Behavioural Processes 103 (2014) 5–8

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Short report

The energy-maintenance strategy of goitered gazelles *Gazella subgutturosa* during rut

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ARTICLE INFO

Article history:
Received 2 April 2013
Received in revised form 28 October 2013
Accepted 28 October 2013

Keywords:
Energy strategy
Feeding
Lying
Rut-related

ABSTRACT

In many polygynous ruminant species, males decrease their food intake considerably during the rut. To explain this phenomenon of rut-reduced hypophagia, two main hypotheses, the Foraging-Constraint Hypothesis and Energy-Saving Hypothesis, have been proposed. In our research, we assessed the behavioral strategy of goitered gazelles (*Gazella subgutturosa*) through the rutting period. According to our findings, male goitered gazelles spent less time feeding during the rut compared to pre- and post-rut feeding times, but then maximized their energy intake during the rutting season when they were not engaged in rut-related behaviors. Females, in contrast, did not change their time budgets across the different stages of the rut. Therefore, rut-induced hypophagia is mainly arising from the constraints of rut-related behaviors for male goitered gazelles, so that the Foraging-Constraint Hypothesis better explains their strategy during rut.

1. Introduction

In general, energy expenditures of male polygynous ruminant species will increase due to their time and energy investments in reproductive activities during the rut (Clutton-Brock, 1989; Descamps et al., 2006). While these investments in rut-related behaviors increase their current reproductive success, they also decrease their energy intake at the same time (Krebs and Davies, 1995). This phenomenon is called rut-induced hypophagia and it has been reported across a range of ruminant species (Komers et al., 1994; Apollonio and Vittorio, 2004; Brivio et al., 2010). Two principal hypotheses were proposed to explain this phenomenon: (1) the Foraging-Constraint Hypothesis, and (2) the Energy-Saving Hypothesis. The Foraging-Constraint Hypothesis states that time normally allocated to feeding is instead allocated to rutting-related behaviors; rutting activities were expected to increase at the expense of acquisition and maintenance behaviors (Mooring and Hart, 1995). However, rutting males continued to optimize their energy balance during the rutting period by maximizing their energy intake by eating whenever possible, in addition to their investments in current reproduction (Geist, 1982). The Energy-Saving Hypothesis suggests that when an animal's efficiency to assimilate energy falls below the level necessary to sustain basic energy requirements, males might be unable to maintain their basic cycle of ingesting and ruminating food, and would shift to another energy-saving strategy by increasing their resting time (Robbins, 1993; Willisch and Ingold, 2007).

It has been reported that the number of females in a group also has a strong influence on the rutting activities of males (Apollonio et al., 1989; Clutton-Brock et al., 1996; Høland et al., 2006). When a group is larger, males must spend more time on rutting activities in order to attain more chances for copulation. As a consequence, the rut-related behaviors of males increase in big female groups, forcing the males to reduce their feeding time (Tennenhouse et al., 2011).

In this paper, we compared the time budgets of goitered gazelles (*Gazella subgutturosa*) during the rutting periods of before, during and after the rut for both sexes to investigate the energy balance strategy of this species. Data of females were considered in order to exclude the influences of environmental factors on time budgets. In addition, the impact of female group size on male activities was also considered.

2. Methods and materials

2.1. Study area and subject

This study was conducted in the Kalamaili Mountain Reserve (KNR) (44°36′–46°00′ N, 88°30′–90°03′ E), located in the eastern part of Junggar Basin, Xinjiang, China. The reserve covers

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http://dx.doi.org/10.1016/j.beproc.2013.10.009

1.8×10^4 km^2 with an average elevation of ca. 1000 m asl. The local climate is a harsh continental-type with an average yearly temperature of +1.99 °C. Winters are long and cold with an average temperature in January of −24.3 °C – absolute minimum of −45 °C and a maximum of +1.4 °C. This climate system influences the vegetation of the region, which also has a number of specific characteristics: ephemerals appear during the rainy period at the end of spring to early summer; plants have only one dormant period in winter; and the vegetation cover is quite sparse, consisting mostly of desert shrubs (40–50 cm) and dwarf shrubs (10–15 cm) from families *Chenopodiaceae, Ephedraceae, Tamaricaceae, Zygophyllaceae* (Unatov, 1960).

