Caro TM. Research plan for successful propagation of captive cheetahs.

Keywords: Acinonyx jubatus/breeding program/cheetah/management techniques/recommendation/reproduction/research plan

Abstract: Several new methods of facilitating breeding cheetahs in captivity are proposed based on extensive observation of their behavior in the wild. The underlying assumption is that mimicing the wild situation is a promising place to start if captive breeding programmes are to show consistent success in the future. After briefly describing cheetah reproduction in the wild, a series of recommendations are made that alter the environmental and social circumstances surrounding captive breeding. These new proposals cover the promotion of mating by both males and females, copulation, gestation, birth and cub rearing and will require alterations in management techniques, as well as behavioral observation of a core group of captive males and females. Attempts to understand the causes of past breeding successes and failures will also be made.

RESEARCH PLAN FOR SUCCESSFUL PROPOGATION OF CAPTIVE CHEETAHS: BEHAVIOURAL ASPECTS

Species Survival Plan (SSP) for the cheetah (Acinonyx jubatus)

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ABSTRACT

Several new methods of facilitating breeding cheetahs in captivity are proposed based on extensive observation of their behaviour in the wild. The underlying assumption is that mimicing the wild situation is a promising place to start if captive breeding programmes are to show consistent success in the future. After briefly describing cheetah reproduction in the wild, a series of recommendations are made that alter the environmental and social circumstances surrounding captive breeding. These new proposals cover the promotion of mating by both males and females, copulation, gestation, birth and cub rearing and will require alterations in management techniques, as well as behavioural observation of a core group of captive males and females. Attempts to understand the causes of past breeding successes and failures will also be made.

INTRODUCTION

Despite the fact that cheetahs have bred in captivity, the factors affecting their successful reproduction are still poorly understood. Though certain breeding programmes have been particularly successful in the number of livebirths and offspring reared to adult age [Marker 1983], at present there are few common themes we can see that link these sporadic breeding successes. In order to understand the nature and extent of environmental and social influences that promote successful reproduction in captivity, different approaches now have to be made. In this part of the SSP proposal, I suggest new avenues of research that may facilitate breeding in captivity. First, and most importantly, new methods of breeding cheetahs need to be instigated firmly based on new information of how free-living cheetahs reproduce successfully in the wild. Then a careful investigation will be made of all the circumstances under which captive breeding has worked well in the past in order to provide a comparison group with which to compare the new methods. In this way, we can experiment with new techniques mimicing behaviour in the wild, and simultaneously learn from previous breeding attempts in captivity.

BACKGROUND TO CHEETAH REPRODUCTION IN THE WILD

Females

Cheetahs reproduce in the wild yet details of the circumstances under which they do so are only just emerging. In the Serengeti National Park, Tanzania where research on this species is most extensive, female cheetahs live alone or with attendant cubs. Each female ranges over huge areas of the Park during the course of a year (c. 800 km2) following their main migratory prey species, Thomson's gazelles [Frame 1984; Durant et al in press]. Only very rarely are adult females ever encountered together (1 out of 390 sightings [Frame & Frame 1976a]), and never during lactation.

Females give birth approximately once every two years or in some cases more frequently. Females have a 3 month gestation period, giving birth in a den from which cubs emerge after 4-6 weeks [Schaller 1972]. Although litters emerge from the den in each month of the year, in Serengeti first sightings of cubs are most frequent in November at the onset of the short rains, and in March at the start of the long rains. Mothers' lactation peaks when cubs are 2 months old, and this period coincides with the appearance of large numbers of neonate Thomson's gazelles, especially in March.

Litters can consist of 6 cubs at time of emergence, but are usually much smaller than this (2 or 3 cubs). Age at weaning is somehat variable but time spent on the nipple has declined to negligible levels by 14 weeks of age. Cubs accompany their mothers until they are between 14 and 22 months old during which period they have most food provided for them by

their mother. Despite increasing participation in hunts during this period of post-weaning dependence, cubs are extremely poor hunters at independence [Eaton 1974].

