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Cheetahs and Their Mating System

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The Cheetah as a Study Animal

The cheetah (*Acinonyx jubatus*) is a blatantly charismatic species that is highly endangered. What student would not jump at the opportunity to work on a species that should easily attract research funding and might even be prevented from declining further as a result of their research? After each spending ten years of our lives working on this species, we are in a strong position to identify the strengths and shortcomings of using the cheetah as a model system.

How did we get involved in cheetah behavioral ecology and later in cheetah conservation biology? In 1979, TMC was finishing his Ph.D. on the behavior of domestic cats (*Felis domesticus*) in Cambridge and wanted to place his understanding of behavioral development in cats in an ecological framework. He had visited eastern Africa before starting as an undergraduate and had been an assistant to researchers at the Serengeti Research Institute, where he had met Brian Bertram. After working with large mammals in Africa, TMC was keen to find a way to go back and Brian, now writing up his lion (*Panthera leo*) work at Cambridge, mentioned that there was no one continuing the cheetah study in Serengeti. It seemed a natural fit: here was an habituated population of a species related to domestic cats, a familiar ecosystem where observations were easy, and there was long-term demographic data on individually recognized animals. For MJK, a senior undergraduate in 1990; the chance to conduct an internship working on a high-profile species was too good to miss. She soon realized that she was looking at a twenty-five-year virtually unexplored demographic data set (Kelly et al. 1998). Early on in her graduate career she nearly switched to a different Ph.D. project related to jaguars (*Panthera onca*) in Central America. But after a rather unsuccessful first field season, she realized that she would probably never get the chance again to analyze twenty-five years of data on a large carnivore with known individual life histories. Despite not studying cats in the wild, the opportunity was too good to pass up, especially for a student interested in conservation topics such as population viability analyses (PVAs) and effective population size (N_e). So from undergraduate to research assistant to master's to Ph.D. student, MJK stayed with the cheetah demography. She has yet to see a cheetah in the wild, whereas TMC has seen more than enough.

What, then, are the conceptual issues that have held the attention of Ser-

engeti cheetah workers over the past twenty years? Initially, TMC was interested in the social and ecological factors that shape the course of behavioral development, particularly of predation (Caro 1994) and play (Caro 1995). However, as he learned more about his subjects in the field, especially about its strange social system compared to other mammals, he realized there were many other interesting questions that could be asked about cheetahs. These centered on the benefits and costs of sociality (Caro 1994) for families, adolescents, and especially males (see below), all of which live in small groups and in the end took up more of his attention than developmental questions. Later, in the second half of the 1980s, Clare FitzGibbon investigated the hunting behavior of cheetahs and the factors that promote hunting failure and success, focusing on many aspects of antipredator behavior in Thomson's gazelles (*Gazella thomsoni*), cheetahs' main prey on the Serengeti Plains (FitzGibbon 1989, 1990; FitzGibbon & Fanshawe 1988). Next, Karen Laurenson discovered that juvenile mortality in cheetahs is extremely high, principally because of lion predation (Laurenson 1994, 1995, 1996). Sarah Durant has extended these analyses to show that cheetahs avoid areas of high lion density (Durant 1998). In the 1990s, we switched attention to conservation issues, challenging prevailing dogma that cheetah populations are vulnerable as a result of genetic monomorphism (Caro & Laurenson 1994; Caro 2000). Now we are interested in the long-term viability of the Serengeti cheetah population (Kelly & Durant, in press) and the influence of demographic variables on its effective population size (Kelly, in press).

Throughout the years, cheetah researchers used a simple methodology (Caro 1994): driving to rises and hilltops in our 2,500 km² study area in the central Serengeti Plains; scanning for cheetahs using 10 × 50 binoculars; driving slowly to our subjects so as not to disturb them; and identifying them immediately from their pattern of spots or their black-and-white bands on the tail (Caro & Durant 1991), or else taking photographs for subsequent identification.

In essence we have used this study animal in the Serengeti to understand what seemed to us to be breaking issues in behavioral ecology and conservation biology at the time. Below we summarize one of the foci of our research, the cheetah's mating system, before reflecting on the successes and mistakes of working with this study animal.

The Mating System

The general conceptual problem in the behavioral ecology that we will address in this chapter is the complexity of mammalian mating systems (Clutton-Brock 1989; Davies 1991). While most mammals are polygynous, others are monogamous, promiscuous, polyandrous, or even lek breeders. The best way of starting to understand mammalian mating systems is to remember

that a male's reproductive success (RS) is limited by the number of females that he can inseminate because his potential rate of reproduction is faster than that of a female, whereas a female's RS is limited by her access to resources (Trivers 1972; Clutton-Brock & Parker 1992). Within this framework, the economics of female monopolization by males are influenced by four key factors: the extent to which female RS can be improved by male assistance, female group size, female range size, and seasonality of breeding (Clutton-Brock 1989). In most mammals males contribute little to parental care for reasons that are poorly understood (Clutton-Brock 1991). In Serengeti cheetahs, females live alone except when they have dependent cubs (Frame 1984), have enormous home ranges of over 800 km² that follow the annual movements of Thomson's gazelles (Durant et al. 1988; Caro 1994), and breed throughout the year (Laurenson et al. 1992). In the first respect, cheetah females are similar to antelopes such as Coke's hartebeest (*Alcelaphus buselaphus*) or Grant's gazelles (*Gazella granti*), where females live in small groups on ranges that are too large to be defended by males (Gosling 1986). In these ungulates, single males defend small mating territories that are visited by females in search of resources.

