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Abstract: A report about the evolution of sociality in the Felidae and other Carnivora. Five of the seven families of Canivora have evolved sociality. Canidae, Hyenidae and Felidae are discussed. Four hypotheses that affect sociality are discussed: H1: Defense against predation, H2: Nature of food resources favors grouping, H3:Intraspecific competition for critically limiting resources, H4: Interspecific competition for critically limiting resources (or for the cheetah: grouping is disfavored by interspecific competition).

However efficient grouping for cheetahs is for capturing prey, in areas with abundant dominants the cost of theft may be too great for grouping to be favored. The conspicuousness of several adults should increase the frequency of theft by dominants. With few or no dominants, hunting efficiency should be sufficient to favor grouping (H2). Thus, in some areas where dominant abound, males must benefit from grouping because of intrasexual competition (H3), the advantages of which are probably sufficient to override the costs of interspecific competition (H4). Grouping by females could be favored because it reduces predation on infants by numerous, smaller predators (H1), by males (H3), and/or because foraging efficiency is enhanced. Intrasexual competition (H3), predation by species subordinate to adults (H1) and increased efficiency of foraging (H2) could account for increased grouping. All of these benefits would be enhanced by removal of interspecific competition from dominants. For example, with removal of the cheetah's dominants, numerous subordinate species should be favored and have higher densities. Last chapter is a reconstruction of social evolution.

THE EVOLUTION OF SOCIALITY IN THE FELIDAE

Randall L. Eaton

Of seven families of Carnivora, five have evolved sociality. For convenience only the Canidae, Hyenidae and Felidae are discussed. The felids have been specialized predators for a relatively long time; of all extant and extinct taxa of the Carnivora, only the Felidae rely exclusively on protein. The social canids and hyenids tend to be more predatory than their asocial relatives, but also exhibit relatively broad diets including plant material. The hyenids, except the modern *Proteles*, appear to have adapted early to a life of scavenging, especially the ability to utilize bone and animal parts left by more effective predators (Ewer, 1973). They have probably always tended to exhibit very broad diets, including smaller mammals killed by themselves (Mills, 1973; Eaton, in press, a; Kruuk, 1972).

Canid, felid and hyenid radiation were stimulated by the appearance of extensive areas of grassland during the late Miocene and Pliocene. Prior to the extensive radiation of herbivores in response to evolution of grasses, the felids were probably the dominant predators, using a high-search, low-pursiit foraging strategy facilitated by relatively high efficiency of killing behavior due in part to the employment of three potent capture and killing weapons, teeth and forelegs with claws. Such a foraging strategy is conducive to a solitary existence, as seen in the majority of extant felids.

Felids diverged early into smaller forms adapted for forest-dwelling and predation on smaller mammals and birds, and several, separate lineages of huge saber-tooths, probably adapted to prey on large, slow herbivores (Ewer, 1973). As grasses evolved and rodents and lagomorphs appeared, canids probably became specialists at foraging in more open habitats by using a pursuit strategy, while the smaller felids continued to monopolize forested habitats and edges. From their outset, felids became highly specialized killers, and canids probably tended towards omnivory and relatively smaller prey then felids.

The canid adaptation to a life of omnivory, utilizing a low-search, high-pursuit foraging mode, was surely conducive to monogamy. Sociality probably did not appear until after the modern, swift ungulate fauna had begun to occupy grasslands where group foraging would have been favored. As huge, slow forest-living herbivores gave way to the smaller, swift ungulates, the clumsy sabre-tooths were displaced by the modern felids, and, possibly hominids. Only one larger felid, the cheetah, adapted to open habitats during the Pliocene. The largest of modern cats, the Pantherinae, appeared in the mid-Pliocene, with the lion evolving most recently, in the late Pliocene, early Pleistocene.

The hyenids became predator-scavengers in open forests and grasslands during the Pliocene, probably scavenging from sabre-tooths, larger Felinae and canids, as well as preying on smaller mammals. For reasons to be discussed below, it is not unlikely that interfamily competition in open habitats contributed to evolution of grouping in modern hyenids. Kleiman and Eisenberg (1973) said that competition between intrafamily and interfamily carnivores has probably always been intense and must be considered a factor in the adaptations made by different groups, and social behavior and evolution must be included.

Among modern carnivores, only one felid, the lion, but four canids -- dhole, bush dog, hunting dog and wolf -- are *highly* social, suggesting that the basic mode of foraging in these species was more conducive to the evolution of grouping in canids. Of only four extant species of hyenids, the spotted hyena is highly social and it uses a pursuit-foraging strategy very similar to the canids and other hyenids. If grouping by large predators has evolved because pursuit by groups is the most effective feeding strategy, it is puzzling why the lion, like most felids, typically a high-search, low-pursuit forager, would have evolved sociality. While obviously less adept at longer-distance pursuit than canids or hyenids, the cheetah relies far more on pursuit than any other felid, and while it classifies as social (below), the level of grouping is rather low compared to the lion and the social canids.

Kleiman and Eisenberg (1973) have discussed the social organization of canids and felids, and how the fundamental differences might account for social evolution in these families. They rely largely on the basic adaptations of primitive canids and felids and how these affected the types of social groups which have emerged. The authors point out the selective benefits in certain habitats of asocial versus social life. They did not pose any major selective benefits other than defense of young against predation or increased efficiency of hunting to account for evolution of grouping. Further, they did not discuss the initial causes of sociality but rather identified selective (maintenance) benefits of grouping.

Asocial canids tend to be monogamous probably because food items are widely dispersed and/or relatively small. The social canids exhibit extended monogamies. Because they are fundamentally monogamous, it has been argued that the asocial canids have a relatively high level of social behavior and thus, for whatever the benefits, grouping could be expected to evolve rather easily in canids. Since felids are fundamentally adapted for solitary foraging and tend to be polygynous, they supposedly do not have a level of social bonding behavior as conducive to grouping as the canids. Accordingly, the phylogenetic inertia of felid and canid social propensities should tend to disfavor and favor grouping respectively. The hyenids have not been as intensively studied, but the asocial species may tend to be monogamous. Thus, everything else being the same, grouping could be expected to evolve more readily in them as well. However, asocial felids possess highly advanced social behavior and exhibit considerable behavioral scaling in regard to grouping. Any difference in the rate of evolution of grouping in canids and felids because of mating systems may be insignificant. Foraging strategies would seem more crucial.

Ecological Correlations with Grouping

It is desirable to identify the ecological conditions necessary for the evolution of grouping in larger carnivores. Also, it is desirable to demonstrate why sociality is not found in similar, but asocial counterparts before any theory can explain its existence. Generally, there are consistent correlations that center around type of habitat: almost without exception social carnivores predominate in more open habitats, asocial counterparts predominate in more closed habitats. The apparent differences include: a) carrying capacity of larger herbivores; b) mode of hunting; c) intraspecific competition; and, d) interspecific competition.

The major habitats of social carnivores are highly productive, for example, tundras, prairies, savannas, wooded savannas and open woodlands. These typically have a relatively high carrying capacity of large herbivores, and, according to Kleiman and Eisenberg (1973), usually have at least one relatively common prey species larger in size than an individual carnivore. However, this rule does not hold for the lion in some and the cheetah in most areas. The habitats of asocial counterparts tend to produce less animal protein, for example, forests, scrub, arid and montane habitats.