Littermates stay together for between 4 and 8 months after they have left their mother, even if the litter is composed of different sexed offspring. Brothers subsequently remain together for life and do not split up. Females are thought to initiate separation from their brothers at first oestrus. However, I know of one suspected case of a littermate having fathered his sister's first litter.

Males

In contrast to females, some males live in permanent groups of two or three individuals for their whole lives while others live alone, in both Serengeti and other habitats [Frame 1984; Caro & Collins 1987a]. About 80% of these permanent coalitions are composed of brothers born in the same litter but a proportion are definitely made up of non-relatives [Caro & Collins 1986].

Male cheetahs employ two different sorts of behavioural strategies to gain access to females: resident cheetahs are those that obtain and hold a territory for a variable number of years, while non-residents range over huge areas (including through territories) apparently following the nomadic females. Coalitions of males are far more likely to become residents than are single males because of their competitive advantage in territorial disputes [Caro & Collins 1987a]. Indeed, competition over territories is severe with observed fatalities and high rates of injuries incurred by many individually known males. The adult sex ratio of the Serengeti and other populations is highly skewed in favour of females as a result of mortality in intrasexual combat between males [eg. McVittie 1979]. Non-resident males are in poor condition, suffer eosinophilia, and are both behaviourally and physiologically stressed compared to resident males, probably as a consequence of their lifestyle [Caro et at under review].

Male territories are small (c. 150 km2) compared to female home ranges. They do not abutt but have wide areas separating their boundaries where no residents are found. All territories contain a certain amount of cover in the form of trees, bushes or rocky outcrops and are centred on areas where disproportionate numbers of females collect during a portion of the year [Caro & Collins 1987b; Caro in prep]. The reason that females collect in these areas is probably related to a combination of large numbers of Thomson's gazelles collecting there, and sufficient cover from which to launch their concealed approach and which provides shade to rest during the heat of the day [Caro & Collins 1987b]. We are currently investigating whether territories also contain larger numbers of denning sites than areas

outside territories. In sum, our working hypothesis is that territorial males encounter more females than non-territorial males, especially in the months of peak conceptions.

At present we do not know whether females chose the territories of certain males in which to collect. Certainly a given female will meet with a number of males (both resident and non-resident) after she and her previous litter have parted company, so there is a potential for a female to chose which male will sire her next litter.

RESEARCH PLAN

General protocol

The number of cheetahs in American zoos is limited [Marker & O'Brien 1987], even if cheetahs are imported from Namibia in the near future. Only where specific physiological knowledge is to be obtained can intensive experimental techniques be justified. In such cases, long term benefits can potentially outweigh short term costs of possible reduced breeding opportunities of a limited number of individuals.

A vast array of environmental and social variables potentially affect reproductive performance, and the number of confounding variables precludes strict comparison of experimental animals (whose opportunities for reproduction are enhanced) with control animals (who are denied such opportunities) without very large sample sizes. Indeed, as cheetahs are an endangered species (CITES, Appendix 1) efforts need to be made to increase the reproductive performance of all captive animals; it would therefore be inappropriate to establish control groups that prejudiced an individual's chance of reproduction. Rather, new techniques need to be tried and compared to past breeding records where such methods were not employed, or to situations where logistics make it difficult to implement new policies.

For these reasons the methods proposed below are relevant to all cheetahs in North American zoos. Thus it will be necessary to be brought into the decision making processes concerning cheetah housing and reproduction programmes in all zoos willing to participate in the SSP for cheetahs.

In general, most of the manipulations put forward in other segments of the SSP proposal will not interfere with those proposed here and can be run simultaneously. Indeed, some behavioural observations require physiological measurements to be taken concurrently, the extent of which is under discussion. Some of the proposals for altering the context in which breeding occurs do require minimal disturbance however, especially during gestation and cub rearing, so that a core group of individuals (numbers to be negotiated) will need to be set aside for behavioural research.

