

{2715}

RESEARCH ARTICLES

Behavior in Adult Pairs of Captive Snow Leopards (*Panthera uncia*)

Helen Freeman

Woodland Park Zoological Gardens and University of Washington, Seattle

Eight adult pairs of snow leopards (*Panthera uncia*) were observed for one to three years in the months December through March to determine the species' social and reproductive characteristics in captivity. To statistically examine the occurrence of behaviors as a function of estrus, the observation weeks were divided into three time blocks: before estrus, estrus, and after estrus. Using percentage of scan samples as an estimate of time spent in various behaviors, 16 behaviors and combined behavior categories were examined for (1) behaviors that differentiated successfully from unsuccessfully breeding pairs, (2) sex differences in behavior, (3) significant correlations between pair members, and (4) behaviors that showed time block effects. The rationale for identifying a behavioral profile of successful breeders in snow leopards was to aid zoos in their captive management programs by increasing their knowledge of the social behavior of this species. By finding correlates to breeding success, informed decisions on whether to change partners after a certain period of time, how to group the cats, and the optimum strategy for a survival plan can be made.

Key words: estrus, behavioral profile, time block, affiliative, statistics

INTRODUCTION

The snow leopard inhabits the high mountains of Central Asia and is considered highly endangered in every region in which it is found [Simon, IUCN Red Data Book, 1970]. Because of its scarcity, and the extremely harsh and often impassable terrain in which it is found, little is known of its habits and behavior in the wild.

There are two genus classifications currently in use for the snow leopard: *Panthera uncia* and *Uncia uncia*. This paper will use *Panthera uncia*, the same classification as that utilized in the studbook for the captive population [Blomquist, 1981].

In January 1981 there were 223 snow leopards in institutions around the world [Blomquist, 1981]. The free-living population was given as 400 ± 200 [Simon,

Received for publication February 7, 1983; accepted March 10, 1983.

Address reprint requests to Helen Freeman, Woodland Park Zoological Gardens, 5500 Phinney Ave N, Seattle, WA 98103.

1970]. However, this may be too low as the estimate in the 1980 Soviet *Red Book* (section translation by K. Braden) gives the general population of the species to be 1,000 individuals, with 500 living in Kirgizia and 200 in Tadzhikistan. A more conservative figure for the Soviet Union of  $300 \pm 150$  is given by V.S. Pokrovskiy, author of the book *Large Predators*.

The number of snow leopards in the wild is decreasing at an alarming rate because of direct annihilation by humans, increased usage of fragile mountain meadows for the grazing of domestic stock, and the declining population of the wild ungulates which are the snow leopard's principal prey [Schaller, 1980; Jackson, 1979; Pokrovskiy, 1974]. Declining numbers coupled with the rugged terrain of the snow leopards' habitat make field observations difficult [Schaller, 1980, 1977, 1976; Jackson, 1978, 1979]. The snow leopard blends so well into its environment that in one instance in Nepal, even though a cat was wearing a radio collar and its location was known, it could not be seen with the spotting scope [Jackson, personal communication]. Thus, much of our knowledge of the snow leopard's biology and behavior must at this time come from captive studies, and it is important to apply any knowledge gained to increase the captive propagation of the species. For this reason I was interested in determining whether a successful pair bond could be identified behaviorally by comparing interactions of breeding pairs and nonbreeding pairs, and if there were differences between newly introduced pairs and pairs with long-term bonds.

My own previous studies [Freeman, 1975, 1977, 1980], as well as references in the literature to "resident pairs" [Dang, 1967], adult pairs [Pocock, 1939, cited in Roberts, 1977; Petzsch, 1968; Ionov, no date, cited in Ognev, 1962; Kuznetsov and Matyushkin, 1962], family groups with adult individuals [Shaposhinikov, 1956], pairs staying together only during a breeding season [Pokrovskiy, personal communication], and a male preferring only one female [Marma and Yunchis, 1968] prompted me to ask if there were characteristics in the interactive behaviors of snow leopard pairs which would indicate pair bonding. It would be useful to know if individuals kept in pairs, and exhibiting the characteristics of long-term pair bonding, produce more offspring than individuals whose mates are changed frequently. Furthermore, if one of the purposes of breeding endangered species in captivity is to provide the option of reintroduction or restocking back into the wild [Campbell, 1980], the optimum social group would be vital to the success of such a project.

In order to determine the snow leopards' social and reproductive characteristics in captivity, behaviors were analyzed for (1) behavioral indicators of breeding success, (2) sex differences in behavior, (3) significant correlations between pair members, and (4) behaviors that showed time block effects.

## MATERIALS AND METHODS

### Subjects

The subjects in this study were 16 adult *Panthera uncia*. They were observed in the months December through March for three years (1978-1981), although not all pairs were observed each season. One pair was observed in December 1978 through March 1979; eight pairs in 1979-1980; six pairs in 1980-1981. The observation time covered a period of 12 months over a three-year span.

There has only been one recorded instance of a female in captivity reproducing before the age of 3 years, and the majority of males are 4 years of age or older before

reproduction occurs [Blomquist, personal communication]. Therefore, all females in this study were 3 or more years of age and all males 4 or older.

The snow leopards in this study were housed at Woodland Park Zoological Gardens, Seattle (two pairs); Washington Park Zoological Gardens, Portland (one pair); Brookfield Zoological Gardens, Chicago (two pairs); Bronx Zoological Gardens, New York (two pairs); and Calgary Zoological Gardens, Calgary (one pair).

Individual captive histories for the subjects in this study are presented in Table 1.

### Procedure

Preliminary studies revealed what behaviors could be observed between adult snow leopard pairs in captivity [Freeman 1975, 1977, 1978]. Because a systematic coding system is a most mathematically sound method for observational research [Altmann, 1974; Crockett, 1977], a broad-based behavior code with categories that are easily distinguishable was developed (Table 2).

In order to establish initial levels of accuracy and reduce observer bias, 35-mm slides illustrating each of the categories were shown to the observers at each zoo. The observers matched the slide to the appropriate behavior code and then participated in on-site training in observing and recording snow leopard behavior on prepared data sheets. A project coordinator was named for each zoo.

In the earlier studies I had found that snow leopards habituate quickly to individuals standing or walking in front of their enclosures, but they become tense or aggressive if the observer stands above them. Therefore all the observations were made from a public viewing area.

In order to minimize the possible effects of the presence of new individual observers, the first week's data for each observer were not used in the final tabulations. This also gave the observer and each zoo's project coordinator an opportunity to discuss the data and eliminate any problems concerning the code or the procedure, minimizing learning problems which might bias the early data.

