy. In the event of rain, deer would increase ruminating proportion when bedding to compensate for the loss of feeding opportunity and increase energy and nutrient intake.

Methods

Study Site and Study Subjects

This study was conducted in the Dafeng Père David’s Deer National Nature Reserve (32°59’–33°03’N, 120°47’–120°53’E) in Jiangsu Province, China. The reserve is located on the coast of the Yellow Sea in Eastern China and lies 2 m to 4 m above sea level. The reserve has an annual average temperature of 14.1°C, an average temperature of 0.8 and 27.0°C in January and July, respectively, and 217 frost-free days. The average precipitation is 1068 mm with rain falling mostly between June and September. The Dafeng Nature Reserve consists of three core zones, two of which are enclosed by fences to allow Père David’s deer to range freely. Deer usually forage in grasslands, which are dominated by Chinese pennisetum (Pennisetum alopecuroides) and cogongrass (Imperata cylindrica), and woodlands, which are dominated by Canadian populus (Populus canadensis) and locust (Robinia pseudoacacia) [16,17].

The Père David’s deer is an endangered species with sexual dimorphism. Adult males are approximately 35% heavier than adult females [18,19]. The mating system is harem polygamous, which means that a strong harem holder dominates the whole harem group and monopolizes nearly all mating opportunities; other stags can only fight or give up mating rights [20,21]. The rutting season is usually from March to May, and the calving season is from March to May.

The Père David’s deer is a formerly extirpated species in China [22]. A herd of 39 Père David’s deer was reintroduced in the reserve in 1986. After 26 years of conservation and development, the total deer population increased to 1789, thus making this herd the world’s largest deer population [23]. The reserve has been implementing a re-wilding program since 1998, and the wild deer population has grown to 182 deer as of 2011. The study was conducted in the first fenced core area, in which a herd of more than 1000 deer live.

Behavioral Sampling

The study was conducted during the late rutting seasons (July to August) of 2011 and 2012. Observations were conducted along the trails of the first core zone every day to study deer that were bedding. Focal bedding deer were randomly selected and observed by using binoculars (8 x56) or a telescope (20–60 x63). The following data were recorded at the beginning of each focal observation: sex-age (fawn, juvenile female, juvenile male, adult female, stag, and harem holder), feeding habitat (grassland and woodland), weather (rainy or rainless), group size and composition (male group, female group, and mixed-sex group), GPS location, date, and time (morning or afternoon). Observations were usually made from a shelter or at a distance of 150 m away from the focal animals to reduce observer effects [24]. Given that the animals were unmarked, sampling the same animal more than once on a given day was unlikely given the large population size.

According to sex-age and reproductive status, deer were classified into six categories: fawns (less than 1 yr, 12.6±1.4 kg, n = 17), juvenile females (between 1 yr to 3 yrs, 100.4±5.7 kg, n = 7), juvenile males (between 1 yr to 4 yrs, 130.1±2.8 kg, n = 8), adult females (older than 3 yrs, 139.0±7.6 kg, n = 22), and stags and harem holders (older than 4 yrs, 184.2±17.2 kg, n = 16) [19]. Although no detailed information was reported regarding the body size of harem holders, they were expected to have larger body sizes than stags because of the competition to monopolize mating rights [21].

During rumination, a bolus of food rises from the rumen; this bolus is then chewed and swallowed (referred to as a bolus cycle) [5]. Focal samples, which consisted of the bedding of randomly selected focal individuals, were observed for 20 min. The 20 min observation of these individuals was only used to analyze the proportion of bedding time spent chewing. Data on deer that ruminated at least five bolus cycles but were observed for less than 20 min were also included in the calculation of bolus processing time and chewing frequency and rate. The data recorded for each individual were the rape time and mean number of chews for a minimum of at least five consecutive bolus cycles. Deer sometimes ruminate while standing. However, this activity is rare; hence, all observations were considered bedding rumination behavior. A bolus usually lasts for approximately 1 min. Thus, each individual was observed for at least 5 min. The four rumination parameters from the observations were quantified as follows: (1) proportion of bedding time spent chewing; (2) mean processing time (sec/bolus); (3) mean chewing frequency (number of chews/bolus); (4) mean chewing rate (chews/sec), which was calculated by dividing mean chews/bolus by mean processing time/bolus.

