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Abstract: Isolation from social competition and associated stress may increase the chances of a successful pregnancy, as well as providing security for the cubs against male attack and resource competition. Social interaction among males may also serve an adaptive function, in that it usually results in a male dominance hierarchy. The results clearly demonstrated the presence of a linear social hierarchy among the male cheetahs. We assume that the hierarchy affects reproduction in two ways: by selecting the most fit male to father offspring and by ensuring male aggression, which serves to elicit receptive behavior in recently isolated, oestrous females.

Male dominance hierarchies and their possible effects upon breeding in cheetahs

Acinonyx jubatus

TED A. BENZON¹ & RICHARD F. SMITH²

¹Hogle Zoological Gardens, Salt Lake City, Utah 84110, USA and ²University of Utah

Few animals have shared a longer or more intimate association with man than the cheetah *Acinonyx jubatus*. But, unlike the dog which in this time has reproduced at an alarming rate, captive cheetahs have hardly bred at all (4). In view of the continuing decline in wild cheetah numbers, preservation of the species may depend upon its captive breeding.

Although little is known about the wild cheetah, two behavioural patterns clearly distinguish it from the captive animal: (1) during much of her life the ♀ is isolated from other adult members of the species, and (2) the ♂♂ move in hunting groups. The isolation period lasts from early pregnancy until the cubs are about 16 months old, when the ♀ again enters

oestrus, is approached by ♂♂ and the reproductive cycle begins once more (1; 4). In zoos, however, the sexes are generally housed together or within visual and olfactory contact. As with other species, the isolation of the ♀ and the formation of ♂ packs may serve adaptive functions. Isolation of the pregnant ♀ may ensure protection of the young in a variety of ways. For example, isolation from social competition and associated stress may increase the chances of a successful pregnancy, as well as providing security for the cubs against ♂ attack and resource competition. Finally, the isolation affords a close association between mother and offspring which allows the cubs to acquire the necessary hunting and social skills.

Social interaction among ♂♂ may also serve an adaptive function, in that it usually results in a ♂ dominance hierarchy. If mating takes place only with the dominant ♂, the offspring are provided the strongest genetic background available (5). While no observations of mate selection in the wild are available, Herdman (4) has recently noted that dominant ♂ selection of mates does occur among cheetahs in captivity.

Clearly, the ♀ can identify and become receptive to the dominant ♂ only if she is in a position to observe aggressive interaction within the ♂ hierarchy. That this may stimulate and direct reproductive behaviour has been known for some time in other species (e.g. 8), but whether such a mechanism is involved in the case of the cheetah is not yet proven. However, the view is supported by reports of captive breedings where reproductive behaviour has followed ♀ isolation and has been accompanied by aggressive interactions (2; 3; 4; 6; 9). Another factor believed to encourage sexual receptivity involves a view of the surrounding landscape (7; 2). We suspect that being able to look into the distance may enhance the ♀'s sense of solitude and as such is an important component of the pre-mating isolation condition.

In summary, we suggest that ♀ isolation (with a view), followed by exposure to ♂♂ engaged in aggressive interaction is necessary to elicit successful reproductive behaviour in captive cheetahs. Although isolation of the ♀ in most cases ought to pose little difficulty, the situation is rarely simulated under captive conditions. The purpose of the present study was to determine whether dominance hierarchies based upon aggressive interaction occur in the zoo environment. If they can be demonstrated, the solution to breeding captive cheetahs may be near.

EXPERIMENTAL CONDITIONS

The subjects of the study were seven cheetahs in the Hogle Zoo in Salt Lake City, Utah. Three of them were wild trapped as infants and raised in captivity by humans. They were docile and two, a ♂ and a ♀, will be referred to as 'domestic'. The third animal, a ♀, was often petted and played with by the keepers - she will be referred to as 'tame'. The other four cheetahs, two ♂♂ and two ♀♀, were trapped as young adults in 1971, and will be referred to as 'wild'.

Observations took place under two sets of conditions, which may be designated 'combined' and 'separate'. In the former, all seven cheetahs were housed in two adjoining and interconnected cages that permitted free interaction among all animals (Fig. 1). In the separate condition, the animals were caged according to sex. The ♂♂ were housed in one of the two cages shown in Fig. 1 while the ♀♀ were kept in an identical cage on the opposite side of the building. When two food pans were used, one was presented approximately ten seconds before the other.

