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Does a temperate ungulate that breeds in summer exhibit rut-induced hypophagia? Analysis of time budgets of male takin (*Budorcas taxicolor*) in Sichuan, China

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ABSTRACT

Mammals maximize fitness by optimizing time and energy allocation between reproduction and survival. Describing time budgets is a way to understand a species' constraints in energy allocation. We describe a time budget for male takin (*Budorcas taxicolor*) in Tangjiahe Nature Reserve, China, to better understand rut-induced hypophagia, which is frequently observed in temperate ungulates that breed in autumn or in winter. Observations generally occurred at two elevations (1200–1600 m and 2600–3200 m), using 20-min focal animal scan sampling from 2007 to 2009. Feeding behaviors accounted for the majority in takin's time budget (61.1%) during daylight hours, relative to the other observed behaviors, such as rest (14.1%), alert behavior (10.2%) and locomotion (6.8%). We found a negative correlation between feeding behavior and rutting behavior during the rutting season. A ratio of feeding time to resting time increased from pre-rut to rut, while resting behavior did not change significantly across seasons. These results suggest the "energy saving" hypothesis could explain reduced foraging in male takin during the rut, but aspects of the species biology suggest that hypotheses for rut-induced hypophagia developed for other temperate ungulates do not apply to takin. We suggest that the unusual summer rutting season of takin releases males from the energy constraints encountered by temperate ungulates that breed in the autumn and has other benefits for offspring survival. Further research should be conducted on ungulates that exhibit rut during the summer and tropical ungulates that might not experience limited food availability following the mating season to improve our understanding on rut-induced hypophagia.

1. Introduction

Maximizing lifelong reproductive success by optimizing energy and time allocation between reproduction and survival is a tactic adopted by long-lived and iteroparous animals. For herbivorous mammals, due to the need to acquire large amounts of plant material for extraction and digestion of nutrients, they devote the largest portion of their time to foraging (Altrichter et al., 2002; Beekman and Prins, 1989; Meldrum and Ruckstuhl, 2009; Styles and Skinner, 2000). Meanwhile, both environmental conditions and physiological state modulate the daily and seasonal foraging patterns (Bourgoin et al., 2008; Boy and Duncan, 1979; Kolbe and Squires, 2007; Nielsen, 1984). For example, among mountain goats (*Oreamnos americanus*), lactating females spend more time feeding and less time bedding compared with the time budget of nonlactating females (Hamel and Côté, 2008).

It has recently been hypothesized that male ungulates face conflicts in time allocation between foraging and mating behaviors during the rutting season (Apollonio and Di Vittorio, 2004; Mysterud et al., 2008; Pelletier, 2005; Willisch and Ingold, 2007; Willisch and Neuhaus, 2009). Hypophagia of male ungulates in rutting season has been observed in studies on bighorn sheep (*Ovis canadensis*) and mountain goats (Pelletier et al., 2009), alpine chamois (*Rupicapra rupicapra*, Willisch and Ingold, 2007), red deer (*Cervus elaphus*, McElligott et al., 2002), alpine ibex (*Capra ibex*, Brivio et al., 2010), fallow deer (*Dama dama*, Apollonio and Di Vittorio, 2004), and moose (*Alces alces*, Miquelle, 1990).

However, all of these studied ungulates have an autumn or winter mating season, which is characterized by low food abundance and associated physiological stress (i.e. low temperature and snow

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cover). During this season, energy expenditure mostly is limited to mating activities, temperature regulation, searching for food, and digestion. But there are some temperate ungulates that breed during the summer when food resources and environmental conditions are better. Therefore, ungulates exhibiting a summer rut may adopt different feeding strategies.

Currently, there are five competing hypothesis (i.e. Foraging constraint hypothesis, Energy-saving hypothesis, Physical rest hypothesis, Physiological hypothesis, and Parasite hypothesis) proposed to explain why male ungulates reduce or cease feeding during the rut (Brivio et al., 2010). Hypotheses for hypophagia differ in their supposition that reduced feeding are either the result of energy-saving behaviors or due to physiological limits on digestion. Pelletier et al. (2009) and Brivio et al. (2010) postulated that these hypotheses can be tested if the observer can estimate the ratio of feeding to resting behaviors from pre-rut to rutting season, as well as the correlation between rutting behaviors and resting during the mating season. Therefore, observations of summer rutting ungulates, such as takin, would provide an alternative test of the competing hypotheses examined in previous studies.