Statistical Analysis

A mixed linear model was used to analyze the effects of the possible factors on rumination indices. The majority of samples were collected from big groups (larger than 20 individuals; these groups were usually stable for hours if not disturbed). Thus, group size was not included in the model. For the proportion of bedding time spent chewing, a group ID was included as a random factor, whereas sex-age (fawn, juvenile female, juvenile male, adult female, stag, and harem holder), weather (rainy or rainless), group composition (male, female, and mixed-sex), time of day (morning or afternoon), and second-order interactions were considered fixed factors in the initial model. The feeding habitat was not included as a potential factor because all data were observed from grassland. In the final model, only sex-age and weather were included among the factors because of the non-significance of group composition, time of day, and second-order interactions (P>0.421).

For the other three rumination parameters, a group ID was also included as a random factor. Sex-age (fawn, juvenile female, juvenile male, adult female, stag, and harem holder), feeding
habitat (grassland and woodland), weather (rainy or rainless), group composition (male, female, and mixed-sex), time of day (morning or afternoon), and second-order interactions were considered fixed factors in the initial models. However, group composition, time of day, and second-order interactions showed insignificant effects on the ruminating parameters (P > 0.100); hence, these factors were excluded from the final models. Values were reported by using mean ± standard error with a significance level of P < 0.05.

Ethics Statement

Permission to undertake the field observation was granted by the Management Bureau of Dafeng Pére David’s Deer National Nature Reserve (Daming Sun, Director). A telescope was used to observe the ruminating behavior of Pére David’s deer from a distance of >120 m to minimize observer disturbance. All experiment procedures in this study were approved by the Chinese Wildlife Management Authority, and all animals used in the experiment were managed according to the guidelines of the Chinese Wildlife Management Authority.

Results

The dataset consisted of 371 focal observations collected during the summer seasons of 2011 and 2012. Among the samples, 42 were from fawns, 43 were from juvenile females, 99 were from juvenile males, 76 were from adult females, 81 were from stags, and 30 were from harem holders. Furthermore, 294 of the 371 observations were collected from grasslands and the rest were from woodlands. The observation days comprised 234 rainy days and 137 rainless days.

A total of 216 observations of 20 min samples were gathered to analyze the proportion of feeding time spent chewing. The final model indicated that both sex-age (F5, 362 = 3.023, P = 0.012) and rain (F1, 362 = 11.836, P = 0.001) had significant effects on feeding time spent chewing (Table 1). Post hoc test results indicated that fawns spent less time ruminating when feeding compared with all other categories. Deer spent a greater proportion of feeding time ruminating on rainy days (0.702 ± 0.053) than on rainless days (0.468 ± 0.045).

For chewing frequency, the model showed that sex-age (F5, 362 = 14.067, P < 0.001) and feeding habitat (F1, 362 = 4.637, P = 0.033) both had significant effects, whereas the effect of rain (F1, 362 = 0.122, P = 0.727) was insignificant (Table 2). Post hoc tests indicated that deer increased their chewing rate in the following order: fawns, juvenile females, juvenile males, adult females, stags, and harem holders. However, no significant difference was observed between stags and harem holders and among adult females, juvenile males, and juvenile females.

For chewing rate, the model indicated that sex-age (F5, 362 = 1.959, P = 0.084; feeding habitat, F1, 362 = 1.414, P = 0.233; rain, F1, 362 = 0.731, P = 0.393; Table 2).

Discussion

Results showed that all three factors, namely, sex-age, feeding habitat, and rain, affected the ruminating behavior of Pére David’s deer. These factors had varying effects on the ruminating parameters. Sex-age influenced almost all four ruminating parameters. Feeding habitat only affected chewing frequency and rate, and rain only had a slight effect on the proportion of bedding time spent ruminating.

