



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.

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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 scabrifida* 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 courting 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

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.

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.

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 sub-alpine 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

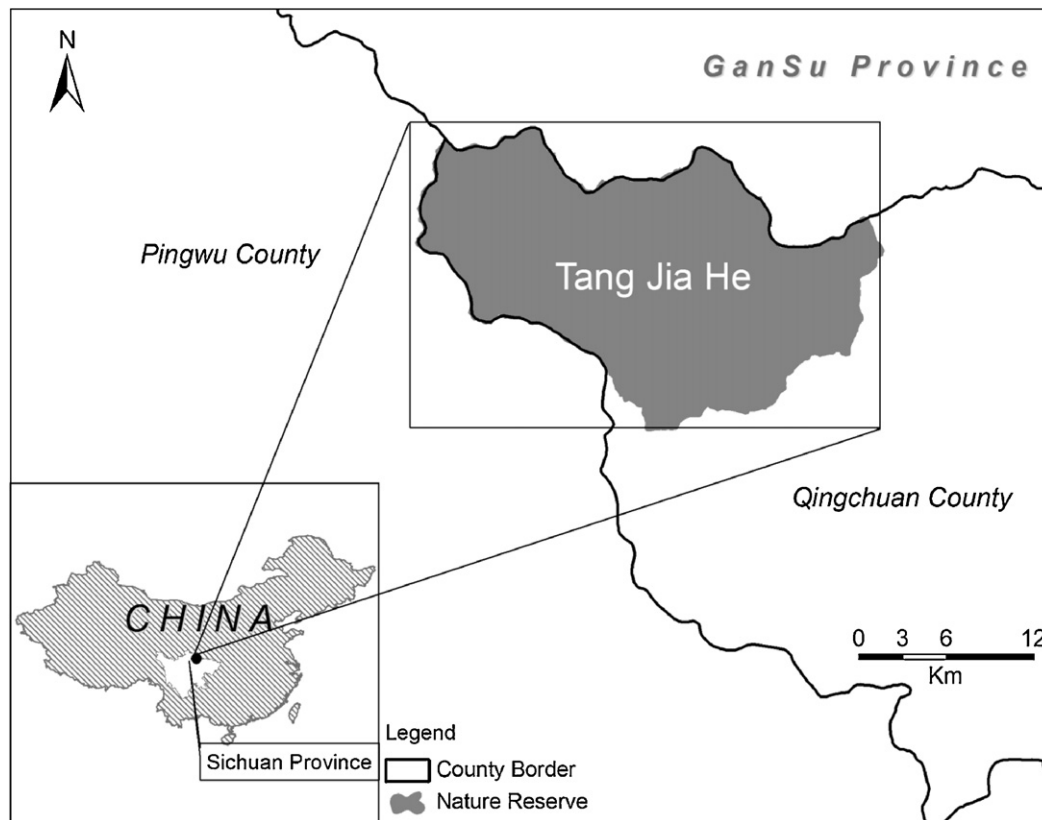


Fig. 1. Location of Tangjiahe nature reserve.

resulting in some observation sessions of less than 20 min in duration. These sessions were discarded from the analysis.

2.3. Data analysis

We divided the field sampling into three seasons according to the annual cycle of takin: pre-rut season (March–May), rutting season (June–August) and post-rut season (September–November) (Hu, 1994). During winter (December–February), takin inhabits the thickly forested bamboo zone (Hu, 1994) which is inaccessible to observers. The percentage of each behavior in every 20-min observation was calculated for each season and represented as mean \pm SE (Table 2). All statistics were calculated using SPSS (version 17.0, SPSS Inc., IL, USA).

For our *F/R* ratio analyses and annual time budget calculations and tests, we combined feeding and foraging into one behavioral category called feed and resting and rumination behavior into one category called rest (Table 1). We considered all of the social behaviors in the rutting season to be rut-related activities and named as social behavior (Brivio et al., 2010).