Open habitats are most amendable to group-hunting: with less cover available, grouping could favor predators. Regardless of any differences in abundance of prey, grouping as a foraging strategy could be favored in open and disfavored in thickly vegetated habitats. The difference may relate to effectiveness of hunting. For example, because of the importance of stealth, two housecats hunting together would surely kill fewer mice than if they hunted separately. Larger felids such as the puma and tiger may forage solitarily not because of lower abundance of prey in their habitats, but because of the advantages of minimizing detection by prey.

There may be relationships between sociality in larger carnivores and their ecological and interspecific behavioral status. The wolf is the most successful of the modern larger carnivores of the northern hemisphere. Other social canids tend to be ecological and behavioral subordinates in their guilds. The lion is exceptionally large among social carnivores, and until very recently was the dominant predator throughout vast regions of Africa and southern Eurasia. With the exception of man, a smaller grouped species, the lion is dominant to sympatric predators, all of which are smaller and several of which are social. The wolf coexists with several larger but asocial carnivores, for example, brown bears and to a lesser degree tigers. While there is no strict relationship between size of carnivores and degree of sociality, the dominant carnivore within many predator guilds is social, including man and the killer whale.

More open habitats support a greater diversity and abundance of mammalian prey species, which also correlates with, and possibly causes, a greater diversity and abundance of predators. Thus, interspecific and intraspecific competition should be far more intense in open habitats. Defense of resources is not only more difficult because of the abundance of competitors, but also because the openness of the habitat increases the probability of information transfer between competitors.

Carnivores can only gain from grouping for any reason so long as the habitat produces a sufficient number and/or size of food items, a necessary but not sufficient cause of grouping. Greater productivity may be conducive to the evolution of grouping because of its effects on density of conspecifics and/or other predators, which influences competition.

To explain the evolution of grouping in the Felidae, two mutually compatable approaches are taken: a) analyzing the causes or selective benefits of grouping; and, b) comparison of the social organization and behavior of asocial and social species to deduce the probable course of social evolution. By combining these, it may be possible to isolate which causes were acting at each stage of social evolution. A predictive theory of social evolution should strive for a sequential reconstruction of grouping.

An Overview of the Social Organization and Behavior of Felids

In order to fully appreciate the evolution of grouping in felids, their social organization and behavior is overviewed.[1] Much information about larger, asocial felid ecology and social behavior is being collected or prepared for publication at this writing. As more intensive field studies are conducted on such species as the puma and leopard, the trend of observations is towards increasing social interactions among individuals (works of C. Koford, T. Bailey, P. and P. Dewar, and others, in preparation).

Asocial Felids

The fundamental pattern of felid social organization is a family unit of one female and her offspring of one litter. No other adults directly assist in rearing young. Males are either territorially established or floaters searching for territory, which may entail aggressive competition with resident males for breeding status (see Eaton 1974a, and this volume, for references).

The mating system typically is polygynous: resident males usually have two or more females within their larger inclusive territory. There normally appears to be an equal sex-ratio at birth, but fewer males are residents and more are floaters. Competition among males should be more intense than among females, and, thus, selection should favor sexual dimorphism with males being larger than females. Field observations indicate greater competition among males than females; serious fights and injuries are not uncommon. Males tend to be larger than females by 15 to 40%, the largest males tending to be

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[1] The reader who is familiar with social organization of felids may go on to the next section.

residents, the smaller, younger males tending to be floaters. Sexual dimorphism may also be favored because it reduces exploitive competition between males and females and offspring (Muckenhirn and Eisenberg, 1973).

The basic reproductive pattern of felids is polyestry, tending towards seasonal polyestry and optimal periods for breeding (Asdell, 1964; Ewer, 1973, 1974). In populations that show a tendency towards seasonality, or in tropical species which tend to respond reproductively to local, unpredicatable fluctuations in food resources, females may reproduce at any time (Rudnai, 1973; Eaton and Velander, in press; Eaton, 1974b,c; Eaton 1976; Robinette et al., 1961; Kleiman, 1974, etc.).

While felids are typically asocial, they are by no means unsociable (see Leyhausen, 1965). Resident males interact fairly often with resident females without mating activity (e.g., Seidensticker et al., 1973; Erickson, 1955; Schaller, 1967; C. Koford, pers. comm.). Resident males appear to communicate regularly with one another, but may rarely associate directly. Subadult or young adult females appear to remain in or close to their native territory (as in bears, Wilson, 1975; falcons, Eaton, in prep., and many asocial predators), and associate periodically with their mothers, even while the mother is accompanied by younger offspring (Seidensticker et al., 1973; Schaller, 1967). Resident females at least communicate indirectly with one another, and it is probable that they are often related.

Previously expelled males may revisit their mother's territory and form temporary associations with a subsequent litter, even form groups which disperse (Seidensticker et al., 1973), though female sibs may settle closer to the native territory as male sibs keep moving. A previously expelled male offspring who later returns should not threaten his sibs, and might even serve his inclusive interests by assisting sibs in adjusting to independence.

In a particular incident (Seidensticker et al., 1973) the mother puma apparently mated with a resident male just after her young adult litter departed with an older male offspring, which would had to have been at least four years old. If such male offspring were to pursue related estrous females (mothers, sisters), they would increase the probability of severe aggression by resident males. Mothers may rebuke their sons' mating attempts not because of "inbreeding" but because the male would be threatened by resident or older males. Normally, the female would serve her interests by refusing sexual relationships with sons. The inhibition of sexual behavior so common between adult littermates or individuals raised together in captivity may represent an evolved incest taboo which has little if anything to do with inbreeding. In any case, resident males should always expell young males because they can succeed in mating unrelated or distantly related females in adjacent female territories.

The primary mode of communication in felids is olfactory, via pheromones produced by exogenous glands and in urine and feces. Males tend to scent-mark far more frequently than females (see Eaton, 1974a; Kleiman, 1974; Schaller, 1967). Resident males expend considerable time and energy marking territories by depositing urine and feces at conspicuous and/or traditionally used features in the landscape (e.g., Seidensticker et al., 1973; Muckenhirn and Eisenberg, 1973). Visual marks have evolved to enhance communication by attracting attention to olfactory marking sites. Scrapes on the ground and scratches on trees visually attract conspecifics to scent posts (Schaller, 1967; Hornocker, 1969; Muckenhirn and Eisenberg, 1973; Shorey and Eaton, 1974). Information contained in scent-marks is as yet only partly deciphered, but includes warnings to potential competitors, advertisement of identity and location in time, sexual attractants, and probably more. Information transferred should vary as a function of who: individuality, sex, age, breeding condition, etc., perceives scent-marks. Usually, intruders appear to avoid residents as much as possible; they may even hide their presence by covering feces and urine (e.g., bobcats, Erickson, 1955).

Resident (breeding) females compete for territory, and, depending on the species, food resources. In larger felids, prey are likely to be highly mobile (Schaller, 1967; Muckenhirn and Eisenberg, 1973; Hornocker, 1970). Aggression between resident or resident and non-resident females appears to be more inhibited and highly ritualized compared to males (e.g., Shorey and Eaton, 1974). Resident females indirectly compete for males. As there invariably are optimal periods to reproduce, females are favored who succeed in attracting males to themselves rather than other females. Females may also benefit by monopolizing the sexual attention of males during false estrous periods if this reduces competition with adjacent females. Excessive mating by females may reduce infanticide by males, for example, floaters or residents established after the female conceived with a previous male (see Eaton, this volume).

