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An ethogram and activity budget of captive Sichuan takin (*Budorcas taxicolor tibetana*) with comparisons to other Bovidae

Abstract: Takins (*Budorcas taxicolor*) are large bovids native to Bhutan, China, northeast India, and northern Myanmar. There is no published comprehensive ethogram for takin and only minimal published data on their behavior. We used captive takin housed in large enclosures in various social groups, ad libitum observation, and video recordings to construct a behavioral repertoire comprising 9 behavioral categories and 24 individual behaviors. Additional 402 h of data collection from a mixed breeding herd were used to examine the time allocated by takin to perform several activities. Most of the time (82.3%) was spent feeding, ruminating and resting, similar to other ruminants. Feeding was particularly common in autumn and winter. In general, the activity budgets of each sex were similar, though social behavior was more common in males than females. The social behaviors suggested that during the breeding season, males follow reproductive females while they are foraging (a behavior termed tending in this study). Many of the behaviors were similar to previously recorded behaviors in other members of the Bovidae.

Keywords: activity; behavior; Bovidae; ethogram; takin.

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Introduction

Takin (*Budorcas taxicolor* Hodgson, 1850) are large antelopes in the tribe Ovibovini, together with the musk ox (*Ovibos moschatus* Zimmermann, 1780)

(Hernandez-Fernandez and Vrba 2005). Takin are stout, with a deep chest, and greater height at the shoulder than the hip. Adult males can weigh over 300 kilograms, and both sexes have massive horns that grow out and back (Neas and Hoffman 1987). Takin inhabit varying elevations from 1000 m to 4000 m; they are found in sub-alpine and sub-tropical forests as well as in alpine meadows across regions of south-central Asia, from Bhutan to central China (Neas and Hoffman 1987, Song et al. 2008). Though locally abundant in some reserves, takin are listed as vulnerable by the IUCN and in Appendix II of CITES (Magin and Groombridge 1994). Sichuan takin (*Budorcas taxicolor tibetana* Milne-Edwards, 1874) are one of four extant subspecies of takin and are restricted to Sichuan, northern Yunnan, and southern Gansu Provinces in the People's Republic of China, although range-wide surveys are lacking (Song et al. 2008). Sichuan takin are afforded protection by sharing many reserves with two charismatic species, namely, the golden monkey (*Rhinopithecus bieti* Milne-Edwards, 1897) and giant panda (*Ailuropoda melanoleuca* David, 1869), and are listed as a Category 1 species of the National Wildlife Law of 1988 by the Chinese government (Song et al. 2008).

Due to the rugged habitat of Sichuan takin, it is difficult to conduct studies on their behaviors; thus, questions remain about their sociality, activity budgets, and foraging behavior. Data from social interactions of golden takin (*Budorcas taxicolor bedfordi* Thomas, 1911) in Shaanxi Province (Zeng and Song 1999, Zeng et al. 2002), and few studies on Sichuan takin (Schaller et al. 1986, Ge et al. 1989), suggest that takin form groups that vary in size and composition depending on the habitat type and season. Takin migrate annually, breeding at higher elevations, and wintering and calving at lower elevations (Schaller 1985, Neas and Hoffman 1987, Zeng et al. 2008). Both subspecies form groups numbering from 2 to 60 animals, but the behavioral dynamics underlying this variation in group size remains unexplored. The courtship, mating, and parturition behaviors of takin are also undescribed. Descriptions of some aggression (Schaller 1977), defending (Zeng and Song 1998), and feeding (Schaller et al. 1986, Zeng et al. 2001a) behaviors from both captive and

wild takin exist in the literature, but a comprehensive behavioral repertoire is lacking. Due to the difficulties of studying takin behavior in situ, captive animals may provide the best opportunity with which to construct a comprehensive ethogram.

The goal of our study was to provide a comprehensive ethogram for takin as well as gather preliminary data on sex and seasonal differences in activity budgets. We also qualitatively compared the behaviors observed with descriptions of behaviors in other ungulates and with our own observations of Sichuan takin in the wild. A subsequent analysis will focus on social behavior and interactions among the takin.

Materials and methods

Observations of captive Sichuan takin to construct an ethogram took place at The Wilds in Cumberland, OH, United States (39°49N, 81°43'W) from May 2006 to January 2008. A total of 117 h of preliminary observations in various enclosures were conducted on breeding and bachelor groups of takin during this period. The breeding group contained 1 adult male, 2 adult females, and a yearling female. The bachelor group contained 7 males, ranging in age from 1.5 to 6.5 years old. Ad libitum notes were combined with digital video recordings to construct a basic behavioral repertoire for use in data collection. Behaviors not included in the initial behavioral repertoire were described in detail as they occurred and then video-taped when possible. New behaviors were analyzed to determine behavioral category, after which they were described and incorporated into the inventory.

To assess activity budgets, we gathered 402 h of systematic observations in six 2-week trips from January 2010 to June 2011, at 2- to 3-month intervals. These observations were placed in each season (i.e., spring, summer, autumn, and winter). We did not collect data in the summer or autumn of 2011 due to logistical problems. The herd of up to 9 adult females and up to 6 adult males (Table 1), in a mixed-sex group, ranged freely in a 90-ha semi-natural enclosure containing grass-covered hillside, lakes, and woodland. The numbers of adult animals increased during the study as individuals became sexually mature. Observations were conducted 5–6 days per week, with randomly determined focal animal order. Observation periods were 0.5 h in duration, made between 07:00 to 18:00 and balanced across the time of day. Individuals were identified by ear tags, horn conformation, and other physical

Table 1 Age and identification of sexually mature takin observed during the study.¹

Males		Females	
ID	Birth date (month/year)	ID	Birth date (month/year)
M74	March 2002	F99	February 2004
M100	May 2004	F105	January 2004
M108	January 2004	F108	March 2005
M114	February 2002	F113	May 2008
M124	May 2005	F116	May 2002
M129	May 2002	F119	June 2008
		F125	May 2004
		F180	July 2005

¹An additional 7 juvenile males and 5 juvenile females were also present in the group during the study.

characteristics. Observations were made by two observers with binoculars from inside a vehicle parked 50+ m away from the group. Observations started 5 min after the vehicle parked at the enclosure and the focal animal was identified. We used a combination of all occurrence and scan sampling (Altmann 1974, Lechner 1992). Behavioral state was scanned every minute, as indicated by a digital stopwatch, and then transcribed to a data sheet. The recording was terminated when the animal was disturbed by unexpected human activities (e.g., arrival of a tour bus arrival, a passing keeper's truck, a helicopter flying over, etc.) during the observation. All observers were assessed for reliability.