We tested difference of time allocation for each behaviors between two years, prior to pooling two years' data together. Due to different time allocations were detected, we classified the period of June 2007–May 2008 as Year 1 and June 2008–May 2009 as Year 2. We calculated the overall percentage of each behavior in each year, and used the Mann–Whitney *U* test to examine the difference of percentage time allocated to four behaviors (i.e. feed, rest, alert, and social) across different seasons.

Non-parametric Spearman correlations were calculated to analyze the relationship between the time devoted to resting behaviors and mating behaviors, and between feeding and mating behaviors, rumination and mating behaviors both during rutting season, pre-rut and post-rut season.

Prior to computing the *F/R* (*F* represents the time allocated to feed and *R* means the time allocated to rest) ratio, a constant ($k = 1$) was added to the proportions of time spent foraging and time spent lying as computed by Brivio et al. (2010) and Pelletier et al. (2009) in order to avoid ratios having a zero in the numerator or denominator.

3. Results

We conducted 198 h of observations including 594 focal scan sessions during September–November 2007, March–November 2008, and March–May 2009.

3.1. Overall and annual time budget

Feeding ($61.1 \pm 0.3\%$), resting ($14.1 \pm 1.2\%$), alert behavior ($10.2 \pm 0.7\%$) and locomotion ($6.8 \pm 0.3\%$) comprised the majority (>92%) of male takin time budgets when we combined both years (Fig. 2).

In Year 1 (Table 2), males spent more time engaged in social behavior in the rutting season than either before ($U = 2044$, $n = 73$, 83 , $p < 0.001$) or after the rut ($U = 3952$, $n = 140$, 83 , $p < 0.001$). The time allocated to feeding was greater in the pre-rut season ($U = 2266$, $n = 73$, 83 , $p = 0.006$) compared to rutting season. There was no significant difference detected of the feeding time between the rutting and post-rut seasons ($U = 5426$, $n = 140$, 83 , $p = 0.407$). Males also were alert for similar amounts of time across periods (rut to post rut: $U = 5121$, $n = 140$, 83 , $p = 0.123$; rut to pre rut: $U = 2935$, $n = 73$, 83 , $p = 0.722$). Time devoted to rest was not significantly different between the pre-rut and rutting season ($U = 3011$, $n = 73$, 83 , $p = 0.934$) or between rutting and post-rut season ($U = 5128$, $n = 140$, 83 , $p = 0.081$) though this difference approached significance.

Table 2

Changes in the amount of time spent (mean ± SE) in various behaviors from the pre-rut to post-rut period in both years of the study. Asterisks represent significant differences from the rut period.

Year	Season	Feed	Rest (rumination) ^a	Alert	Social
Year 1	Rut (N=83)	52.83 ± 3.61%	17.89% ± 3.75% (10.74% ± 2.84%)	5.24 ± 0.67%	10.36 ± 3.44%
	Post-rut (N=140)	55.00 ± 3.10%	24.93 ± 3.28% (8.84% ± 1.95%)	13.29 ± 1.72%	0.04 ± 0.04%**
	Pre-rut (N=73)	64.79 ± 3.86%*	16.44 ± 3.78% (11.74% ± 3.38%)	8.56 ± 1.59%	0**
Year 2	Rut (N=74)	44.74 ± 4.43%	4.81 ± 2.29% (3.49% ± 1.82%)	16.30 ± 3.25%	16.76 ± 3.99%
	Post-rut (N=118)	71.10 ± 2.17%*	6.14 ± 1.91% (2.75% ± 0.99%)	9.49 ± 1.02%	0.34 ± 0.34%**
	Pre-rut (N=106)	69.72 ± 2.28%	8.54 ± 2.28% (3.5% ± 1.18%)	8.58 ± 1.31%	0.33 ± 0.17%**

^a We considered rumination time, in parenthesis, as part of the testing resting time in these analyses.

* $p < 0.05$ Mann–Whitney U test.