In cheetahs, however, some males live in small permanent coalitions of two or three animals whereas others live alone. Most of these coalitions are composed entirely of littermates, but approximately 30 percent included an unrelated male (Caro 1994). For cheetah males, there are some parallels with waterbuck (*Kobus defassa*) (Wirtz 1982), white rhinoceros (*Ceratotherium simum*) (Owen-Smith 1972, 1975; Rachlow et al. 1998), and oribi (*Ourebia ourebi*) (Arcese 1999; Arcese et al. 1995), species in which territorial males living on small territories tolerate satellite males that contribute to territorial defense. Cheetah male coalitions also resemble species in which groups of (usually related) males defend groups of females against other males as in chimpanzees (*Pan troglodytes*) (de Waal 1992) or horses (*Equus caballus*) (Berger 1986; Feh 1999) and perhaps bottlenose dolphins (*Tursiops* sp.) (Conner et al. 1999). The most closely related of these species is the lion, where females live in social groups (prides) and permanent groups of males, often composed of relatives, jointly defend the pride against other coalitions (Packer et al. 1988). Answering the question of whether the cheetah's mating system resembles the mating territory system of certain ungulates, or the multimale spatial defense system of lions, or neither, will help to broaden our understanding of how common ecological factors produce similar social systems in different species, and whether social organization is constrained by phylogeny. Thus we are using the strange mating system of our study animal as the starting point to answer a theoretical question. This is the way that many field-oriented behavioral ecologists work: they use the organism's behavior to generate new questions that they would never have thought of sitting in a library or in front of a computer screen.

MALE REPRODUCTIVE TACTICS

We found that adult male cheetahs exhibited two distinct behavioral tactics. Resident males held and urine-marked small territories whereas nonresident (floater) males roamed over large parts of the Serengeti study area and rarely urine-marked. Nonresidents were less relaxed than residents in that they sat up and lay alert more often; they exhibited signs of physiological stress, specifically elevated cortisol levels; and they were in poor condition as determined from higher white blood cell counts, higher eosinophil levels, lower muscle mass, and more sarcoptic mange (Caro et al. 1989). Resident male territories were 37 km² on average whereas nonresident ranges were huge, 777 km² on average. Territories were not occupied continuously by males throughout the study. All males started out as floaters. Whereas some remained nonresidents all their lives, others became territorial; yet others first encountered as a resident subsequently floated. Some of these findings started out as anecdotal observations, which led TMC to record quantitative information on these behaviors, supplement them with additional measures, and finally analyze the numbers statistically. Quantifying what appears to be biologically significant, be they morphological, behavioral, or physiological features, allows scientists to test their intuition objectively.

During the first five years of TMC's study, coalitions of males were more likely to obtain a territory than were singletons (9 percent of 35 singletons versus 60 percent of 25 coalitions). The most plausible explanation was coalitions' numerical advantage in fights. Fights over territories were an important source of mortality (Fig. 25.1) as males were more likely to die inside or on the immediate borders of territories than outside them and many males died on territories at the time they were occupied (called active territories) (Caro 1994). Coalitions were more likely to displace residents from a territory than singletons, the latter of which usually acquired territories obtained by taking over a vacancy (Table 25.1a).

Nevertheless, there was no statistical effect of coalition size on the length of time that residents held territories. This was surprising since single residents were more likely to be displaced by other males than were coalitions (Table 25.1b). In contrast, resident coalitions were rarely displaced, implying they vacated their territories voluntarily. Lack of association between tenure length and coalition size was probably due to reduced competition over territories in the second five years of the field study (see below). In addition, larger groups of males did not hold larger territories than smaller groups (Caro 1994). Thus the key benefit of being a coalition member was that it gave a male a greater chance of acquiring a territory. Data on fights was particularly difficult to obtain because fights were seen so rarely; instead TMC used territory takeovers and location of dead males to piece together the dynamics of intrasexual contests.