A scan sampling method [Altmann, 1974] was used. Observations were recorded every 20 seconds on a pair simultaneously. Observation periods were conducted between 0830 and 1100 hours and 1400 and 1630 hours. Each observer was supplied with behavior code; data collection sheets; worksheets for tallying behaviors; written instructions on methods; pencil or pen and clipboard; and a stop watch, watch with a second hand, or a beeper which gave audio clues every 20 seconds.

The code was exhaustive in that the subjects were always recorded as doing something, even if the behavior was one of inactivity or out of view. Some behaviors were not mutually exclusive because the subject could be doing more than one behavior at the same time (example: showing *flehmen* while sniffing). In this case one behavior was noted in one column while the second behavior was noted in a separate column. In this way the combination occurrences were measured as separate events and the coding system became mutually exclusive. Proximity relationship was also noted by categories of contact of greater or less than 1 m.

Although infrequent behaviors of short duration (ie, aggressive swipe with forepaw) can be missed using scan or sampling, the previous snow leopard studies showed that very little information would be lost using 20-second intervals. Twenty-second, rather than 60-second, sampling permits unambiguous interpretation of the on-going activity because it allows only one behavior to have occurred in most

TABLE 1. Captive history of snow leopards in study

Name, sex, studbook no.	Location	Arrival (A) or birth date (B)	Wild caught (WC) or captive born (CB)	Pair no. (this study)	Offspring produced prior to this study	Reproductive success during this study	Length of observations (months)
Nicholas Male Seattle 1	Seattle	A 3/71	WC	1	Yes	Litter b. 5/31/79 Litter b. 5/4/81	12
Alexandra Female Seattle 2	Seattle	A 3/71	WC	1	Yes	Litter b. 5/31/79 Litter b. 5/4/81	12
Igor Male Omaha 2	Seattle	B 5/72	CB	4	No	No	8
Marya Female Seattle 7	Seattle	B 5/75	CB	4	No	No	8
Piotr Male Seattle 5	Portland	B 5/75	CB	5	No	No	8
Natashe Female San Antonio 12	Portland	B 7/77	CB	5	No	No	8
Shiva Male Brookfield 7	Chicago	B 6/76	CB	7	No	No	4
Masha Female Seattle 9	Chicago	B 5/77	CB	7	No	No	4

Captive Snow Leopard Behavior

Yeti Male Orange 1	Chicago	B approx 1963-64 A 1967	WC	8	No	No	4
Sonjah Female Brookfield 3	Chicago	B 5/68	CB	8	No	No	4
Mr. Cin Male Cincinnati 3	New York	B 5/69	CB	3	Yes	Cub b. 5/29/80	5
Olga Female Seattle 10	New York	B 5/77	CB	3	No	Cub b. 5/29/80	5
Kahn Male Lincoln Park 17	New York	B 6/75	CB	2	No	Litter b. 5/26/81 Litter b. 5/26/81	4
Shanda Female Bronx 21	New York	B 6/75	CB	2	Yes	Litter b. 5/26/80 Litter b. 5/26/81	4
Cheyenne Male Cheyenne 8	Calgary	B 5/75	CB	6	No	No	8
Irina Female Seattle 8	Calgary	B 5/77	CB	6	No	No	8

instances, with little lost between the samples. This method is particularly suited for activity cycle studies [Altmann, 1974] and using a pair-sampling method, interactive behaviors were also collected.

To statistically examine the occurrence of behaviors as a function of estrus, the observation weeks were divided into three time blocks: before estrus, estrus, and after estrus. The estrus time block was determined by the occurrence of certain behaviors as described in the Results. Analyses were also made using the percentage of time spent in each behavior for the total time period. Using percentage of scan samples as an estimate of time spent in various behaviours, 16 behaviors and combined behavior categories were examined.

Two percentages, titled "Cat-Year Data" and "Cat-Mean Data," were used in the statistics. Cat-Year Data is the percentage based on observations collected on one individual during one breeding season ( $N = 15$  cat-years per sex). Cat-Mean Data is the percentage averaged over the cat-years that an individual cat was studied ( $N = 8$  cat-means per sex).

Three statistical tests [Siegel, 1956] were used: Mann-Whitney U test for analyzing differences between successful and unsuccessful cats; Wilcoxon Matched-Pairs Signed-Rank for testing sex differences and time block effects (significant differences in percentage of time before estrus versus estrus and/or between estrus and after estrus); and the Spearman Rank Correlation Coefficient to examine the similarity in the percentage of time spent engaging in the same behavior by both members of a pair.

Successful pairs or individuals were defined as those that produced offspring in either 1979 or 1980 or 1981.

## RESULTS

Scan sample totals for each observation period were entered into a data file at the University of Washington Academic Computer Center. Observation period totals were summed for each behavior category yielding the total number of 20-second scan samples that each behavior was recorded for each cat per week of observation (up to 18 weeks per cat per year) and the total number of scans per cat. To examine the frequency of behaviors as a function of estrous cycle, the observation weeks were divided into three time blocks. Since it was not possible to take vaginal smears or other physiological indicators of estrus, the occurrence of copulation, or in its absence, anal genital sniffing, was used.

Previous observations suggest that estrus normally lasts from three to six days. Since it was not possible to observe all copulations and since estrus could extend into more than one observation per week (each observation week consisted of one calendar week, Sunday through Saturday), a two-week block was used for the estrus time block to assure an equal sample size for each pair.

The central time block consisted of the consecutive two weeks which most likely coincided with estrus, based on the occurrence of copulation and other sexual-related behaviors (example: anal genital sniffing). For pairs 7 and 8, no indicative behaviors occurred, and weeks 9-10 were classified as the estrus time block. The preestrus time block averaged 8.5 weeks (range 3 to 11;  $n = 14$ ; pair 2 had no preestrus observations during one year of study); the estrus time block was two weeks for all 15 pair-years; the postestrus time block averaged six weeks (range 3 to 9 weeks,  $n = 15$ ). Total

observations were based on an average of 14.5 weeks of study (range 9 to 18) per pair year.

A Statistical Package for the Social Sciences (SPSS) program [Nie et al., 1975] summed the frequency of scans per behavior per cat-year within each of the three time blocks and for the total observation period. The frequency of scans per behavior was divided by the total scans on that animal for the time block in question to yield a percentage of scans. The percentage was considered to be an estimate of the percentage of time spent by the cat engaged in the behavior in question during the specified time period. All subsequent analyses used these percentages.