Differences in male and female activity budgets were initially compared using G-tests. To identify the behaviors that differed between males and females, we conducted a confidence interval (CI) analysis (e.g., Powell et al. 2006). We considered the CI around the mean with the highest number of subjects (males or females) in that observation session as the standard (i.e., if the other sex's mean fell outside this CI, it was considered significantly different), so that our estimate was as robust as possible. As a result, we used the CI around the mean of the males' behavior for each observation period except spring 2011. The CI around the mean of the females' behavior was also used in the comparison of total activity budget across periods for the same reason. We used CI analysis because our analyses included repeated observations of a small number of individuals and represented an initial exploratory assessment of behavior. We also compared activity budgets of takin (males, females, combined) across observation periods using CI to assess seasonality of behavior. We analyzed seasonal activity budgets by comparing data from one observation period to data from the previous observation period.

Results

After conducting preliminary observations to identify and describe takin behaviors, we defined 24 individual items gathered into 9 behavioral categories that include the following: feeding, foraging, ruminating, maintenance, moving, alert, resting, social, and other. Social behaviors were further subdivided into aggression, courtship, affiliative, maternal, and vocalizations based on similarities to recorded behaviors in other ungulate species. In all cases, the G-test indicated that the total activity budgets of males and females were different ($p < 0.0001$, individual tests not shown).

Feeding

Feeding was defined as actual consumption of food items. Overall, takin spent 35.5% of their time feeding (Table 2). No systematic record of grazing versus browsing was made during scan sampling, but the observed feeding type was predominantly grazing on non-woody grasses and forbs. Males spent more time feeding than females (48.6% vs. 32.8% of time) in winter 2010, while the reverse was true in spring 2011 (19.5% vs. 40.1% of time). There were no other gender differences in feeding time.

Generally, takin grazing is similar to other ungulates: slow walking with momentary pauses to crop grass with the lips. Grazing takin paused to raise their heads for surveillance every 5–10 s. The bachelor group enclosure provided some opportunities for browsing, although the predominant bush, autumn olive (*Elaeagnus umbellata*),

was not favored. In the winter, when non-woody plants became scarce, male takin were observed to browse by grasping small branches with the lips and pulling with the head to strip several leaves from the branches of the evergreen bushes.

Foraging

Foraging included any search for, or handling of, food before feeding. Foraging behavior was relatively rare (1.5% of the overall activity budget), and the sexes only differed in spring 2011 when females foraged more than males (3% vs. 1.8% of time). During ad libitum observations, takin were observed to use their head and neck to break or bend branches to browse leaves beyond their reach. An adult male takin was also observed to stand fully upright with the forelegs supported by a tree to reach branches that were 2–3 m above the ground. Takin were not observed to kick snow away to expose ground forage, but were observed eating snow on several occasions. Captive takin were never observed to dig with hooves or teeth for minerals or salt.

Ruminating

Ruminating occupied 19.7% of the overall activity budget (Table 2). Females ruminated more than males in summer 2010 (25.4% vs. 4.4% of time) and winter 2010 (18.5% vs. 3.7% of time). The predominant position for ruminating was lying on the sternum with the muzzle lowered, often with the eyes closed. Takin also stood to ruminate, with the

Table 2 Seasonal activity budgets of adult male and female takin at The Wilds.¹

Period	Sex (n)	Feeding	Foraging	Ruminate	Maintenance	Moving	Alert	Rest	Social
Spring 2010	F (4)	19.63±6.56	0.77±0.30	35.01±3.19	1.32±0.15	1.24±0.95	1.52±0.57 ²	32.56±11.19	0.87±0.72
Summer 2010	M (6)	13.49±5.02	0.44±0.34	41.06±6.11	2.23±1.04	1.98±0.80	0.89±0.21	35.31±3.22	3.85±2.24
Autumn 2010	F (5)	38.07±8.09	0.00	25.37±9.97 ²	1.94±0.49	2.06±0.31	0.74±0.21	27.33±4.50 ²	0.20±0.20
Winter 2010	M (5)	20.51±10.25	0.00	4.40±3.02	6.93±5.84	7.93±3.34	1.33±1.33	47.82±9.88	4.16±2.84
Spring 2011	F (5)	53.08±7.08	1.69±0.75	20.83±4.46	0.56±0.39 ²	1.83±0.42 ²	1.53±0.26	5.47±2.46	0.06±0.06
Summer 2011	M (5)	44.81±8.01	1.20±0.47	21.54±6.73	3.08±0.42	1.01±0.30	2.33±0.65	15.11±4.90	1.86±1.45
Autumn 2011	F (4)	32.81±7.80 ²	2.88±1.07	18.47±8.04 ²	0.83±0.50	3.86±0.48	6.26±1.80 ²	34.24±3.76	0.00
Winter 2011	M (6)	48.57±4.07	2.94±0.71	3.70±2.10	2.00±0.66	8.66±4.09	11.06±1.38	19.94±8.13	0.85±0.62
Spring 2012	F (8)	40.07±3.31 ²	3.05±0.51 ²	19.72±2.87	1.78±0.50 ²	1.52±0.43 ²	1.58±0.51	28.61±2.53 ²	0.71±0.41 ²
Summer 2012	M (5)	19.50±5.67	1.81±0.89	17.21±6.58	4.15±1.41	2.58±1.97	1.17±0.62	22.66±9.89	24.45±19.03
Autumn 2012	F (4)	40.61±4.93	0.89±0.30	19.63±2.04	1.22±0.45	3.31±1.50	0.82±0.31	31.05±5.26	0.19±0.13
Winter 2012	M (6)	47.67±5.22	0.93±0.52	11.12±5.17	3.41±0.96	6.57±3.83	0.72±0.35	27.65±9.11	0.86±10.63
All	F (9)	38.28±5.22	1.70±0.56	22.71±4.21	1.34±0.37 ²	2.18±0.56 ²	1.95±0.76	26.14±4.63	0.37±0.28 ²
Data	M (6)	32.80±8.39	1.24±0.64	16.70±7.09	3.53±2.14	4.87±2.86	3.03±1.76	28.04±8.17	5.63±7.13

