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CIRCADIAN ACTIVITY RHYTHMS OF CHAMOIS IN NORTHERN TYROL, AUSTRIA

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Abstract: Circadian activity of chamois (Rupicapra rupicapra) was studied both by direct observation and by radio-tracking. Activity rhythms were characterized by two main peaks which coincided with the crepuscular intervals. Secondary peaks were apparent at mid-morning, mid-afternoon and midway through the nocturnal period. Individual activity patterns varied within a herd during most of the diurnal period but were highly synchronized at dawn and dusk. On the average, chamois were active between 13.6 and 14.5 hours per solar period throughout the year. General activity was highest in late fall and winter and lowest during the spring and early summer. During the snow-free months, feeding bouts/24-hour period were more numerous and of shorter durations than during winter. The length of activity bouts varied from 10 minutes to over 10 hours in the course of the year (mean: 2½ hours). Resting periods were considerably shorter than feeding bouts and ranged from 7 minutes to 5 hours (mean: 1½ hours). The pattern of resting and feeding shown by an individual varied from one day to another. Nocturnal activity was substantial (up to 5½ hours/night) especially in the fall. Nocturnal feeding bouts were significantly shorter than diurnal bouts. Clouds, fog and light to moderate rainfall had no effect on chamois activity rhythms. Chamois sought shelter and became inactive during thunderstorms and blizzards accompanied by high velocity winds. Very high (21°C to 30°C) temperatures, deep or heavy, coarse snow as well as non-supporting crust reduced chamois activity.

Activity rhythms of a species may be influenced by season, habitat type, disturbances, social interactions or climatic conditions. Changes in feeding and resting rhythms reflect the energy requirements of an animal at different times of the year.

The chamois, being an ungulate endemic to the alpine and subalpine zones, feeds mostly in treeless, open habitat. Resting periods on the other hand, are spent primarily in deep, cool gullies or creek beds, underneath cliffs or in the shade of trees. Chamois are thus easier to census and to hunt when active.

Studies of the activity rhythms of free-ranging chamois have been limited to observations during the daylight period and to a particular season (Briedermann 1967, Daenzer 1978, Pachlatko 1980). Zuber (1977) observed activity rhythms of captive chamois in a large enclosure for one year. He used an infrared night-viewing device and reported extensive nocturnal activity, especially in fall and winter. Daenzer (1978) noted that free-ranging chamois grazed before sunrise and after sunset during wither. None-the-less, the existing literature on chamois life history presents the species as an almost exclusively diurnal ungulate (Fuschlberger and Nerl 1969, Knaus and Schroeder 1975, Briedermann 1976).

The present study investigated activity rhythms of free-ranging chamois on a year-round basis both by direct observation and by radio-tracking. To establish the extent of nocturnal activity, one animal was monitored continuously through all seasons using an activity sensitive radio collar and an automatic event recorder.

STUDY AREA

The study area measured roughly 30 km^2 and was part of the Karwendel Mountain Range in Northern Tyrol, Austria. Elevations ranged from 920 to 2060 meters. Forest, composed mainly of fir, spruce and beech comprised 60 to 65 percent of the study area. Extensive alpine pastures above elevations of about 1600 meters were rarely interrupted by patches of mountain alder or dwarf pine. Precipituous cliffs, screes and fellfields with locally extensive growth of dwarf pine occupied the highest elevations. Mean annual precipitation in the study area varied between 1450 and 1850 millimeters.

Summer and winter temperature extremes were measured at +32°C and -25°C respectively with an average of +5.5°C during three years of study. Yearly snow accumulation reached about 400 centimeters. Continuous snow cover was present from mid December to mid April.

Chamois in the study area were subjected to a number of disturbances. A system of hiking trails allowed tourist access to all elevational zones during the snow-free period. Hikers frequented the region from early June until late September. An alpine ski-resort comprised about 20 percent of the study area. Skiers frequented the study area from late December until early April. Use of habitat by livestock was intensive both above and below timberline from July to September. Logging was practiced year-round. Chamois hunting season lasted from August 1 to December 31 each year.