For statistical analyses, 16 behaviors and combined behavior categories were examined (Table 2 lists 16 categories; Table 3 lists statistics used). Three other behaviors were tabulated but not analyzed because of low frequency of occurrence (eg, bite/swipe; snarl/growl; caterwaul). Several other behaviors which were recorded are not considered here (eg, eating, defecation).

The eight snow leopard pairs studied represented 15 pair-years; pair 1 was observed during three breeding seasons, pairs 2-6 were observed for two seasons,

**TABLE 2. Behavior categories**

Category	Description
Pace	Repetitious movement over the same area in a stereotypic pattern, either alone or within 30 cm of mate
Locomote	Directional movement, either alone or within 30 cm of mate
Autogroom	Self-grooming by licking
Social groom	Licking the fur of mate
Sniff	Sniffing of an inanimate object or mate's anogenital area
Flehmen	A grimace with open mouth, wrinkled nose, retracted lips, and tongue that may or may not protrude past the lips
Roll on back	Individual in dorsal recumbancy, rubbing back on floor while forepaws in air
Sedentary	Lying motionless, eyes open or shut, at a distance of more than 30 cm from mate
Social sedentary	Lying motionless, eyes open or shut, within 30 cm of mate
Not visible	Individual is out of sight of the observer
Prusten	The sound of short, single snorts of air expelled through the nostrils
Social affiliative	The combined active behaviors of standing, locomoting, or pacing within 30 cm of mate; social grooming or headrubbing; and social play
Sexual	Sniffing of anogenital area of one individual by the other; or sexual mount ventral ventral; or mount ventral dorsal; or mount unspecified
Mark horizontal	Scraping of floor surface with hind paws
Mark vertical or spraying	Tail raised, squirting liquid caudally upward at an angle of 30° to 40°
Combined marking	The combined behaviors of horizontal marking, vertical marking, or spraying, and headrubbing of an inanimate object

TABLE 3. Statistics used

Comparison	Test	Percentage
Successful vs unsuccessful	Mann-Whitney U	Cat-year and cat-mean
Male-female differences	Wilcoxon matched-pairs signed rank	Cat-mean
Pair correlation	Pearson r and Spearman rank correlation coefficients	Cat-year and cat-mean
Time block (before vs estrus; estrus vs after)	Wilcoxon matched-pairs signed rank	Cat-year

and pairs 7 and 8 were observed one season. Percentages per cat for each of the 16 behavior categories for each time block (pre, estrus, post, total) for each year studied were entered into an Apple II Plus computer [Statpro statistical program; Imhof et al, 1982]. Analyses of "pair-year" records had a sample size of 15 percentages per time block (15 pair-years; 14 for preestrus). Further analyses used pair-means, the average of the percentages for a given cat recorded during the one to three years studied (sample size = 8 pair-means).

As outlined in the previous section, the behavior categories were analyzed for the following:

#### Behavioral Correlates of Breeding Success

Three of the eight pairs studied produced cubs and were considered to be successful pairs. Two of these (pairs 1 and 3) failed to produce cubs one of the years studied. This produced a problem in analysis of behavioral correlates of breeding success, since the 15 pair-years could be grouped into three categories: successful pair-successful year ( $n = 5$ ); successful pair-unsuccessful year ( $n = 2$ ); unsuccessful year ( $n = 8$ ). For each sex separately, the behaviors were analyzed using a Mann-Whitney U statistic; first, the data from unsuccessful years of successful pairs were grouped with "unsuccessful" and next these data were grouped with "successful." In all cases where the latter grouping yielded a nonsignificant result, so did the former. In all other cases, grouping the unsuccessful years of successful pairs with the successful years produced significant differences, either changing a nonsignificant result to a significant one, or reducing the probability level. This suggested that successful pairs during unsuccessful years behaved more like themselves during successful years than like unsuccessful pairs. Thus, for all subsequent analyses of behavioral correlates of breeding season, pair means were used (three successful pairs versus five unsuccessful pairs).

Mann-Whitney U tests were run again on the 16 behaviors, this time comparing, by sex, the three successful pairs with the five unsuccessful pairs. Three behavior categories showed significantly different percentages for successful males and females: Successful pairs spent less time "not visible" than unsuccessful pairs, and



successful pairs spent more time in "sexual" (Fig. 1) and "roll on back" (Fig. 2) behaviors than unsuccessful pairs. Furthermore, successful males spent significantly more time in "autogroom" (Fig. 3) and "sniff" compared to unsuccessful males. To yield a significant Mann-Whitney U value for these sample sizes (three and five) (two-tailed test), there can be no reversals in rank; in other words, for all significant results, all successful pair-means ranked above (or below) the unsuccessful pair-means.

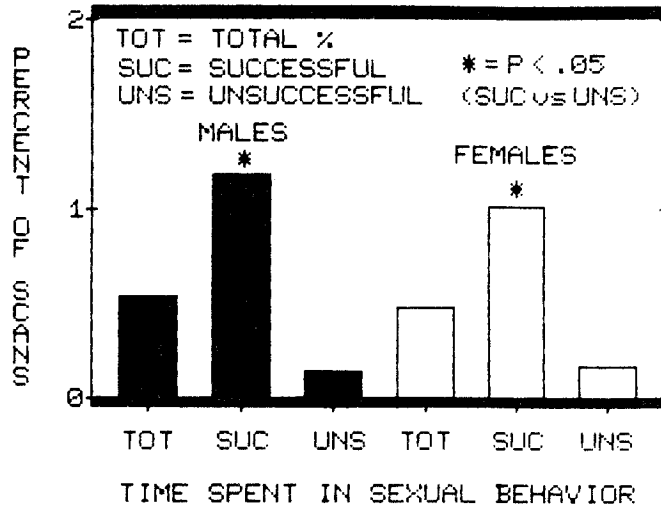


Fig. 1. Comparison between successful and unsuccessful pairs in time spent in sexual behavior (cat-mean data).

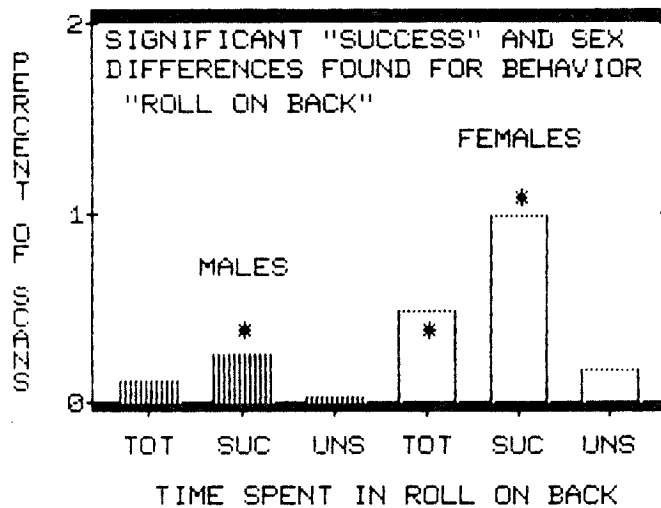


Fig. 2. Comparison between successful and unsuccessful pairs in time spent in the behavior "roll on back." There was also a significant difference between successful and unsuccessful females in this behavior (cat-mean data).