The goitered gazelle is a polygynous ungulate whose rutting season starts in early winter when the availability of food is quite low (Kinswood and Blank, 1996). During the rut, males divide up the areas around the daily routes of female groups into individual ranges, with each owner of a territory courting just those females within his range. As females past through these territories, the male owners chased them to try to keep as many females as possible within his borders for as long as possible (Blank, 1998).

2.2. Data collection

The behavior of the goitered gazelles was investigated using the focal animal sampling method (Altmann, 1974) from November 2009 to January 2010. Observation period consisted of the entire time of daylight hours. Each sampled gazelle was observed for 10 min, and we took samples from as many groups as possible; we selected only a portion of the females from each group for observation. Each territorial male, was observed only once to reduce the occurrence of pseudo-replication, and the male's courtship behaviors were recorded to assess the timing of the rut (Blank, 1998). Three different stages were defined: pre-rut (8–24 November), rut (8–24 December), and post-rut (10–15 January). In total, 135.67 h were spent on the observation of goitered gazelle.

Five behavioral categories were classified. *Feeding* was defined as a gazelle standing or walking slowly with its head below shoulder level, biting or chewing plants, or walking with its muzzle close to the ground. *Lying* was defined as the animal lying down. *Moving* was noted when the gazelle walked or ran with its head at or above shoulder level. *Standing* was defined as an animal remaining still with its head above its shoulders. And *social behaviors* included any conspecific-related actions and reactions. When females were present in the focal males' territory, feeding and lying of males were considered as non-rutting behaviors, while standing, moving and social behaviors belonged to rut-related behaviors because of their contribution to reproduction (Relyea and Demarais, 1994; Lima et al., 1999). The relationship between a male's activities and the number of females in the group was considered only when the group size within a territory did not change during one observation period.

2.3. Statistical analysis

The percentage of time spent on each behavior was arcsin square root transformed to test for normality using the Kolmogorov–Smirnov test. All data were normally distributed, and a one-way ANOVA combined with a post hoc test was used to compare different rutting stages for each behavior. *T*-test was used to compare pre- and during-rut stages for females. Spearman's rank correlation tests were performed to show relationships between time spent engaged in rutting-related behaviors and time spent on non-rut behaviors (feeding or lying), and also the influence of the number of females on a male's activities. The data are shown as mean ± error. The level of significance is set at 0.05. All statistical analyses were carried out using the SPSS18.0 software package.

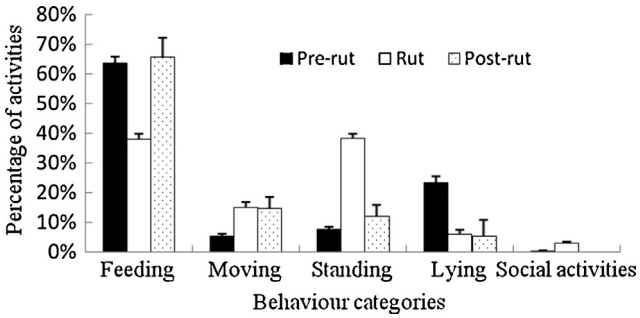

Fig. 1. Time budget of male goitered gazelles in pre-, during- and post-rut.

3. Results

Males spent less time feeding during rut than in pre- and post-rut periods ($F = 28.198$, $P < 0.001$, Fig. 1). During the rut, the average time spent feeding decreased by 25.66% compared to the pre-rut period ($n = 320$, 147, respectively). After the rut, the males' feeding time increased sharply to 65.75% ($n = 55$). The time a male spent lying also changed significantly over the three different biological periods of before, during and after the rut ($F = 13.899$, $P < 0.001$, Fig. 1). Males spent 23.21% of their daytime hours lying down before the rut ($n = 320$), 5.99% during the rut ($n = 147$) and 5.44% after the rut ($n = 55$).

