A TECHNIQUE FOR PROPAGATING CHEETAHS

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The responsibility of zoos and wildlife parks to aid in the preservation of endangered species has increased with the disruption of natural habitats. In an effort to assume such responsibility, the Hogle Zoological Gardens has combined resources with animal behaviorists at the University of Utah to deal with the problem of captive cheetah breeding. Herdman (1972) states that only 18 births have been recorded among captive cheetahs. Further, these births resulted from the activities of only nine females. Myers (1972) estimates that only 7,000-10,000 cheetahs remain in the wild. The problem of cheetah breeding must be considered within the constraints of the typical zoo environment. That is, a breeding technique must be developed which not only works in large, semi-natural wildlife parks, but can also be applied within a variety of limited habitats. The work described below suggests such a technique as well as providing a more general example of combining the practical experience obtained in the zoo with the academic methodology of animal behavior. The authors are deeply indebted to Mr. Lamar Farnsworth, Director of the Hogle Zoo, for his interest and support in the use of the facilities. Portions of this work were supported by Public Health Service Grant HD 05026.

Since cheetahs breed in the wild, but rarely in captivity, we began our work by comparing the behavior of wild cheetahs with the more limited behavior permitted by the captive environment. Although recorded observations of wild cheetahs are limited, two behavior patterns have been observed which fail to occur in captivity because both sexes are commonly caged together. In the wild, females are isolated from conspecifics for most of their lives and some males live in roving groups. The female isolation period lasts from early pregnancy until the cubs are about 13 to 14 months old. The female then enters a period of "pre-estrus"; contact with males occurs (either male or female initiated); and the reproductive cycle is repeated (cf. Eaton, 1970). We suspect that "pre-estrus" rather than an estrous period occurs in isolation since such a period affords a greater opportunity for mate identification and is well known in canids (Patricia J. Berger, personal communications). Data obtained in our work further support use of this term. As with other species, the isolation of the female may serve adaptive functions. That is, isolation from social competition and associated stress may enhance the likelihood of a successful pregnancy. The isolation also provides security for the offspring against male attack and resource competition. Finally, the isolation affords a close association between mother and offspring which provides the cubs an opportunity to acquire necessary adaptive skills involving hunting and social interaction.

Social interaction among the males may also serve an adaptive function. Such interaction is expected to result in a male dominance hierarchy. If future mating occurs only with the dominant male, the offspring are provided the strongest genetic background available (Lorenz, 1963; Barnett, 1967; Dethier and Stellar, 1961). While no natural observations of mate selection are available, Herdman (1972) has recently noted that selection of dominant males does occur among captive cheetahs.

Female observation of aggressive interaction among males may stimulate and direct reproductive behavior (see: Tinbergen, 1951; Parks, 1960). This view is supported by reports of captive matings in which we note that reproductive behavior followed female isolation and her exposure to aggressive interactions among the males (Eaton and Craig, 1973; Herdman, 1972; Florio and Spinelli, 1967, 1968; Manton, 1970; Rawlins, 1972; Vallat, 1971). An additional factor believed to reduce stress and thereby facilitate sexual receptivity involves visibility of the surrounding landscape (Rawlins, 1972; Florio and Spinelli, 1967). We suspect that a view of the landscape simulates the female's definition of isolation and as such is an important component.

In summary, the following events, rarely present in the zoo, seem to occur prior to mating: (1) the female is isolated with her cubs for approximately one year; (2) she enters a period which we will label "pre-estrus" and confronts single males and/or a roving male group(s); (3) the males either fight in her presence revealing their dominance hierarchy, or the dominant of a group has priority; (4) observation of the male-male aggression and/or the courtship behavior by males excites the female facilitating receptivity and the probability of ovulation.

The project described below includes a brief description of our work on male dominance hierarchies reported in the 1974 *International Zoo Yearbook* and two new studies involving attempts to detect pre-estrus. It also includes the results of subsequent introductions of a pre-estrus and a control female to the male group.