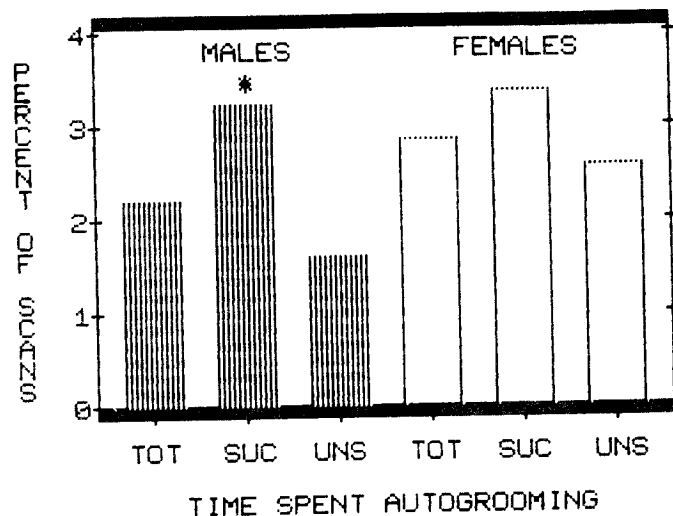


Fig. 3. Comparison of successful and unsuccessful males in the time spent autogrooming (cat-mean data). The difference between females is not significant.

Eight comparisons using pair-year data that yielded significant Mann-Whitney U results failed to achieve significance when pair-means were used. In all eight of these cases, one or both members of pair 4 had a higher mean percentage than one or more of the successful pairs, and in all but one this was the single reversal. In other words, if it were not for the single reversal by the same unsuccessful pair, the following seven categories would also have reached significance: male "combined marking," male "vertical marking," female "sniff," female "*prusten*," male "social grooming," and "*flehmen*" by both sexes. Thus, these seven categories may also prove to be correlated to breeding success. However, since pairs contributed different numbers of years to the pair-year data set, a particular pair (especially pair 1) could bias the outcome of statistics, and individual differences independent of real correlates of breeding success might produce misleading results. Until more data are available, the pair-mean statistics are more appropriate.

### Sex Differences

Sex differences were assessed using a Wilcoxon Matched-Pairs (Sign Rank) test on pair-means, each male's percentage matched with his mate's percentage. Seven of the 16 behavior categories in Table 4 revealed significant sex differences (paired t-tests on pair-year percentages found the same behaviors to have significant sex differences, but the assumptions of the t-test are not met by these data). Females spent significantly more time in "roll on back," "autogroom," and "*prusten*" than their mates; males spent significantly more time than females in "horizontal," "vertical," and "combined marking" and "social grooming." This indicates that females receive more total grooming than males, since they groom themselves more than do males, and males groom them more than females groom males.

TABLE 4. Percentage of time and sex differences\*

Behaviour	Male %		Female %	Sig.
Not visible	12.4		11.8	
Sedentary	41.2		43.9	
Social sedentary	14.7		14.5	
Total "inactive"	68.3		70.2	
Social affiliative	3.5		3.2	
Pace	6.6		5.8	
Locomote	8.0		8.6	
Social groom	0.5	>	0.2	***
Autogroom	2.2	<	2.9	**
Sexual	0.5		0.5	
Sniff	3.0		2.3	
Roll on back	0.1	<	0.5	***
Combined marking	2.5	>	0.7	***
Horizontal Marking	1.1	>	0.1	***
Vertical spraying	0.5	>	0.1	***
Flehmen	0.8		0.7	
Prusten	0.2	<	0.5	**

\*Wilcoxon Matched-Pairs (Sign Rank) Test.

\*\*P < .05.

\*\*\*P < .01.

### Pair Correlations

Correlation coefficients were calculated to determine whether the percentage of time spent in each behavior category was similar for each pair member (Table 5). Correlations of pair-year percentages were done using the Pearson correlation coefficient. Correlations of pair-mean percentages, comparing the mean percentage of each male with that of his mate, were calculated for each behavior category using Spearman's rank order correlation. Eleven of the 16 categories were significantly positively correlated: ie, when a male had a high percentage for a behavior, his mate tended to have a high percentage, and when a male had a low percentage, so did his mate. Not surprisingly, the highest correlation was for "social sedentary" since this behavior is defined as being in proximity to the mate (Fig. 4). The behaviors that were not significantly correlated were "sedentary," "autogroom," "social groom," and "horizontal" and "vertical marking." Only the latter two behaviors were found to be uncorrelated in both pair-year and pair-mean correlations; the former three were significant in pair-year comparisons. "Roll on back," "pace," and "prusten" were significantly correlated when pair-means were used but not for pair-year data.

The difference between these two correlations is that one compares the average percentage of time for both pair members, years of observation combined, while the other compares the percentage of time for both pair members during a particular breeding season. Therefore, sedentary and grooming behaviors are more correlated for a pair within a year while roll on back, pace, and prusten are correlated only when pair averages are used. Behaviors that are significantly correlated for both measures include not visible, social sedentary, social affiliative, sexual, combined marking, locomotion, sniff, and flehmen.

TABLE 5. Correlation between pair members

Behaviors listed from highest to lowest	
Social sedentary	1.00 $P < .01^*$
Sexual	.95 $P < .01^*$
Sniff	.95 $P < .01^*$
Locomote	.95 $P < .01^*$
Not visible	.93 $P < .01^*$
Social affiliative	.90 $P < .01^*$
Roll on back	.83 $P = .01^*$
Combined marking	.83 $P = .01^*$
Pace	.79 $P < .05^*$
Flehmen	.76 $P < .05^*$
Prusten	.74 $P < .05^{**}$

\*Spearman Rank and Pearson r Correlation Coefficients.

\*\*Spearman Rank Correlation Coefficient.