As a female and/or her daughters approach breeding condition, daughters are expelled and the female reproduces again. It is probably normal for the female to conceive while still associated with her litter (Robinette et al., 1961). If her sons have not already voluntarily dispersed or been expelled by a resident male, they should be expelled during the female's estrus, when the resident male may attack and kill them (e.g., Schaller, 1967; Goldman and Young, 1946). While nonresident females may tend to wait for a vacancy or a suitable portion of their mother's territory, males tend to disperse, then search, and, if necessary, later fight. Thus, neighboring females are likely to be related while neighboring males are likely to be unrelated, which may partly account for greater aggressiveness between males.

Females spend considerable time away from infant litters. When the litter is older and mobile (from six to ten weeks), it spends more time closer to or with the female. Floater males are a threat to offspring as most are unrelated to the mother. Resident males cannot fully exclude other males, which kill and eat infants and, to a lesser extent, smaller juveniles. Most nonresident males which encounter families will be relatively young and small, a factor which may be conducive to defense of offspring by the female. Perhaps more important, a female should be more aggressive (willing to assume greater risks) in defending her young than a male would be to prey on them. Females may employ sexual deceit to reduce infanticide, for example, the weaning estrus. Any male in the area is likely to either mate the female, though she may not necessarily conceive, or be expelled by a resident male. A nonresident male who only manages to sneak one or a few copulations before being ousted by the resident male, cannot later afford to kill offspring in the female's area or with the female.

Because floater males are a threat to a resident male's success: they can prey on offspring, mate females, extract resources from breeding territories, and may challenge for territorial status, resident males can benefit by attacking and killing floaters. With younger, smaller males the risks to a resident may be relatively small; however, with larger, more potentially dangerous adversaries, residents may tend to use more ritualized expressions of aggression to attempt expulsion (domination). In the event that an intruder is not submissive, the resident male should attempt domination by fighting or otherwise lose breeding status. The tenacity with which residents defend their status is to be expected as they have everything to lose and nothing to gain by yielding.

It is important to recognize that the highly specialized killing techniques used by felids are enhanced by transmission of information by parent females, which favors prolonged family ties (Ewer, 1974). This in itself has favored a higher degree of social behavior than might otherwise be expected in basically solitary-hunting predators. In spite of considerable association of adults and probably related adults and family units, cooperative hunting has not been observed (Erickson, 1955) except rarely by courting pairs (McCord, 1974).

Other than the lion and cheetah, at least two species appear to have evolved a basically different form of social organization than described above. The black-footed cat occupies a harsh environment and feeds on sparsely distributed, small food items (Visser, 1976). Sexual dimorphism in body size is small or lacking, although males may be distinctively marked (Leyhausen and Tonkin, 1966). The estrous period of the black-footed cat is exceptionally short and breeding is probably very seasonal. Males may behave parentally (U. Schurer, pers. comm.). Both the black-footed cat and the snow leopard appear to be monogamous, but do males play a parental role comparable to males of monogamous canids? It is predicted that the canid-like foraging strategy surely used by black-footed cats, combined with a high threat from predation, would result in a pair's use of a central den where kittens are hidden. Males may help provision females and offspring, as in foxes and jackals. The snow leopard's foraging strategy could be more representative of large canids. Births may be timed according to a high abundance of large and small prey in alpine habitats. Both parents might provision infant offspring at a den located in lower watersheds frequented by wintering ungulates. When the offspring are mobile, they probably relocate with both parents in the alpine habitats during the late spring and summer.

At least for felids, monogamy is probably rare and may only evolve under relatively unfavorable conditions; it probably originated from extension of temporary pair bonds between unrelated adults, possibly between sibs. Contrary to Kleiman and Eisenberg (1973), monogamy was surely not the origin of grouping in social felids.

Social Felids

Most all felids studied to date appear to be asocial; however, the cheetah exhibits a degree of sociality, as males tend to group (type 4, see Alexander, 1974), and in one population, family groups include two or more adults (probably females) and/or two different litters (extended type 3, Alexander, 1974). Lions also form type 3 and 4 groups but males or male groups are usually associated with related females and their offspring, the pride.

The Cheetah

Cheetahs are only about 25% the size of lions, and their average prey is disproportionately smaller than the lion's. The cheetah is highly specialized; its fundamental niche is that of a diurnal predator on smaller, swift antelope such as gazelles (Eaton, 1970a, 1974a; Kruuk, 1972; Schaller, 1972). The smaller ungulate prey are typically migratory and occupy very open terrain (Schaller, 1972). Defense of a territory is normally impractical but temporal spacing is achieved by mutual avoidance and scent-marking (Eaton, 1970). Confrontations and congestions are rare. In the vast majority of populations, females live alone with one litter, but males tend to group everywhere (Eaton, 1974a; Pienaar, 1969; Gaerdes, 1973-74; Schaller, 1972). Apparently these groups consist only of siblings (Eaton, 1974a).

Females normally conceive prior to separation from their subadult litter, then either drive them away or leave offspring just prior to parturition. Male offspring are not expelled from family groups by mating males. Quite often the entire litter including males and females remain together for several weeks; the females become solitary and the males either separate or remain together, sometimes for several years. There is no evidence that unrelated males ever group. It is not unlikely that a female's first estrus attracts older males which expel male littermates.

Females exhibit smaller home ranges and probably tend to remain closer to their mother's range than do males (Adamson, 1971; McLaughlin, 1970). Females may periodically associate with their mothers and thus form temporary groups, or, in exceptional circumstances, remain with their mother through the raising of a subsequent litter.

Males mark at high frequencies, females do so only rarely (Eaton, 1970b, 1974a) compared with females of asocial, territorial species, for example tigers, or female lions (Schaller, 1967; Rudnai, 1973; Eaton, 1973). Females probably mark only to attract males for mating. Males who have not mated a female are probably dangerous to the female's offspring (Herdman, 1972). The high mobility of cheetahs, especially males, is such that females may lose by advertising their presence, and, thus, rely on vision to space themselves. Females with offspring less than about 10 months old exhibit great avoidance of males (Eaton, 1974a) by moving away and/or hiding their young. In the cheetah, breeding-age females probably associate with adult males only for mating.

Experiments in naturalistic settings indicate that grouping behavior in cheetahs is readily expanded and probably adaptable to local settings. In a large, semi-natural compound in Kenya abundantly stocked with gazelles, a cheetah family (female and offspring) were enclosed. The female later bred with a son and her mature offspring assisted in rearing the female's second litter (W. York, pers. comm., and in Eaton, 1974a). In Rhodesia's miombo woodland, a cheetah family was reported to be geographically territorial (W. Garst, pers. comm.); however, relationships with other adults were not observed.

The Lion

The lion has a broad fundamental niche. It hunts singly or in groups; it kills a vast array of species including larger species than killed by any terrestrial predator except man. The lion tends to hunt nocturnally but also diurnally, and freely scavenges and steals from other species. The lion occurs in such diverse habitats as miombo woodland, wooded savanna, grassland plains, semi-arid and true deserts. Based on biomass, it tends to be the dominant predator wherever it occurs, and in larger groups behaviorally dominates all other predators.