Dominance Hierarchies

Method

The subjects were seven resident cheetahs of the Hogle Zoological Gardens in Salt Lake City, Utah. Three of the animals were wild trapped as infants and raised in captivity by humans. These cheetahs were docile and two of them, a male and a female, will be referred to as the "domestic" cheetahs. The third animal, a female, was often petted and played with by the keepers--this animal

ll be referred to as the "tame" cheetah. The other four cheetahs (2:2) were ld trapped as young adults in 1971. These animals will be referred to as the vild" cheetahs.

e experiment consisted of a "combined" and a "separated" condition. In the mbined condition, all seven cheetahs were housed in two adjoining and inter- nnected cages that permitted free interaction among all animals. Figure 1 ows the cage sizes, arrangement, and facilities for this condition. In the parated condition the animals were caged according to sex. The males were used in one of two cages shown in Figure 1. The females were housed in an entical cage located on the opposite side of the feline building.

both conditions, an observer recorded social interactions daily with emphasis on agonistic encounters. Behavioral events considered agonistic included ssing, teeth baring, attack, and displacement. Displacement was defined as the t of one animal forcing a second animal to vacate a location which was sub- quently occupied by the first animal. Following each incidence of aggressive teraction, both the type of behavior and the individuals involved were noted.

the combined condition, the data comprise a simple description of the frequ- cy with which various interactions occurred. In the separate condition, two pects of the environment were experimentally manipulated in order to instigate nflicts believed to reveal the dominance hierarchy. The manipulations involved vement of animals to a new cage and food dispersal. The movement manipulation volved opening an access door to a new cage and permitting either free move- nt or forced movement to the new cage. In the forced movement condition, animals re hosed in the old cage and could escape the aversive stimulus (water) only by vement through the access door.

e food dispersal manipulation consisted of presenting either one or two food ns at feeding time. Again, the order that individuals approached and ate was corded. The total amount of food provided, whether in one or two pans, was d constant throughout the experiment.

ervation periods scheduled at various times during the day were 90 min. long occurred five times per week for eight consecutive weeks in October and ember, 1972.

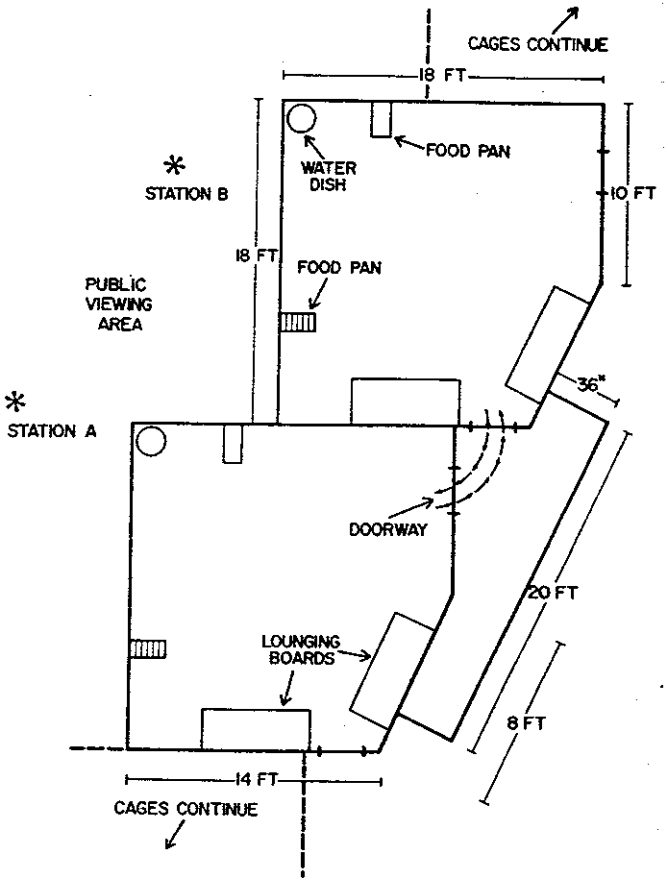

Figure 1. Cage sizes, arrangement, and facilities for the combined condition. In the separate condition, the males were housed in the upper cage shown and females were housed in an identical cage on the opposite side of the feline building. Shaded food pans were used in the combined condition; unshaded food pans indicate secondary pan location for the separate condition. Station A represents observer location in the combined condition; Station B represents relative observer position in the separate condition. The access route between cages is indicated by arrows between the doorways.