¹Numbers in parentheses represent the number of subjects observed during that observation period.

²Significant differences in behavior between the sexes during a given observation period, as revealed by confidence interval analyses.

muzzle lowered and eyes closed. They were also observed to lie flat out on their sides for short periods when resting after rumination bouts.

Maintenance

Overall, takin spent 2.4% of the time engaged in maintenance behaviors. Males performed more maintenance behavior than females in autumn 2010, spring 2011, and in all observation periods combined (Table 2). Takin performed self-directed body maintenance behaviors described for most other ungulates, which include scratching the body with the hoof, licking fur, rubbing the body on an object, rubbing the face on an object, or shaking the head or the entire body.

Takin males and females also rubbed their horns on fence posts and trees in both solitary and group-housed animals. Maintenance horn-rubbing was performed with little force, and was done at a slower pace than the male display termed object horning (described below). Males in the wild and in captivity were also observed to rub their entire flank against hillsides, eventually denuding the vegetation (B.S. personal observations). Both males and females rubbed their flanks against fence posts, walls, and trees.

Moving

Moving occupied 3.5% of the overall activity budget (Table 2) and was more common in males in the overall activity budget (2.2% vs. 4.9% of time) and in spring 2011 (1.5% vs. 2.6% of time). Females moved more than males in autumn 2010 (1.8% vs. 1% of time). Takin were observed to be amblers that moved their legs on the same side of the body with the head held low. Takin moved slowly, but were capable of explosive speed and jumped with all four feet leaving the ground. They were agile for their size and climbed steep terrain with ease. In dense brush, takin moved powerfully, often breaking limbs and other barriers, rather than moving around them. Takin ran quickly for a short distance when startled and then turned to face the threat; they were also observed to wade in chest deep water for periods of time during the heat of summer, and a young male (2 years old) was even observed swimming a short distance.

Alert

Takin showed alert behavior 2.5% of the time overall (Table 2). Females were more alert than males in spring

2010 (1.5% vs. 0.9% of time) while the reverse was true in winter 2010 (6.3% vs. 11.1% of time). Alert behavior was defined as the animal being attentive, with the eyes open. The head of an alert takin was typically horizontal or above, and the ears were often moving or aligned along the line of sight. Alert behavior occurred in several positions including standing and sternal recumbent (animal lying on the stomach with the head up).

Resting

Takin rested 27.1% of the time. Males rested more than females in summer 2010 while the reverse was true in spring 2011 (28.6% vs. 22.7% of time). Resting in takin was defined as the animal being stationary with the head at the horizontal or below. Resting was differentiated from rumination by a lack of visible mastication. Their eyes were partly or completely closed, and the ears were often to the side or partially lowered. Resting in takin occurred in several positions including standing rest (animal standing with head lowered), sternal recumbent (animal lying on stomach with head lowered at or near ground level with the rear legs tucked under the body with the forelegs extended or tucked under the body), and lateral recumbent (animal completely on side with head resting on ground).

Aggression

Arched back display

Adult male takin performed a ritualized lateral display in a nose-down, arched-back posture that was called a “head down display” by Schaller (1977). The performing male lowered the nose and horns, while drawing the rear legs forward and arching the back. The body was lateral to the recipient, possibly to enhance apparent size. The performer was sometimes stationary, but often the display was performed in combination with a slow, exaggerated, stiff-legged walk. When two males simultaneously performed the arched back display, they would often tilt the horns and head toward the opponent, and circle while engaging in stiff-leg walking.

During preliminary observations of a bachelor group of takin, this behavior was relatively common (n=35 occurrences) and in 34% of observations, the display was reciprocated within 1 min. Among the observations of such display, 49% were followed by an additional arched back display or one animal was supplanted by the performer within

2 min; moreover, 31% were followed by sparring or charging by the performer within 1 min. The two most dominant males performed 85.7% of these observed displays ($n=35$). In comparison, the arched back display was not observed in males under 2 years of age, and was never observed in females.

Sparring

For this study, several fighting techniques were combined under the general behavior termed sparring. Sparring in takin took several forms depending on the severity of the encounter. In low intensity encounters, takin stood face to face with their horns in medial presentation and the chin drawn in to make contact with the horns (i.e., boxing or nod-butting). Takin also maintained contact with the horn bosses and tilted and twisted the head to wrestle with the horns. When horns were engaged, takin lightly pushed back and forth, but not strenuously. In higher intensity encounters, takin exchanged powerful blows from short distances with the impact focused on the bosses, often circling or turning rapidly toward an opponent to increase force as described for the arched back posture. Sparring takin did not separate by more than 1 to 2 m and did not run at each other from long distances. The massive shoulders and forelegs compared with the smaller hindquarters of the takin may prevent any rearing behavior. However, takin did transfer their weight to their hindlegs and raised their head and shoulders before bringing them down to make contact, but the forelegs did not leave the ground.