Adult females and offspring live together and the average relatedness is probably high, about 0.25. The adult male or male group with a pride of females is usually not related to the females. Males are probably closely related, having originated in most cases from the same pride, but not usually from the same females. The normal sex-ratio of a group is 1:2-3. Males are considerably larger than females. Group-size and composition tend to vary in different habitats, partly as a function of carrying capacity. Spacing by groups may be territorial in more productive habitats, or temporal in poor habitats as in the cheetah.

Males compete for pride status, and turnover rates may be high (Schaller, 1972). New males may cause the death of offspring sired by ousted or dispersed males. Juvenile and subadult males are expelled from prides by resident males, or leave voluntarily (Rudnai, 1973). Females tend to perpetuate themselves within the same group and territory for many generations. Most female offspring are expelled as young adults by pride members (females), with some being admitted into the matricarchy. Expelled females may wait within the territory for a vacancy; others become nomadic and probably have little reproductive success (Schaller, 1972).

Communication is via scent-marking as in other felids, with males marking more frequently than females. Vocalizations are more complex in lions than in any other felid, and both sexes roar though males roar more loudly and more often. Fighting within groups is inhibited, but between strangers may be combative and lethal (Schaller, 1972, Schenkel, 1967; Rudnai, 1973, Eaton, 1973). Competition between male groups is often peaceably settled by differences in group size (Schaller, 1972).

Why Groups Form

Sociality is group living. Sociobiological theory predicts that sociality evolves because the average fitness of individuals in groups in higher than individuals not in groups. Except in clones, the genetic interests of individuals within groups are never the same as the group as a whole. Therefore, Alexander (1974) argues that in order to understand sociality the conflicts of interest among individuals must be specified. According to the theoretical development of Alexander (1974) there are many automatic detriments to group living, such as: subordination of males thus prevented from reproduction; the threat to the dominant male of being overthrown by subordinates; the individual who must constantly be in competition for preferred space or food; increased conspicuousness; greater probability of transmission of disease and parasites, and so on.

While it is valid to argue that group living evolves because individuals benefit, some of the detriments listed by Alexander may actually favor grouping. As to the increased probability of disease and transfer of parasites constituting a detriment to sociality, an equally good case can be made for the opposite: that immunities can be acquired by exposure to conspecifics within groups, effectively reducing the probability of mortality or impaired reproductive performance of individuals living in groups. Ticks are serious disease vectors for many mammals, and in areas of higher mammalian density, which also are more open habitats, grouping could benefit rather than cost them. Lions are highly susceptible to ticks, which may transmit potentially lethal diseases. Rudnai (1973) observed that allogrooming is directed at the body parts not reachable by autogrooming; apparently ticks are being removed.

Regardless of detriments, it still must be demonstrated for any social species what gains accrue to individuals over the alternative of asociality. Alexander (1974) says that these are chiefly of three kinds: 1) susceptibility to predation must be lowered, for example, through group defense (first hypothesis, H-1); 2) the nature of food resources may disfavor splintering (second hypothesis, H-2); 3) there may be an extreme localization of some critically limiting resource (third hypothesis, H-3).

Alexander (1974) argues that H-1 and H-2 are probably far more significant as causes of sociality. Brown and Orians (1970) consider intraspecific defense of clumped resources a benefit to individuals of groups; however this cause may apply to some species, the examples given by Alexander--safe sleeping sites in the Hamadryas baboon and breeding sites for some marine mammals and birds--could just as well be included in H-1, a lowering of susceptibility to predation. Neither Brown and Orians (1970) nor Alexander (1974) have postulated direct interspecific competition for clumped resources as a primary force favoring evolution of sociality. Interspecific competition for clumped resources may have caused evolution of sociality in carnivores, thus, a fourth hypothesis is added to the basic causes of grouping. It will be argued that intrasexual competition may cause grouping; however, this is best considered as intraspecific competition for a critically limiting resource, for example, mates (H-3).

There has been no real attempt to explain grouping in the cheetah. In fact, the cheetah has been considered basically solitary by some workers, for example Schaller (1972) who observed them in the least social population known. Eaton (1970b; 1974a) established an inverse relationship between frequency of grouping by males and the density and diversity of competing species, and suggested that predation on litters (H-1) and degree of direct (behavioral) interspecific competition for food (H-4) may explain populational differences in grouping.

Schaller (1972) has given an account of why lions are social. To explain sociality in lions, Schaller (1972: 357-8) mentioned eight selective forces which could be consolidated into the four hypotheses. Individuals in groups hunt more successfully than solitary individuals. He says, "A lion group uses its food more fully than an individual. Wildebeeste and zebra may be consumed within an hour or two by several lions but a solitary lion must guard the remains against other predators and vultures. A single lion is not always able to do this, and hyenas, for example, often drive (even kill on occasion) it from a kill." Another explanation by Schaller is division of labor, for example, one lion may protect the carcass while others seek shade, fetch cubs, or are otherwise employed. He mentions that a lioness often rests near small cubs, thereby functioning as a guard, without the need to hunt because other pride members may kill something and provide meat for all. These benefits to individuals from grouping fall variously under H-1, H-2, and, probably H-3 for competition between females of different groups.

In still a third explanation, Schaller (1972) points out that interspecific rank is enhanced by group living; however, he believes this is largely based on size. For example, a single lion always wins against a single hyena, but a single lion is put to flight by a hyena pack. Actually this implies that interspecific hierarchy is not dependent on size of individuals but on size of individuals which comprise groups. Other selection forces which Schaller attributes to grouping by lions are prolonged development and possibility of learning which could fall under any or all of the hypotheses.

The Hypotheses

H-1. *Defense against predation*. This hypothesis tends to be overlooked as a cause of grouping in larger carnivores, probably because it is believed that these species have few or no enemies. Like several of the larger felids, the wolf is the dominant carnivore in most of its range. Bears could be serious predators on young wolves protected by only one or two parents. The point is that the *initial* cause of grouping may be less apparent than the selective advantages *after* grouping has already been favored by presently obscure selective pressures.

Wilson (1975) discounted risks from predation as important in the larger felids, but all of them studied to date are killed as adults by other species and they incur predation on offspring. Thus, it is reasonable to propose that felids evolved grouping because of advantages against predation.

The Cheetah

The cheetah's exceptionally large litter size, nearly twice as large as the similar-sized leopard or puma, probably reflects a high mortality rate of offspring. The cheetah may incur higher levels of mortality from predation than any larger felid. In East and South Africa (Eaton, 1974a; Abbot and Fuller, 1973; Adamson, 1971; etc.) about 50% of the kittens born are killed by dominant predators (lion, leopard and hyena). Adults are also preyed upon by sympatric carnivores; however, almost all cases to date have been of females of single-adult family groups, rarely of males living solitarily or in groups.

If defense against predation favored grouping, then there should be a direct correlation between grouping by females and males and densities of dominant predators. The proportion of males which are grouped in a population inversely correlates with the diversity and density of predator species which prey on cheetah kittens. The Serengeti area has a great density and full complement of dominant species, and a relatively small portion of male cheetahs occur in groups (Schaller, 1972). In Nairobi Park, spotted hyenas and hunting dogs are absent; grouping by male cheetahs is prevalent and larger groups are found (Eaton, 1970b; McLaughlin, 1970). Very few females have been observed with two different litters (Graham, 1966) and there are only rare observations of two adult females together with one litter.