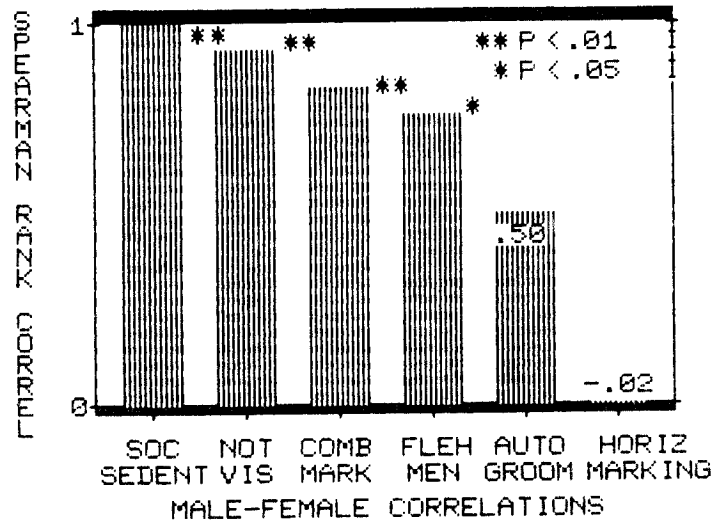


Fig. 4. Significant correlations between pair members were found in the behaviors social sedentary, not visible, combined marking category, and flehmen (Pearson r and Spearman Rank Correlation coefficients).

In general, the behaviors that are not significantly correlated are the same behaviors for which sex differences in percentages were found.

**Time Block**

The effect of time blocks (before estrus compared to estrus and estrus to after estrus) was assessed for males and females using a Wilcoxon (Sign Rank) test. The following behavior categories had significant differences in the time spent performing that behavior when comparing before, during, and/or after estrus:

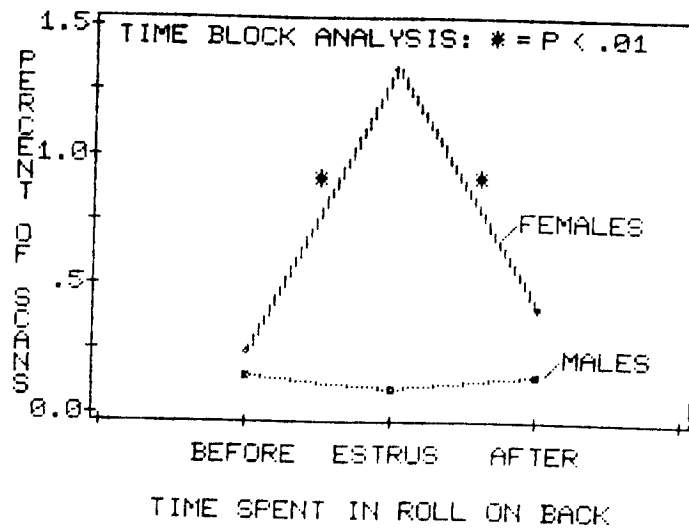


Fig. 5. Time block analysis of time spent in behavior "roll on back." There is a significant increase for females during estrus (Wilcoxon Sign Rank test).

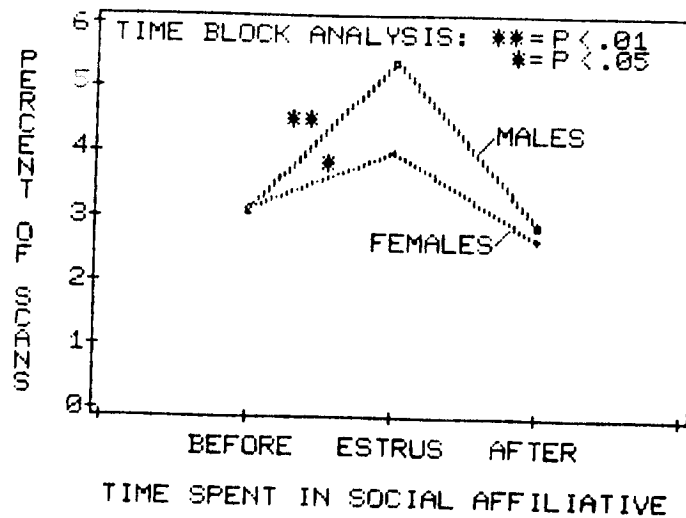


Fig. 6. Time spent in social affiliative behaviors increases prior to the estrous time block. The increase is highest for males (Wilcoxon Sign Rank test).

In "roll on back" (Fig. 5) there is a significant increase in percentage of time spent by females during estrus compared to before estrus or after estrus. Males did not exhibit a change over the breeding season in the frequency of this behavior.

Increase in percentage of time spent in social affiliative behaviors (Fig. 6) between before estrus and estrus is significant for both sexes but the increase is highest for males. This indicates that males peak their contact behaviors with females prior to copulatory activity.

During estrus the incidence of pacing (Fig. 7) drops significantly when compared to before estrus and after estrus for all females. This precipitous drop in pacing during the estrus time block also occurs with successful males, but unsuccessful males continue pacing at a constant rate during the female's estrous cycle.

The percentage of time spent in sexual behaviors (Fig. 8) is at its highest peak for both sexes during estrus.

Females spend little time performing the marking behaviors of spraying, scraping, and headrubbing, but this incidence drops even lower between the before estrus and estrus periods.

## DISCUSSION

Male and female interactions during the breeding season are characterized by an increase in the precopulatory contact behaviors of sniffing of the anogenital area of one individual by the other (Fig. 9); social grooming, particularly by the male (Fig. 10); head and body rubbing of one individual by the other; the incidence of the low-intensity vocalization of "prusten," particularly by the female; standing and moving in close proximity; and playful stalks and pounces (Fig. 11). These types of precopulatory interactions are typical of canid reproductive behavior [Kleiman and Eisenberg, 1973].

Interactions are not performed at a high level of intensity but instead are subtle and brief, resulting in minimum energy expenditure by each pair member. This in turn makes the on-going sexual dance of the snow leopard intricate and synchronized.

The incidence of ritualized threat behavior (ie, where the female strikes out at the male with her forepaws) is extremely low. The highest occurrence is when pairs are newly introduced.