Sex-age had a significant effect on ruminating proportion while bedding, chewing frequency, and chewing rate, as well as a marginal effect on bolus processing time. Numerous studies have addressed the importance of sex and age on shaping ruminating behavior [25–27]. However, the majority of these studies consider sex-age effects to be closely related to body size [3,5,6,9,28], which is commonly regarded as the most important variable [2]. When controlling for body size, the effect of sex-age on human chewing effectiveness disappears [29] because body size is isometric with the occlusal surface area of the teeth, which is an important parameter that determines tooth effectiveness [27,30,31]. Thus, chewing behavior, which also affects chewing effectiveness [2], compensates for the possible reduction of tooth effectiveness.

Chewing behavior is strongly related to the quantity and quality of food processed [2]. However, food selectivity may also be related to body size. Considering metabolic rates and feeding abilities (e.g., picking out small items), smaller animals tend to select low quantities of high quality food, whereas larger animals forage conversely [8]. When consuming low quality food, a slow chewing rate increases the chewing efficiency of larger animals [14]. Given the difficulties of catching and identifying wild animals, the body weight measurements of each focal individual were not obtained. Therefore, the scaling effect of body weight on ruminating parameters could not be analyzed. However, body weight might probably be the most important factor.

Fawns spent approximately 30% on chewing time ruminating, which was only approximately half of the other sex-age categories. Fawns can obtain extra (or maybe basic) energy and nutrition from sucking, and the pre-weaning period can last for approximately half a year [32,33]. No significant difference was observed among other categories, thus indicating that all sex-age levels maintained a certain ruminating proportion for nutrition and energy intake when they have grown up.

Although certain studies have reported that reproductive status affects feeding and ruminating behavior [3,34,35], this effect was

| Table 1. Proportion of ruminating/bedding of Pére David’s deer with respect to sex-age and rainfall in Dafeng Nature Reserve. |
|---------------------------------------------------------------|
| **Rainy day** | **Rainless day** |
| Mean(SE) | N | Mean(SE) | N |
|---|---|---|---|
| Fawn | 0.468(0.085)a | 7 | 0.210(0.077)a | 17 |
| Juvenile Female | 0.684(0.080)b | 8 | 0.625(0.072)b | 20 |
| Juvenile Male | 0.733(0.055)b | 28 | 0.475(0.055)b | 30 |
| Adult Female | 0.752(0.062)b | 18 | 0.494(0.055)b | 34 |
| Stag | 0.721(0.069)b | 12 | 0.462(0.059)b | 30 |
| Harem holder | 0.664(0.108)b | 10 | 0.405(0.116)ab | 2 |

Same letter in the same row denotes no significant difference at P > 0.05. doi:10.1371/journal.pone.0066261.t001
not observed among male deer. Harem holders even fast during the peak of rut season [21,32], which probably affects rumination behavior. However, this study was conducted in July and August when the rut season was nearly finished. Moreover, even if harem holders are larger than other stags, the body size difference might not be significant to change rumination behavior.