Sparring took the same form in females, although the force of impact was greatly reduced. Sparring occurred much less frequently in females than in males. One incidence of low-intensity sparring was observed between the breeding male and a female during preliminary observations in November 2006.

Supplanting

Passive avoidance occurred frequently in males and females when confronted with animals of apparently higher rank; such passive avoidance helped avert fighting. Supplanting was observed in both males and females and usually occurred when animals were given their supplementary diets. In males, the actor sometimes performed the arched back display while supplanting a subordinate animal; however, the act of walking toward the recipient was often enough to cause them to cede ground. The recipient never adopted a posture that may be associated with

submission in other ungulates, but only walked or jumped away depending on the proximity of the aggressor.

Charge

A charge was differentiated from a supplant by the performer's rate of approach. Charging takin approached a recipient by taking several bounding strides from a short distance with the head lowered. A charge also included taking one or two rapid steps and swinging the head at a recipient from close proximity. Takin did not chase the recipients for any distance after they retreated following a charge or a supplant, but instead, occupied the ceded territory or resource.

Object horning

Takin males were observed to thrash vegetation with their horns and to forcefully rub and gouge large tree trunks with their horns. Although aggressive object horning was observed only in males, both females and males rubbed their horns on posts and trees in a self-directed maintenance behavior discussed above. Maintenance horn-rubbing and object horning by males were differentiated by the degree of force applied. In the presence of other males, male takin pushed their horns against a tree or post with exaggerated force, often tearing the bark from trees, and engaged in some of the same motions used in sparring, suggesting this could be a type of aggressive display. In the bachelor group vegetation thrashing was recorded twice in the same observation period as 25 other aggressive encounters.

Courtship

Anogenital sniff

An animal placed its nose near the recipient's anogenital region and inhaled, with the animal approaching from behind or from the side of the recipient. This behavior was relatively common in both the bachelor ($n=14$) and breeding groups ($n=24$) during preliminary observations. In the breeding group the male performed such behavior more frequently ($n=19$) than females ($n=5$). Both sexes directed sniffing behaviors at individuals of both sexes. The two most dominant males in the mixed sex group performed 85.7% of observed male-female anogenital sniffing behavior.

Flehmen

Flehmen in takin is similar in form to the behavior described for most ungulates where the head was raised above horizontal and the lips opened, usually after smelling dung or urine. Flehmen was observed only in males, and was more common in the breeding males ($n=7$) than in bachelor males ($n=1$) during preliminary observations.

Urine sampling

Directly sampling the urine stream was not observed during this study, but urine testing from the ground by males was observed preceding the flehmen behavior.

Tending

The main courtship behavior in takin was termed tending. Takin males tended a female by standing parallel with the head near the female's flank. If the female was stationary (feeding or standing), the male would stand with his muzzle contacting the female's flank and occasionally rest his chin on the female's back. As the female moved, the male would follow closely, not allowing the female more than 1–2 m of separation, and sometimes maintaining contact with his muzzle on the hindquarters. When moving, a tending male would adopt a chin-out posture with the head held at shoulder height. The female was always positioned ahead of the male, and the female controls the direction of movement because her path is not intercepted or changed by the male.

In 57 h of preliminary observations, only 11 tending bouts were observed during 7 different observation periods in the breeding group. The longest bout of tending that was uninterrupted by other behaviors lasted 2 min; 4 other tending bouts were preceded within 3 min by aggression by the breeding male toward another female. Anogenital investigation preceded 2 tending bouts, and 3 tending bouts were initiated with no observed social behaviors preceding them.

Dominant males were observed tending subordinate males on 13 occasions. Subordinate males never tended more dominant males. In these 13 cases of male-male tending, the tending behavior was never followed within 1 min by any aggressive behavior. Tending was never performed by females.

Mounting

During tending bouts, males attempted to mount by throwing their forelegs onto the back of the female. The female did not stand for any of the attempted mountings, and no copulation was observed during preliminary observations. Dominant male takin were observed mounting subordinate males five times during tending bouts. Female takin were never observed to mount males or other females.

Affiliative

Face-sniff

A behavior we termed face-sniff has a greeting or investigative function. An animal placed its nose near a recipient's facial region and held the position while smelling the recipient's face or head. By definition, the face-sniff was always reciprocated with both animals raising their heads and muzzles near the other animal's face. Physical contact between the animals was observed, although it did not occur in most of the interactions. Of 60 observed face-sniff behaviors during preliminary observations, 26 were followed within 1 min by another social behavior. In 25 observed face-sniff behaviors in the bachelor group, 4 were followed within 1 min by an aggressive act directed toward the same animal as the one giving the face-sniff.

Social play

Social play was observed in a 2-year-old female. The intention to play was indicated by repeatedly tossing the head and jumping back and forth in front of the breeding male. The male did not reciprocate the play behavior and ignored the young female.

Maternal

No systematic observations of dam-calf behaviors were completed during ethogram development. The birth of 5 takin calves occurred after the completion of the study, but ad libitum observations were provided by animal care staff at The Wilds. Takin calves were usually up and mobile within 30 min after birth and did not hide away from the dam for any period of time. They were able to travel with the entire herd within a couple of days (personal observations, The Wilds). Individual dams fiercely defended offspring when animal care personnel performed neo-natal

exams. Calves that vocalized attracted the attention of all females, but only the dam continued with defensive behavior. Calves were observed to form crèche-like associations when managed in the natal herd. These crèche-like groups were often attended by 1 or 2 adult females, although all other dams usually remained in sight of their calves. We also observed similar crèche groups of takin calves attended by one or more females in the wild in China (D. Powell, B. McShea, personal observations). Further observations indicate that takin dams groom and interact with their calves in similar ways as the ungulates.

Vocalizations

Snort

The snort vocalization is produced by explosively expelling air through the nose. The snort served as a threat, and could be directed at other takin or other species, including humans. Startled takin often produced the snort as they fled. The snort was recorded four times during preliminary observations in both males and females.