Other analyses showed that per capita foraging returns were greater for

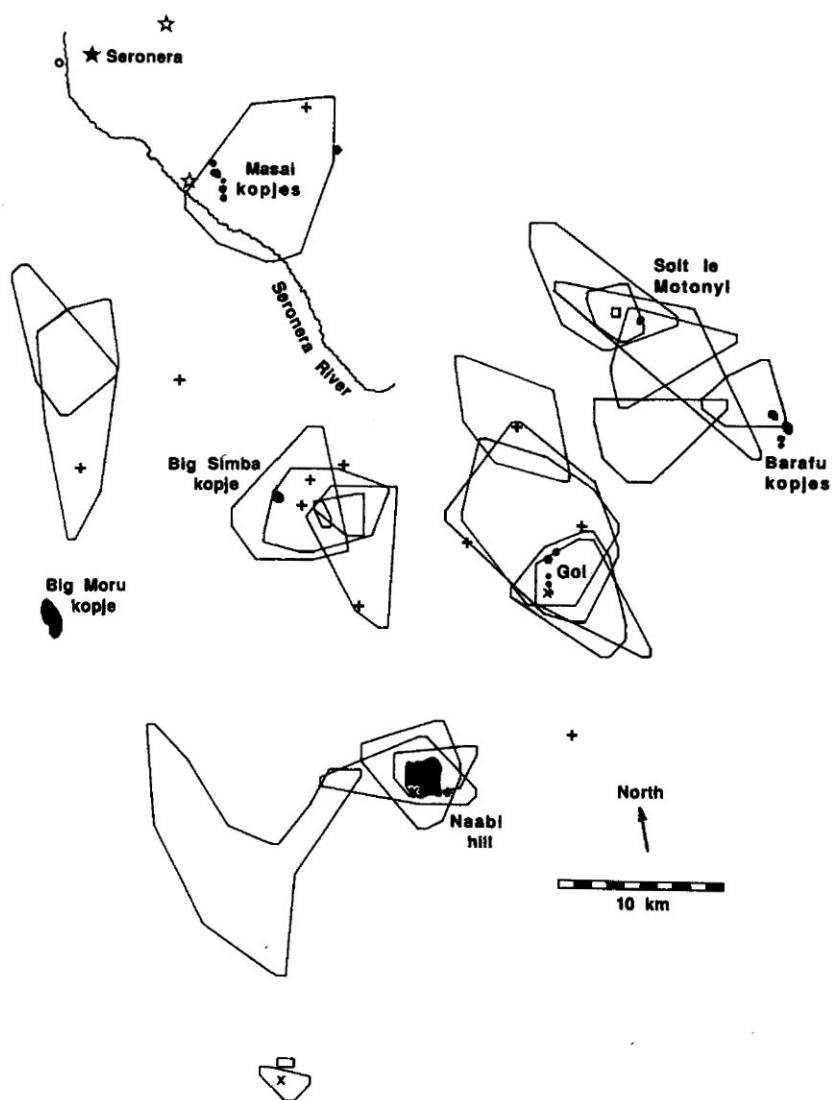


Figure 25.1. Location and extent of twenty-six territories on the Serengeti Plains, derived by the minimum polygon method for all males that were residents from March 1980 to July 1990. (The most southwesterly territory was not derived in this way.) Note that territories overlap as a result of sequential not simultaneous residence. Also shown are locations of dead cheetahs: radiocollared males (+, $N = 11$); males that were not radiocollared (solid diamonds, $N = 2$); females (open circles, $N = 1$); cheetahs of unknown sex located by chance (crosses, $N = 3$); and male cheetahs that died after being very ill (open stars, $N = 2$) (from Caro 1994).

Table 25.1

(a). Methods by Which Male Cheetahs Took Up Residence on a Territory. (b) Number of Instances of Termination of Residence by Males Under Different Circumstances

<i>Male group size:</i>	1	2	3
(a)			
Displaced residents	0	4	3
Took up a vacant territory	5	2	2
Retained even though companion(s) disappeared	2	1	0
Unknown	3	7	2
(b)			
Ousted from territory by other males	5 or 4	1	1
Territory left vacant because male or his coalition partner died	2	1	2
Territory left vacant because male or his coalition partner disappeared	0	2	0
Territory left vacant but reasons unknown	2 or 3	7	0
No longer held a territory but circumstances completely unknown	1	2	1

Note: Number of entries in (b) is four fewer than in (a) because three instances of coalition partners retaining the territory after loss of companions are omitted, and one territory was still occupied at the end of the study period. a: it was unknown whether one singleton vacated his territory or was displaced by another singleton male (from Caro 1994).

coalition members as a result of choosing to hunt larger prey items (rather than increased hunting success) but it was the competitive arena that had the key influence on survival, not food intake. Recent analyses have shown that male survival was strongly affected by the interaction of two variables: number and size of coalitions present in the study area (Durant et al., under review). Coalitions had higher survivorship than singletons when, and only when, there were many other coalitions on the Plains, pointing to the import of enhanced competitive abilities in promoting survivorship.

BENEFITS OF TERRITORIALITY

What were the advantages of territoriality? Since theory suggests that male distribution will depend on that of females and since TMC observed males rushing toward females and investigating their reproductive status at almost every opportunity, we examined the distribution of females in and outside territories, taking the area that TMC spent searching for cheetahs into account. Results showed that there were significantly more females sighted on active territories than were seen outside territories or on those that were not occupied. Moreover, TMC was more likely to see females pass by when he was conducting behavioral observations of territorial than of nonterritorial males. In addition, sightings of males guarding females were 4 times more common on active territories than elsewhere, devalued for areas searched

(Caro 1994). Thus territories held by males were female "hotspots." In this set of analyses, we were merely trying to determine whether empirical data on male and female ranging patterns conformed to theoretical expectations (e.g., from Trivers 1972) as to where males should distribute themselves in relation to females.

DO FEMALES CHOOSE MATING PARTNERS?