Behaviour prior to mating: males

In the wild, males spend large portions of the day scanning their environment locating both prey and passing females. Territorial males spend about 12% of their daytime resting period above ground (on rocky outcrops) surveying their surroundings, while non-residents spend considerably more time hiding in vegetation at ground level. When a female is sighted, most males will quickly approach, but in almost every case I have witnessed the female attempts to escape by running off as soon as she sees the male. Males, whether singletons or in a coalition, outrun the female and will slap her hindquarters to the ground preventing further escape.

As soon as the female is halted, the male starts to sniff the surrounding vegetation and sometimes the female herself, although males appear fearful of approaching too close in case they get slapped by her. Every time she moves, he tries to sniff where she has sat but then quickly follows her in order to prevent further escape. Females usually emit high pitched yips in the presence of males, and occasionally growl at them. The length of time that a male and a female associate together appears highly variable: I have seen associations for as little as 5 minutes to those lasting over 36 hours. My impression is that the level of hunger of both individuals, but especially of the male, can account for some of this variability.

Among coalitions, one male is usually more assiduous in keeping in close contact with the female than is the other. Some mild aggression between coalition partners is shown in the presence of females, such as growling or slapping but I have never seen males biting or wounding each other.

Methods for improving the chances of males mating

The above considerations suggest a number of useful avenues in which aspects of the wild situation can be brought into the captive context.

Raised perches provided in male's enclosures

Territorial males, those that achieve most matings, spend much of their day scanning their surroundings from elevated promentories. Ability to see over large views on a day to day basis, may be important for these males. At best, this might be achieved by moving cheetah males to enclosures that are outdoors and contain high rocks and terraces (up to 20 metres in height). At worst, cheetahs could be housed in enclosures where they can see other species and watch human activity every day.

Enhance the possibility of males exhibiting territorial behaviour

Free-living non-territorial males show symptoms of ill-health compared to territorial males. They are also both behaviourally and physiologically

stressed as shown by lack of relaxed resting posture, elevated resting serum cortisol levels and acute adrenal response following electro-ejaculation [D. Wildt unpubl. data; Caro et al under review]. Although no differences in serum testosterone, LH concentrations or sperm characteristics were found in the two sorts of males [Wildt et al 1987], differences in stress could well be associated with differences in reproductive behaviour in the presence of a female. Moreover, if poor health is also a correlate of lack territorial behaviour in the captive situation, it would be highly beneficial if males were encouraged to be territorial in zoological settings.

Territorial behaviour in the wild is characterized by scent marking (particularly spray urinating, but also defaecation and perhaps clawing) prominent landmarks in restricted areas, and is most often exhibited by males living in coalitions. The proximate factors affecting this behaviour are unknown: for example it may be that having males living in adjacent pens would promote this behaviour. Alternatively, housing males in olfactory or visual contact with other males might inhibit scent marking for all the individuals concerned. Differential housing of males could distinguish these possibilities and the one that facilitates territorial behaviour should be employed. Males that scent mark should be those that are used preferentially for mating.

Allow males to cohabit with each other permanently

In the wild, coalition members are larger than are single males (probably as a result of preferential provisioning by their mothers when they are dependent on her for solid food [Caro under review]). As stated above, they are usually in better condition because they are more likely to become territory holders. It is my impression that coalition members are more behaviourally confident than males that live alone, perhaps because they can rely on support in social situations or because of their larger size. Confidence might contribute to enhanced reproductive performance in the presence of a female.

If, as suggested below, pairs or trios of males are given access to females so as to allow her the possibility of mate choice, it will be important to have let groups of males cohabit together for a considerable time so as to minimsze any aggression when they are introduced to a female.