Bellow

The bellow vocalization is a low stuttering call produced deep in the throat, with the sound coming from an opened mouth. The bellow is a low intensity sound, but can be heard at distances of up to 200 m. The bellow occurred 19 times in males during preliminary observations. The bellow was recorded 11 times in one observation period when the focal male was separated from another male by a fence. The other male bellowed in response, and thus the vocalization served as a locator call or a vocal display. The bellow was not recorded in females during preliminary systematic observations, but was recorded in females during ad libitum observation.

Overall social behavior occupied only 2.9% of the activity budget of the takin (Table 2). Males spent more time engaged in social behavior (all forms combined) than females overall (0.4% vs. 5.6% of time) and during spring 2011 (0.7% vs. 24.5% of time) (See Figures 1 and 2).

Other

Other was recorded when an activity could not be included in the eight other categories.

Solitary play

Solitary play behavior was observed in a 4-year-old female and a 2-year-old male. Both instances involved the animals repeatedly flipping feed pans in the air with their horns. This is possibly an early form of object horning behavior described above.

Horn licking. During ad libitum observations, a yearling takin female was observed licking another female's horns. No aggression followed the behavior, nor was it reciprocated. The behavior was not observed in males, and no additional encounters were observed in females.

Seasonal changes in the activity budget

Feeding, resting, and rumination occupied most of the activity budgets of male and female takin (82.3% on average). All other behavior categories observed never occupied more than 6% of the activity budgets in a given season; therefore, only changes in feeding, rumination, and resting are reported here.

In males, feeding increased significantly from summer to autumn and winter in 2010 (20.5%–44.8% and 48.6% of time). Feeding in winter 2011 was higher than in spring 2011 (47.7% vs. 19.5% of time). Meanwhile, rumination was significantly higher in spring (41.4% in 2010 and 17.2% in 2011) and autumn 2010 (21.5% of time) compared with the adjacent seasons (Table 2). Resting behavior increased from spring to summer 2010 (35.3%–47.8% of time) and decreased significantly during autumn 2010 (15.1%). No other significant changes in these behaviors were seen (Figure 1).

Female takin showed significantly increased feeding from spring to summer 2010 (19.6%–53.1% of time), although this activity decreased in autumn 2010 (38.1%) and in winter 2010 (32.8% of time). Rumination was significantly higher in spring compared with summer 2010 (35.0% vs. 25.4% of time). Resting behavior was significantly higher in summer and winter 2010 (27.3 and 47.2% of time, respectively) compared with autumn 2010 (5.5% of time). No other significant changes in these behaviors were observed (Figure 2).

Discussion and conclusion

Takin are generalist herbivores, vertically migrating to follow phenological changes and feeding on well over 100 different plant species (Schaller et al. 1986, Zeng et al.

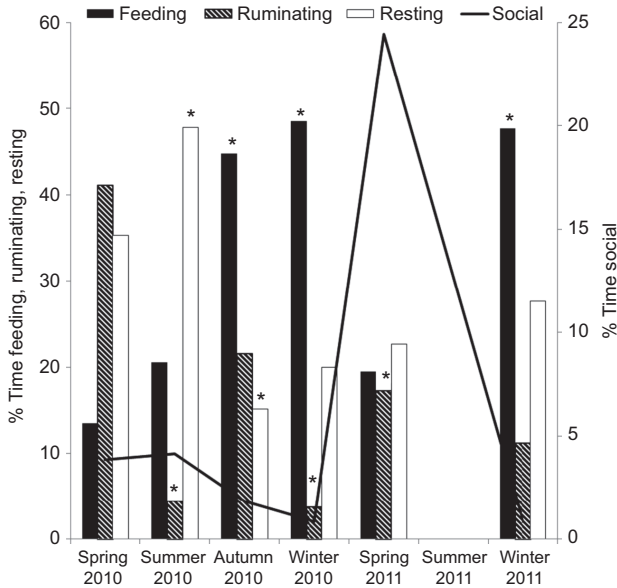


Figure 1 Feeding, ruminating, and resting behaviors of male takin observed at The Wilds (Ohio) during the study. Social behavior is included as a line on the secondary y-axis. Asterisks represent significant differences in that behavior compared with the previous observation period.

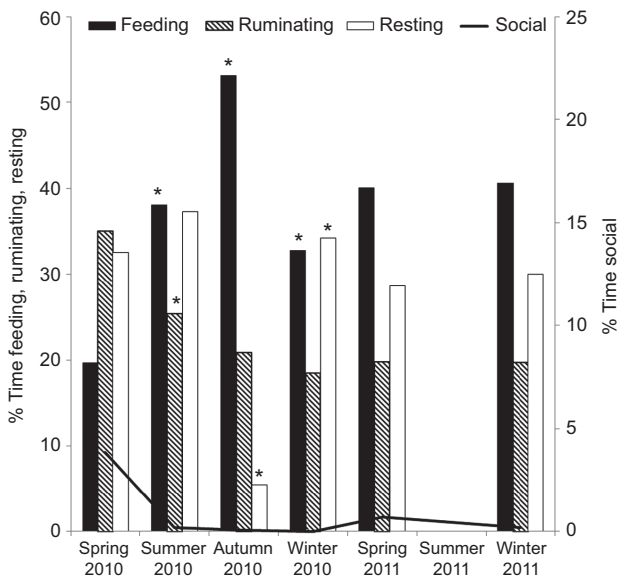


Figure 2 Feeding, ruminating, and resting behaviors of female takin observed at The Wilds (Ohio) during the study. Social behavior is included as a line on the secondary y-axis. Asterisks represent significant differences in that behavior compared with the previous observation period.