** $p < 0.001$ Mann–Whitney U test.

In Year 2 (Table 2), social behavior occupied more time during the rutting season compared to both pre-rut ($U = 1880$, $n = 106$, 74 , $p < 0.001$) and post-rut ($U = 2033$, $n = 118$, 74 , $p < 0.001$) seasons. Compared to the rutting seasons, the time devoted to feeding was significantly higher in both the pre-rut ($U = 1595$, $n = 106$, 74 , $p < 0.001$) and post-rut ($U = 1595$, $n = 118$, 74 , $p < 0.001$) seasons. Although the time devoted to rest in Year 1 was much higher than in Year 2 (see Table 2), in Year 2, there was no statistical difference between rut and pre-rut ($U = 2733$, $n = 106$, 74 , $p = 0.463$) or post-rut ($U = 3133$, $n = 118$, 74 , $p = 0.774$). We also found no significant difference in the time allocated to alert behavior between the rut and pre-rut ($U = 2582$, $n = 106$, 74 , $p = 0.295$) or post-rut ($U = 3161$, $n = 118$, 74 , $p = 0.933$) seasons.

3.2. Correlation between feeding, resting and social behavior across seasons

During both rutting seasons observed, there was a significant negative correlation between social behavior and both resting (Year 1: $r = -0.301$, $n = 83$, $p = 0.002$; Year 2: $r = -0.285$, $n = 74$, $p = 0.037$) and feeding (Year 1: $r = -0.266$, $n = 83$, $p = 0.015$; Year 2: $r = -0.362$, $n = 74$, $p = 0.007$) behaviors.

During the pre-rut, there were no significant correlations between social behavior and either feeding (Year 2: $r = -0.196$, $n = 106$, $p = 0.054$) or resting (Year 2: $r = 0.152$, $n = 106$, $p = 0.120$) behaviors. However, since social behavior was never recorded during the pre-rut season in Year 1, we cannot determine whether there were correlations between social behavior and resting or feeding during that period. During the post-rut, there was no

significant correlation in either year between social behavior and either resting (Year 1: $r = -0.063$, $n = 140$, $p = 0.459$; Year 2: $r = -0.038$, $n = 118$, $p = 0.685$) or feeding (Year 1: $r = 0.013$, $n = 140$, $p = 0.882$; Year 2: $r = -0.139$, $n = 118$, $p = 0.133$) behaviors.

3.3. F/R ratio change between rutting season and non-rut season

Previous studies (Brivio et al., 2010; Pelletier et al., 2009) examining feed to rest ratios have used resting behavior as a proxy measure when rumination was not discernable. We were able to identify rumination behavior and did find significant positive correlations between rumination and rest during pre-rut (Year 1: $n = 73$, $r = 0.301$, $p = 0.01$; Year 2: $n = 106$, $r = 0.263$, $p = 0.004$), rut (Year 1: $n = 83$, $r = 0.365$, $p = 0.001$; Year 2: $n = 74$, $r = 0.570$, $p < 0.001$) and post-rut (Year 1: $n = 140$, $r = 0.184$, $p = 0.031$; Year 2: $n = 118$, $r = 0.679$, $p < 0.001$) seasons. We have continued the practice of combining rumination and rest to facilitate comparison with previous studies (Brivio et al., 2010).

We compared the F/R ratio between rut and both non-rut (pre- and post) periods in both years, and three of the four comparisons demonstrated significant changes, with lower F/R ratios during the rutting season (Table 3). The seasonal comparison of rut to post-rut ratios in Year 1 was in the same direction but the difference was not significant (Table 3).

4. Discussion

4.1. Overall time budget

As has been demonstrated in other temperate ungulates (Hudson, 1985; Brivio et al., 2010), we found that male takin spent more time engaged in social behaviors during the rut compared to before or after this period. Similarly, although feeding times ranged from 44% to 71% seasonally, it occupied more time than any other behavior throughout the year as predicted. During each of the ruts observed, social behavior increased 10–16% and foraging time reached its lowest levels, again consistent with a number of studies of hypophagia in male ungulates during the breeding season (Apollonio and Di Vittorio, 2004; Brivio et al., 2010; McElligott et al., 2002; Miquelle, 1990; Pelletier et al., 2009; Willis and Ingold, 2007). In Year 1, feeding behavior decreased by about 12% during the rut and remained low during the post-rut period. In contrast, during Year 2, feeding behavior during the rut was about 25% lower