Allow cohabiting males access to females simultaneously

When members of a coalition encounter and surround a female, observations suggest she then makes little choice in whom has closest proximity to her, at least out of the mating situation. However, the presence of a number of males may affect probability of ovulation. At present, it is not clear the extent to which cheetahs are spontaneous or induced ovulators [D.Wildt, this proposal] so the possibility remains that ovulation may subsequently be facilitated if many males are present and

competing over a female, irrespective of whether they all achieve intromission or whether the female is in oestrus at the time.

Behaviour prior to mating: females

Less is known about the reproductive behaviour of females in the wild than it is of males. In the field, observers of this species find it particularly difficult to agree on whether an individual is exhibiting oestrus behaviour because there is a great deal of individual behavioural variability amongst females. For example,I have only ever seen a free-living female spray urinate once (which may not indicate oestrus), although other observers report it [Frame & Frame 1981]. Moreover, individual mothers and dependent daughters (that are almost certainly not in oestrus) show extensive rolling, head rubbing and short bursts of playful running characteristic of oestrus behaviour.

We do know however, that there are peaks in conception in wild cheetah populations. Given that day length varies little in the tropics, and that birth peaks are not pronounced in captive populations in the northern hemisphere where daylength varies considerably, conceptions are likely to be linked to other factors. One possible factor contributing to a female coming into oestrus is change in the food supply although it is difficult to see how this occurs in Serengeti because the months in which peak mating must occur are June and July, dry season months, and October and November, respectively dry and wet season months. Moreover, female cheetah ranging patterns, which closely follow their migratory prey, buffers them against changes in food supply in this ecosystem. Nevertheless changes in food intake, the precise nature of which are not yet understood, may be important in stimulating the onset of oestrus.

As described, female cheetahs in all phases of their reproductive cycle are approached by males. This contact with males may in itself alter the chances of ovulation.

Methods for improving the chances of females mating

Determining oestrus through behavioural observation

It would be particularly helpful if oestrus could be recognised in all captive females rather than just those individuals where it is particularly obvious [see Seal et al 1987]. A number of females without cubs need to be observed carefully by a relatively experienced observer to document subtle behavioural changes that occur throughout the reproductive cycle. These changes can then be matched to physiological oestrus and ovulation based on hormonal measures taken as part of the SSP reproductive physiology programme If we can provide future observers with a suite of key behaviours to look for that indicate whether females are in oestrus, it will help considerably in promoting successful mating.

Change food supply to stimulate oestrus

Food quality and quantity are easy to both change and maintain. It is now recognised that feeding regimes are extremely important in maintaining health of captive populations [eg. Fitch & Fagan 1982], with whole carcasses of small animals being an important dietary element. Nevertheless, it is known that captive animals are fed greater amounts than females are estimated to eat in the wild. For example, at Whipsnade captive non-mothers were fed an average of 1.7 kgs per day, whereas free-living mothers (some of whom were lactating), whose energy requirements were presumably greater than non-mothers and who moved much greater distances each day, ate only an estimated 1.3 kgs per day [Caro et al 1987]. This feeding regime is almost certainly replicated in other zoos. The first suggestion then, is to reduce food intake to 80% for periods initially as long as a month to simulate the wild situation.

Second, changes in food supply need to be made because of the possibility that this stimulates oestrus. Two tactics are possible: either reducing food supply by say 10% for short (weekly) periods because the dry season peaks in conception suggest that oestrus may be correlated with a reduction in food intake. In another group of subjects, food intake should be increased by 10% for short periods because there is also evidence that better diet facilitates oestrus across a broad range of species [eg. Mitchell & Lincoln 1973].