During the precopulatory period both sexes are able to evaluate each other and close-range interactions become a necessary overture to copulation. The female has

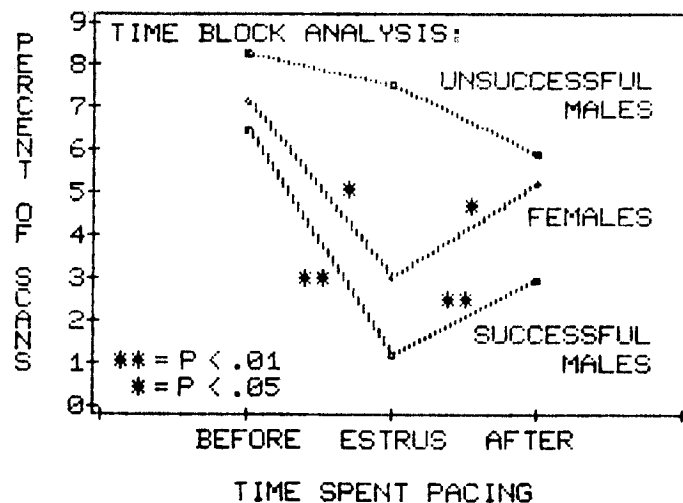


Fig. 7. During estrus the time spent pacing decreases significantly for all females and for successful males (Wilcoxon Sign Rank test).

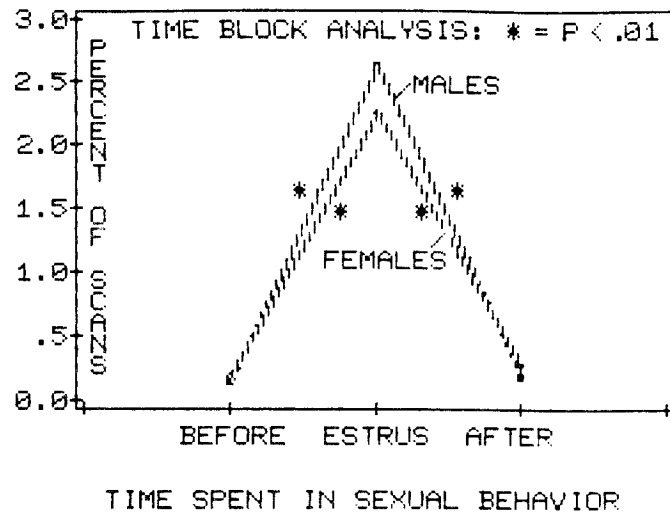


Fig. 8. The percentage of time spent in sexual behaviours is at its highest for both males and females during the estrous time block (Wilcoxon Sign Rank test).

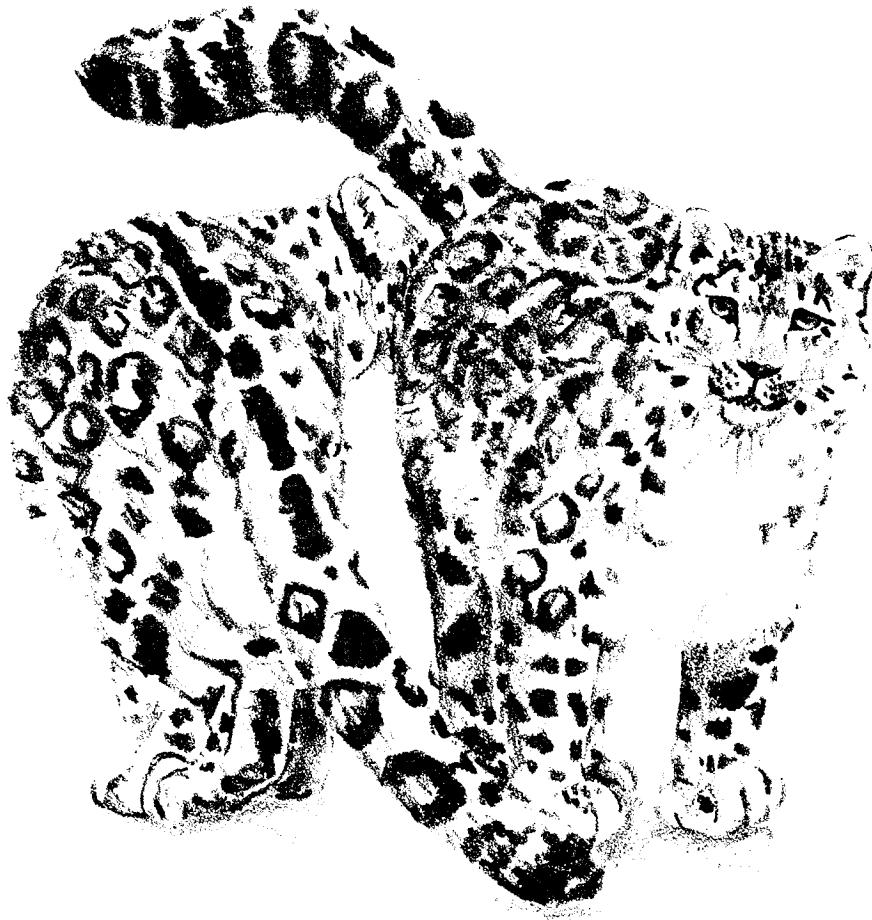


Fig. 9. Anogenital sniffing.



Fig. 10. Social grooming.



Fig. 11. Playful stalk and pounce.

more behaviors on which to form an opinion as there are more behavioral differences between males than between females.

There are no significant differences between males and females in the percentage of time spent in performing the majority of the behaviors. This indicates a reduction in role differences between males and females.



The high degree of synchrony between individuals results in within-pair consistency. The percentage of time in which the sexes had significant differences in the time spent in a behavior was approximately 10% of the total time.

A high degree of tolerance for close proximity is demonstrated by the percentage of time pairs spend resting together. This increases in relation to the length of time a pair has been together.

Copulation occurs over a 3-6-day period. The male usually grips the fur on the female's neck when he mounts. After the last thrust, and with the occurrence of full immissio penis, the male gives a loud piercing yowl. This vocalization during copulation is probably a derivative of the continuum mew/main call of the large felids, though specific to this behavioral situation [Peters, 1978].

The most common copulatory posture is for the female to lie on her belly, rump raised in a lordosis posture and tail turned aside. The male mounts here in a ventral/dorsal position. Snow leopards were also observed copulating in a ventral/ventral position, with the female on her back, forepaws clasp the male (Fig. 12). This is an unusual copulatory posture for felids as it places the female off balance and in a vulnerable position.