METHODS

Field Observations

The studied population (approximately 350 to 400 animals) included 12 individuals with ear-tag radio-transmitters (powered by solar energy) as well as 26 animals with numbered plastic ear-tags and 27 naturally recognizable individuals (broken horns, pelage anomalies). Telemetry and visual surveys of known chamois were conducted 2 to 6 times per week from 1981 to 1983. Surveillance routes and times were altered from one session to the next. The activity of each known animal was recorded upon location. If on its feet, the chamois was considered active. All recumbent animals were considered as resting. Wherever the focal individual was sighted in association with other chamois, both the predominant activity and the degree of activity synchronization in the group was recorded. Activity rhythms of known chamois were observed for extended periods and comparisons were made between simultaneously observed animals. During late summer, when female chamois formed large herds (up to 90 individuals), the numbers of active and resting animals in a herd were recorded at 15 minute intervals throughout the diurnal period. Checks or nocturnal activity were made whenever light conditions allowed.

Event Recording

A Burchard and Reinchenbach, type 294078-A radio collar with a mercury activity switch was used. Activity was monitored and recorded by a B. and R. receiver, type 287178, connected to a Metrawatt recorder, type Miniscript-D. The unit was weather-proofed, equipped with a whip antenna positioned 5 meters above ground and installed in the test animal's home range. Activity records were printed on a calibrated carbon paper ribbon which was replaced every 11 days.

To calibrate the equipment, a captive, ten-year-old female was initially fitted with the activity collar. She was fed supplements regularly, but also consumed natural food available in the enclosure. The activity rhythms of this female were recorded simultaneously by the event recorder and by an observer for 48 hours. A 95 percent correspondence was found between visual and mechanical records.

The event recorder distinguished three distinct behavioral modes. A continuous movement of the mercury switch was apparent when the animal was feeding and moving around (Figure 1a). Field observations revealed that undisturbed chamois grazed almost continuously even during long-range, goal-oriented movements. When no activation of the mercury switch took place, the test animal was resting. This was the case whenever the neck was held upright during rumination or surveillance of the environs in a sternally recumbent position (Figure 1b). The recorder could also identify sleep with the head down whenever the animal lay flat on its side or on the sternum (Figure 1c). Both the sleep (head down) and rumination (head up) modes were pooled and treated as rest for data analysis.