2001b). In the wild, the amount of time they spend feeding, foraging, and ruminating is expected to vary with changes in the predominant available food type. The floral composition of the enclosures in this study was predominantly

grassland, which differed greatly from forage found in the wild. Takin in this study were also given daily supplemental feed, consisting of hay and concentrated pellet, which may have affected diurnal rhythm, as the supplemental feeding caused immediate activity regardless of the time of day. The overall activity rhythm we observed for takin resembled the pattern observed in most large bovids, with the time spent feeding peaking in early morning, followed by a resting and ruminating period in the late morning and early afternoon (unpublished data). We conducted no evening or night observations, but ad libitum observations suggest that takin actively feed in the evening as well.

The social behaviors described for takin in this study are expected given the unstable and varied social structure observed in wild takin (Schaller et al. 1986, Zeng and Song 1999, Zeng et al. 2002). The core social unit of takin in the wild comprises adult females and their offspring of different generations (Schaller et al. 1986, Zeng et al. 2002). In the current study, only two affiliative behaviors were seen in takin, and no mutual grooming or other bonding behaviors were observed in takin females. The face-sniff behavior was the most frequently observed affiliative behavior, although it could not be strictly defined as a bonding behavior, as it was never followed by distinctly affiliative behaviors such as mutual grooming. However, the close contact of the behavior with few observations of subsequent aggression indicated that it was more affiliative or investigative than aggressive.

Takin males, when not in mixed groups, are mostly solitary, but occasionally form small, unstable bachelor herds consisting of 2–3 animals (Schaller et al. 1986). The 7 males in the captive bachelor herd observed during ethogram development did not form a cohesive group. Individual males left and rejoined the group, and smaller groups formed and dissolved. Dominance could not be clearly defined for every male in the group, but older animals tended to be dominant to younger ones, and coexisted with moderate aggression and minimal injury. Meanwhile, the arched back display and low-intensity sparring emphasized size and strength without severe aggression. Dominant males had priority access to supplemental feed, and it is assumed that these males would also gain access to reproductive females in mixed groups (B.S., personal observation). A subsequent analysis will focus on behavioral events, such as aggression and sexual behaviors, to test this hypothesis.

The arched back display was a ritualized lateral display performed in a nose-down, arched-back posture, similar to that described for other bovids, including nyala (*Tragelaphus angasii*, Gray, 1849), greater kudu

(*Tragelaphus strepsiceros*, Pallas, 1766) (Estes 1990), markhor (*Capra falconeri*, Wagner, 1839) (Walther 1974), and mountain goats (*Oreamnos americanus*, de Blainville, 1816) (Geist 1965). The arched back display was often performed in combination with a slow, exaggerated, stiff-legged walk, as described for kob (*Kobus kob*, Erxleben, 1777) and topi (*Damaliscus lunatus*, Burchell, 1823) (Estes 1990). A broadside posture can either be a threat or dominance display, and the arched back display in takin may function as both, depending on the situation and the response of the recipient (Walther 1974). The low incidence of charging or sparring observed after an arched back display suggested that the arched back posture was a display rather than a threat. However, when two males simultaneously performed the arched back display in close proximity, they often tilted the horns and head toward the opponent and circle one another while stiff-leg walking. This indicated an intention to fight, as sparring bouts involved circling and angling the horns toward an opponent. The response of the recipient appeared to be determined by the distance between the performer and the recipient during the arched back display, although this was not quantified.

Sparring in takin was low intensity, and high intensity fighting was never observed. Sparring takin pushed with the horns, but the fighting style could not be classified as true push-fighting or front-pressing as in oryx (*Oryx* sp.) or eland (*Taurotragus* sp.) (Estes 1990). This was because takin males never tried to lift or twist an opponent by the horns. Sparring takin did not separate by more than 1–2 m and did not run at each other from long distances as described in other Caprinae such as mountain sheep (Geist 1971) and Punjab urial (*Ovis orientalis punjabiensis*, Gmelin, 1774) (Schaller and Mirza 1974). Takin also did not threat-jump as described in mountain sheep (Geist 1968), or rear up on their hind legs before impact as in Marco Polo sheep (*Ovis ammon poli* Blyth, 1841) (Walther 1974).

The severity of fighting in a species was predicted by horn conformation according to Geist (1966). Animals with horns that are short and do not curve are predicted to fight infrequently but severely, while animals with horns that are branched or curved tend to fight frequently with less severity. Thus, takin were predicted to fight frequently with less severity, and this seemed to be true in the 25 sparring interactions observed. As in American bison (*Bison bison*, Linnaeus, 1758), no hooking was observed and horn blows were never delivered anywhere but to the opponent's horns (Lott 1974). During the observation period from 2006 to 2008, only one injury occurred that required medical treatment – an eye trauma that could have resulted from non-combat or combat-related causes.

In aggressive encounters, in both males and females, the recipient never adopted a submissive posture, such as the head-low/chin-out posture seen in dorcas gazelle (*Gazella dorcas*, Linnaeus, 1758), or lying down in front of a dominant opponent as seen in black wildebeest (*Connochaetes gnou*, Zimmermann, 1780). Instead, takin only walked, jumped, or ran away depending on the proximity of the aggressor (reviewed in Walther 1974).

There is no indication from the literature or personal observation that takin males are territorial, but rather, they move to different elevations with shifting vegetation phenology, while joining and leaving mixed groups throughout the year (Schaller et al. 1986, Zeng et al. 2002, 2008). Mountainous terrain with fragmented resources would decrease group stability and select against male territoriality as a stable strategy. Whether the rubbing of the body or horns on an object has a scent marking function is not known. Scent marking behavior has not been described in *Budorcas*. Neas and Hoffman (1987) reported that takin spray themselves with urine but did not spray on objects. In this study, we did not observe chasing or driving subordinate males, as described in territorial antelope such as gerenuk (*Litocranius walleri*, Brooke, 1879) (Estes 1990) or impala (*Aepyceros melampus*, Lichtenstein, 1812) (Jarman 1979).