Finally, the possibility that the stimulus of live food plays some role in stimulating oestrus should be reviewed provided that the costs, in terms of suffering to the prey (usually lagomorphs), are carefully weighed up against the possible benefits of increasing breeding opportunities. For this reason and because it is known that free-living cheetahs do scavenge [Caro 1982] and can be maintained in good condition in captivity eating dead food, such a practice should only be considered as a last resort

Alter housing conditions to separate females

Female cheetahs and most other cats live alone in the wild, show mutual avoidance when they see each other and may also avoid each other by olfactory means [Leyhausen 1979]. The reasons that females do live apart are still the subject of debate [Packer 1986; Caro in press] but the lengths to which female cheetahs go to stay apart in Serengeti suggests that it may be important that they are not housed next to each other in captivity. Females may well benefit then if they have no visual contact with other females, and if they cannot smell each other. Indeed Marker's data suggests that zoos which have only one female cheetah have average breeding records as good if not better than those with several.

Introduce males to females regardless of their reproductive condition
Males might periodically be allowed to enter females' enclosures. This procedure might facilitate the probability of successful mating in two ways. First, the presence of males might prime females to ovulate, as suggested above. Actually allowing the male to enter and contact the female, rather than be housed in an adjacent pen, is likely to be more effective in achieving any priming.

Second, prior familiarity with a mate may be important in a females' willingness to mate with a suitor. Clearly the issue of familiarity of mating partners is a controversial one, but it is amenable to empirical investigation. Altering the amount of time, and frequency, with which potential mating partners are allowed prior interaction is probably the only way to determine the importance of familiarity for successful mating. At first, three regimes each with two females each would be set up, from no exposure, a rather limited amount of exposure to much more extensive contact. In another parallel study, females would be exposed to two different males instead of one, in case choice of males further stimulates oestrus.

Mating behaviour

The above observations of free-living males and females associating together refer to situations in which mating did not occur. To my knowledge, the mating of cheetahs in East Africa has been seen only four times in the wild [Caro & Collins 1987a]. In these cases intromission lasted approximately 30 seconds only, but the opportunistic nature of the observations makes it unclear whether the males had been in association with females a long time prior to mating. However, the extended periods of time that some adult (and therefore experienced) males remain with a female suggests that some do eventually mate with males after a period of association. Nevertheless from one of the reports of mating in the wild, it is my impression that a free-living female will also quickly mate with males once she has been located by them if she is in oestrus.

In one report, a pair of males were seen to mate with a female. The coalition members competed over matings by pushing each other off the female and then thrusting for about 25 seconds. Interest in mounting seemed to overshadow any direct combat between the two males who normally showed amicable relations.

Methods for facilitating successful mating

Give potential mating partners every opportunity to stay together
To mimic the wild situation sudden introduction of a male to a female may be appropriate, if provision is made for partners to be separated if necessary. When seeking matings, zoos do allow cheetahs several days

together but the point needs reiterating. Minimum disturbance during this period of acquaintance is only likely to be beneficial; associating cheetahs that are not used to tourist vehicles will leave each other if approached closely. Furthermore, during association both males and females are often extremely thin, particularly the former. Associations disband when one member leaves to hunt. If food is provided during this period, it has the potential of disrupting mating if one partner leaves to eat; failure to eat during the mating period may be the normal state of affairs in this species.

Allow a group of two or three acquainted males to mate

Coalitions of males appear to gain access to most females, so it possible that females may actually prefer to mate with coalitions, either because of the increased social stimulation or vaginal stimulation during copulation that two or three males provide, or because it gives enables them to chose partners. The finding that males form coalitions in so many different habitats [Caro & Collins 1987a] implies that it is of real importance for successful reproduction. Thus the possibility of furthering matings in this way should be explored much more fully; indeed it has been tried successfully in South Africa on a regular basis. Routine blood sampling, proposed elsewhere, will allow us to determine whether members of the same litter can be sired by more than one male.

Allow females to chose their mating partner

Given that females may exercise some choice with whom they mate because they pass through many male territories during the course of a year, female mating performance may be enhanced if they are allowed to chose partners. Irrespective of introducing a group of males to mate with a female, females could be allowed to chose with which males they prefer to associate. To determine female preference, two males could be simultaneously placed in enclosures directly adjacent to a female and her behaviour recorded by an observer. If association preferences with one male are marked during anoestrus (measured in terms of proximity and affiliative interactions), then this male may be a far more promising candidate for subsequent mating efforts because he might heighten female receptivity or probability of conception.