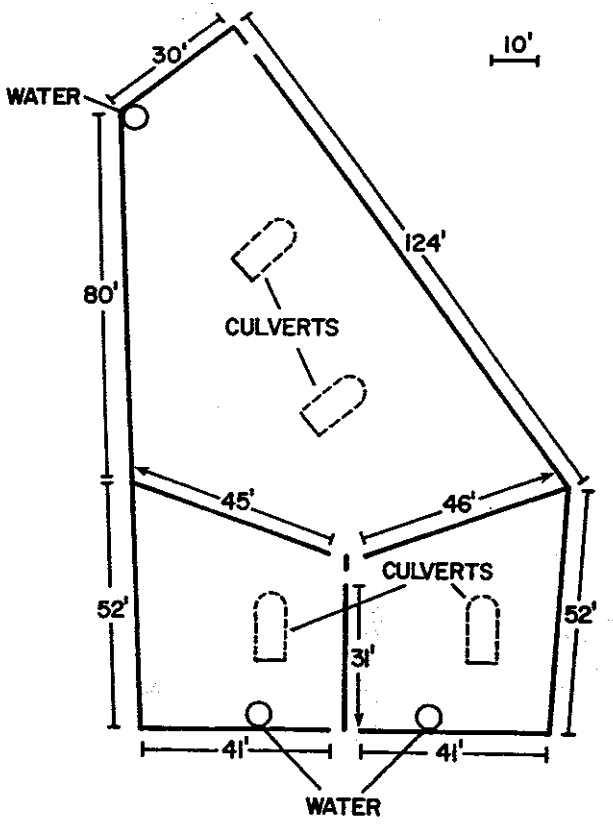

Figure 2. Cage size, arrangement, and facilities for the outside cheetah run. Access routes between cages are indicated by breaks in the solid lines. The culverts are not drawn to scale (see text for dimensions).

Results

Combined Condition

The observational data for the combined condition may be summarized as follows: agonistic encounters occurred frequently and most of these encounters involved conflicts between the wild and the domesticated cheetahs. In nearly all cases, the encounters were initiated by wild cheetahs and the domestics were displaced.

That is, the wild males dominated; the wild females dominated the domestic male and tame female, and the domestic female was dominated by all. We failed to ascertain the relationships between the wild males, between the wild females, and between the domestic male and tame female. These failures resulted from two sources: the large number of moving animals made it difficult to keep track of the participants in each interaction and either the presence of resident females inhibited male dominance relationships or the concerted conflicts between wild and domesticated cheetahs over-shadowed such relationships. For these reasons, the animals were separated according to sex.

Separate Condition

In the separate male cage, the bond between the wild cheetahs remained obvious. Nevertheless, a dominance relationship between these two animals soon became evident. The wild males were estimated to be of approximately the same age, but differed slightly in size. The larger male was dominant over the other wild male, and both remained dominant over the domestic who was intermediate in size.

In the separate female cage, a less definite dominance hierarchy was observed. In general, the two wild females were dominant over the tame and domestic cheetahs. There was no evidence for a dominance relationship between the wild females, but the tame cheetah cat frequently aggressed the domestic cheetah cat as did her wild cagemates. However, the occasions on which the tame female cat aggressed the domestic typically followed displacement of the tame individual cat by the wild pair. Thus, the relationship between the tame and domestic female was primarily revealed through redirected aggression.

These results are summarized from a variety of tests detailed in Benzon and Smith (1974).

Discussion

The results clearly demonstrated the presence of a linear social hierarchy among the three male cheetahs. It is equally clear that the recently captured (wild) animals were dominant over the "domesticated" animals and that the wild cheetahs often obtained their advantage by concerted action. While there was little evidence of a dominance hierarchy among the separated females, concerted threats and/or attacks by the wild cheetahs gave them a general advantage.

We have tentatively concluded that the dominance relationships among females are unlikely to be important in cheetah breeding. We arrived at this conclusion for two reasons: (1) in nature, the females are often isolated (during pregnancy and approximately 13-14 months after giving birth), and (2) if a social hierarchy exists, it is weak. However, the possibility exists that proximity of unrelated females is stressful and could inhibit reproduction (Eaton, pers. comm.).

On the other hand, the clarity of the male hierarchy suggests that it is functional. We assume the hierarchy affects reproduction in either of two ways: (1) it is stable in which case there is little competition between males; (2) an unstable hierarchy causes male competition, which may heighten courtship behavior and elicit receptive behavior in recently isolated, pre-estrous females.

Pre-estrus Identification and Attempted Breeding

Based on the results of the hierarchy experiment, we concluded that the following breeding technique should be tested: (1) isolate the females; (2) discern the male hierarchy and remove the dominant male; (3) when the female is suspected of entering pre-estrus, return the dominant male in order to elevate the frequency and intensity of male aggressive interactions; (4) approximately one day after return of the male, place the pre-estrousfemale in the group and permit access to a private area adjoining the cage; (5) after sexual behavior is observed to have ceased, return the female to her isolation area in order to reduce social stress during the pregnancy.