If H-1 explains grouping by males then in areas with fewer predators, as Nairobi Park, grouping should be less prevalent, not more, and in areas of extremely high predator density, females should group. Thus, in an area devoid of dominant predators, cheetahs should group least. In much of South West Africa (throughout the vast ranchlands) all dominants have been extirpated for 80 to 100 years. Males typically occur in groups, the average size of which exceeds all other regions (Gaerdes, 1973-4). It is not uncommon for one female to be observed with a young, adult litter and a second, small litter and almost one-half the family units have more than one adult (Gaerdes, 1973-4). Grouping must not benefit cheetahs because of the relative advantages of individuals in groups to escape predation.

The Lion

While cheetahs may tend to reduce predation on offspring by living in open grassland with a lower density of predators, they still lose about 50% of their offspring to predation. The lion's only effective defense of offspring in wooded savanna, densely saturated with grouped predators, should be grouping.

It is apparent from field studies (Eloff, 1973; Rudnai, 1973; Schaller, 1972) that lions incur mortality from predation, particularly on young but also on solitary adults (e.g., Pienaar, 1969; Kruuk, 1972). Unfortunately, there are no data which compare mortality from predation on young of solitary-living lions as opposed to pride-living lions. However, as single lions are not only dominated by groups of hyenas and wild dogs, but also are killed and sometimes eaten, surely the offspring of solitary adults would receive much higher predation than offspring of grouped adults.

It is known that the younger lions are, the more vulnerable they are to predation (Eloff, 1973; Rudnai, 1973; Schaller, 1972). Thus, if predation causes grouping then it is to be expected that offspring would be born and raised from birth in the presence of group members which could provide defense, for example, as in many primates. Female lions leave their groups and parturate in concealment, raising their young in isolation for several weeks before integrating them into the group (Schaller, 1972, Rudnai, 1973). The simplest explanation for the female's separative behavior for parturition and early rearing of young is that the best strategy against predation is to conceal small, immobile young, but later have them near other adults. When offspring are very small, they are virtually immobile and unable to stay with a moving group of adults and older young. By hiding them, the female can either hunt for herself or utilize the kills made by the pride (Schaller, 1972) returning periodically to suckle the litter without risking transport of young--a one at a time affair--as the pride relocates. Myers (unpubl. ms.) provides accounts of how vulnerable the litter is to predation when a female attempts to relocate her as yet immobile litter. Since the litter is normally introduced to the group just at the age when they can remain close to their mother or other pride members, it would appear that there has been selection favoring group defense of young as soon as it is practicable. If lions group because of H-1, then where major predators are absent grouping should be less prevalent. In Nairobi Park hyenas and wild dogs are virtually absent and females group more loosely than anywhere (Rudnai, 1973). H-1 is supported for the lion.

H-2. *Nature of food resources favors grouping* is almost universally accepted to explain grouping by larger carnivores (e.g., Alexander, 1974; Wilson, 1975; Kleiman and Eisenberg, 1973). Alexander (1974) mentions wolves, hyenas, and hunting dogs as examples; others have mentioned the lion (Schaller, 1972; Kleiman and Eisenberg, 1973). Group-living benefits individuals because: a) they utilize larger prey than could be acquired by an individual; b) the same size (or smaller) prey could be captured more efficiently; c) regardless of these, fewer risks are involved in grouping. The usual argument is based on "a" or "b", especially "a": if each individual in a group gains more food at higher predictability than it could by hunting alone, sociality should be favored.

Ability to kill large prey (H-2a) and risks involved (H-2c) are not completely separable. As the ratio of prey to predator size increases, the risks should also increase. As the number of predators in a group increases, the risks decrease but the amount of food per individual also decreases. Albeit, H-2 is supported if grouped individuals kill prey too large for solitary individuals to kill.

It is well known that cheetahs experience difficulty in dispatching larger and/or potentially dangerous prey. Similarly, lions have been killed or injured by species ranging from warthog to oryx, buffalo and giraffe. Data that compare risks to single and grouped cheetahs or lions are lacking; however, judging from combined attack and killing behavior, grouped individuals should incur fewer risks.

The Cheetah

The largest prey normally killed by a single cheetah is about 150 pounds, for example, impala and Grant's gazelle, although difficulty and failure at killing are not uncommon, and risks must be relatively high. In most areas, the average and largest prey of single and grouped cheetahs is generally about the same. However, in Nairobi Park, a group of four (later two) males regularly killed exceptionally large prey, such as hartebeest and even zebra weighing 300 to 400 pounds or more (Eaton, 1974a). Since groups of males are able to kill significantly larger prey, and also forage most efficiently in terms of hunting success (H-2b), it is puzzling that in areas such as the Serengeti and Kruger Parks, the size of prey of individuals and groups appears virtually the same. There are insufficient data at this time to strictly compare hunting efficiency of solitary versus grouped cheetahs in these areas. However, cooperative tactics much as described for wolves (Mech, 1970) are used by male and subadult family groups (Eaton, 1974a; J. Gaerdes, pers. comm.; H. Theron, pers. comm.) in

Nairobi Park and South West African ranchland, which implies greater efficiency of predation (H-2b) and probably reduced risks (H-2c).

If grouping can benefit males because of enchanced hunting, it is puzzling why only males normally group. If groups of two and four adult males can be *very* successful, and the average litter-size at 6-8 months is two or three, then females should be able to enhance their reproductive success by grouping. While individuals in some rather peculiar environments benefit from group-hunting, H-2 does not fully explain the lack of grouping in many other areas.

The Lion

If groups of lions can kill larger prey than an individual lion, and the carrying capacity and mode of hunting in more open habitats are conducive to group-hunting tactics, then it would appear obvious why lions are social. Field observations (Eloff, 1973; Bertram, 1973; Rudnai, 1973; Schaller, 1972; Smuts, 1976) suggest that individual lions of social groups often hunt alone successfully. In the dry season when larger prey are not as available, individual hunting by pride lions is the rule, not the exception, and single females may prey largely on Thomson's gazelles which weigh a mere 50 pounds and which are considered very wary. Moreover, they occupy extremely open habitats and are very swift (Schaller, 1972; Walther, 1970). As the majority of food is acquired by individual hunting effort, perhaps grouping for hunting is relatively unimportant overall as a cause of sociality.

The data (e.g., Schaller, 1972) suggest that a lion pride, say of six adults (2:4), almost always kills the same size of larger prey as a single lion. When a lion pride of merely four adults (1:3) kills a 600 lb. zebra each lion gains less food than when a single lion kills a zebra or anyone of a number of smaller species and the young of large species. If the size of prey killed by groups is no greater then individuals of groups must gain in the economy of hunting in terms of time and energy spent relative to amount of food gained (H-2b).

An advantage to group hunting whether or not it entails cooperation is that more than one prey animal can be acquired. Schaller (1972) mentions cases in which several larger prey were captured by as many lions in single, group efforts. In Nairobi Park (Rudnai, 1973) and in Zambia (Ansell, 1969) multiple killings occurred in single hunts. These usually occurred during seasons of resource abundance.

Schaller (1972) demonstrated that two or more lions hunting together had a success rate of 52% and that single lions succeeded at a rate of 29%. Success ratios vary with the time of year, abundance and type of prey available as well as habitat type. While grouped lions are nearly twice as successful measured by attempts as solitary hunting lions, only in 29 of over 500 hunts did Schaller (1972) report cooperation, as he defined it. In accordance with Schaller's interpretation, real cooperation by hunting lions is relatively rare, and occurred only between females. Ability to kill the largest prey species apparently requires the active assistance of males, thus males should be considered as cooperators, even if their role is that of killing and not capture per se.