The courtship behaviors described in this study also corresponded to the social structure observed in wild takin. During breeding season, from June to August, takin inhabit higher elevations, and are often observed in alpine meadows (Schaller et al. 1986, Zeng et al. 2008). A mating system termed “following” has been described by Gosling (1986), in which a male follows a female or multiple females as they forage, while defending against other males. This mating strategy is also described in Himalayan goral (*Nemorhaedus goral*, Hardwicke, 1825), a Caprine that inhabits similar habitat to takin (Lovari and Apollonio 1994). Data from wild takin suggest that solitary males move alone between female groups in search of females in estrus (Zeng et al. 2002). Upon locating a female in estrus, tending the female would help the male guard against mating attempts from other males until copulation was achieved.

The “following” strategy is common in Caprinae, due to mountainous, fragmented habitat that makes territoriality unlikely (Lovari and Apollonio 1994). The tending behavior described in this study fit the “following” mating strategy, as takin males stayed close to females while they foraged. In this study, the longest bout of tending that was uninterrupted by other behaviors was 2 min in length. Lott (1974) described the tending relationship in American bison as varying in length from seconds to days.

Dominant male feral Soay sheep establish tending bonds that continue for the duration of an ewe's estrus period (Grubb 1974). However, the longest tending bond observed in Punjab urial lasted for only 20 min (Schaller and Mirza 1974). In 2006 a breeding male was observed charging or supplanting an immature female nine times in the same observation period while he tended an adult female. It seems likely that males would attempt to displace any individual attempting to disrupt courtship.

Dominance displays during courtship are widespread among bovids, although this behavior has yet to be observed in takin (Walther 1974, Estes 1990). In our study, the arched back posture was not observed during tending, and was never performed by the breeding male while in the breeding group. The only aggressive behaviors observed in the same observation period as tending were directed toward the females not being tended. Although dominance displays during courtship were not seen in takin, tending and mounting may have served as a dominance display when directed toward other males. Homosexual mounting is more prevalent in captive animals than in wild animals (Dagg 2008), and dominant musk ox males housed together in a paddock with other males performed genital sniffing, foreleg kicking, and mounting behaviors on subordinate males (Reinhardt 2005). Here, males tended ($n=13$) and mounted ($n=5$) other males, and these behaviors were never followed within 1 min by any aggressive behavior by the recipient or tending male. Thus, takin males appeared to use these courtship behaviors to impose dominance without overt aggression, whether it was performed on subordinate males or females. Alternatively, male-male sexual behavior may have reflected sexual frustration among non-breeding males.

Overall activity budgets did not differ markedly between the sexes, with the exception of moving, maintenance and social behaviors, which were more common in males than in females. Most seasonal sex differences in behavior were not consistent over time, but there were some exceptions. Females ruminated consistently more than males in summer and winter 2010, and males exhibited more maintenance behavior in autumn 2010 and spring 2010. However, the biological significance of these seasonal sex differences is not clear.

Meanwhile, male takin significantly increased the amount of time they spent feeding after summer and going into winter during 2010. This presumably represented a strategy of increasing intake prior to the onset of cold weather after additional energy expenditure during the summer breeding season. This is similar to the pattern observed in wild takin in China (Guan et al. 2012), where males decreased feeding behavior during the rut and then

increased feeding afterwards. Generally, captive male takin do put on additional weight during spring and lose it during the summer rut even though they are fed a high quality diet year round (San Diego Zoo Global, personal communication). Even though the differences were not significant when measured as a behavioral state, social behavior did increase in spring and summer for male takin and was lowest in autumn and winter, coincident with the events leading up to and during the rut. Males significantly increased their resting behavior during the rut and decreased it in autumn. This is somewhat in contrast to Guan et al.'s (2012) observations of wild takin, where resting behavior did not differ significantly between rut and non-rut periods, but perhaps captive male takin could afford to take more time to rest during the rut, given a higher plane of nutrition and decreased distance to estrous females in captivity.

No field data are available to assess seasonal changes in female takin activity budget. The females in this study increased their feeding behavior in summer and fall in 2010 but decreased feeding in winter, though the amount of winter feeding was similar to that observed in summer, occupying about one-third of their time. As with males, this likely represented the accumulation of calories in anticipation of cold weather.

We described 24 behavioral items for takin in varying social groups. Overall, the social behaviors observed suggested that males were non-territorial and followed reproductive females during the breeding season. Takin did not appear to form strong social bonds in groups of unrelated animals, but more affiliative behaviors occurred in dam-calf and sibling groups. We plan to more closely analyze social behavior in a subsequent analysis, because activity budget analysis provides little insight into social relationships. Compared with their closest relatives, the gregarious musk oxen, the lack of social cohesion behaviors in takin may have been due to the forested mountain habitat of takin, which decreased the likelihood of large, cohesive herds compared with the open tundra habitat of musk oxen. The large size of takin and the scarcity of their two potential predators (Schaller et al. 1986), the snow leopard (*Uncia uncia*, Schreber, 1775) and Asiatic wild dog (*Cuon alpinus*, Pallas 1811), may minimize the need for the social defense behaviors recorded in musk oxen (Lent 1988). Overall, the social behaviors observed in takin more closely resembled the behaviors of the mountain goat than those of the musk oxen.