Problems of familiarity and relatedness

In cheetahs, data suggest that sons move greater distances from their natal home ranges than do their daughters [Frame 1980] implying that reduction in the probability of breeding between close relatives is still important in this homozygous species (O'Brien et al 1983; 1985). Many species have sophisticated mechanisms that serve to reduce inbreeding and in mammals familiarity is often found to be important [Fletcher & Mitchener 1987]. In general, mating between mothers and sons, and between brothers and sisters who are familiar with each other is not so likely to be as successful as between unfamiliar animals. Some observations in the field suggest that close relatives can recognise each other years after they have parted, and

in cheetahs relatives are known resemble each other closely in coat pattern [Caro & Durant under review].

In addition, genetic considerations which normally advocate reduction of inbreeding as far as possible, suggest that mating between fathers and daughters, and first cousins, should be discouraged because of the consequent reduction in genetic variability. The importance of this is management plan is not diminished in this relatively monomorphic species because certain other genetic loci, not sampled in previous studies, are likely to be polymorphic [O'Brien et al 1987].

Gestation

In many rodents and other mammals, the presence of males, especially strange males, can cause females to abort [Huck 1984]. There is no evidence to support or refute this in cheetahs, but as male cheetahs contribute no further reproductive effort after copulation, the safest paradigm for captive breeding is to keep gestating females out of both visual and olfactory contact with males during their gestation.

During gestation, energetic demands on mothers increase progressively. These demands require compensation in terms of food intake especially during the last trimester. Data being collected at present suggests that females' diet changes dramatically during gestation; pregnant mothers turn to catching smaller prey (hares and newborn Thomson's gazelles) whose bones they can eat in entirely. (Cheetahs' relatively weak jaw musculature compared to other cats, prevents them from eating bones of even adult gazelles [see van Valkenburgh & Ruff 1987]). Increased calcium uptake is probably of central importance at this and later stages of reproduction.

Towards the final stages of pregnancy, free-living females search out suitable denning sites. Choice of den may depend on a number of factors related to safety from aerial predators which take cheetah cubs [Maugham 1914] and terrestial predators which are still common in cheetah habitats [Caro 1987]. Good views, warmth and quality of the substrate may also be involved. As we dont yet know the relative importance of these features, sensitive management should provide a number of alternative dens which a female can chose as her pregnancy nears an end, not just one which may only partially satisfy her needs.

Birth and cub rearing

Understanding of free-living cheetah mothers' behaviour at birth and during the first six weeks of cub life is rudimentary but is currently the subject of ongoing investigation [Laurenson in prep]. Preliminary data show that mothers give birth alone high up on rocky outcrops in caves or crevaces while others seek out thick stands of herbs (>1 metre tall).

Mothers have been seen to move dens [Frame & Frame 1981] in response to disturbance from tourists (one known case) and other predators (one known case) but the frequency and the reasons that they do this are still not clear.

Data now being collected shows that mothers change their feeding and ranging habitats dramatically between pregnancy and lactation. Mothers hunt up to 4 times more frequently after their cubs have been born and will travel up to 15 kms from the den to secure sufficient food. This evidence suggests that having cubs sequestered in a den puts a strain on mothers because they may not be able to encounter sufficient food nearby to support the demands of lactation. Cubs are probably brought out of the den as soon as possible so that mothers can move to new feeding grounds.

Once cubs emerge from the den they are vulnerable to predation from a variety of different carnivores, including male cheetahs [Burney 1980]; mothers are extremely vigilant at this time and will attack predators [Caro 1987]. At 14 weeks old cubs can outrun most predators and lose their natal coat.