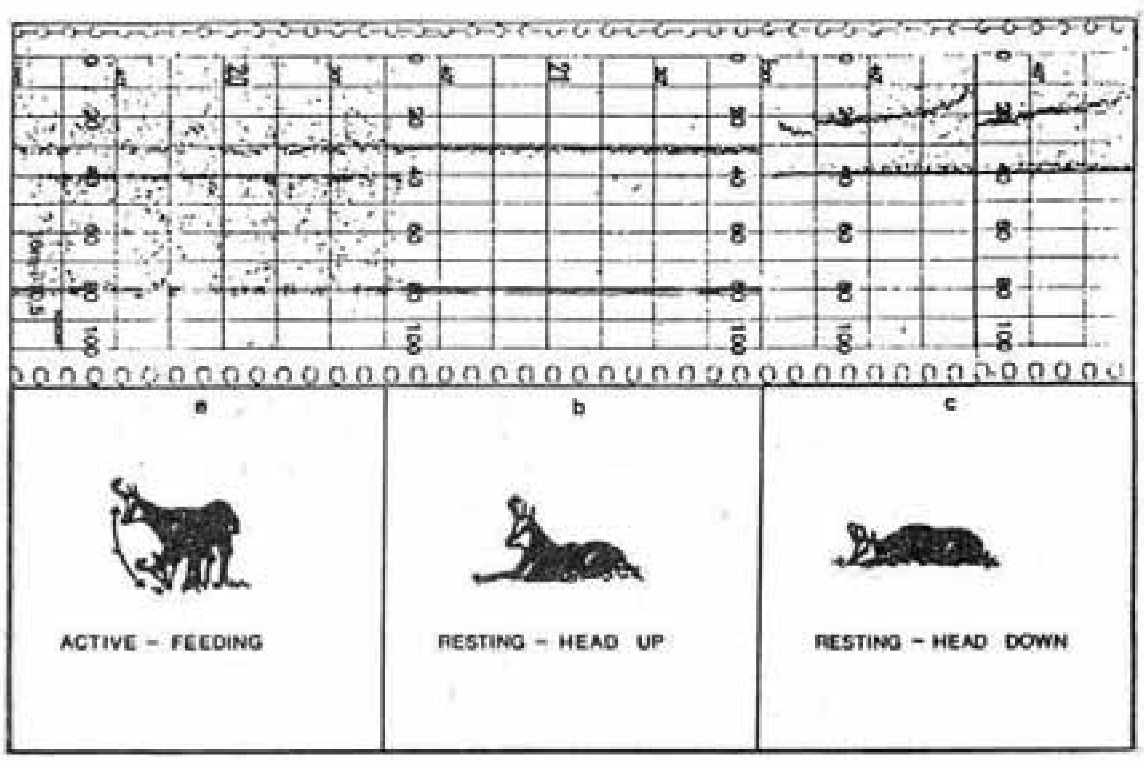

Figure 1. Three behavioral modes distinguished by the event recorder: a. activity, b. rest-rumination, c. rest-sleep. Horizontal number sequences on carbon paper ribbon indicate signal frequency; vertical number sequence indicates time.

A possible source of error arose whenever the test animal browsed or fed on cliff vegetation. In such cases, the neck remained upright, thus preventing switch activation. Since chamois in the study area clearly preferred ground vegetation to other food throughout the year (Perle and Hamr 1985), the chance of error occurrence was presumably very small. Nevertheless, the mechanical records may somewhat under estimate actual activity totals. This would be the case especially during winter when chamois preferred steep, snow-shedding cliffs and when thick snow crust induced browsing.

A free-ranging yearling male was fitted with the activity collar in the beginning of August 1983. The animal was darted with a Tel-inject-Vario 2 air gun and narcotized by a mixture of Rompun (Xylazine) and Vetalar (Ketamine). The yearling was monitored for almost 10 months. During this period, continuous recording of activity rhythms was attempted. Reception was usually interrupted whenever the test animal moved more than 1 km away from the recorder. Depending on the accessibility of the new location and on the snow conditions, up to one month elapsed before recording could be continued. Signal reception was also sporadically subject to disturbances by planes vehicles and by portable radio-transmissions. Twenty-four hour records with interruptions amounting to more than 72 minutes (5 percent) were not used for data analysis. The yearling was periodically located during daylight and observed continuously for up to 7 hours. His activity was compared to that of simultaneously observed animals belonging to the same herd.

Climatic Influences on Activity

Weather records (daily temperature, duration and amount of precipitation, snow depth) were obtained for the 1981 to 1984 period from a meteorological station located in the study area. In addition, a number of weather data were recorded with each field observation: wind speed (0-3), fog density (0-3), snowfall or rainfall intensity (0-3), cloud cover (0-¼-½-3/4-1), depth of snow (cm), quality of snow (5 categories).

Data Analysis

Data was examined for solar period as well as seasonal and climatic influences on several chamois activity parameters. Analysis of field observations was performed by utilizing SPSS programs (Nie et al. 1975). The numbers of "active" and "resting" records were cross-tabulated with respect to each temporal or climatic factor. Raw chi-square was used to test for significance. Seasonal differences in activity rhythms obtained by the event recorder were tested by Kruskal-Wallis one-way analysis of variance (Siegel 1956). In all tests, a significance at p 0.05 was accepted. Mechanical recordings of activity were chronologically charted and tallied by computer using a program developed during the study (Mayr 1984).

RESULTS

Field Observations

A total of 1239 activity records were compiled by observations during 2.5 years. The diurnal data produced a biomodal activity curve. The main peaks coincided with the crepuscular periods. Two secondary peaks were apparent at mid-morning and mid-afternoon.

Seasonal differences in the frequencies of active chamois sightings were significant. Activity was observed more frequently during winter than during the other seasons (Table 1). The highest percentages of active records were registered in February, March and April (84, 82.5 and 86 percent, respectively). Chamois activity decreased in late spring and early summer. In May, June and July, the sightings of active animals comprised 74.5, 67 and 71 percent respectively. A marked increase in the frequency of active chamois sightings was registered again in September (78.5 percent).

Table 1. Seasonal differences in the proportion of "active" to "resting" field records.

Records	Winter	Spring	Summer	Fall	Totals
active	328	78	259	295	960
resting	67	32	87	93	279
% active	83	71	75	76	p .005

Continuous observation of individual chamois revealed an activity pattern composed of feeding bouts alternating with resting periods typical for most ungulates. The length of 62 diurnal feeding bouts recorded mostly during the snow-free period varied from 9 minutes to 2.5 hours (mean: 73 minutes). Activity bouts tended to be shorter from mid-morning to mid-afternoon (9-90 minutes) and rather extended just after sunrise and before sunset (45-150 minutes). The length of 35 recorded resting periods varied between 7 minutes and 1.7 hours (mean: 47 minutes).