This technique was followed in the summers of 1973 and 1974. Since the work in 1973 represented a pilot program and will be reported in Benzon and Smith (1975), only the results of our most recent tests will be discussed below. However, two outcomes from the pilot study were important in determining the design of the present study: (1) female isolation was indeed found necessary and (2) a practical pre-estrus identification method was needed as we failed to accurately identify pre-estrus in 1973. The females were housed together and casual daily

observation revealed a subtle increase in mutual grooming and activity which correlated with subsequent mating behavior in another study (Eaton and Craig, 1973). On the basis of this observation, both were introduced to the males but only one turned out to be receptive. Thus, we concluded that our decision to introduce the females was fortuitous. The problem is one of maintaining females in both visual and olfactory isolation while simultaneously attempting to detect pre-estrus. Presumably this is accomplished via scent deposits in the wild (Eaton, 1970) and thus a reconstruction of the way in which the sexes locate each other provides a key to the identification problem.

In nature, most of the females lead a solitary life while providing cubs with adaptive skills (Eaton, 1970; Schaller, 1972). At the approach of a male group she moves away with her cubs (Eaton, 1970). Prior to the cubs reaching an age of relative independence, the female is again ready to begin the reproductive cycle. At this point, there are three alternatives to the method by which the sexes make social contact: (1) the males seek the female and initiate the reproductive behavior, (2) the female seeks the males and initiates the reproductive behavior, or (3) both processes are active.

The male initiation hypothesis assumes that upon crossing the spoor of a pre-estrus female, males are excited by the olfactory cues in her urine, track and locate her, and initiate the mating ritual. If this description is correct, then a simple method for determining pre-estrus in captivity would involve soaking a rag in the female's urine and introducing the rag to the male group. Presumably, when the female enters pre-estrus a change in her urine would occur. If the time when the males attend to the rag is monitored, we would then expect a sudden increase in attending time correlated with the onset of pre-estrus. In order to insure that the males can detect a change in olfactory cues, novel odors would be introduced periodically and the males' response monitored.

The female initiation hypothesis assumes that the female entering pre-estrus seeks males and initiates reproductive behavior. If this description is correct, we might expect a change in the females' behavior to occur during the onset of pre-estrus. To determine this, a careful observation of the females' behavioral profile might detect such a change. If both hypotheses are involved, positive results should be found during both urine testing and observation of female behavior.

A second issue which needs to be looked at is the importance of pre-estrus, i.e., is pre-estrus in a recently isolated female a necessary condition upon introduction to males in order to induce successful reproduction? This issue could be answered by simply using a control female who is introduced to the male

group before demonstrating any signs of pre-estrus. This issue and the two hypotheses will be considered in the following experiment.

Method

Subjects

The subjects were the same as those described in our first study (Benzon and Smith, 1974). Males were marked with ear tags, and the females, being easily identifiable, were simply referred to as female #1 and female #2.

Experimental Area

In May, 1974, the males were placed in a 8,100 sq. ft. enclosure affording a wide view of the Salt Lake Valley. This enclosure is diagrammed in Figure 2. As shown, the animals could be shifted to any one of three parts of the enclosure. Of special interest were the culverts indicated in the diagram. These were of two sizes, those contained in the smaller enclsoures were 8 ft. long and 2 ft. in diameter and those contained in the larger enclosure were approximately 4 ft. long and 4 ft. in diameter. All culverts were closed at one end and covered with dirt to form a semi-natural cave. The enclosed areas were barren with only a few bushes and two small trees in the large enclosure. The two smaller enclosures were covered with fine wire mesh some 15 ft. above the ground.

Urine Testing

Female #1's urine was tested every other day at the beginning of summer (1974) and female #2's urine was tested every other day towards the end of the summer. This was done since female #1's suspected pre-estrus occurred before that of female #2's. At various times throughout testing, a novel odor (lion or leopard urine) was presented to the males to determine if detection of odor change was possible (i.e., to determine if habituation to the rag had occurred). The females were kept separated from each other in order to obtain urine samples from specific animals.

A piece of white cotton cloth, 10" by 10" was soaked in the urine each testing day at approximately 7:00 A.M. The rag was then placed in the outside enclosure in a cleared area where the males would encounter it. Total amount of time spent with the rag, number of males attending, number of times the rag was picked up, rolled on, and aggressive displays between the males due to the

presence of the rag were monitored. The urine testing was started on June 20 and continued throughout the summer until October 19. Female #1 was tested every other day from June 20 to August 31. During the period of June 25 to August 31, female #2 was tested once a week; from August 31 to October 19, she was tested every other day.