Takin are large bovids (adult weight 250–500 kg) living in high elevation regions from the eastern Himalayas to south-central China. They inhabit sub-alpine coniferous forest with three bamboo species (*Fargesia denudate Yi*, *Fargesia scabrida Yi* and *Fargesia rufa Yi*) and rhododendron (*Rhododendron*. spp.) understory in Tangjiahe nature reserve (hereafter referred to as Tangjiahe), as well as alpine meadows. Takin may be distinct among temperate ungulates in that their mating season occurs in summer from June to August. During this period, takin aggregate from small groups (3–8 takin) into large groups (>30 takin), and most males exhibit tending and coursing behaviors to obtain mating opportunities (Wu et al., 1998). So unlike other temperate ungulates, male takin are rutting during a season of high food availability, and thus the conflict between foraging and mating confronted by other ungulates might not be as critical for takin. Any trade-offs between foraging and social behavior may be different from those factors affecting fall/winter breeders. Takin also make seasonal altitudinal movements (Zeng et al., 2008, 2010), which might impact investment in foraging versus mating.

In this paper, we address two main questions: Do male takin exhibit hypophagia during the summer mating season, as observed in other large ungulates; and does the pattern of time investment in foraging/digestion versus resting or rutting behavior match any of the predictions of competing hypotheses for rut-induced hypophagia in male temperate ungulates as outlined by Brivio et al. (2010)? We postulate takin should allocate less time to foraging and digestion during the rut to meet the same level of energy balance as pre-rut (spring), but foraging and digestion should still encompass a significant portion of the time budget so that males can gain weight for winter. We also predict that social behavior should occupy more time during the rut compared to non-rut periods

2. Methods

2.1. Study area

This study was carried out in Tangjiahe (104°E, 32°N), in the northwest of Sichuan province, China (Fig. 1), from March 2007 to May 2009. Tangjiahe is located on the south piedmont of the Motianling Mountains, a branch of the Minshan Mountains range and covers 40,000 ha with a broad elevation range from 1100 to 3864 m. The climate at Tangjiahe is temperate, with January as the coldest month (mean −1.2 °C) and July as the warmest (mean 19.7 °C). The vegetation within the reserve possesses a distinct altitudinal gradient, with evergreen and deciduous broadleaf forest below 1700 m, mixed coniferous and deciduous broadleaf forest from 1700 to 2100 m, subalpine coniferous forest from 2100 to 3000 m and alpine meadows and rock outcroppings above 3000 m (Schaller et al., 1986). No human settlements exist within the reserve boundary, but there are eco-tourism (wildlife observation and watching along road and trails) activities along the main valley from April to October.

Table 1
Ethogram of takin behaviors based on Speeg et al. (in preparation).

Category	Description
Locomotion	The animal is traveling regardless of intent or motivation. This behavioral state includes walking, running and leaping.
Inactive	The animal is stationary and the head is at the horizontal or below. The eyes are partly or completely closed, and the ears are often to the side or partly lowered. The animal may be standing or lying down.
Alert	The animal is attentive, with the eyes open. The head is typically at horizontal or above, this behavior may occur in several body positions.
Feeding	Feeding includes any activity whereby the animal takes food into the mouth and chews, regardless of the type of food item.
Forage	Includes any search for, or handling of, food before feeding.
Rumination	Rhythmic chewing of cud and occurring well after a feeding bout has ended. Usually occurs while the animal is at rest.
Maintenance	Self-directed body maintenance behaviors; scratching body with hoof, licking fur, rubbing body, rubbing horn, or rubbing face on object, shaking the head or entire body, and dirt bathing.
Social behavior	Behaviors occurred between individuals. Including sexual behavior, aggressive behavior and affiliative behavior.

2.2. Data collection

Observations were conducted within two elevation bands: a low open area covered by brush and less dense forest (1200–1600 m) during March–May and September–November, and high subalpine coniferous forest and alpine meadow above the tree line (2700–3200 m) during June–August. Data were collected from 06:00 to 19:00 and all observations were conducted by at least two observers (range 2–4) at a distance 100–150 m at the low elevation area and 150–300 m at high elevation. All observers had been tested for reliability prior to the beginning of the study.

Focal animal scan sampling (Altmann, 1974) was used as our primary observation method. All males were selected according to the sequence of direction (e.g. from left to right or right to left) and no more than two individuals were observed in one group as the focal animal and scanned once a minute for a 20-min sampling duration. Males and females were distinguished by the size and the width of horns (the horns of males are larger and wider than that of female), the size of body and the color of fur (females are smaller and have lighter fur and males are larger and have dark fur around neck and head). We followed the ethogram developed by Speeg et al. (in preparation) based on semi-captive takin, which classified all takin behaviors into eight categories (Table 1). All behaviors beyond these categories were recorded as “Other”. When the focal animal was not visible to the observer, it was marked as “Not-Visible (NV)”. Here, we merged “NV” into “Other” prior to analysis. Bushnell spotting scopes (15–45 × 60) were used at distances >100 m. The takins’ movements in the rugged terrain, thick bushes as well as forest would occasionally block our ability to identify the exact behavior conducted by the focal individual