Did females take note of male presence on territories? For seven territories for which there were data, females were sighted significantly more often on territories when males were in residence than when they were not, but on three there was no difference, and on one females were encountered by TMC more often when residents were absent (Caro 1994). If females had visited territories to choose mates, they should have left vacant territories and searched elsewhere. Since they did not, we can be confident that cheetah territories were not leks despite their small dimensions (Hoglund & Alatalo 1995). Second, there was no relationship between the number of females on active territories and resident male coalition size. This shows that males were not settling on territories in a ideal free fashion (Fretwell 1972). If they had been, 3 times as many females should have been found on territories occupied by trios as those occupied by singletons. Here, we were again trying to match empirical data to theoretical expectations in order to determine what class of mating system we were dealing with.

REPRODUCTIVE PAYOFFS FOR COALITIONS

It was not possible to estimate the reproductive payoffs of coalition formation because matings were never observed by TMC in the wild despite collecting over five thousand hours of behavioral data. Matings that have been witnessed since are very rapid affairs lasting less than a minute. Moreover, in captivity, coalitions often mate sequentially, which would hinder estimates of per capita breeding success. DNA analyses would have been the best method (Packer et al. 1991) but in practice it was difficult to locate wide-ranging floaters over such a large study area, and many residents and non-residents were too shy to approach to within the 15 meters necessary to immobilize them using a blowpipe or dart rifle. Using a gun to obtain biopsy samples might have splintered a bone or injured a muscle. These difficulties were a major impediment to the study but abandoning the idea of large-scale blood or tissue sampling is the appropriate stance in relation to conservation ethics. Instead, we carried out rough calculations as follows.

The ratio of females inside and outside active territories was 0.0128 and 0.0078, respectively, when observer's searching was taken into account. The average number of sightings of floaters devalued by searching was 0.0026

inside and 0.0014 outside active territories, that is, a 0.65:0.35 ratio. Thus floaters had potential access to $(0.0128 \times 0.65) + (0.0078 \times 0.35) = 0.0111$ devalued females whereas resident males had access to $(0.0128 \times 1) = 0.0128$ devalued females per unit time. Resident males were estimated to live 1.78 times as long as floaters as determined from times of disappearance from the study area individually adjusted to incorporate each male's intersighting intervals (Caro 1994; Kelly et al. 1998). Lifetime encounter rates with devalued females had to be adjusted accordingly (residents $0.0128 \times 1.78 = 0.0228$, non-residents $0.0111 \times 1 = 0.0111$). These calculations assume that floaters inside active territories were as likely to encounter females as were residents, which seems reasonable as there was no significant difference in the percentage of sighting that the two sorts of males were seen with females once they were inside active territories.

To estimate fitness payoffs of living in groups of differing size, the proportion of singletons, pairs, and trios that were residents and nonresidents must be known. These were 8.8 percent and 91.2 percent, 70.6 percent and 29.4 percent, and 37.5 percent and 67.5 percent, respectively, during the period when data on female distribution was taken. Multiplying lifetime encounter rates for the two strategies for each male group size ($\times 100$) gives payoffs of $0.021 + 1.101 = 1.213$ for singleton males, $(1.610 + 0.326)/2 = 0.968$ for each member of a pair, and $(0.855 + 0.694)/3 = 0.516$ for each member of a trio. These calculations assume that reproductive payoffs were divided equally among coalition members and we have no direct evidence for this. In the absence of witnessing matings, the best we can say is that there was no obvious behavioral dominance in relation to initiating social activity or starting hunts, in sharing food, or in obtaining proximity to females (Caro 1993). Thus per capita estimated lifetime reproductive payoffs for males in each group size was 1.101:0.968:0.516 or 45.0 percent for singletons, 35.9 percent for males in pairs, and 19.1 percent for males in trios. The distribution of payoffs corresponds closely to the proportion of males in different sized groups. Of 110 males, 40.9 percent were singletons, 40.0 percent lived in pairs, and 19.1 percent lived in trios (Caro & Collins 1986). In short, these crude calculations suggest that males were behaving in an ideal free way by distributing themselves according to group size and territorial status in such a way that each encountered equivalent numbers of females. In essence, for single males, reduced reproductive benefits of floating were balanced by not having to share matings with coalition partners.

The problem with this data is that we do not believe it! First, ideal free models assume individuals are free to go to their area of choice but we know from direct observations and locations of dead males that intruding males were prevented from occupying a territory by the residents. Second, floaters were in poor condition and physiologically stressed compared to residents, suggesting they were disadvantaged (Caro et al. 1989). Third, it is likely that floating coalitions took up residence outside the study area because they

quickly passed through it; it was the floating singletons that remained in the study area. If coalitions settled outside the study area, it means our calculations of their reproductive returns are an underestimate of unknown magnitude. Fourth, the calculations are extremely crude, simply a product of mean values that can produce great error. Currently, then, the reproductive payoffs of coalition formation are not known with accuracy. This rather censorious self-analysis reflects our belief that it is important to be critical of one's own results even to the point of refuting them in later publications. Scientists are not judged by sticking doggedly to a point, be it right or wrong, but whether their observations stand up to scrutiny.