During the period mothers are lactating more than half of the prey they catch consists of neonate gazelles and hares. This proportion of small prey declines progressively until mothers are capturing mostly adult gazelles when cubs are 8 months old. Either lactating mothers need to eat frequently, and hence concentrate on easy-to-catch neonates and hares, or they focus on small-sized prey because they can completely consume the carcass (except for skin) including the bones. Mothers catch slightly more food for larger litters than they do for smaller litters, though not appreciably; cubs with many siblings each receive somewhat less food. Mothers allow preferentially provision litters containing 2 or more sons compared to those containing only one son [Caro under review].

Cubs remain with their mothers for an extended period during which time they learn some hunting tecniques. However, by the time they leave their mother (varying between 14 and 22 months) they are still poor at hunting. After independence, adolescents subsist almost exclusively on hares and neonate gazelles (even rodents are caught) because they consistently fail to catch larger prey; they may suffer increased mortality at this time. Adolescents remain together as a sibling group for several months.

Methods for improving successful raising of cubs

No contact with other cheetahs during gestation and lactation

Female cheetahs never join up to rear offspring, as they do in lions [Schaller 1972], and being out of visual and olfactory contact with conspecifics may be of significance in the successful reproduction of this species. In particular, males commit infanticide in a variety of free-living species of cats [Packer & Pusey 1984] and probably do so in cheetahs, thus

the presence and also the odour of a male may be extremely stressful to a mother with small cubs. For these reasons females should be housed apart from other cheetahs.

Keep all forms of disturbance to an absolute minimum after birth

Mothers show extreme vigilance near their den and probably move dens if other predators are seen nearby [Frame & Frame 1976b]. Thus mothers may be more reluctant to continue to nurse properly, or may even abandon cubs, if their dens are entered by zoo staff. Though careful monitoring of newborn cubs may be necessary for treatment of disease, new technology such as video cameras, and specially constructed dens that allow temporary removal of cubs while the mother is away from the den need to be looked into. Disturbance should be minimised not only for the first month (until after cubs voluntarily explore outside their den) but also beyond this period because peak lactation is not reached until 6 weeks and even minor stresses to the mother may reduce her milk supply in ways not yet appreciated.

In a similar way, mothers' enclosures should be well away from those of other carnivores. In Serengeti, the sight of spotted hyaenas and lions even a kilometre away makes mothers with young cubs completely alter their behaviour: nursing stops, mothers sit up and remain vigilance for up to half an hour until the danger has passed. Simply hearing the roar of a lion also stops relaxed resting and evokes a considerable increase in vigilance.

Provide several dens so that mothers can move their cubs.

If disturbance is the main factor causing mothers to move cubs in the wild, then several should be provided in captivity. This will allow mothers who have heard or seen events unknown to zoo staff, to move their progeny to what they may perceive as a safer place. Given that mothers spend whole days away on hunting trips from even young cubs, the fear that some cubs will be moved but not others, or that different cubs may be nursed in different dens, may be more apparent than real.

Whole carcasses need to be provided for lactating mothers

The problem of nutrition for captive cheetahs is addressed elsewhere, but field observations show that total consumption of carcasses (especially small bones and brains) if an integral part of the feeding habits of all cheetahs, but particularly of lactating females. The pattern of hunting at this time suggests that several small whole carcasses eaten in fairly quick succession over the course of 6 hours, followed by up to a day with no food, may be the normal situation for mothers with young cubs; attempts might be made to mimic protocol. Total food provided should be stepped up to compensate for increased energetic demands during lactation.

Let cubs remain with their mothers for many months

Some of the reasons that free-living cubs remain with their mothers for so long are understood. Certainly young cubs cannot catch prey for themselves and could only develop if they have food provided for them. However, despite being able to practice hunting skills on live prey that mothers release in front of them, make ill-formed concealed approaches at prey, and play with each other, they are very incompetent hunters at independence. Thus mothers may allow their offspring to reach a threshold of predatory competence before separating from them, but cubs may also gain from being with their mother in other ways.