Observational Procedure

Female Profile. Observations were taken on the females in order to better understand the behavioral changes that might occur during the onset of pre-estrus.

A behavioral sample was obtained from the females from June 18 to October 19. An interval method of observation consisting of 10 seconds of observation followed by 10 seconds of recording time was repeated for two 10 minute sessions. An audio timer was used to clue the observer when to record and when to observe. The two sessions were divided by a 10 minute break of no observing to help prevent observer boredom and to spread the behavioral sample out over a longer period. The behaviors recorded are defined as follows: activity was considered as the action of an animal moving from one point to another, i.e., the animal had to be in the process of walking or running other than pacing. Pacing was defined as the act of an animal moving in the same path along a fenceline in a rigid figure-eight pattern. Auto-grooming was noted when an animal groomed (licked) herself on any area of her body. Rub-roll was recorded when a female rolled on the ground, usually on its back, or rubbed its body (face, stomach, flank, etc.) on any object in the pen. Vocalization was noted whenever an animal made an audible sound such as a chirp, stutter-call, growl, etc. Tail flagging consisted of the female moving her tail in wide horizontal sweeps. Observations were taken on the females from station A as shown in Figure 1.

Female Introduction. Following the introduction of a female, observations were taken for approximately five minutes every half-hour and continuously during the three hours prior to darkness.

The observations were taken from any area around the outside run (Figure 2) that provided a good view of the animals. During these observations, special note was made of courting behaviors seen in the pilot study.

Results

Urine Test

Female #1. The total amount of time the males spent each day attending to the urine rag of female #1 is plotted in Figure 3. The males show habituation to the female's urine by July 6, spending approximately 20 seconds with the rag. Following habituation, the males never demonstrated a sudden increase in attending time, even during her suspected pre-estrus period. The lack of male response cannot be attributed to habituation since they were entirely capable of detecting changes in odor as shown by the sudden increase of attending time when novel odors were introduced on July 16, July 27, and August 31.

The males' ability to detect changes in odor appears to indicate that either the female did not enter pre-estrus during her urine testing period of June 20 to August 31, or that males do not detect pre-estrus through olfactory cues in the urine. As seen by the figure, after habituation the males spent approximately 100 seconds or five times longer with the novel odors than with female #1's urine. We can therefore conclude that males can detect changes in olfactory cues, but were unresponsive to the female's urine. This would appear to favor the female initiation hypothesis (i.e. females seek males during pre-estrus), unless pheromones are secreted from anal glands. Secondly, time of day that urine was collected could be a factor.

Female #2. The total amount of time the males spent with the rag of female #2 is plotted in Figure 4. As can be seen the males habituated by July 19 with a baseline response of approximately 20 seconds. Again, the males never demonstrated a sudden increase in attending time to the urine of the female throughout the testing period of June 25 to October 19. When the novel odor of leopard urine was introduced (September 29), the males did increase their attending time. Further, the males responded differentially to female #1 versus female #2 during habituation (e.g., compare July 1 for the females) indicating they could identify individuals. This provides further evidence for the female initiation hypothesis.

Female Profile Observation

Female #1. The results of the evening observations of female #1 demonstrated that definite behavioral changes occurred. The profile is plotted in Figure 3 and shows that until mid-July, activity, grooming, and vocalization had fairly low rates. However, beginning around July 20, all three behaviors began to increase in frequency. High rates of grooming, activity, and vocalization continued until approximately August 5, at which time, the rate of these