COMPARATIVE DATA ON MATING SYSTEMS

Given data on territoriality and group size, how do cheetahs fit in with other mammals? Parallels with ungulates are few. First, there was no behavioral dominance in cheetahs but this was characteristic of relations between waterbuck males and oribi males. Second, male associations lasted many years in cheetahs but for much shorter periods than in ungulates, for example, less than 2 years in oribi (Arcese 1999). Third, territory acquisition was different: in only 3 of 18 (17 percent) instances did a cheetah coalition partner inherit his territory after his partner disappeared whereas this occurred in 42 percent of instances in waterbuck. Fourth, only 2 out of 17 (12 percent) new occupations of adjacent territories were by cheetah males that had previously held a territory in the study area. This contrasts with satellite male waterbuck, white rhinoceros, and oribi acquiring adjacent territories in 17 percent, 27 percent, and 43 percent of cases, respectively. Thus the benefits experienced by supernumerary male ungulates did not apply well to cheetahs.

In regard to primates, male coalitions appear far less egalitarian than in cheetahs. In species in which males form coalitions that repel extra-group males such as gelada baboons (*Theropithecus gelada*) (Dunbar 1984) or expel a breeding male from a single-male group as in gray langurs (*Presbytis entellus*) (Hrdy 1977), only one of the two males eventually obtains access to females. In savannah baboons (*Papio anubis*), where males cooperate directly for females, it is unclear whether reproductive benefits are shared evenly between coalition partners (Bercovitch 1988; Noe 1990). In addition, alliances between primates are commonly short-lived, terminating when a rank reversal or takeover has occurred. Turning to lions, larger coalitions are better able to obtain a territory and hence access to females. Moreover, behavioral dominance between males is absent in this species. The main difference between lions and cheetahs, however, is that larger coalitions of male lions enjoy greater per capita RS on average whereas larger coalitions of cheetahs do not encounter greater numbers of females on territories. Thus the cheetah seems to emerge as a species with no direct parallel mating

system among mammals, being different from ungulates in the way males obtain reproductive benefits, from primates in regards to male relationships, and from lions in the way females are distributed.

MALE SOCIALITY

If localized or high densities of females are responsible for group-living in both cheetahs and lions, then females should be widely dispersed or live at low densities in all the other felids where males are solitary. When MJK collated ranging data on the felids, we were able to separate species into those in which densities were higher than the median, and species in which female ranges overlapped each other. We found that males usually lived in groups in these species where both these factors pertained but that they lived alone in species in which these two factors were not congruent (Table 25.2). In conclusion, high female densities and extensive home range overlap together apparently drive male sociality in felids.

FEMALE ASOCIALITY

The reasons that female cheetahs and all other felids except lionesses live alone is poorly understood. Packer (1986) proposed that in those species that usually capture large prey and that live in open habitats, and where female density is high, females will be social. This is because large carcasses will last for some time and would be seen and stolen by conspecifics especially if they were numerous. It therefore benefits a female to live with relatives and

Table 25.2
Species of Felids Separated According to Whether Densities Were Higher Than the Median and Female Ranges Overlapped (from Caro 1994)

	<i>Densities higher than median and female ranges overlap</i>	<i>Densities lower than median and/or female ranges are exclusive</i>
Males may live in groups	Cheetah Lion	
Males live alone	Serval	Bobcat Cougar European lynx Leopard North American lynx Ocelot Snow leopard Tiger

share food with them rather than inevitably relinquish it to nonrelatives. Packer argued that these conditions pertain only to lions. Cooperative defense against infanticidal males in lions is not sufficient reason for female sociality because other male felids commit infanticide (Caro 1994). An alternative hypothesis is that females of most species cannot afford to share prey because prey items 1 to 2 times the weight of an adult female are unavailable in most ecosystems (Caro 1989). This argument pertains to seventeen out of twenty-one field sites where felids have been studied. Only for lions are large prey sufficiently numerous to support groups of females living together. While the hypotheses differ, and the reasons for felids being asocial are not yet resolved, both hypotheses stress foraging costs as preventing the formation of groups. A subsequent, more formal model of female felid sociality (Macdonald et al., in press) suggests that relative prey size, felid population density, day range, prey capture rate, maximum prey consumption rate per day, and rate of searching for prey all need to be incorporated in order to predict when daily per capita food intake requirements can be met by females living in groups.

Always it is important to compare one's own observations to those of related species since they provide an additional test of whether conclusions are robust. If a behavioral ecologist's findings stand in marked contrast to those of others, they need to be reexamined. An additional benefit of the comparative approach at a small scale (e.g., within felids) or at a large scale (e.g., across mammals) is that it may throw out generalizations that the researcher would not have considered otherwise.

Strengths of the Study

Our cheetah study has three main strengths. First, the detailed behavioral work on male territoriality spanned eleven years, which allowed us to examine changes in patterns of residency over time. For example, between 1980 and 1985, very few singleton males became resident on the Plains, but from 1986 on single males began to acquire territories at an increasing rate (Fig. 25.2). The most convincing hypothesis for this change was reduced competition over territories: sightings of floating coalitions declined from the first to the second half of the study from 23 percent. This may have been related to increasing lion and spotted hyena (*Crocuta crocuta*) numbers, the main cause of mortality for cheetah cubs (Laurenson 1994). Relaxed competition would allow more singletons to hold territories.