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References

- Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49: 227–267.
- Dagg, A.I. 2008. Homosexual behavior and female-male mounting in mammals – a first survey. *Mammal Rev.* 14: 155–185.
- Estes, R.D. 1990. The behavior guide to African mammals. University of California Press, Los Angeles, CA. pp. 660.
- Ge, T., J. Hu, M. Jiang and Q. Deng. 1989. The herd compositions, numbers and distribution of Sichuan takin (*Budorcas taxicolor tibetana*) in Tangjiahe Natural Reserve. *Acta Theriol. Sinica* 9: 262–268 (in Chinese with English abstract).
- Geist, V. 1965. On the rutting behavior of the mountain goat. *J. Mammal.* 45: 551–568.
- Geist, V. 1966. The evolution of horn-like organs. *Behaviour* 27: 214–257.
- Geist, V. 1968. On the inter-relation of external appearance of social behavior and social structure of mountain sheep. *Z. Tierpsychol.* 25: 199–215.
- Geist, V. 1971. Mountain sheep: A study in behavior and evolution. University of Chicago Press, Chicago, IL. pp. 399.
- Gosling, M. 1986. The evolution of mating strategies in male antelopes. In: (D.I. Rubenstein and R.W. Wrangham, eds.) *Ecological aspects of social evolution*. Princeton University Press, Princeton, NJ. pp. 244–281.
- Grubb, P. 1974. Mating activity and social significance of rams in a feral sheep community. In: (V. Geist and F. Walther, eds.) *The behavior of ungulates and its relation to management*. International Union for Conservation of Natural Resources, Morges, Switzerland. pp. 457–476.
- Guan, T.P., B.M. Ge, D.M. Powell, W.J. McShea, S. Li and Y.L. Song. 2012. Does a temperate ungulate that breeds in summer exhibit rut-induced hypophagia? Analysis of time budgets of male takin in Sichuan, China. *Behav. Proc.* 89: 286–291.
- Hernandez-Fernandez, M. and E.S. Vrba. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biol. Rev.* 80: 269–302.
- Hoefs, M. 1974. Food selection by Dall's sheep (*Ovis dalli dalli*). In: (V. Geist and F. Walther, eds.) *The behavior of ungulates and its relation to management*. International Union for Conservation of Natural Resources, Morges, Switzerland. pp. 759–785.
- Jarman, M.V. 1979. Impala social behavior: territory, hierarchy, mating and the use of space. *J. Comp. Ethol.* 21 (suppl.): 1–92.
- Lehner, P.N. 1992. Sampling methods in behavior research. *Poultry Sci.* 71: 643–649.
- Lent, P. 1988. *Ovibos moschatus*. *Mammal. Spec.* 302: 1–9.
- Lott, D. 1974. Sexual and aggressive behavior of adult American bison (*Bison bison*). In: (V. Geist and F. Walther, eds.) *The behavior of ungulates and its relation to management*. International Union for Conservation of Natural Resources, Morges, Switzerland. pp. 382–394.
- Lovari, S. and M. Apollonio. 1994. On the rutting of the Himalayan goral (*Nemorhaedus goral*). *J. Ethol.* 12: 25–34.
- Magin, C. and B. Groombridge. 1994. *Budorcas taxicolor*. In: CITES Appendix II. <<http://www.cites.org>. Accessed on 04/07/2010.
- Neas, J. and R. Hoffman. 1987. *Budorcas taxicolor*. *Mammal. Spec.* 277: 1–7.
- Powell, D.M., K. Carlstead, L.R. Tarou, J.L. Brown and S.L. Monfort. 2006. Effects of construction noise on behavior and cortisol levels in a pair of captive giant pandas (*Ailuropoda melanoleuca*). *Zoo Biol.* 25: 391–408.
- Reinhardt, V. 2005. Courtship behavior among musk ox males kept in confinement. *Zoo Biol.* 4: 295–300.
- Schaller, G.B. 1977. Mountain monarchs: wild sheep and goats of the Himalaya. University of Chicago Press, Chicago, IL. pp. 444.
- Schaller, G.B. 1985. Talking of takin. *Animal Kingdom* 88: 22–29.
- Schaller, G.B. and Z. Mirza. 1974. On the behavior of Punjab Urial (*Ovis orientalis punjabiensis*). In: (V. Geist and F. Walther, eds.) *The behavior of ungulates and its relation to management*. International Union for Conservation of Natural Resources, Morges, Switzerland. pp. 306–323.
- Schaller, G.B., Q. Teng, W. Pan, Z. Qin, X. Xiaoming, J. Hu and H. Shen. 1986. Feeding behavior of Sichuan takin. *Mammalia* 50: 311–322.
- Song, Y.L., A.T. Smith and J. MacKinnon. 2008. *Budorcas taxicolor*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.1. <<http://www.iucnredlist.org>. Accessed on 04/07/10.
- Walther, F. 1974. Some reflections on expressive behavior in combats and courtship of certain horned ungulates. In: (V. Geist and F. Walther, eds.) *The behavior of ungulates and its relation to management*. International Union for Conservation of Natural Resources, Morges, Switzerland. pp. 56–106.
- Zeng, Z.G. and Y.L. Song. 1998. Observations of defending behaviors of the golden takin. *Acta Theriol. Sinica* 18: 8–14 (in Chinese with English abstract).
- Zeng, Z.G. and Y.L. Song. 1999. Preliminary observations on the phenomena of solitary individuals in golden takin (*Budorcas taxicolor bedfordi*). *Acta Theriol. Sinica* 19: 169–175 (in Chinese with English abstract).
- Zeng, Z.G., Y.L. Song, W.Q. Zhong, H.S. Gong, J. Zhang and G.D. Dang. 2001a. Food habits of golden takin. *Chin. J. Zool.* 36: 36–37 (in Chinese with English abstract).
- Zeng, Z.G., W.Q. Zhong, Y.L. Song, H.S. Gong, X.J. Wang and K.W. Wang. 2001b. Feeding behavior of golden takin. *Chin. J. Zool.* 36: 25–28 (in Chinese with English abstract).
- Zeng, Z.G., W.G. Zhong, Y.L. Song, J.S. Li and F. Guo. 2002. Group size, composition and stability of golden takin in Shaanxi Foping Nature Reserve, China. *Folia Zool.* 51: 289–298.
- Zeng, Z.G., A.K. Skidmore, Y.L. Song, T.J. Wang and H.S. Gong. 2008. Seasonal altitudinal movements of golden takin in the Qinling mountains of China. *J. Wildl. Manage.* 72: 611–617.