Feeding habitat displayed significant effects on chewing rates, thus demonstrating that deer found in grasslands chew faster than deer found in woodlands. The effect of habitat on rumination behavior might be attributed to the different diet composition between grasslands and woodlands. Dominant plants in grasslands include Chinese pennisetum and cogongrass, whereas woodlands are populated by Canadian populus and locust; all of these plants can be utilized by deer [16]. Chewing behavior is influenced by cell toughness, particularly cellulose fibers and lignin in cell walls [1,10]. Certain studies reported that the relationship between cell toughness and feeding time or chewing effectiveness is uncertain. Spalinger et al. [1996] hypothesized that particle breakdown rate in the rumen should be positively related to the lignin concentration. However, they found that the results they obtained are inconclusive [36]. Nevertheless, this uncertainty may precisely reflect the importance of chewing behavior. When feeding on tough foods, the decision to spend more time on chewing or to slow down chewing rates can consequently increase chewing efficiency. The exact concentrations of cellulose fibers and lignin in the four plants in the two habitats were not measured. However, the two latter trees should contain more vegetable fibers, particularly lignin, even only in their epicormic shoots and branches. High vegetable fibers would lead to a reduction of chewing rate in woodlands. Another possible reason might be the different intensities of sunlight. Many studies have addressed the importance of sunlight on sleeping, rumination, and other behaviors of herbivore [37,38]. Sheep would change their ruminating patterns under different lighting conditions [38]. When in darkness or low intensity sunlight, animals easily succumb into a rest or relaxed state. The intensity of sunlight and temperature are higher in grasslands than in woodlands. Dominant plants in grasslands are populated by Canadian populus and locust; all of these plants can be utilized by deer [16]. Chewing behavior is influenced by cell toughness, particularly cellulose fibers and lignin in cell walls [1,10]. Certain studies reported that the relationship between cell toughness and feeding time or chewing effectiveness is uncertain. Spalinger et al. [1996] hypothesized that particle breakdown rate in the rumen should be positively related to the lignin concentration. However, they found that the results they obtained are inconclusive [36]. Nevertheless, this uncertainty may precisely reflect the importance of chewing behavior. When feeding on tough foods, the decision to spend more time on chewing or to slow down chewing rates can consequently increase chewing efficiency. The exact concentrations of cellulose fibers and lignin in the four plants in the two habitats were not measured. However, the two latter trees should contain more vegetable fibers, particularly lignin, even only in their epicormic shoots and branches. High vegetable fibers would lead to a reduction of chewing rate in woodlands. Another possible reason might be the different intensities of sunlight. Many studies have addressed the importance of sunlight on sleeping, rumination, and other behaviors of herbivore [37,38]. Sheep would change their ruminating patterns under different lighting conditions [38]. When in darkness or low intensity sunlight, animals easily succumb into a rest or relaxed state. The intensity of sunlight and temperature are higher in grasslands than in woodlands. Thus, during the hottest periods of the year, woodlands can provide enough shade for the deer, thus causing them to become relaxed, rested, and ruminate slowly [39,40].

Weather conditions, including temperature, wind, and rain, affect feeding and rumination behavior [5]. However, unlike the bighorn sheep (Ovis canadensis), which spend less time processing per bolus under rainy conditions [5], Pe`re David’s deer devote more time to rumination while bedding. When raining, the deer have to spend extra energy to search and feed because of low visibility and tough feeding paths. More importantly, rain decreases herbage acceptability because of the palatability effect, which results in a reduction of dry-matter intake [41]. Excessive water in the rumen might not decrease forage intake but would reduce saliva production during the ingestion of low dry-matter forages [42,43]. Thus, ungulates are usually observed to reduce feeding time, biting rate, and intake per bite on rainy days [3,41]. For compensation, prolonging rumination time would increase chewing efficiency, thus leading to a higher utilization of forages in the rumen.

In conclusion, rumination behavior could be considered a plastic behavior constrained by sex-age, feeding habitat, rain, and other factors. Among all the abovementioned factors, body size might be the basic characteristic that binds other factors. Rumination should be further explored, such as whether/how deer change their rumination behavior when provided with supplemental food during food-limited seasons (i.e., late November to April) and whether/how harem holders allocate their rumination behavior during the peak of rut season. These studies would help in understanding how Pe`re David’s deer rapidly adapted and recovered in their native land, as well as provide information on how to implement better conservation and management strategies for this species.

Acknowledgments

We thank Prof. Yuhua Ding, Prof. Daming Sun and other staff members at Dafeng Mili National Natural Reserve for supporting our field research in the reserve. I also thank Rongrong Wang, Jiahui Wei, Xiaoxiao Zhou, Wei Zheng, and Bin Liu for help with the field work, Eve Fernandez for language improvements, and Cheng Huang, Iain Gordon, Guy Beauchamp, Kathleen Ruckstuhl, Jia Chen for useful discussion. I also thank two reviewers for their insightful comments.