Second, inheriting a long-term demographic data set allowed us to determine demographic parameters such as lifetime reproductive success (LRS) and annual rates and relate these to changing environmental variables. For example, we could show that average litter size at independence was 2.5 between 1969 and 1979 when lion abundance was low on the Plains but

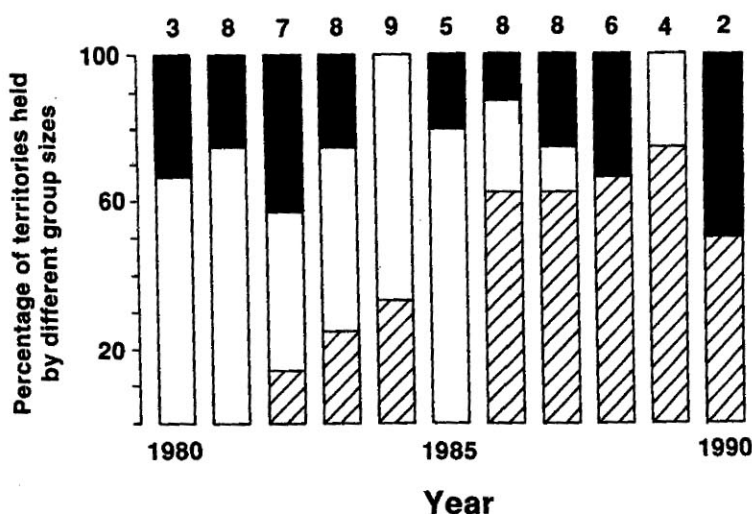


Figure 25.2. Percentage of territories held by resident singletons (hatched), pairs (open), and trios (solid) each year of the study. Number of territories held each year is shown above the bars (from Caro 1994).

averaged 2.0 between 1980 and 1994 when lion abundance increased by 60 percent (Kelly et al. 1998). In contrast, other environmental factors such as changing rainfall or prey abundance did not seem to be responsible for these changes.

Third, the fact that we are working on an endangered species has allowed us to address questions of conservation significance (Caro 1998). For example, we can use observations of behavior in the wild to inform captive breeding plans in zoos. As an illustration, Laurenson (1993) documented the type of lairs that cheetah mothers favor for giving birth in Serengeti and the rapidity with which litters are moved between them, allowing zoo breeders to mimic these situations in captivity. Also, we used demographic data to construct a PVA. (Kelly and Durant first built a deterministic model of the population and found that, in spite of increasing lion density, on average, the cheetah population is nearly self-replicating, i.e., $\lambda = 0.997$.) Nevertheless, we also know that lion density and presumably lion predation has increased over a twenty-year period. Although we would expect cheetahs to be able to withstand predation as they have evolved with sympatric larger predators, and their litter sizes and rapid reproduction are thought to be adaptations to intense predation (Caro 1994), it is surprising that $\lambda \approx 1.0$ given the marked recent increase in lion numbers (Hanby et al. 1995). Either lion densities are returning to "normal" as their main prey, wildebeest (*Connochaetes taurinus*), recover from rinderpest (Sinclair 1995), or cheetahs may move between areas of differing lion densities. For example, the Maswa Game Re-

serve to the southwest of Serengeti National Park, where lions are hunted (Caro et al. 1998), could provide a refuge for cheetahs. Alternatively, if lion densities are higher than "normal" because they are being forced into protected areas, as some have argued, λ values may be more optimistic now than in the future.

Populations with a $\lambda = 1.0$ are still subject to extinction due to stochasticity (Shaffer 1990; Burgman et al. 1993; McCarthy et al. 1995). Hence Kelly and Durant constructed a stochastic model of the cheetah population and used our long-term records to compare actual cheetah population size to the model's predictions under demographic and environmental stochasticity. They then conducted a sensitivity analysis of extinction risk. They found extinction risk to be sensitive to adult survival, but juvenile survival, especially of 0 to one-year-olds and not one- to two-year-olds, also had a strong effect on extinction risk. Since adult cheetahs are well protected within Serengeti National Park, it is unlikely that adult survival could be enhanced. Juvenile survival, on the other hand, is likely to fluctuate with amount of predation. In fact, by combining the cheetah and lion long-term data sets, we determined the influence of different lion numbers on cheetah recruitment through a generalized linear model (Durant et al., under review). Then Kelly and Durant (in press) simulated different levels of lion abundance and found that maximum lion abundance (120 lionesses) and average lion abundance (98 lionesses) resulted in the extinction of nearly all cheetah populations in 50 years, but that cheetah populations remain extant when lioness numbers were low (72 lionesses) (Fig. 25.3). Parameterizing vital rates in areas of different lion abundance and quantifying immigration to and from such areas would add greatly to population modeling effort by including the spatial heterogeneity that likely contributes to the coexistence of these predators (Durant 1998).