The activity of individuals within a herd was heterogeneous during most of the day but became highly synchronized at dawn and at dusk (Figure 2). Uniform group activity was seen less frequently from late spring to late fall than during the winter. This was apparently due to the break-up of large summer-fall herds on winter ranges. The smaller the group the greater were the chances of observing uniform behavior of all its members.

Nocturnal data collected by observation were of a highly anecdotal nature. Several records of chamois activity were made during late summer and fall in open terrain on clear, full-moon nights. Feeding activity could also be monitored in total darkness by listening to the sounds of falling rocks, released by chamois grazing on steep slopes. Nocturnal rutting activity was apparent from courtship vocalizations of males competing for mating rights.

Event Recording

The yearling male covered an area of approximately 6 km^2 while his activity was monitored. The event recorder had to be relocated five times.

Although several gaps occurred in the recording, distinct seasonal and daily activity patterns are apparent. The test animal was active at night throughout the year. The onset of diurnal activity correlated with relatively high light intensity during or just after sunrise. Evening activity on the other hand, usually continued until well after sunset. The longest feeding bouts usually occurred at the start and at the end of the day. The pattern of feeding and resting bouts produced by the test animal on successive days was at times very similar but never identical.

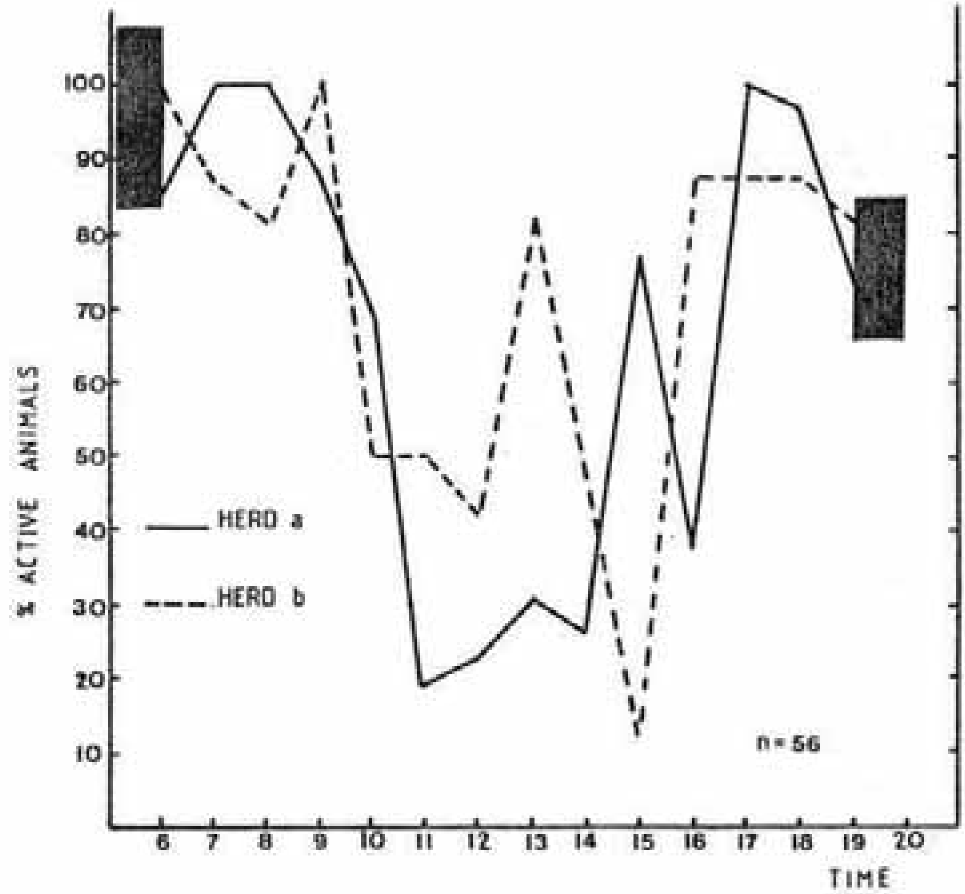

Figure 2. Diurnal variability in activity synchronization among the members of two female herds observed simultaneously in late summer. There were 26 chamois in herd a and 16 in herd b. The number of active animals in each herd was recorded every 15 minutes from dawn to dusk. Data were pooled for each hour. Shaded regions represent crepuscular periods.