In many mammals, proficient mothering is crucially dependent on being raised with both mother and peers [Hinde 1974]. The social environment during development also affects the ability of males to mate appropriately [Simpson 1978]. In primates, access to peers does not compensate fully for separation from the mother, so that the most cautious approach to breeding programmes is to allow mothers and cubs to remain together for at least a year. Then, rather than separating daughters from their male siblings at the same time as separating them from their mothers, females should be allowed to stay with their brothers until first oestrus. Finally, sons should remain together for life, even if they are transferred between zoos. Coalition members are acutely affected by even temporary loss of their partner in the wild.

COMPARISON OF NEW METHODS TO PREVIOUS PROTOCOLS

As stated at the head of this section, strict experimentation is inappropriate for a small number of individuals of an endangered species: comparisons between new breeding techniques must be made with those already in existence and with situations where environmental and social circumstances cannot be altered for logistical reasons.

The circumstances surrounding past breeding successes and failures therefore needs close examination. All the variables listed in the main body of this proposal need to be recorded for every documented breeding attempt. Compared to the majority of captive species, we are in a strong position to make such a survey because the location and breeding records of cheetahs are well documented [Marker 1983; in press]. Some of the variables (eg. separation of females, multiple mating partners, familiarity of partners) can be examined through correspondence with zoo personel and gleaned from the literature. However, a number of the more subtle effects (eg. territorial behaviour, proximity to carnivores) require personal interviews with zoo staff to get a fuller understanding of the contexts surrounding successful breeding. Visits to Whipsnade and de Wildt breeding programme will therefore be an important priority for the behavioural section of the SSP for the cheetah.

In brief, the thrust of this part of the projects is (a) to determine the circumstances under which breeding successes have occurred; (b) pinpoint at which part of the reproductive cycle animals have failed to breed; (c) and then to decipher the circumstances which caused failure. In this way, we hope to be able to establish trends which lead to consistent success. Moreover, such a survey will allow us to group together past breeding attempts which employed a particular routine (eg. using single males for mating) with which to compare new methods advocated here (eg. using groups of males for mating). Although such comparisons may not always exclude confounding variables (eg, familiarity), they provide rough and ready comparison groups, without disadvantaging large numbers of potential breeders for experimental purposes.

Detailed analysis of past breeding records will also enable us to screen individual differences in breeding performance: rate of litter production, offspring number, and sex ratio of litters. These variables are of both considerable practical and theoretical interest.

BUDGET

The methods advocated in this part of the SSP proposal rely almost entirely on the ready cooperation and goodwill of zoo personel at every level. Aside from a number of changes in management techniques requiring varying sums of money depending on current practice, behavioural observation of animals is required in a number of situations. Primarily these focus on:

1. Observing the factors that promote territorial behaviour of males,
2. Preferences for males made by anoestrus females,
3. Nature of males' and females' behaviour with different degrees of familiarity,
4. Behaviour at mating, especially with groups of males,
5. Changes in females' behaviour just before and after birth,
6. Unavoidable effects of disturbance on lactating mothers,
7. Unavoidable proximity of predators near enclosures.

In addition, close examination of previous breeding successes and failures is required for comparison with the new regimes.

In my experience, and that of colleagues, providing a person with their own project is the strongest motivational incentive leading to hard work and carefully considered results and discussion. For this reason, a minimal salary for a university PhD student would be required. In addition, regular internal travel between zoological sites and the university base would be necessary. Equipment for behavioural projects is minimal, requiring pen and paper only. A single visit to UK and then on to southern Africa is also included.

Three year salary for student (including a year's writing up)	$ 36000
Internal travel (only estimated until site locations are known)	5000
Per diem allowance during observations (estimated $20/day)	6000
Stationery and accessories	500
Monitor & MacIntosh portable computer, image printer writer & data managing program	2800
Return airfares to UK and southern Africa	2500
Correspondence costs to zoos worldwide	500

ESTIMATED TOTAL REQUESTED: $ 53,300

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