Author Contributions

Conceived and designed the experiments: ZL. Performed the experiments: ZL. Analyzed the data: ZL. Wrote the paper: ZL.
References

1. Wilson JR (1994) Cell-Wall Characteristics in Relation to Forage Digestion by Ruminants. J Agr Sci 122: 173–182.
2. Perez-Barberia FJ, Gordon IJ (1998) Factors affecting food comminution during chewing in ruminants: a review. J Anim Sci 76: 233–256.
3. Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, Ovis canadensis. Behav Ecol Sociobiol 53: 329–338.
4. Blanchard P, Fritz H (2008) Seasonal variation in rumination parameters of free-ranging impalas Aepyceros melampus. Wildlife Biol 14: 372–378.
5. Moquin P, Curry B, Pelletier F, Ruckstuhl KE (2010) Plasticity in the rumination behaviour of bighorn sheep: contrasting strategies between the sexes? Anim Behav 79: 1047–1053.
6. du Toit JT, Yetman CA (2005) Effects of body size on the diurnal activity budgets of African browsing ruminants. Oecologia 143: 317–325.
7. Bell RHV (1971) A grazing ecosystem in the Serengeti. Sci Am 225: 86–93.
8. Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48: 215–267.
9. Perez-Barberia FJ, Perez-Fernandez E, Roberton E, Alvarez-Enriquez B (2008) Does the Jamaran-Bell principle at intra-specific level explain sexual segregation in polygynous ungulates? Sex differences in forage digestibility in Soay sheep. Oecologia 157: 21–30.
10. Deboever JL, Andries J, Debrabander DL, Cotyn BG, Bayse F (1990) Chewing Activity of Ruminants as a Measure of Physical Structure - a Review of Factors Affecting It. Anim Feed Sci Tech 27: 281–291.
11. Gram RJ, Colenbrander VF, Albright JL (1990) Effect of particle size of forage and rumen cannulation upon chewing activity and latidity in dairy cows. J Dairy Sci 73: 3150–3164.
12. Mysterud A (1998) The relative roles of body size and feeding type on activity time of temperate ruminants. Oecologia 113: 442–446.
13. Chumpasawadee S, Pimpa O (2009) Effects of Non Forage Fiber Sources in Total Diet Composition on Ruminal Fermentation and Chewing Behavior of Cattle. Grass Forage Sci 64: 291–297.
14. Van Soest PJ (1994) Nutritional ecology of the ruminant: Cornell University Press.
15. Ding Y (2004) Physiology and Biochemistry. In: Ding Y, editor. Chinese Milu Research. Changchun, Jilin, China: Jilin Publishing House for Science and Technology. 92–111.
16. Liang C, Li B (1991) The habitat vegetation of semi-free range Milu and their eating plant species in China. Forest Sci 27: 425–434.
17. Yu S, He Q (2011) Vegetation. In: Jiang Z, Ding Y, editors. Milu and Biodiversity in Dafeng. Beijing: Beijing Forestry Press. 18–22.
18. Yu C, Liang C, Lu J, Ding Y, Shen H (1996) The growth and breeding habit of Milu in Dafeng Nature Reserve. Acta Theriol Sin 16: 19–24.
19. Ding Y, Ren Y, Hou L, Xie S, Liu B (2011) Morphological Features of Milu. In: Jiang Z, Ding Y, editors. Milu and Biodiversity in Dafeng. Beijing: Jilin Publishing House for Science and Technology. 92–111.
20. Li CW, Jiang ZG, Jiang GH, Fang FM (2001) Seasonal changes of reproductive behavior and fecal sterol concentrations in Pere David’s deer. Horm Behav 40: 518–525.
21. Jiang ZG, Li C, Zeng Y (2008) "Harem defending" or "challenging": alternative individual mating tactics in Pere David’s deer under different time constraint. Acta Zootax Sin 33: 706–713.
22. Jiang ZG, Yu CQ, Feng ZJ, Zhang LY, Xia JS, et al. (2000) Pere David’s deer in China. Wildlife Soc 28: 681–687.