In the combined condition the observer was stationed 2 m from the cage wall and in a position that gave the best view of both cage areas (Station A). From this position, only a small area, the passage between the cages, was invisible. Since, with only two exceptions, animals moved singly through the passage, the lack of visibility did not restrict observation of social interactions. In the separate condition, the observer was also stationed 2 m from either the ♂ or ♀ cage (Station B).

In both conditions the observer recorded social interactions with emphasis upon agonistic encounters, e.g. hissing, teeth baring, attack and displacement behaviour. Displacement was defined as the act of one animal forcing another to vacate a spot which the former subsequently occupied. In the combined condition no experimental manipulations of the environment were attempted; we merely recorded the frequency with which various interactions occurred. In the separate condition, two aspects of the environment were experimentally manipulated in order to investigate conflicts believed to reveal the dominance hierarchy: (1) the animals were moved from one cage to another through an open access door; they were either permitted to enter the new cage freely, or were forced to do so with a jet of water - in both cases their order of movement was recorded; (2) food was presented at feeding time, in either one or two pans; again, the order in which individuals approached and ate was recorded. The total amount of food provided, whether in one or two pans, was held constant throughout the observation.

Observation periods scheduled at various times of the day were 90 minutes long and occurred five times a week for eight consecutive weeks in October and November 1972.

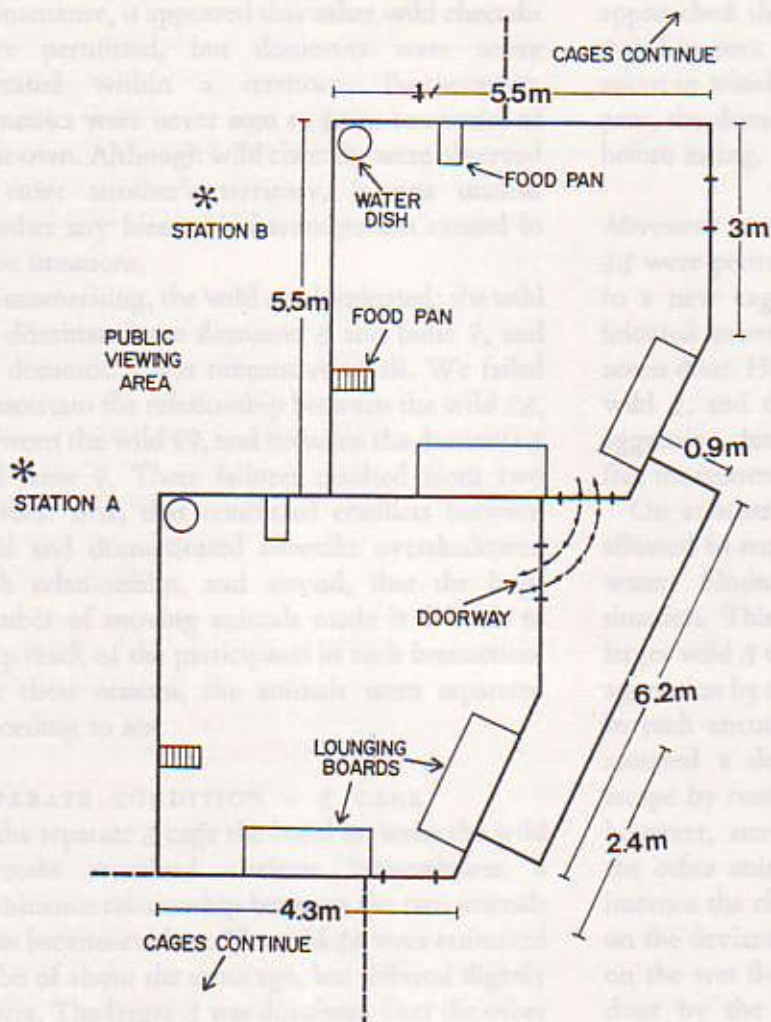


Fig. 1. - Interconnected cages provide free interaction (combined condition) among cheetahs observed experimentally at Hogle Zoo. When the sexes were separated, ♂♂ were housed in the upper cage, ♀♀ in an identical cage on the opposite side of the house (separate condition). Shaded food pans were used in the combined condition; unshaded pans show location of secondary pans used in the separate condition. Station A (combined) and B (separate) show positions of observers. Arrows indicate access route between cages.