The bidmodal nature of chamois activity rhythms was confirmed by the yearling's 24-hour activity cycles both in the winter and in the snow-free period. The diurnal portion of both curves corresponded closely to the activity cycle obtained by field observations (Figure 3). The overall degree of diurnal activity (measured by the percentage of active records at a particular time of day) shown by the yearling was somewhat higher during the winter than in the snow-free period. This was also in accordance with field observation data. The peak in nocturnal activity was shifted from around midnight during the snow-free period to around 02:00 hours during winter.

Seasonal differences in activity parameters between four time periods characterized by several close to perfect 24-hour records were tested for significance. These periods corresponded to: a. late summer - early fall b. early winter c. later winter - early spring d. late spring. Although a slight increase was apparent from early fall to early winter, the circadian activity totals remained more-or-less constant throughout the year at about 14 hours per solar phase. The daily and nightly activity totals for the yearling correlated with the length of daylight and darkness respectively. The number of activity bouts per 24 hours was significantly higher during the snow-free period than during the winter. The number of activity bouts per diurnal period during

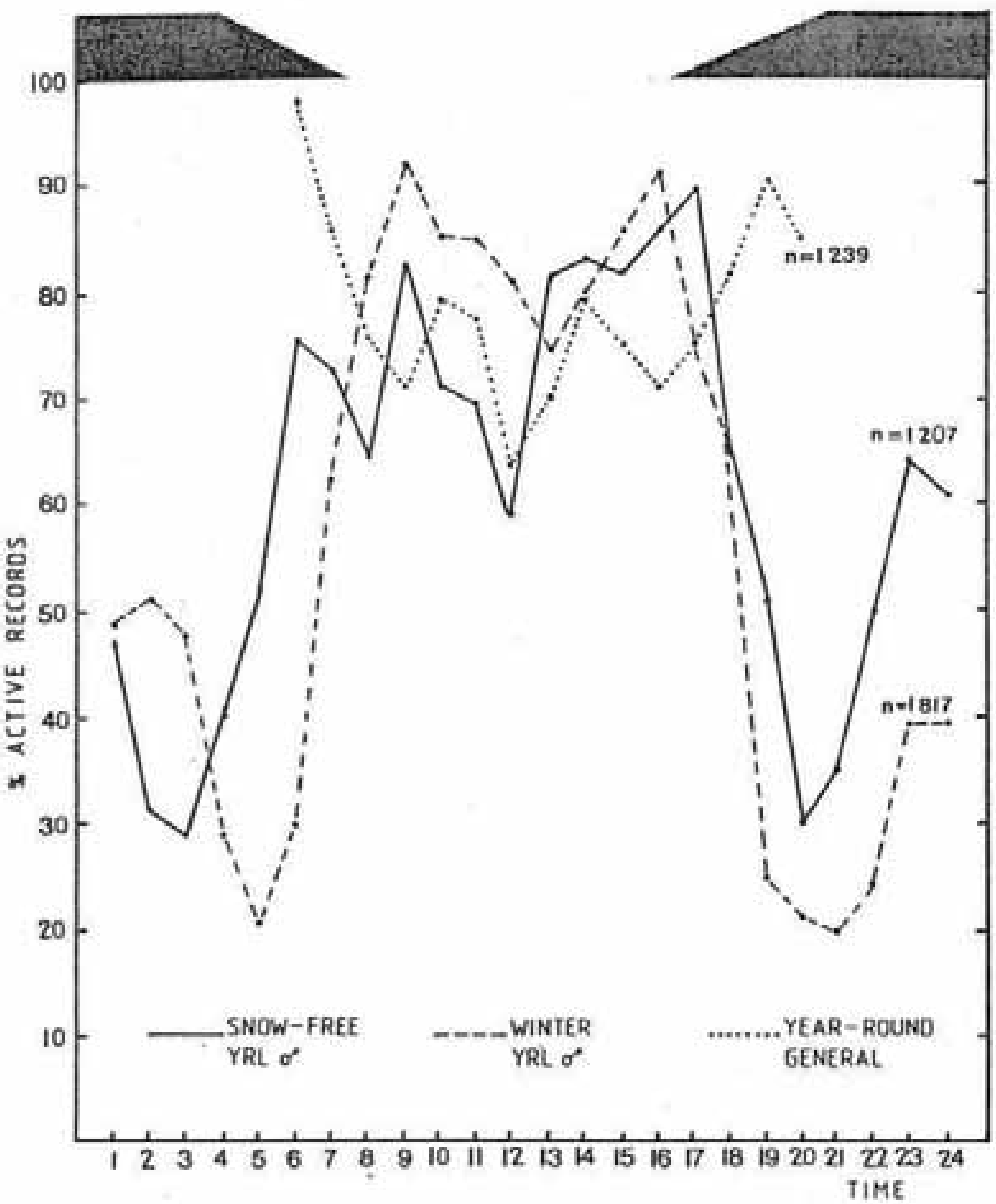

Figure 3. Daily activity rhythms of the studied chamois. Dotted curve represents pooled data obtained by year-round field observations of diurnal activity. Solid curve represents circadian activity data from the snow-free period recorded mechanically for the yearling male. Dashed line shows the yearling's winter activity rhythm. The curves were constructed by computing the percentage of "active" records for each hour of the solar phase. Shaded regions represent the duration of darkness at different times of the year.

spring was more than double that in early winter. Also the difference in the length of diurnal activity bouts between these two seasons was striking (Table 2).

The highest number of activity bouts per night was recorded in early fall (mean: 4.36). This number gradually decreased in the course of the winter until it was reduced by ½ in late spring. Diurnal activity bouts lasted two to three times the length of nocturnal activity bouts regardless of season. The duration of nocturnal feeding bouts remained relatively constant throughout the year (Table 2).

Sporadic visual comparisons of the yearling's activity rhythms to those of other chamois revealed no major differences. As expected, adult females were somewhat less active than the physically and socially developing male. Even though individual differences in the distribution of activity bouts were apparent, the total amount of activity shown over an extended period varied only little from one animal to another within a herd.