What is probably most significant is that groups had greater success hunting large prey, while single lions had higher success hunting smaller prey Only groups tend to hunt the largest species, buffalo and giraffe. It would appear that lions acquire more food when they hunt in groups. Schaller (1972: 356-7) argues that size of prey (H-2a) is a factor in maintaining the social organization of the lion as compared with more solitary felids: "Lions are able to increase their food resources by hunting together. A solitary lion usually hesitates to attack a buffalo or giraffe but a group does so readily and presumably more successfully, a point of particular importance in the Serengeti, where some three-fourths of the resident prey biomass consist of these two species." It is plausible that ability to kill very large prey even occasionally would sufficiently favor grouping by lions, especially as their largest prey are year-round residents while their major prey species are migratory and more mobile generally. The ability to kill exceptionally large and risky prey *during the limiting season* could explain grouping; the same principle could apply as well to other dominant or codominant predators such as the killer whale and hominids.

If lions group because of the advantages to individuals of being able to obtain very large prey during the limiting season, then lions living in habitat which do not support large herbivores should not group. Lions live socially in small groups where their largest prey species is smaller than prey frequentl killed by solitary effort elsewhere. In the Kalahari, the lion's largest prey is the gemsbok, smaller than a zebra. The majority of prey species are quite small, such as rodents and small carnivores (Eloff, 1973; 1974). Group hunting of gemsbok is successful; moreover, it may greatly reduce risks of injury from sabre-like horns and cooperative, anti-predator defense. While Kalahari lions may not benefit from grouping because of killing extremely large prey (H-2a) cooperative tactics of individuals may reduce risks (H-2c) (Eaton, 1970c).

All that is important for grouping to be favored is some relative advantage in predation efficiency be it large prey, more food per unit of effort or reduced risks; thus, H-2 is supported for the lion.

H-3. *Intraspecific competition for critically limiting resources.* Defense of limiting resources has not been given adequate consideration as a cause of grouping in carnivores, but it would a priori seem probable. (Depending upon how extensively one defines critically limiting resources, ultimately, all grouping relates to intraspecific competition.) In larger, predatory carnivores a single kill must often be a critical resource, the use of which may affect survival or reproductive success. For carnivores, a large kill can only be thought of as a clumped resource. Defense of a kill against conspecifics could be sufficient to cause grouping. It is conceivable, for example, that monogamous asocial wolves initially evolved grouping because of competition for kills with other pairs or simple family units with larger, competitive offspring.

A kill or any food item could be critically limiting, and so could offspring, mates, allies or territory. R. Alexander (pers. comm.) suggests that males can be forced into groups by sexual selection. Alexander believes that this selection could be powerful enough even to offset increased risks of predation of individuals from grouping. This is relevant to felids because of the implications that sexual competition can lead to unisexual grouping.

Given that open habitats are productive enough, felids could gain by grouping to:

a) reduce intraspecific predation, aggression or infanticide (intersexual competition), for example, by strangers or new mates;

b) gain access to mates (intrasexual competition);

c) defend or steal clumped resources (kills) from conspecifics; and,

d) increase resource base via spacing or acquisition of territory.

The Cheetah

Typically, cheetahs are not geographically (fixed) territorial; individuals and groups tend to use common areas and to migrate after herds of antelope. Females may breed anytime of the year, thus, males are *always* in competition for estrous females. Fighting has been observed between males pursuing a female, and the only cases of lethal aggression between cheetahs occurred between adult males (Eaton, 1974a; H. Theron, pers. comm.), which possibly were competing for a female. Studies in captivity established that the most severe aggression between males occurs in competition for estrous females (Eaton and Craig, 1973; St. Louis Zoo, pers. comm.).

Grouping should benefit males. The largest group of males in an area is likely to achieve more matings than all other groups or individual males in that area. Males in groups exhibit great cohesiveness and cooperation, and there is a clear, apparently uncontested linear heirarchy of members. Unlike lions (Eaton, 1973), unrelated male cheetahs seem incapable of forming cohesive, stable groups. Groups of apparently related males kept together cooperate in competition with other males for estrous females. Subordinates actually assist dominants in competition for females, but only the dominant male may copulate (Eaton and Craig, 1973; Eaton, 1974a). Apparently this is the most efficient strategy for subordinate males as it benefits them inclusively. If males of cheetah groups-are siblings, which seems very probable (Eaton, 1974a), their genetic relatedness is 0.5 on the average. In a hypothetical case of 100 offspring surviving to adulthood, it is assumed that the average solitary male achieves a fitness of 0.01. If by grouping, one of three grouped sibs increases its fitness to 0.4, the nonmating, subordinate males average inclusive fitness would equal 0.02, which is higher than for solitary males. As long as the inclusive fitness of every male in a group exceeds the average fitness of nongrouping males, selection will favor altruism and grouping should evolve.

The Lion

Male lions of floating groups and prides are probably fairly closely related on the average, having probably been born in the same pride at about the same time (Schaller, 1972). Groups of males are cohesive and apparently stable. They compete with one another for pride status, and normally a larger group wins (Schaller, 1972). As numbers carry success in competition between males (Eaton, 1973; Schaller, 1972), intrasexual competition for mates obviously favors grouping by males. It is true that male lions in groups do not contribute appreciably to parental investment, but they obviously play a role in group defense, particularly of young (Schaller, 1972). Thus, males do control resources important to females by their territorial and defensive behavior. In the lion, intrasexual competition appears to favor unisexual grouping by males, as in the cheetah.

Female lions group in every population which has been investigated; they are probably almost always close relatives. A major advantage of grouping by females is division of labor in offspring care, including cross-suckling and the option of adoption (see Rudnai, 1973), which can favor mother and step-mother alike if they are closely related.

In some populations, the rate of male turnover tends to be rather high As a consequence, infanticide by new males is common, which favors them but disfavors females. Females may deceive new males by mating with them, thus reducing the frequency of infanticide and serving their personal and inclusive fitnesses (H-3a). By employing excessive mating, to sexually gratify males, groups of females can increase the bonding of males to their group, and the males should tend to assume greater risks in defending their status against other males, which favors females, in several ways: reduction of infanticide by new males; aggression or predation of offspring by foreign lions; and, maintenance or expansion of territory.

Synchronous estrous periods of grouped females may reinforce male grouping and thus serve the females' interests (Eaton, this volume). Synchronous reproduction also favors females in additional ways: a) division of labor in offspring care, and, b) females which produce the largest surviving groups of male offspring should have higher reproductive success (H-3b).

Lion groups compete for real estate. Although the fluctuation in territory size in dense populations such as the Serengeti may be slow, some prides have gained resources at the cost of adjacent groups (Bertram, 1973). Success in intragroup competition is probably influenced most by numbers of males, which generally should correlate with size of female groups (H-3b), the best indicator of territory quality and potential productivity of males which settle there.

Lions of different groups sometimes compete for clumped food resources. Groups of males without prides can get much of their food by driving prides with fewer males off large kills (Ansell, 1969) (H-3c). Floating males can benefit by grouping because it reduces the risks of attack by resident (pride) males, which are likely to kill younger, transient males, and because grouping by floaters enlarges their resource base, for example stealing from solitary pride lions or defending food against pride subunits smaller in group size.