Weaknesses of the Study

Over the course of the project, we have made a number of mistakes and it is important for researchers to make these explicit so that they can be rectified or avoided in future. One of these was failing to recognize cheetahs in the field. At the time, there were good reasons to do this: pictures took up to four months to be incorporated into the photographic reference index because of processing time, sifting through photographs could take an hour or more, and time was limited to only four hours of searching in the mornings before cheetahs went to sleep under bushes. Nonetheless we were left with a backlog of ten thousand pictures at the end of the project! We solved this problem by using a matching program (Hiby & Lovell 1990). This involved capturing black-and-white photographs of cheetahs using video stills fed into a desktop computer. Digital images were then processed to extract a sample

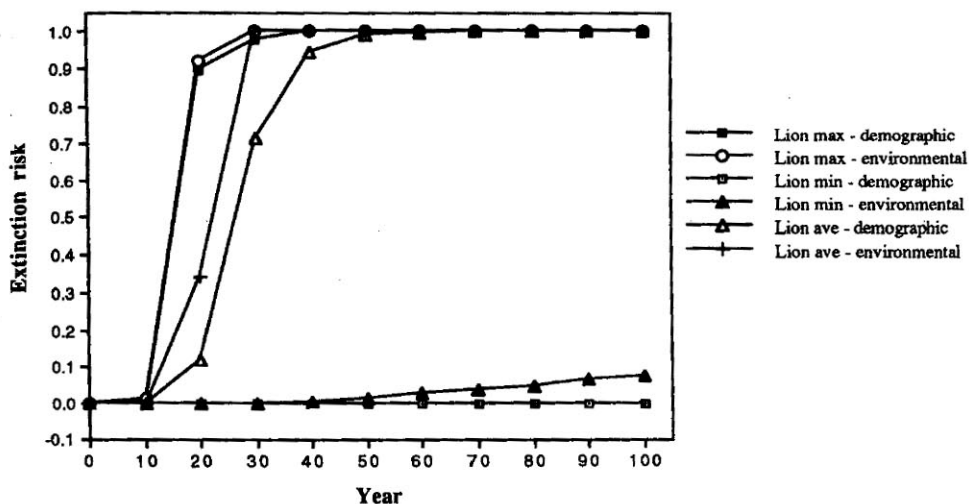


Figure 25.3. Projected extinction risk out of a hundred simulations under both demographic and environmental stochasticity for cheetah populations subject to different lion densities. Lion minimum was 72 adult lionesses, corresponding to the minimum recorded over 20 years in the study area, while lion maximum was 120 female lions, corresponding to the maximum density recorded. Average lion density was 98 lionesses.

of the coat pattern to act as a “fingerprint.” The computer program compensated for differences in lighting by removing gray-level patterns. Fingerprints were stored as a matrix of numbers termed an identifier array. To determine whether two sightings are of the same or different cheetahs, the computer compared four different areas of the animal’s pelage, calculated a correlation coefficient between array elements, and then generated a weighted average. All potential matches greater than 0.370 were inspected by eye to determine a true match. MJK found that the percentage of positive matches as determined by eye increased with increasing correlation coefficients (Fig. 25.4). With a coefficient of 0.500 or higher, the computer program was almost 100 percent accurate in matching different sightings of the same cheetah.

The advantage of using this technique is that it is noninvasive, accurate, can be used for any species with pelage patterns remaining constant through life, and is suitable for a laptop computer in the field. Moreover, it can be used to explore quantitatively the extent to which relatives have similar morphological phenotypes: we found an increasing proportion of mother-offspring and sibling pairs as correlation coefficients of match probability increased from 0.370 to 0.499 (see Fig. 25.4). With hindsight, we found a way to work around our mistake by developing a new methodology. There is an important lesson here. Faced with an obstacle that occurs sooner or later

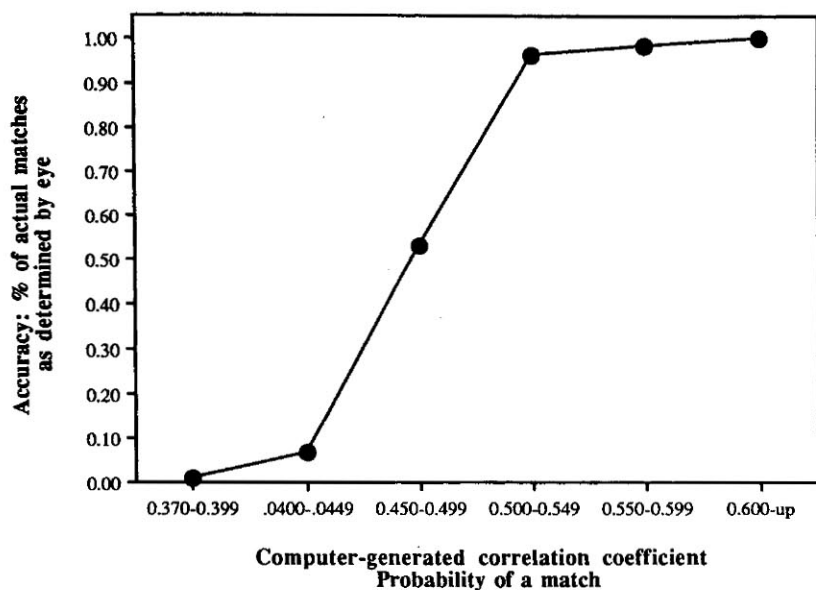


Figure 25.4. Accuracy of computer-generated correlation coefficients between two cheetah photographs in determining whether two photographs of cheetahs are the same animal. Accuracy was determined by examining a subset of a thousand potential matches with correlation coefficients ranging from 0.370 to 0.600 and above, and then inspecting these by eye to determine a true match. The proportion of true matches in each correlation coefficient category is plotted on the y-axis.

with most data sets, researchers need to use it as a springboard to generate new approaches or analyses to overcome the problem rather than allow it to demoralize them or cause them to abandon a piece of research.