Table 2. Seasonal differences in the activity rhythms of a yearling male chamois.

	SEASON								
	a. Late summer-early fall		b. Early winter		c. Late winter-early spring		d. Late spring		
Parameter	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	p
total activity/ 24 hrs.	8	14.53	8	14.14	23	13.65	16	14.01	0.3
total activity/ day (hrs)	8	9.78	8	8.43	23	10.75	16	11.71	.001
total activity/ night (hrs)	8	4.47	8	5.53	23	2.68	16	2.16	.001
no. of activity bouts/24 hrs	8	8.13	8	5.38	23	4.79	16	8.11	.001
no. of activity bouts/day	8	4.58	8	2.45	23	3.32	16	6.39	.001
no. of activity bouts/night	8	4.36	8	3.56	23	2.31	16	2.25	.001
length of diurnal bouts (hrs)	38	2.22	20	4.39	73	3.57	101	1.93	.001
length of nocturnal bouts (hrs)	27	1.09	23	1.61	37	1.23	30	1.01	.05

Climatic Factors

Cloud cover, fog density and rainfall intensity did not alter chamois activity rhythms. Low to moderate snowfall seemed to stimulate chamois activity (Table 3). Chamois sought shelter and reduced feeding activity during extreme weather fluctuations (thunderstorms, blizzards) accompanied by strong winds.

The frequency of sightings of active chamois was indirectly proportional to temperature (Table 3). On extremely hot days (temperatures: 28°C to 32°C) diurnal feeding activity was virtually limited to early mornings and late afternoons. At mid-day, chamois rested in shady, cool locations. Although there was some evidence that chamois reduced feeding activity during extremely cold winter nights (temperatures below -15°C), sufficient data could not be obtained to prove this.

Table 3. The effects of climatic factors on chamois activity.

Climatic factor	Intensity	Resting records	Active records	% Active records	p
cloud cover	0	69	279	80	
	¼	61	197	76	
	½	35	126	78	0.55
	3/4	27	88	76	
	1	89	266	75	
fog	0	248	852	77	
	1	2	13	87	
	2	23	76	77	0.44
	3	8	15	65	
rainfall	0	238	842	78	
	1	20	45	69	
	2	22	68	76	0.29
	3	1	1	50	
snowfall	0	248	834	77	
	1	18	48	72	
	2	11	70	86	0.04
	3	4	4	50	
wind speed	0	182	708	74	
	1	35	105	75	
	2	43	101	70	0.02
	3	21	42	67	
temperature (°C)	-10- 0	46	200	81	
	+1-10	73	267	78	
	+11-20	126	412	77	0.049
	+21-30	36	78	68	

The depth and the quality of snow significantly influenced chamois feeding activity. The frequency of activity chamois sightings decreased with increasing snow depth. Coarse, heavy late winter snow and non-supporting crust also decreased chamois activity. On the other hand, compact or dry, light snow as well as a supporting crust favored foraging activity. A marked increase of chamois activity was noted whenever snow was shed off steep, south-facing slopes (Table 4).