If intraspecific competition causes grouping in lions, then a small, disjunct population might exhibit a lesser degree of grouping. Competition between males might result in one larger group totally dominating the area. Younger males born in the population could be expelled from the habitat and forced to disperse so far through poor habitat that they would have high mortality and/or groups of expelled males would not be able to maintain group cohesion long enough to be able to return and compete with the resident, dominant group. For the same reasons, *groups* of males expelled from other populations would immigrate at low frequencies if at all.

Nairobi Park is more productive per unit of area than the Serengeti, but is a mere 44 square miles, and is virtually an island of habitat suitable for lions; it has the higest density of lions known (Rudnai, 1973). The Park has had one, resident group of three males for several years. The males are extremely aggressive, attacking and killing foreign males, and even females (Rudnai, 1973). Females do not form tight-knit prides and pride sizes are very small, perhaps not really prides at all, yet kinship is obviously important to female interactions and reproductive success (see Rudnai, 1973). The group of males wanders between the different prides' territories, mating with females of each. The ability of a single group of males to dominate several prides is probably favored by a lack of challenging males in the population. Floating males are rare, and until an equal-sized or more vigorous group of males arrives, the resident males should retain their status.

In Zambia's miombo woodland, lions live in small, unimale prides as well as relatively large prides. Some clearly dominant groups of males may not become resident with female groups (Ansell, 1969). Instead they appear to steal from prides and mate females of several prides. Marauding male groups would be favored as long as they were relatively uncommon in a population. If abundant, infanticide might be too high, and single pride males would either achieve too few fertilizations, or, they would be selected against because of inability to defend their own young or for contributing to the survival of unrelated young. The presence of a single pride male reduces male turnovers and thus infanticide and provides defense against grouped predators (H-1), but the male would have to achieve some reproductive success. Unimale prides should succeed in areas with male groups only because the latter are low in density.

It is to be expected that in poorer habitats, female groups would be minimal in size, and thus could support only one male. Unimale prides predominate in harsh, arid environments such as the Kalahari desert (Eloff, 1973). Groups of floating males also are found and they should be successful competitors for grouped females. In such habitats, however, food items tend to be small and sparsely distributed. Territories are not defendable and lion groups tend to be highly mobile, sharing common areas but temporally separated (Eloff, 1973), as in the cheetah. Groups of related males probably overpower single pride males but the expulsion should be only temporary. Moreover, the pride male can be assured of achieving most fertilizations anyway because densities are so low that male groups would not be able to locate estrous females in time.

There could be apostatic selection acting on the behavior of males, resulting in a polyephism for grouping and marauding versus competition for pride status and defense by single males. On the other hand, separate strategies employed by males could be determined by individual circumstances. In more productive habitats, female groups would be larger and capable of supporting male groups. Thus, grouping by males with prides would be highly advantageous.

It was argued that grouping by male cheetahs benefits subordinates even if they do not mate but are siblings. Aside from the advantages to females that minimize selfish mating by dominant male lions, why is it that male lions share, albeit unequally, in mating? The probability of males in groups being siblings is relatively small; their average relatedness is probably 0.25 or less. One male would not normally have enough personal reproductive success to sufficiently reward allies more distantly related than sibs. Each male of a group must assume equal risks including warfare with other males; thus, dominant males might serve their own interests by sharing with subordinates.

H-4. *Interspecific competition for critically limiting resources.* Almost all carnivores readily scavenge, and competition for kills can be very intense. Regardless of how apt a species is at capturing prey, ability to defend food against other species may favor grouping. Grouping could benefit individuals because of its advantages in defending or stealing food from competing species. Cooperative defense or theft of food is a logical precedent to group hunting (H-2) (Eaton and Hutchins, in press).

If a carnivore were the largest member of a predator guild but a smaller, subordinate species grouped, the largest member might be prevented from stealing kills from the smaller species. If the smaller species grouped because of advantages in defense of resources against its dominants, then the smaller species might also benefit by stealing from dominants. Such an occurrence might in turn favor grouping by the larger species, and so on (Eaton, 1975). For example, a single grizzly bear can exclude a wolf from its kill, and then feed for several days from the carcass. But the ability of even a small pack of wolves to expell a grizzly bear (Mech, 1970) suggests that wolves may have evolved grouping to defend clumped resources against a stealing species. As a consequence, the wolf may have achieved dominant behavioral and ecological status in its guild.

The following arguments largely ignore quantitative analysis of indirect or exploitive competition as at least in the predator guilds of the lion and cheetah in Africa, behavioral rank correlates with ecological status, which in turn corresponds with overlap of resources. For example, the lion and hyena overlap most, the wild dog overlaps most with its closest-ranking subordinate, the cheetah, and so on. A detailed study of ecological competition and its relationship to interspecific, behavioral hierarchy and grouping is under preparation.

While the fundamental foraging behavior of felids is basically less suited to predation in more open habitats, the typical felid can dominate an equal-sized or larger canid or hyenid in a one-to-one encounter. It is probable that a single 25-pound bobcat can win an encounter against two 30-pound coyotes, or a single wolf weighing 100 pounds. A leopard readily wins against an equal-sized hyena (Kruuk, 1972) but loses against several. A solitary, large felid entering the savannas could benefit purely by scavenging from a number of solitary predators and small groups of inferior predators. However, it would lose against larger groups so long as an individual of the species is capable of inflicting harm. Because a single felid typically kills larger prey than a single canid or hyenid of equal size, these species might benefit by stealing from solitary felids, and grouping to do so.

If grouping were favored because of advantages in defending or stealing food from other species then the degree of grouping by cheetahs should directly correlate with the density and/or number of competing species. Grouping by cheetahs inversely correlates with density and number of competitors (Eaton, 1974a).

Lions, hyenas and leopards frequently steal from cheetahs (Eaton, 1974a; Schaller, 1972; Kruuk, 1972); however, cheetahs *never* steal from them. Moreover, even when cheetahs outnumber equivalent-size competitors, the competitiors almost always win. Sacrifices in weaponry--teeth, musculature, claws--required to prey on small swift gazelles has severly limited the interspecific competitiveness of cheetahs against equal (leopard, hyena) or larger (lion) predators. Because two or more cheetahs are hardly if any more effective in defense of kills than a single cheetah, grouping is disfavored by interspecific competition with dominants.

The behavior of cheetahs at feeding sites reflects fear (risks) of dominants: cheetahs eat quickly and often move off before the kill is consumed (Eaton, 1974a). Cheetahs have evolved imitative, interspecific displays, quite terrifying in appearance but largely ineffectual against dominants, as they are rarely backed up with actual combat (Eaton, 1974a), and then only against a *smaller* leopard or a single hyena.

H-4 is not upheld for the cheetah; however, an alternative hypothesis, H-4: *that grouping is disfavored by interspecific competition*, should be tested.

An apparent inverse relationship between the frequency of theft by dominants and grouping by cheetahs suggests that interspecific competition is the limiting factor on most populations. The cheetah has--by far--the narrowest niche in its guild, which probably has reduced overlap with dominants. By living in very open habitats and relying on speed to capture small, elusive prey during daylight, the cheetah indirectly competes with only a mobile, low-ranking and relatively uncommon species, the wild dog. The wild dog rarely scavenges or steals (Pienaar, 1969); the cheetah is not known to scavenge or steal (Eaton, 1974a), which indicates that niche breadth is directly related to interspecific rank (Morse, 1975) and, for the cheetah, degree of sociality. The cheetah's niche may minimize theft of food by larger species but may tend to maximize predation because the major predators are more active at night, indicating that theft of food is more limiting than predation. If large populations of lions and hyenas can subsist on solitary hunting of gazelles for extended periods during the dry season, (Schaller, 1972; Kruuk, 1972) then cheetahs (and wild dogs), which are specialists at preying on these and-similar species, may pursue migratory prey not because prey is limiting on the plains but because of threat of dominants.