A second difficulty that we encountered were inconsistencies among observers' records over the twenty-five-year history of the project (Kelly et al. 1998). While observers uniformly paid attention to taking rigorous demographic notes at each sighting (such as number and sex of cheetahs, and date and location), they differed in the amount of environmental information that they collected, such as presence of prey and predators. In addition, some observers would rigorously go through cleaning up question marks in their sightings notebooks at the end of the day but others forget to do this, making interpretation difficult for MJK years later. Finally, our differing foci of research interests, an undoubted strength of our project, resulted in researchers devoting different amounts of effort to searching different parts of the study area. This meant that we missed reproductive events for several females because females had temporarily quit the core of the study area. This greatly reduced the numbers of females for which we could calculate LRS. This parameter is difficult to determine in long-lived species and we regret the

number of missed opportunities due to observer absence during six months to a year of a particular female's life. Additionally, LRS has important conservation ramifications for effective population size (Kelly, in press). In short, consistency is absolutely critical in long-term data sets.

One advantage of inheriting such a data set is that population size trends and LRS can only be examined with long-term data and such a data set could not have been obtained for long-lived species during the course of a single Ph.D. dissertation. On the other hand, incomplete or inconsistent data collection over time makes analyses difficult and, at times, frustrating.

The Future

The most important aspect of the cheetah's mating system is that female movements, themselves dependent on migratory Thomson's gazelle prey, result in temporary aggregations of females on the Serengeti Plains. Males compete intensely over areas where these aggregations occur and increase their competitive ability by being in a coalition. A key question is whether we will observe male coalitions in other ecological circumstances where females are more evenly dispersed or live at lower densities. In short, we need a new study of cheetahs in a different part of Africa where prey densities are lower and less aggregated. If males do form coalitions under these circumstances, it will point to other factors, including perhaps phylogenetic constraints, that drive sociality in male felids. Currently we do know that males live in coalitions in other regions (Nairobi National Park, McLaughlin 1970; Kruger National Park, Bowland 1993) but we do not know whether females form temporary aggregations in these areas. Although there is currently no fieldwork being done on this topic, MJK is using the long-term data set to examine philopatry, or the extent to which related individuals overlap in space and time.

A second important issue that needs to be addressed is paternity: how reproductive success is shared among males in general, and between coalition members in particular (Packer et al. 1991; Feh 1999). While DNA paternity exclusion studies are constrained by difficulties in collecting blood and tissue samples of many cubs and putative fathers, we believe that it might be possible to collect DNA from hair in scats deposited by cheetahs (Hughes 1998). The chief difficulty is that whereas resident males defecate frequently (Caro et al. 1989), nonresidents, cubs and, to some extent, mothers do not do so, forcing prolonged follows of these individuals in the field. This is also an open field of study as no work is currently being carried out to determine paternity of cheetahs in the wild.

Our other avenues of research on cheetahs have raised a number of issues too. Laurenson's discovery that lions are the chief source of mortality of cheetah cubs suggests that in protected areas where adult survival is high, it

will be necessary to monitor the relationship between cheetahs and lions, particularly juvenile cheetah survival, as this parameter exerts strong control over population growth. Outside protected areas, where lions are hunted, cheetahs may have reasonably robust population sizes, although evidence for this is controversial (Laurenson 1995; Gros 1998). In other areas, where both large predators and cheetahs are hunted, it is likely that protection of adult cheetahs would be the most effective conservation strategy. Fieldwork is being conducted outside the Serengeti Plains in woodland areas to determine cheetah population size and reproductive rates, but nevertheless this is still a protected area.

MJK has also found that certain matriline in Serengeti are far more successful than others (Kelly, in press) with five lineages contributing 45 percent of the cheetah population. Although we do not yet understand the reason why reproductively successful mothers produce reproductively successful daughters and granddaughters (Kelly, in press), Durant (in press) has used playbacks of lion roars to demonstrate that female cheetahs that react most strongly to lion roars by moving away from the speaker are those with the highest RS. Since lion predation is so important in affecting RS in this species, her finding raises the interesting possibility that daughters inherit some aspects of their mothers' wariness or antipredator tactics. This in turn generates questions about the extent to which such behavior is environmentally, genetically, or culturally transmitted. These sorts of questions are best answered in zoos, where cross-fostering is possible. Moreover, work on cheetahs' temperaments has actually been carried out in zoos (Wielebnowski 1999). Nevertheless, Wielebnowski's work has shown quite the opposite result. In zoos, female and male cheetahs that had never bred successfully scored higher on tense-fearful components of personality than did breeders! Although the nature of stress is likely to be different in captivity, we have contradictory findings on the association between temperament and RS which need to be resolved in order to inform managers about which subjects to use in reintroduction programs and to inform behavioral ecologists of which behavior patterns are under strong selection in the wild. There is still plenty to do!

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