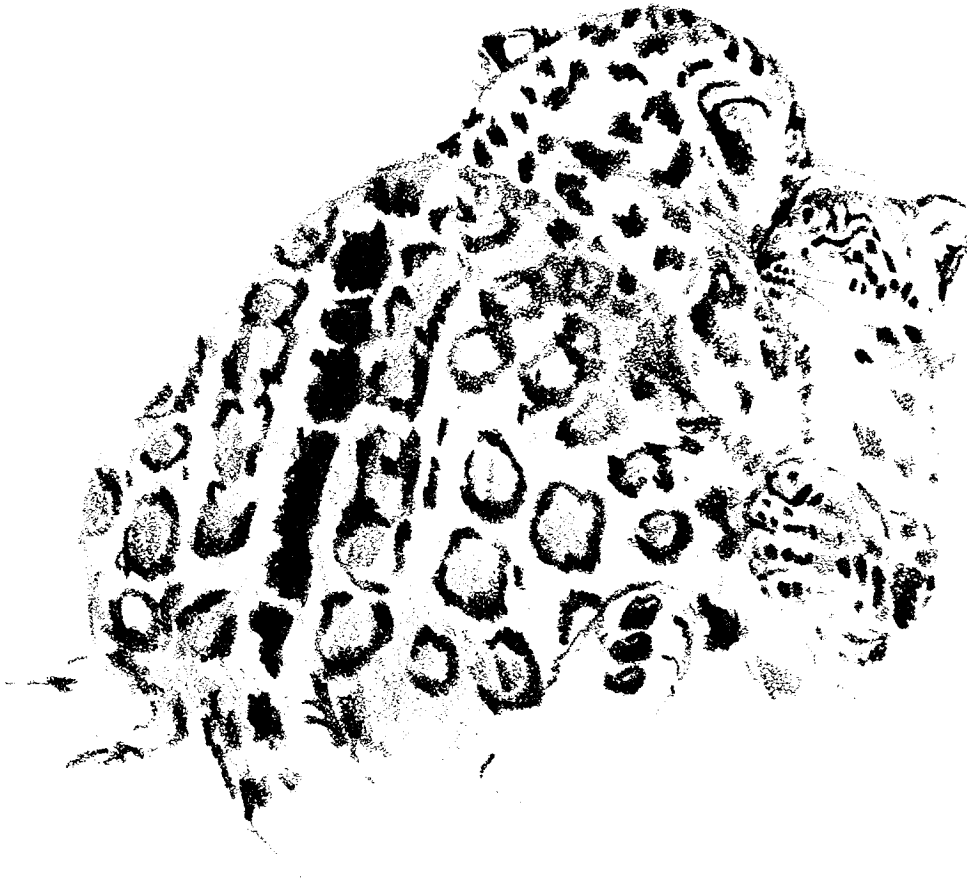


Fig. 12. Copulation in ventral/ventral position, female on her back.

After mating, the female rolls, rubbing her back on the ground and stretching her body.

Three basic scent-marking postures are seen in the snow leopard: turning the hindquarters toward a vertical surface, raising the tail and squirting or spraying a liquid caudally upward at an angle of  $30^\circ$  to  $40^\circ$  (Fig. 13), with flagging or twitching of the tail occurring after spraying; scraping the floor surface with hind paws; and alternately rubbing the cheeks on the sides of the face against a surface which has sometimes been used also for spraying (Fig. 14).

These marking behaviors are performed significantly more often by males than females. This sexual difference was also noted in the study by Rieger [1978]. In snow leopards marking may be a behavior trait midway between the lion, where it is a male activity [Schaller, 1972] and the tiger, where scent marking is performed frequently by both sexes [McDougal, 1979].

Successful individuals of both sexes demonstrate a higher degree of activity than unsuccessful animals. More time is spent investigating the enclosure, interacting with each other, grooming themselves, and showing the behavior "*flehmen*" in response to sniffing.

Unsuccessful males continue to pace during the female estrous cycle, while males whose mates become pregnant have a dramatic drop in this behavior during the estrus time block. This suggests the possibility that males may be able to detect a female's reproductive capability, continuing to be restless and pacing if the female is unlikely to become pregnant.



Fig. 13. Marking by spraying or squirting.



Fig. 14. Marking by rubbing cheek.

Because the snow leopard in captivity spends a high proportion of its day resting and sleeping, a great many observations are necessary to record behavior in meaningful terms.

At the onset of this study I was hoping it would be able to provide concrete guidelines for the breeding of this species in captivity. In fact, I found correlates to breeding success.

Clearly the methodology in future research could be improved. But since this is one of the first attempts at this type of approach in zoological gardens, it is my hope that others will follow this example of inter-zoo comparisons and larger samples.

## CONCLUSIONS

1. Results indicate that the amount of time spent in "being visible," "sexual behavior," and "rolling on back" distinguishes successfully from unsuccessfully breeding pairs. There was a reversal of one pair, but in the other seven pairs the incidence of "*flehmen*" (Fig. 15) was also an indicator of breeding success.



Fig. 15. *Flehmen*. Figures 9-15 illustrated by Gretchen Daiber.

2. There are more behavioral similarities than differences between males and females in how they spend their time. Males and females differ significantly in seven of the 16 analyzed behavior categories. The most significant differences between the sexes are: Males spend a higher percentage of time social grooming and in the marking behaviors of headrubbing, scraping, and spraying; Females spend a higher percentage of time in "autogrooming," "rolling on back," and giving the vocalization "*prusten*."
3. There are 11 significant behavioral correlations between members of a pair, resulting in a high degree of within-pair consistency.
4. The following behavior categories show a time block effect and may be indicators of the estrous time period: Both sexes show an increase in social affiliative behaviors prior to copulatory activity and an increase of sexual behaviors during estrus: females show a significant increase in "roll on back" during estrus while males stay relatively constant at a lower rate; all females and successful males exhibit a significant drop in pacing frequency during the female's estrous period; males mark at a constant rate throughout the three time block periods but females exhibit a significant drop during estrus in the combined marking behavior category (headrubbing, scraping, and spraying).
5. Snow leopard pairs have a high degree of tolerance for each other and exhibit little aggressive behavior.
6. This study has identified some behaviors that seem to correlate with reproductive success. Hopefully, this may inspire others to employ systematic manipulation with concomitant data collection so that the effects of these manipulations can be evaluated.