Table 4. The effects of snow conditions on chamois activity.

		Resting records	Active records	% Active records	p
snow depth (cm)	0	144	476	77	
	1-20	26	103	80	
	21-50	27	92	77	
	51-100	16	40	71	0.001
	101+	2	1	33	
	shed	20	167	89	
snow quality	dry	25	109	81	
	wet	47	169	78	
	non-support. crust	17	53	76	0.005
	coarse	29	41	59	
	support. crust or compact	16	80	83	

DISCUSSION

The present investigation confirmed and enhanced the results obtained in previous studies of chamois diurnal activity rhythms. It also showed that free-ranging chamois are active at night throughout the year.

Feeding activity of ungulates is not uniformly distributed over the 24-hour period. The characteristic bimodal pattern with overt peaks at dawn and dusk was shown by chamois in different parts of their domain (Briedermann 1967, Daenzer 1978, Pachlatko 1980) and in captivity (Zuber 1977). Such activity rhythm is also typical for red deer (Cervus elaphus) (Georgii 1980), roe deer (Capreolus c.) (Turner 1980) as well as the mountain goat (Oreamnos americanus) (Fox 1978). These results suggest that the crepuscular periods serve as cues ("Zeitgeber") for the synchronization of these species' activity rhythms. In accordance with the results of the present study, both Briedermann (1967) and Zuber (1977) noticed that sunrise was much more effective as an initiator of chamois feeding activity than sunset was as an activity terminator.

Turner (1978) suggested that de-synchronization of activity during the day is due to the variable digestion times of foods selected by the individual animals. There is also some evidence that food intake of subordinate chamois in a group is less efficient than that of more dominant animals due to social stress (Lovari and Rosto 1985). Nutritional requirements and therefore food intake presumably differ between sexes, age classes and barren as opposed to nursing or pregnant females. These factors further contribute to activity de-synchronization within a population. De-synchronization of individual activity rhythms within a chamois group seems to function as a method of danger detection. Resting animals usually survey the surroundings and alarm feeding group members if danger approaches. This was especially apparent from mid-morning to mid-afternoon during the snow-free period when the highest numbers of human intruders frequented the study area.

Considering how little quantitative data has been obtained on chamois nocturnal activity, it is surprising how many authors labeled the ungulate as entirely diurnal (Knaus 1960, Christie 1967, Briedermann 1967, Pachlatko and Nievergelt 1985). Briedermann (1967) cited several reports by incidental observers on chamois activity during full-moon nights but considered these cases unusual. He correctly estimated the total duration of chamois diurnal activity at 10 to 10½ hours in summer and compared this figure to the activity budgets reported for roe deer and red deer by Bubenik (1959 and 1960). Since the estimate of total diurnal activity for chamois already exceeded the 24-hour activity totals for both cervids, Briedermann (1967) concluded that any additional chamois activity would not be possible during the night at the expense of rumination and sleep.

Ungulate circadian activity budgets differ from one species to another and the direct application of results obtained for the member of one taxonomic group to another is highly questionable. For example, ibex (Capra ibex) are active predominantly during daylight (Georgii 1978, Daenzer 1978), whereas red deer feed mostly at night and during the crepuscular intervals (Georgii 1980, Georgii and Schroeder 1983). The two species also show differences in the length, number per unit time and temporal location of feeding bouts.

A herd of 9 captive chamois was night-active on the average 51 minutes during summer and 4.5 hours during winter (Zuber 1977). Diurnal activity totals varied from 6.5 to 8.5 hours in the course of the year. Generally lower activity would be expected in animals fed ad-libitum year-round and restricted in movement as compared to those in the wild. However, all seasonal activity trends shown by the captive chamois were remarkably similar to those found in the present study. The captive chamois also gradually increased their general activity from a low during the summer to a high in winter. The changes in circadian activity totals were not as pronounced in the course of the seasons as the changes in diurnal and nocturnal activity which varied with the length of each respective solar phase. The marked similarities among activity rhythms shown by captive as well as free-ranging chamois in different habitats suggest that the activity pattern is endogenous to the species. Unless extreme, environmental factors probably have only a minor effect on activity budgeting.