COMBINED CONDITION

Agonistic encounters occurred frequently and most of these involved conflicts between wild and domestic individuals. In nearly all cases, the encounters were initiated by wild cheetahs and the domestics were displaced.

Food competition: During feeding periods, the wild cheetahs always took control of the first food pan offered, and the domestics were forced to eat from the second. If a domestic individual ventured near the first pan, it was aggressively displaced with concerted threats or attacks from the wild cheetahs.

¹ The domestic ♀ appeared physically weak throughout the study and was subsequently isolated from the colony for medical treatment.

General displacement: This resembled feeding interactions. At various times the wild ♂♂ displaced all other animals and the wild ♀♀ displaced all domestics. The relationship among the domestic cheetahs was unclear. However, several observations of re-directed aggression suggest that the domestic ♀¹ was least dominant. Both the domestic ♂ and the tame ♀ displaced her immediately after their own displacement by other individuals.

Territorial maintenance: The dominance of wild over domestic animals became most apparent in observations of territorial behaviour. The wild cheetahs frequently established private territories

in the corners of the cages, which were maintained for several hours to several days. During territorial maintenance, it appeared that other wild cheetahs were permitted, but domestics were never tolerated within a territory. Furthermore, domestics were never seen to form territories of their own. Although wild cheetahs were observed to enter another's territory, it was unclear whether any hierarchical arrangement existed in these situations.

Summarising, the wild ♂♂ dominated; the wild ♀♀ dominated the domestic ♂ and tame ♀, and the domestic ♀ was submissive to all. We failed to ascertain the relationship between the wild ♂♂, between the wild ♀♀, and between the domestic ♂ and tame ♀. These failures resulted from two sources: first, that concerted conflicts between wild and domesticated cheetahs overshadowed such relationships, and second, that the large number of moving animals made it difficult to keep track of the participants in each interaction. For these reasons, the animals were separated according to sex.

SEPARATE CONDITION - ♂ CAGE

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

Food dispersal tests: On ten occasions only one food pan was available at feeding time. The larger wild ♂ would arrive first and begin eating. Soon after his arrival, the smaller wild ♂ approached and was permitted to eat. Twice the domestic approached while the wild cheetahs were eating; in the first attempt he was displaced by vocal expressions (growling), and in the second, by physical attack. On the remaining eight occasions the domestic ♂ waited until the wild ♂♂ had finished and then approached the food pan without incident.

On ten other occasions two food pans were offered. In each case the larger wild ♂ selected a pan and began eating first. On seven occasions the smaller ♂ soon began eating from the pan chosen by the larger ♂; three times he chose the

alternative pan. On two of the seven occasions the smaller ♂ was displaced. In both instances he approached the pan occupied by the domestic ♂ and in turn displaced him. On the three occasions in which the wild cheetahs chose different pans, the domestic waited until one was vacated before eating.

Movement manipulation: On five occasions the ♂♂ were permitted to move freely from the old to a new cage. Each time, the larger wild ♂ initiated movement and was first to enter the access door. He was always followed by the other wild ♂, and the domestic was always last. No aggressive interactions were observed during free movement.

On another five occasions, the cheetahs were allowed to enter the new cage to escape a jet of water. Hosing reliably produced a conflict situation. This took the form of attacks by the larger wild ♂ on both cagemates, and re-directed aggression by the smaller on the domestic cheetah. In such encounters the domestic animal either assumed a defensive posture or attempted to escape by running around the cage. He did not, however, attempt to use the access door until the other animals had done so. In all but one instance the cheetahs escaped in the usual order; on the deviant occasion, the large wild ♂ slipped on the wet floor and was preceded through the door by the smaller ♂ and followed by the domestic, which waited until the large ♂ had exited before moving.

General displacement: More than 20 cases of displacement behaviour resulting from threat (posturing or growling) were observed in the ♂ cage. As usual, the large wild ♂ was seen to displace both cagemates, the small wild ♂ displaced the domestic and the latter was never observed to either initiate or win an encounter. Similarly, about 15 cases of displacement resulting from direct attack were observed. The outcome was identical to threat produced displacement.