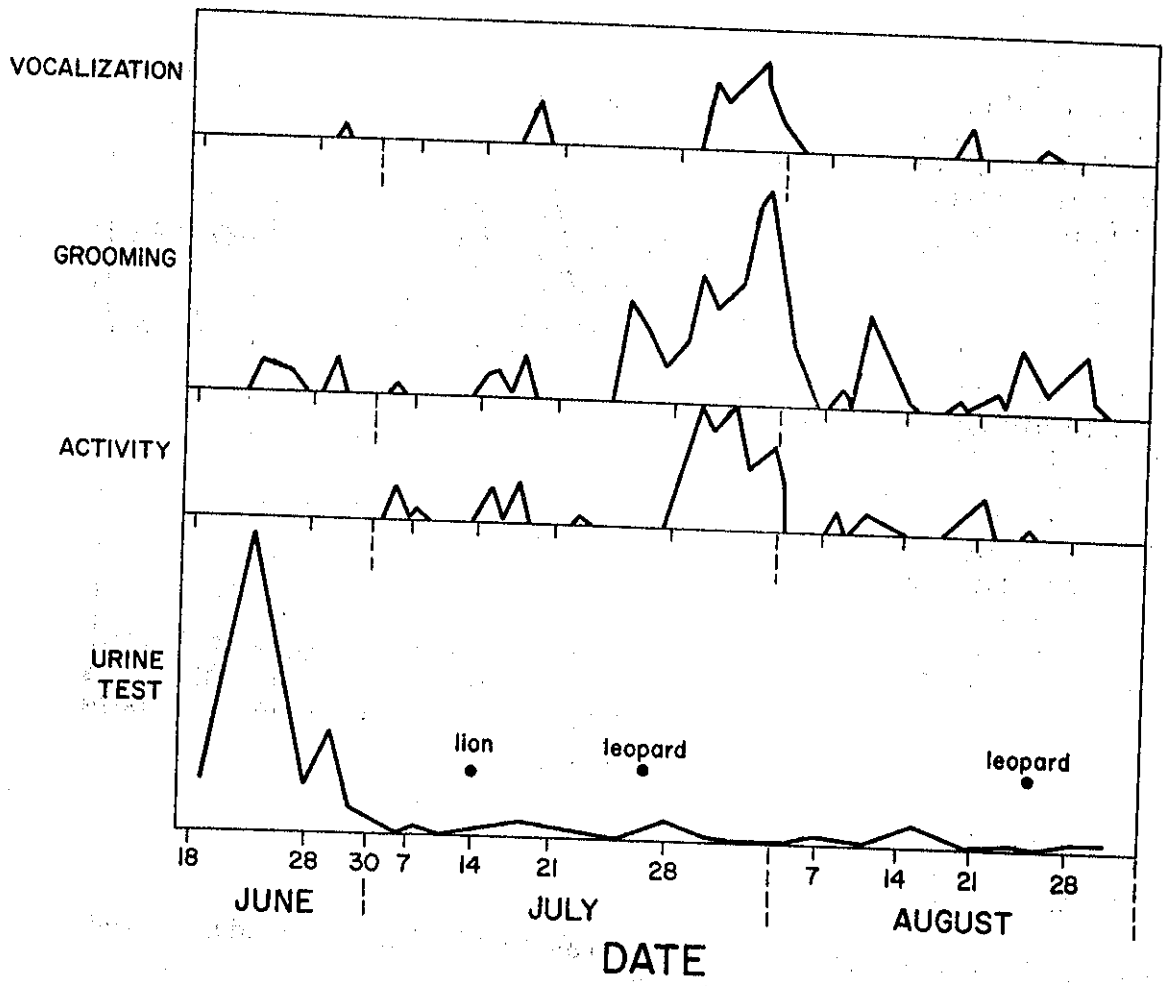

Figure 3. Profile and urine test for female #1. The novel odors tested (lion and leopard) are noted in positions shown.