The present results showed that chamois interrupted normal feeding activity cycles only at very high temperatures or during periods of high velocity winds and extreme precipitation. Chamois in the Elbe Sandstone Range (Czechoslovakia) also decreased their activity during intense rainfall and thunderstorms. Cases of chamois summer mortality due to lightning are frequently reported by game wardens in the Alps. Turner (1980) found that winds of high speed negatively influenced the activity of roe deer and hypothesized disruption of scent-localizing abilities important in predator avoidance.

Chamois in the Alps seem to increase feeding time during winter in order to compensate for the decline in forage quality and availability. The same strategy was observed in red deer on the island of Rhum (Clutton-Brock et al. 1982). However, when snow conditions are adverse, energy losses incurred by locating widely spaced, not readily attainable forage probably override the gain represented by ingested food and chamois remain stationary. In the spring, chamois slowly recover from the hardships of the winter. Still in winter pelage, they avoid heat stress by reducing activity and rest in the shade of trees or on the remaining snow patches. The new vegetation is abundant, attainable with minimal effort and of high nutritional quality. As summer progresses, days become shorter, temperatures gradually drop and the quality as well as palatability of forage worsen. These changes induce chamois to feed longer and to rest less. A high level of activity is reached by the rutting season in late fall. The about two week long rut represents the yearly activity peak especially for mature bucks.

Although the present study did not consider differences in activity rhythms among chamois sexes or age classes, some variations are likely. In bands of ibex, yearlings fed over 1 hour longer and rested about 2 hours less during daylight than six-year-old males (Schaerer 1977). Briedermann (1976) observed old chamois males resting and feeding in longer spurts than younger animals thus producing fewer activity bouts per day. Zuber (1977) compared the seasonal activity rhythms of three age classes of captive chamois: mature females, yearlings and kids. The year-round activity of yearlings was higher than that of mature females and slightly higher or equal to that of kids. This would be expected since neither kids or yearlings have completed body-growth and thus have higher nutritional requirements than adult animals. These findings can be used in the present study as a reference for relating the activity rhythms of the radio-tracked yearling to the rest of the population.

Although frequent, human induced disturbances had limited effect on chamois activity. It was expected that diurnal activity cycles would be disrupted during the period of most frequent human intrusions into chamois ranges (June-September). However diurnal activity showed no unusual fluctuations during these months. This suggests that chamois in the present study area were strongly habituated to the presence of humans in their environment. In view of the alarming increase of year-round recreational activities inside preferred chamois ranges during the last two decades, further investigation of human influences on chamois behavior is necessary.

The present study answers only some of the questions important to efficient chamois management. It is intended as an impulse to initiate a larger scale, more detailed study of those factors which influence chamois activity rhythms. Thorough knowledge of how a game species' behavior is affected by man-induced changes to the environment should allow the wildlife manager to adjust management practices according to the objectives of both the public and the animal concerned.

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QUESTIONS AND ANSWERS

Mike Scott, Idaho: I'm curious to know how long those animals were on a lichen diet and what their general condition was in the spring time?

Joseph Hamr: They were never on a purely lichen diet. That was only after periods of very intensive snow fall. Sometimes there would be up to 1 or 1 1/2 meters of snow dumped within 3 or 4 days. During these periods they would take primarily lichen off branches and tree trunks. But generally they would feed on grass through the winter that they pawed up, or as soon as bare patches appeared on south facing slopes they would go to those. Even so, there's quite a bit of winter mortality every year, especially during severe winters because chamois will not accept supplementary feed during the winter. Except for a few males that will pop up at deer feeding stations, you can't feed them. Winter mortality was quite high in some years...up to 50 or 60 animals within that study area, and those were just the ones that were found. The dead were mostly kids and males seven years old and older. Most dead chamois were usually found in April.

No Name: I was wondering why they don't winter above the tree line? Are there open slopes above tree line? Ecologically they seem similar to our sheep during the summer, but very different during the winter.

Hamr: Yes, generally above the tree line there's a lot of snow and a very high danger of avalanches. Chamois tend to move into the forest because they find more food there. There's no food above the tree line. There is a lot of snow, and perhaps the ski resort in my study area was a factor in pushing chamois into the forest. But there are ibex in the study area that stay on the highest ridges throughout the winter.