23. Zheng W, Beauchamp G, Jiang XL, Li ZQ, Yang QJ, et al. (2013) Determinants of vigilance in a reintroduced population of Pere David’s deer. Curr Zool 59: 265–270.
24. Li G, Jiang Z, Tang S, Zeng Y (2007) Evidence of effects of human disturbance on alert response in pere david’s deer (Elaphurus davidianus). Zoo Biol 26: 461–470.
25. Oakes EJ, Harmens R, Elveh C (1992) Sex, Age, and Seasonal Differences in the Diets and Activity Budgets of Muskoxen (Ovibos Moschatus). Can J Zool 70: 605–616.
26. Das N, Maitra DN, Bisht GS (1999) Genetic and non-genetic factors influencing digestive behavior of sheep under stall-feeding conditions. Small Ruminant Res 32: 129–136.
27. Mellado M, Rodriguez A, Villarreal JA, Rodriguez R, Salinas J, et al. (2005) Gender and tooth wear effects on diets of grazing goats. Small Ruminant Res 57: 105–114.
28. Gross JE, Demment MW, Allon PU, Kotzman M (1995) Feeding and Chewing Behaviors of Nubian Ibex - Compensation for Sex-Related Differences in Body-Size. Funct Ecol 9: 383–393.
29. Julien KC, Buschang PH, Throckmorton GS, Dechow PC (1996) Normal mastiatory performance in young adults and children. Arch Oral Biol 41: 69–75.
30. Perez-Barberia FJ, Gordon IJ (1998) The influence of molar occlusal surface area on the voluntary intake, digestion, chewing behaviour and diet selection of red deer (Cervus elaphus). J Zool 245: 307–316.
31. Shipley LA, Gross JE, Spalinger DE, Hobbs NT, Wander BA (1994) The Scaling of Intake Rate in Mammalian Herbivores. Am Nat 143: 1055–1082.
32. Ding Y (2004) Reproduction. In: Ding Y, editor. Chinese Milu Research. Changchun, Jilin, China: Jilin Publishing House for Science and Technology. 112–126.
33. Zeng Y, Jiang Z, Li C, Yan G, Zhang L, et al. (2004) Activity synchrony and aggregation tendency in Pere David’s Deer calves. Acta Theriol Sin 24: 78–81.
34. Blanchard P (2005) On lactation and rumination in bighorn ewes (Ovis canadensis). J Zool 265: 107–112.
35. Hamel S, Cote SD (2008) Trade-offs in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. Anim Behav 75: 217–227.
36. Spalinger DE, Robbins CT, Hanley TA (1986) The Assessment of Handling Time in Ruminants - the Effect of Plant-Physical and Chemical Structure on the Rate of Breakdown of Plant-Particles in the Rumen of Mule Deer and Elk. Can J Zool 64: 312–321.
37. Oshiro S, Nakamae H, Hirayama T, Furuta K, Hongo F, et al. (1996) Effects of duration of photoperiod on the rumination behavior of goats. Small Ruminant Res 22: 97–102.
38. Gordon J, McAllister I (1970) The circadian rhythm of rumination. J Agr Sci 74: 291–297.
39. Blackshaw JK, Blackshaw AW (1994) Heat-Stress in Cattle and the Effect of Shade on Production and Behavior. Aust J Exp Agr 34: 285–293.
40. Ainsworth JAW, Moe SR, Skarpe C (2012) Pasture shade and farm management effects on cow productivity in the tropics. Agr Ecosyst Environ 155: 103–110.
41. Butris GY, Phillips CJ (1987) The Effect of Herbage Surface-Water and the Provision of Supplementary Forage on the Intake and Feeding-Behavior of Cattle. Grass Forage Sci 42: 259–264.
42. Thomas J, Moore L, Okamoto M, Sykes J (1961) A study of factors affecting rate of intake of feeders fed silage. J Dairy Sci 44: 1471–1483.
43. Meyer R, Barley E, Morrill J, Stewart W (1964) Salivation in cattle. J. Anim Feed and Animal factors affecting salivation and its relation to bloating. J Dairy Sci 47: 1339–1345.