## ACKNOWLEDGMENTS

This study was supported by grants from the Wildlife Preservation Trust and each of the participating zoos. Portions of these data were presented at the Third International Snow Leopard Symposium, June 22-25, 1982, in Seattle, Washington. Because this was a cooperative research project between institutions, a number of individuals have assisted. Special recognition should go to the observers: Chicago Zoological Park: Gayle Pluta, coordinator; Nancy Bagley, Joyce Barloga, Aggie Blesy, Bruce Brewer, Dorothy Connell, Darcy Donald, Penny Korhumel, Mary Nicholas, Susan Rice, and Linda Whatley. New York Zoological Park (Bronx Zoo): Dan Wharton, coordinator; Susan Bauer, Bethanne Beck, Ginger Finkelstein, Kathy Fitzgerald, Margaret Gaughan, Amy Schacter, Pat Thomas, and Laura Westphal. Calgary Zoo, Botanical Gardens and Natural History Park: Greg Tarry, coordinator; Bill Dubreuil, Sue Flood, Bryan Isaac, Bob Kam, John Lehnhardt, Jim McConnell, and Curt Schroeder. Washington Park Zoo: Jill Mellen, coordinator; J. Arriaga, J. Baer, M. Boone, A. Driscoll, Cherie Hensley, J. Jouck, M. Strayce, and A. Walther. Woodland Park Zoological Gardens: Evelyn Burt, coordinator; Kathleen Braden, Carola Burroughs, Laura Eisen, Alison Fujino-Miller, Marie Anne Johnson, Terry O'Connor, Phyllis Riggs, and Les Riggs. There was continuous support from the staff of Woodland Park Zoological Gardens, particularly David Hancocks, James W. Foster, Gwen Boyer, Gordon Swanberg, Les Harbert, and Bill Cowell. The author wants to express a special thanks to Gretchen Daiber for her illustrations. I am much indebted to Carolyn Crockett for her guidance and expertise on the statistical analysis, and to Kathleen Braden and Stan Freeman for their invaluable assistance and encouragement.

## REFERENCES

- Altmann, J. Observational study of behavior; sampling methods. *BEHAVIOUR* 49:227-267, 1974.
- Blomquist, L. The 1980 annual report of the captive snow leopard (*Panthera uncia*) population and a review of the breeding results during the 1970's, pp. 32-50 in the *HELSINKI ZOO ANNUAL REPORT 1980*. Helsinki, Finland, 1981.
- Campbell, S. Is reintroduction a realistic goal? pp. 263-269 in *CONSERVATION BIOLOGY: AN EVOLUTIONARY-ECOLOGICAL PERSPECTIVE*. M.E. Soule; B. A. Wilcox, eds. Sinauer Associates, Sunderland, Massachusetts, 1980.
- Crockett, C. Methods of Observational research in the zoo setting, pp. 51-73, in *APPLIED BEHAVIORAL RESEARCH: WOODLAND PARK ZOOLOGICAL GARDENS*. C. Crockett; M. Hutchins, eds. Pika Press, Seattle, 1977.
- Dang, H. The snow leopard and its prey. *CHELTAL* 10(1):72-84, 1967.
- Freeman, H.; Hutchins, M. Captive management of snow leopard cubs: an overview. *DER ZOOLOGISCHE GARTEN* Jena 50:377-392, 1980.
- Freeman, H.; Braden, K. Zoo location as a factor in the reproductive behavior of captive snow leopards. *DER ZOOLOGISCHE GARTEN*, Jena 47:280-288, 1977.
- Freeman, H. A preliminary study of the behavior of captive snow leopards. *INTERNATIONAL ZOO YEARBOOK* 15:217-223, 1975.
- Imhof, M.A.; Hewett, S.W.; Imhof, K.M. *STATMOD USERS MANUAL*. Madison, Wisconsin, Blue Lakes Software Ltd., 1982.
- Jackson, R.M. Snow leopards in Nepal. *ORYX* 15(2):191-195, 1979.
- Jackson, R.M. *A REPORT ON WILDLIFE AND HUNTING IN THE NAMLANG (LANGU) VALLEY OF WEST NEPAL*. Unpublished manuscript, 21 pp. Submitted to His Majesty's Government Office, National Parks and Wildlife Conservation, Kathmandu, 1978.
- Kleiman, D.G.; Eisenberg J.F. Comparisons of canid and felid social systems from an evolutionary perspective. *ANIMAL BEHAVIOUR* 21:637-659, 1973.
- Kuznetsov, G.V.; Matyushkin, G.V. The snow leopard hunts. *PRIRODA* 12:65-67, 1962.
- Marma, B.B.; Yunchis, V.V. Observations on the breeding, management, and physiology of snow leopards at Kaunas Zoo from 1962-1967. *INTERNATIONAL ZOO YEARBOOK* 8:66-73, 1968.
- McDougal, C. *THE FACE OF THE TIGER*. Rivington Books and Andre Deutsch, London, 1979.
- Nie, N.H. et. al. *SPSS, STATISTICAL PACKAGE FOR THE SOCIAL SCIENCES*, second edition. New York, McGraw Hill, 1975.
- Ognev, S.K. *MAMMALS OF U.S.S.R. AND*

- ADJACENT COUNTRIES. Vol. III. Carnivora. Israel Program for Scientific Translations. Jerusalem, 1962.
- Peters, G. Vergleichende Untersuchung zur Lautgebung einiger Feliden. Ph.D. Dissertation, in *SPIXIANA: ZEITSCHRIFT FÜR ZOOLOGIE* (1), Munich, 1978.
- Petzsch, J. *DIE KATZEN*. Leipzig, Urania-Verlag, 1968.
- Pocock, R.I. Cited in *THE MAMMALS OF PAKISTAN*. T.J. Roberts, ed. London, Ernest Benn Ltd., 1977.
- Pokrovskiy, V.S. *THE SNOW LEOPARD*. Lesnaya Promyshlennost', Moscow, 1974.
- Rieger, I. Scent marking behavior of ounces. *Unciannia*, pp. 78-103 in *INTERNATIONAL PEDIGREE BOOK OF SNOW LEOPARDS*, Vol. 1. L. Blomquist, ed. Helsinki Zoo, 1978.
- Schaller, G.B. *STONES OF SILENCE: JOURNEYS IN THE HIMALAYA*. New York, Viking Press, 1980.
- Schaller, G.B. Notes on the habits of several predators. pp. 138-159 in *MOUNTAIN MONARCHS: WILD SHEEP AND GOATS OF THE HIMALAYA*. Chicago, University of Chicago Press, 1977.
- Schaller, G.B. Mountain mammals in Pakistan. *ORYX* 13:351-356, 1976.
- Schaller, G.B. *THE SERENGETI LION*. Chicago, The University of Chicago Press, 1972.
- Shaposhnikov, F.D. The snow leopard in the Western Tien Shan. *PRIRODA NO. 7*:113-114, 1956.
- Siegel, S. *NONPARAMETRIC STATISTICS FOR THE BEHAVIORAL SCIENCES*. New York, McGraw Hill, 1956.
- Simon, N., ed. Vol. 1. *MAMMALIA. RED DATA BOOK*. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland, 1970.