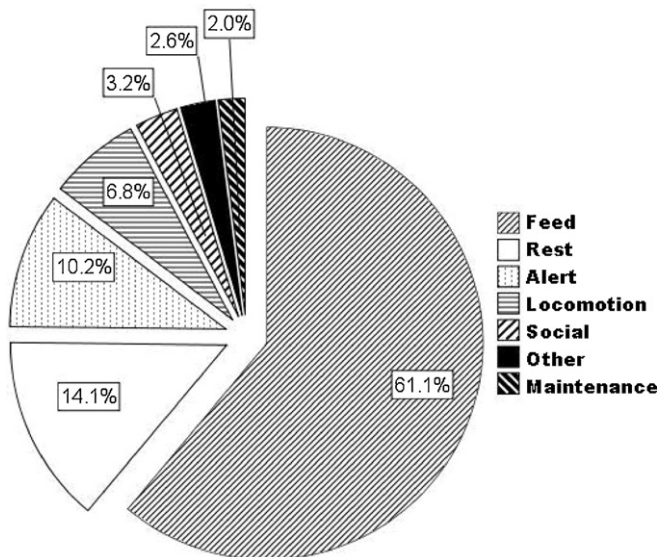


Fig. 2. Overall time budget of male takin.

Table 3
Comparison of F/R ratio between rut and non-rut periods during the study.

Year	Rutting season	Non-rutting season	F/R	U test/ p value
Year 1	1.41 ± 0.05 (n=83)	Post-rut (n=140)	1.40 ± 0.06	5646/ $p = 0.724$
		Pre-rut (n=73)	1.54 ± 0.06	2360/ $p = 0.016$
Year 2	1.40 ± 0.05 (n=74)	Post-rut (n=118)	1.67 ± 0.03	1738/ $p < 0.001$
		Pre-rut (n=106)	1.63 ± 0.04	1752/ $p < 0.001$

than both the pre- and post-rut periods. The reason for the annual differences in feeding time is unclear. Takin increased their resting time from rut to post-rut in Year 1 by about 7%, whereas resting only increased 1.3% in the following year. The amount of time taken spent resting did not change significantly across rut and non-rut seasons but they did appear to rest significantly more in Year 1 (19.7%) than Year 2 (6.5%). The increased resting time may reflect annual differences in forage quality or environmental conditions (Pipia et al., 2008), or unintended differences in demographics of those animals selected for observation (Miranda et al., 2005). We do not have sufficient information to deduce the reason behind the annual difference in feeding behaviors during the post-rut. Possibly the breeding investment of observed males differed between the two years which would influence post-rut feeding.

4.2. Hypotheses for hypophagia in ungulates

Social behavior increased significantly during rut and was negatively correlated with feeding, resting, and rumination behavior during both rut periods in this study. The *F/R* ratio during rut was significantly lower than outside the rut periods for most of the comparisons, while resting behavior did not change within years across the rut and non-rut periods. These results seem to support the energy saving hypothesis (Brivio et al., 2010), though not perfectly. The energy saving hypothesis predicts no change or an increase in resting from the non-rut to rut period, a decreased *F/R* ratio during the rut, and a negative correlation between resting and rutting behavior. According to this hypothesis, feeding and rutting behavior will have an inverse relationship until males cross a threshold food storage level where it is more beneficial to spend the majority of their non-rutting time resting rather than foraging. Below this threshold the rumination cycle would be disrupted by the increase in social behavior (VanSoest, 1994), and they would maintain a better energy balance by resting. We detected an inverse relationship between feeding and rutting in our analyses, but visual inspection of the data did not reveal a threshold below which feeding behavior ceased; in fact feeding behavior was a large part of the activity budget throughout the study.

The energy saving hypothesis is reasonable to explain the behaviors of winter rut ungulates that reduce their foraging effort on poor food resources to avoid a negative energy balance (Willisch and Ingold, 2007), but it is an unlikely explanation for takin hypophagia during the rut, as forage quality and quantity remains high during this period and takin have the autumn to recover and alternative food sources available during the winter (see below). Indeed it may be more accurate to describe a 12–25% reduction in feeding time as mild hypophagia, as takin are spending 45–53% of their time feeding during the rut.