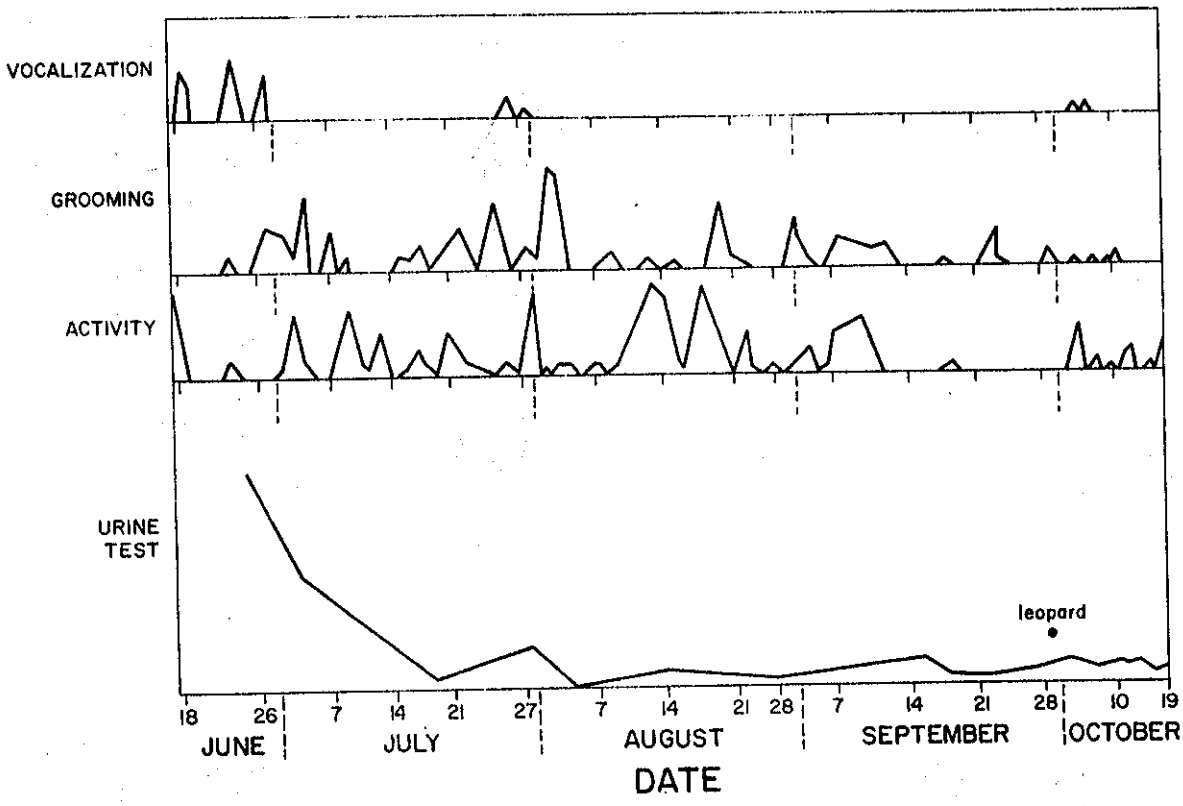

Figure 4. Profile and urine test for female #2. The novel odor tested (leopard) is noted in position shown.

behaviors decreased, although they were maintained at rates higher than those observed prior to July 20. The other behaviors (pacing, rub-roll and tail-flagging) were recorded at low rates throughout the profile and are not included in the figure.

It will be recalled that in the pilot study female #1 was introduced during the period of increased activity, mating occurred, and a birth resulted. It was thus assumed in that study that the female had entered pre-estrus. However, in this experiment, the female was not introduced to the males until one month after the peak in her behavioral profile. If the sudden increase in behaviors indicated that the female was in pre-estrus as suspected previously, then the males did not or could not detect it in her urine.

Female #2. As shown in Figure 4, female #2's behavior failed to demonstrate any systematic changes during the experiment. This female's profile did reveal fluctuations in activity, grooming, and vocalization, but unlike the correlated changes recorded for female #1, these changes appeared independently. Thus, for female #2, both the profile and the urine test failed to detect pre-estrus. Therefore, we must conclude that either: (1) the urine test and behavioral observations are a poor indicator of pre-estrus, or (2) female #2 failed to enter pre-estrus. Since the correlated changes in female #1's behavior were noted during observations, we can assume that if female #2's behavior had changed, it would have been detected (i.e., the observations are a good indicator). The data suggests, therefore, that female #2 did not enter pre-estrus during this experiment. This view is further supported by the following observations of behaviors elicited by the introduction of the females.

Female Introduction

As described previously, the cheetahs were separated according to sex at opposite ends of the feline building from October, 1973, until the summer of 1974. In May, 1974, the males were transferred from the feline building to the outside enclosure, and the females remained inside the building in individual display areas.

It was decided to introduce female #1 to the males on August 31. Though the males attending time to the rag was still very low, it was felt that the sudden increase of activity, grooming, and vocalization around July 31 indicated that the female had entered pre-estrus. It was also taken into account that in the pilot study the female had demonstrated a similar increase in behavior around July 31 and introduction during this time had resulted in mating and a birth.

Upon introduction at 9:30 A.M., the males immediately began surrounding female #1 and slowly pushed her into a corner. Whenever the female moved a few feet, the males sniffed the ground where she had been sitting. Every time the males approached the female, she would attempt to fight them off while vocalizing with high-pitched chirps as described for estrous females by Eaton and Craig (1973). The males kept the female in the corner of the pen and did not leave to eat when food was placed in the pen at 2:20 P.M. At 7:30 P.M., the female attempted to leave the corner. All three males attacked her, pulled her to the ground, and male #1 attempted mounting for 10-15 seconds. The female finally fought the males off and ran toward a culvert. The males caught her and again pulled her down and male #1 attempted mounting. She fought the males off, and ran into the culvert where she stayed for the next few days. The males oriented themselves around the female and maintained this "suitor siege" for three days. An example of this dramatic ritual is shown in Figure 5. The pattern was identical to one observed prior to mating in 1973.