SEPARATE CONDITION - ♀ CAGE

A less definite dominance hierarchy was observed among ♀♀. In general the two wild ♀♀ were dominant over the tame and domestic cheetahs. There was no evidence for a dominance relationship between the wild ♀♀, but the tame ♀

frequently attacked the domestic, as did her wild cagemates. However, the occasions on which the tame ♀ attacked the domestic typically followed the former's own displacement by the wild pair. Thus the relationship between the tame and domestic ♀♀ was primarily revealed through re-directed aggression.

Food dispersal tests: On the occasions on which one food pan was offered, the wild pair arrived first and the domestic pair followed slowly. The four ate simultaneously amidst considerable growling which failed to displace any participants. In the ten instances where two pans were offered the wild pair selected a pan and the domestics ate from the other.

Movement manipulation: On the five instances when the ♀♀ were permitted to move freely between cages, the wild pair typically preceded the domestics through the access door. However, this was not always the case. In general the wild pair remained close together and the domestic pair moved independently. The free movement produced no aggression, but conflict was induced when the animals were hosed. The aggressive encounters did not, however, result in a fixed order of movement. Aggression was mostly directed at one or both of the domestic ♀♀, often in the form of a concerted attack.

General displacement: With the exception of frequent displacement of the domestic ♀, our observations provided little evidence of a social hierarchy among the ♀♀. The wild ♀♀ were able to displace the tame animal by concerted threat or attack, but when dealing with a single wild ♀ the tame one was seen to win and lose encounters about equally. The domestic ♀ never won or instigated such interactions. In general, the frequency of displacement behaviour was lower in the ♀ cage than in the ♂ cage.

DISCUSSION

The results clearly demonstrate the presence of a linear social hierarchy among the three ♂ cheetahs. It is equally clear that the recently captured (wild) animals were dominant over the domesticated animals and that the wild cheetahs often attained their advantage by concerted action. While there was little evidence of a dominance hierarchy

among the separated ♀♀, concerted threats and/or attacks by the wild cheetahs gave them a general advantage.

We have tentatively concluded that the interactions observed among ♀♀ are unlikely to be relevant to breeding. In the wild the ♀♀ are often isolated (during pregnancy and for about 16 months after parturition); moreover, if a social hierarchy does exist, it appears to be weak.

On the other hand, the very distinctiveness of the ♂ hierarchy suggests that it is functional, especially since it is the wild ♂♂ which are dominant and primarily responsible for maintenance of the hierarchy. We assume that the hierarchy affects reproduction in two ways: first, by selecting the most fit ♂ to father offspring, and second, by ensuring ♂ aggression, which serves to elicit receptive behaviour in recently isolated, oestrous ♀♀.

As the isolation of ♀♀ is easily arranged, the conditions exist for testing the second assumption. We suggest the following method for making such a test.

A. Facilities

(1) Female isolation cages. The cages should isolate ♀♀ from visual and olfactory contact with adult ♂♂ and, if possible, afford the isolate a view of the landscape. Since the cages will be used for rearing the young, they should contain a den area and be as large and natural as possible.

(2) Male cage. The cage need not be large but a scattering of furniture (logs, small den areas, etc.) useful as territorial props may facilitate the development and maintenance of hierarchies. It should also have an access door to a second cage isolated from public view; this may be used by the breeding pair.

(3) Animals. A minimum of two ♂♂ and one ♀ is necessary. As the frequency of agonistic encounters decreases with the time since capture and increases with the number of ♂♂ present, several recently captured ♂♂ are preferable. We may assume that a selection of ♀♀ will also enhance the likelihood of successful pregnancies.

B. Procedure

(1) Isolate the ♀♀.

(2) Identify the ♂ hierarchy and remove the dominant animal.

(3) When a ♀ is observed to enter oestrus, return

the dominant ♂ to the ♂ cage. This is expected to heighten the frequency and intensity of ♂ interactions.

(4) About a day after the return of the ♂, place the oestrous ♀ in the ♂ cage and allow access to the adjoining isolation area.

(5) If pregnancy is determined, return the ♀ to her own isolation area.

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