During the rut, males devoted most of their time to rutting-related behaviors (56.08%) (Fig. 1), via more time spent standing ($F = 89.058$, $P < 0.001$), moving ($F = 85.677$, $P < 0.001$) and social behaviors ($F = 62.116$, $P < 0.001$). Of non-rutting behaviors during the rut, 86.38% of time was used for feeding, and only 13.62% was allocated to lying down. Rut time spent feeding significantly correlated to the duration of rutting-related behaviors ($P < 0.001$, $R_s = -0.343$, $n = 135$, Fig. 3), while lying time, in contrast, did not have a significant correlation with the time spent rutting ($P = 0.391$, $R_s = -0.074$, $n = 135$, Fig. 3). The ratio of feeding to resting times increased across the biological periods of observation, with 2.74 in pre-rut, 6.34 during-rut, 12.08 in post-rut.

Males spent more time feeding with fewer females available ($P = 0.002$, $R_s = -0.905$, $n = 103$), compared to more time spent on rut-related activities in the presence of more females ($P = 0.002$, $R_s = 0.905$, $n = 103$, Fig. 4).

During the rut, females spent more time moving ($t = 3.469$, $P = 0.001$) and lying ($t = 2.351$, $P = 0.019$), while the duration of their feeding ($t = 0.288$, $P = 0.773$), standing ($t = 1.218$, $P = 0.224$), and social behaviors ($t = 0.437$, $P = 0.662$) did not change between the pre-rut and during-rut periods ($n = 132$, $n = 160$, respectively. Fig. 2).

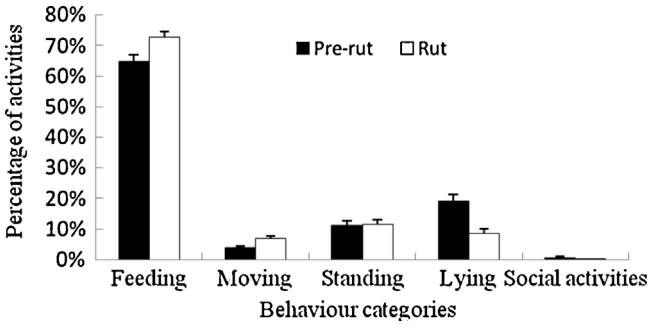

Fig. 2. Time budget of female goitered gazelles in pre- and during-rut.

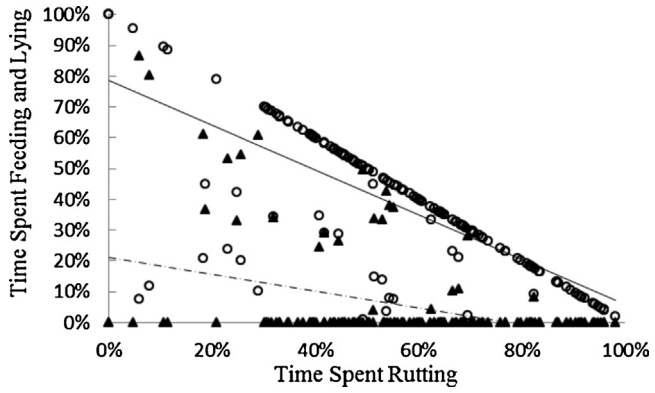

Fig. 3. Time spent feeding and lying in relation to time spent rut of male goitered gazelle during rut. Open circles with continuous trendline for feeding, filled triangles with dashed lines for lying.

4. Discussion

Like many ruminants, male goitered gazelles spent more time on rut-related behaviors during the rut, while they reduced their feeding and lying time in their daily time budgets (Fig. 1). However for females, time spent feeding did not change significantly before and during the rut (Fig. 2). This means then that the rut-induced hypophagia in males cannot be explained by environmental factors, since if it was, feeding activities would change similarly for both sexes. Therefore it follows that the feeding reduction in rut time for males is a result of their investment in rut-related behaviors to improve their reproductive success.