During the evening of September 3, a fight between the males began and the courtship shifted into the "fighting circle" phase. This pattern was also observed in 1973 and involves a series of male-male fights with the female laying nearby. Eaton and Craig (1973) described this pattern as a "mating circle" and gave an excellent photographic example in their article. However, since we observed no mating during the ritual in either 1973 or 1974, we prefer the term "fighting circle". The circle seemed to break down on September 8 and the dominant male again attempted to mount. We concluded the ritual had ended and isolated the pair. For the next two days, they were constantly together though no mating was observed. On September 14, the other two males were allowed access to the female, and they displayed no interest toward her. The female was isolated on September 15, and transferred to the feline building on September 19 where she stayed isolated until giving birth. During the period of December 14 to December 16, the female aborted her litter. Number and development of the cubs could not be determined since immediately following the abortion, the litter was eaten.

Female #2. It will be recalled that female #2 was to be a control subject. She was to be isolated, then periodically introduced to the males to determine the necessity of the pre-estrus. She was introduced to the males on May 21 and October 1. The males' response to female #2 was drastically different from their response to female #1. The suitor siege and fighting circle never developed. In fact, after the first few minutes, the males ignored female #2 on both of her introductions.

Discussion

The major concern of this paper was to investigate the problem of captive

cheetah breeding. Our first study (Benzon and Smith, 1974) demonstrated the presence of a linear social hierarchy among the three males. The data suggest that the hierarchy is functional and we assumed it facilitated reproduction. Based on the results of that study, a possible breeding technique was developed.

A pilot study in 1973 involved a preliminary test of the technique. The results revealed two important factors: (1) premating isolation appeared to be necessary; and, (2) a more sophisticated pre-estrus identification technique was needed.

The final study invetigated pre-estrus identification methods and the necessity of pre-estrus prior to introduction to males. The male initiation hypothesis assumed that males detect a pre-estrus female through olfactory cues in her urine, and then locate her for mating. In order to investigate this hypothesis, the urine testing technique was developed. The female initiation hypothesis assumed that females enter a pre-estrus period and seek the males and are aroused by inter-male aggression which results in a true estrous period. In order to investigate this hypothesis, the behavioral profiles were recorded. Contrary to field observations, the results of this study suggested that the male initiation hypothesis was unlikely, and that a pre-estrous period occurred for female #1 at which time she became increasingly active. It seems plausible that the increased activity recorded in this confined female would translate into male searching behavior in an unconfined environment. It will be recalled that female #1 was introduced to the males one month after the change in her profile and a litter resulted from that introduction. Therefore, the behavioral changes demonstrated by the female were apparently indicative of pre-estrus since estrus only lasts about two weeks (Eaton, 1974). Furthermore, pre-estrus appears to be a necessary condition for successful mating. This is suggested by the treatment of the control female #2, who was introduced twice without evidence of pre-estrus, and in both cases the males ignored her.

The results of our work suggest three necessary conditions for cheetah breeding: (1) pre-mating isolation, (2) pre-estrus prior to the introduction, and (3) female observation of inter-male aggression. The third conclusion is based on the length and rigidity of the mating ritual; it would be strange indeed if such a ritual lacked function--in this case the function of inducing estrus. On the other hand, it must be the case that in those populations with few or no male groups, single males achieve mating success (Eaton, unpbl.). On the basis of these three conditions, the breeding technique outlined in our first study (Benzon and Smith, 1974) should be modified as follows: (1) isolate the females; (2) discern the male hierarchy; (3) when the female demonstrates she has entered pre-estrus, place her into the male group; (4) when the courtship behavior has

reached it's peak, isolate the female and dominant male from the other cats; and, (5) after mating has occurred, isolate the female in order to reduce social stress during pregnancy.

There still exists a behavior that appears to be involved in mating but was not investigated during these studies. Following the introduction of female #1, the males were observed to smell the ground where she had sat. This behavior has been reported by Eaton (1974) who believes that a female in estrus does provide olfactory signals where ever she sits or urinates. The results of our study indicate that the female was not providing such signals prior to her introduction to the male group, but within approximately 15 minutes with the males some olfactory cue was emitted from her anogenital area. The female had not urinated, so we might assume that she was leaving an anal pheromone other than a urinary one. An investigation to isolate the source of the pheromone could be helpful in simplyfying the identification of pre-estrus.

Figure 5. The "suitor seige." The female is lying at the culvert entrance and is completely surronded by the males. The seige was maintained for approximately 30 hours.

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