Hypotheses for rut-induced hypophagia have been elaborated for species that are considered to be capital breeders, species in which energy expended for reproduction comes from storage rather than on-going intake (Jonsson, 1997). Capital breeders acquire energy resources in advance of breeding, whereas income breeders acquire energy during the breeding season. Are takin capital or income breeders? Energetic demands on male takin likely increase during the breeding season as they fight with other males for access to females. Data from captive takin indicate that adult males do put on weight during spring and then lose it during the summer breeding season (San Diego Zoo Global, personal communication) even though the animals are fed a high quality diet throughout the year; takin in our study spent a significant amount of time foraging during the breeding season. These data suggest that male takin do not conform to a single strategy, and thus hypotheses for rut-induced hypophagia in capital breeders may not be relevant to this species. Takin appear to be somewhat unique among temperate ungulates in that they rut only during the summer when

food is abundant (Schaller et al., 1986; Wu et al., 1990). There is still a trade-off between energy expenditure (rutting) and energy gain/conservation behaviors (foraging, rumination, resting) but the costs of reduced foraging must be more easily recovered in male takin. Even post-rut, food of intermediate quality is available for several months because takin migrate to lower elevations (Zeng et al., 2008), thus male takin may enter the winter in better physiological condition than most temperate ungulates.

4.3. Possible explanation of summer rut in takin

Most temperate ungulates time their mating so that parturition coincides with periods of food abundance (Bowyer, 1991); this timing results in females being on a high plane of nutrition during lactation and young having high quality forage. Due to gestation time constraints, this means most temperate species breed in fall and giving birth in spring. Takin, bison (*Bison bison*) and musk ox (*Ovibos moschatus*) breed during the summer (Nowak, 1999); whereas bison and musk ox give birth in the spring (Heard, 1992; Rutberg, 1984; Wu et al., 1990), takin give birth in winter mid-December to early April (Wu et al., 1990).

Why do takin pursue such a counter-intuitive strategy? We believe the answer lies in the takin's ability to make altitudinal migrations (Zeng et al., 2008) and their incorporation of bamboo into the diet (Hu, 1994; Schaller et al., 1986). Severe topography allows for significant variation in phenology along an elevation gradient in mountain areas (Fryxell and Sinclair, 1988). Better food quality is the main reason temperate ungulates conduct seasonal elevational movements (Myserud et al., 2001). When the calves are born during the winter, females occupy an elevation band of 1900–2400 m where evergreen bamboo is readily available (Hu, 2005). Bamboo serves as a nutritional, above-snow food source for females in the early months of lactation, as the leaves of bamboo species found in this region are known to contain 7–15% crude protein in winter (Edwards et al., 2006; Tabet et al., 2004) which is adequate for maintenance in ruminants (BANR, 2007). In March, females begin to migrate down to 1300–1400 m elevation to feed on new shoots and vegetation and remain there until mid-spring. During this time, lactation is supported by new spring vegetation, which also serves as food for young takin that begin to take solid food at one to two months of age (Neas and Hoffmann, 1987; Nowak, 1999). Most temperate ungulates, including takin, are weaning their offspring in late summer or fall (Walther, 1990; Wilson and Reeder, 2005). Elevational migration to nutritious food sources, and incorporation of bamboo into the diet as winter forage, enables takin calves to have a longer growing season than most temperate ungulates and to be weaned at larger relative body weights which should promote better survival during their first winter.

In conclusion, rut-induced hypophagia appears to be relatively minor in takin though it does share features in common with other temperate ungulates. Hypotheses to explain rut-induced hypophagia in capital breeding temperate ungulates do not appear to apply to takin as this species seems to pursue a mixed capital-income breeding strategy and ruts during a period of high food availability. It is suggested that the unique timing of the rut in takin and subsequent atypical birth season are the results of the takin's ability to seasonally migrate to high quality food sources and incorporate bamboo into the diet as winter forage. Further studies of summer rutting species such as bison and musk ox would be beneficial in understanding hypophagia during rut in temperate ungulates.

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