Like other polygynous ungulates (Pelletier, 2005; Mainguy and Côté, 2008; Pelletier et al., 2009; Brivio et al., 2010), male goitered gazelles decreased their feeding duration during the rut, but still spent most of their non-rutting time feeding, with only a small part spent lying down. Moreover, a significant correlation was found only between feeding and rut-related behaviors, indicating that the males' rutting activities increased at the expense of their feeding time (Fig. 3). These results then seem to support the Foraging-Constraint Hypothesis for male goitered gazelles rather than the Energy-Saving strategy during the rut. Furthermore, our data demonstrated that the feeding time of males decreased when more females appeared in his territory, which implies that in the presence of few females, males spend more time feeding activities (Fig. 4); this also confirmed that male goitered gazelles tend to maximize their energy acquisition. Similar results were also found for Arabian sand gazelle (*Gazella subgutturosa marica*) (Cunningham and Wronski, 2011a,b), fallow deer (*Dama dama*) (Apollonio et al., 1989) and reindeer (*Rangifer tarandus*) (Tennenhouse et al., 2011).

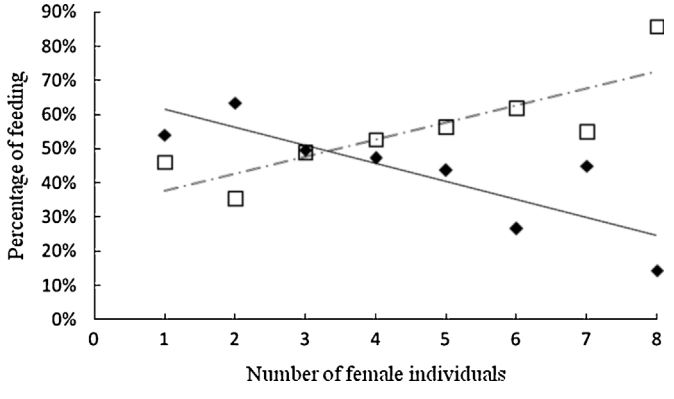

Fig. 4. Influence of the number of females on time spent feeding and rut-related behaviors (the number "8" in the horizontal ordinate including eight or more than eight females). Filled diamonds mean feeding time, open squares mean rut-related time.

We did discover a potential contradiction to the Foraging-Constraint Hypothesis however. Since the lying time decreased more significantly compared to feeding, the ratio of feeding time to lying increased through the pre-rut to post-rut cycles. Gazelles (Antilopinae) usually ruminate in a lying position, but to do so males would lessen their control over their territories and females. Standing, on the other hand, provides a better visual field and faster response times to keep females from leaving their territories (Blank, 1998), which is an incentive for males to spend more time in a standing position. From this, then, we inferred that rutting males ruminated longer and more often in a standing position to compensate for the reduction in rumination time in a lying position. This need to be investigated further.

Male goitered gazelles decreased their food intake to increase the time available for their reproduction efforts. However, this strategy also had an apparent cost in the reduction of their fitness, with males decreasing their body weight by 30% during the rut (Zhevnerov, 1984). This fact, along with a very adverse winter environment during the breeding season, caused the deaths of some male gazelles, which resulted in a sharp decrease in the ratio of males to females from 1:1.4 to 1:9.4 (Zhevnerov, 1984). Similar results have also been found for the species *Rangifer tarandus* (Mysterud et al., 2003; Tennenhouse et al., 2011) and *Dama dama* (Apollonio and Vittorio, 2004) as well.

Acknowledgements

We are grateful to The National Natural Science Foundation of China (U1303301), West Light Foundation of the Chinese Academy of Sciences (Breeding ecology and human disturbance on great bustard; Sustainable grazing research in Ili Valley; XBBS201102), Chinese Academy of Sciences Visiting Professorships for Senior International Scientists Program of the Chinese Academy of Sciences (2011T1Z42) for financing this research. We thank Doctor LI Zhongqiu, Patricia Johnston and two anonymous reviewers for reviewing our manuscript.

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