According to H-4', as interspecific competition decreases, the density of cheetahs and proportion of cheetahs in groups should increase. For whatever benefits accrue from grouping, a reduction in density and number of dominants should lead to more advanced sociality as well as a broader niche. Greater sociality, for example, extended family, can be expected to evolve if only a small portion of individuals display rudiments of grouping and this tendency has a genetic base; rapid evolution can be expected in 10 to 100 generations (Wilson, 1975), which is normally equivalent to 20 to 200 years in the cheetah. More than rudiments of grouping exist in the cheetah.

In South West African (SWA) ranchlands, all dominants have been extirpated for 80 to 100 years (Gaerdes, 1973-74), or 40 to 50 generations of cheetahs. Interspecific competition is non-existant. Cheetahs exhibit the greatest degree of grouping, as well as the highest density of any larger region (Myers, 1976). In SWA's Etosha Park, which has a full guild, Lowry's (1975) impression was that cheetahs, "are being kept down (i.e., very rare) in game reserves by other predators taking their potential food as well as their young."

The SWA ranchlands population may be ranked as more social as females with offspring often have adults and/or older offspring accompanying them. This more advanced stage is known to occur, although much less frequently, in only one other opoulation, Nairobi Park, which lacks two (hyena and wild dog) competitors. And, also in accordance with the predictions of H-4', Nairobi Park has the highest density of cheetahs known for a discrete area (Eaton, 1974a).

Cheetahs in South West Africa's Ranchlands

Clearly, H-4'is supported. Thus, it is important to substantiate in greater detail that grouping in cheetah populations is inversely related to interspecific competition.

Through the survey results and over 50 years of observations by Gaerdes (1973-4) plus data in correspondence (J. Gaerdes, pers. comm.; H. Theron, pers.

comm.) I have compiled information on sizes of groups--there is much less on group compositions--in SWA. In compiling the data I assumed that groups without offspring, individuals smaller than adults, were composed entirely of adults, although these could be young adult offspring.

The average number of adults in groups *unaccompanied by young*, including sightings of single cheetahs, was 3.92 (n = 200), with a range of 1-9, possibly 14 (Table 1). Average group size is probably minimal since many multiple sightings of groups of four and more were tabulated only once. All but four of the groups were sighted after 1955, or after 60-80 years of near complete extirpation of dominants.

As to the composition and size of groups with offspring, I assumed that at least one female was among adults of a group. The average number of adults accompanied by offspring is nearly double the typical single-adult family elsewhere (Table 1). There was a total of 19 females and 44 other adults with 106 offspring of 32 litters. Fifteen of 32 groups with offspring had 2 or more adults; 17 groups had only 1 adult. In the groups which had 2 or more adults, the average number of adults was 3.0, with a maximum of 5. In addition to these, 2 mixed-age groups with at least 2 adults in each were reported to have 8 and 12 individuals.

The sex-ratio of 2:1 (Table 1) for adults observed singly, in groups and single-female groups, was 85:44 (males: females) with 158 unknown. Data on sex-ratio of offspring are lacking, but in 4 family groups with one adult each, the sex-ratio of litters was 9:5 plus 1 unknown. With a group of 6 adults there were 4 males and 1 unknown offspring. In another groups were 1 adult female, 2:1 nearly adult cubs and three 6-month old cubs, which suggests the composition and origin of multi-adult family units as typically consisting of mother and offspring (probably daughters). The sample indicates a sex-ratio at birth in favor of males, but it is too small to be accurate. The sex-ratio of over 40 first generation captive born litters of imported SWA cheetahs was 2:1 (Eaton, in press, b).

The age structure is as follows: 252 adults in all-adult groups plus 67+ adults with offspring. Offspring include 106 reported plus an assumed one-half of mixed age groups of 8 and 12, for an added 10 and a total of 116 offspring. The age structure is about 3:1, as reported elsewhere (Eaton, 1974a). However, as it appears that young adult offspring may group with parents in SWA more than in other populations, age structures may not be comparable.

Comparisons with Cheetahs of other Populations

The average size of adult groups in Nairobi Park, which lacks hyenas and hunting dogs, is between 2 and 3. In the Serengeti with a full guild it is only 1.6 (Schaller, 1972). The largest and rarest group size (3%) in the Serengeti was 4; groups of 4 adults have been fairly common (possibly 20%) in Nairobi Park. In the ranchlands of SWA, the average adult group is at least 3.9 (Table 1).

If interspecific competition disfavors grouping in cheetahs then wherever there is a full complement of guild members, group size should be small and only males should group according to H-3. Most cheetahs in Kruger are in groups of 2 (Pienaar, 1969). Although the composition of these groups is unknown, there is no indication, such as presence of young, which would suggest grouping by other than males. Apparently family groups consist of a single adult and one litter (Wroggeman, 1976). Like the Serengeti, Kruger has all dominants plus a small population of the brown hyena which can dominate cheetahs and prey on them (Mills, 1973; Eaton, in press, a). Kruger cheetahs may have incurred reduced interspecific competition until 1960 because of intensive control of larger predators. The cheetah produces more offspring per unit of time than any of its major *direct* competitors, lions and hyenas. The cheetah's major indirect competitor, the wild dog, probably was *most* seriously reduced by control effort. During predator control, the cheetah population probably expanded relative to populations of competitors, thus, grouping should have become more prevalent. Since control, average group size of adults (probably only males) should have declined. Just recently, limited control of lions was resumed (Smuts, 1976); hopefully, social behavior of other predators is being monitored.

Sex-ratio should increase under good conditions and decrease under poor conditions (Pianka, 1975). Where interspecific competition has been reduced, the sex-ratio of a cheetah population should be high, and male groups should be larger. In Kruger Park the adult sex-ratio of 51 cheetahs was 2:1, while after control, the ratio of 471 cheetahs was 1 4:1 (Wroggeman, 1976), taken over several years (Table 1). In the Serengeti Park, the sex-ratio of cubs and juveniles was about 1:2, and for adults 1:3 (Schaller, 1973). Eaton (1970b) and McLaughlin (1970) observed a high adult sex-ratio in Nairobi Park, and McLaughlin (1970) recorded nearly a 5:1 sex-ratio for cubs. (Nairobi Park

Table 1. A comparison of cheetah populations (see text for particulars).

Population	Number of Dominants	Ave. Size All-Adult Groups	Largest Adult Group	Ave. No. Adults with Offspring	Adult Sex Ratio	Kitten and Juvenile Sex Ratio	Source
Serengeti	4	1.6	4	1	1:2	1:2 1:1 (approx)	Schaller, 1972 G. Frame, pers. comm., 1976
Kruger	4-5	2	?	1	2.1:1* 1.4:1**	?	Pienaar, 1969 Wroggeman, 1976
Nairobi	2	2-3	5-6	1	2.6:1	4.5:1 5:1	Eaton, 1970 McLaughlin, 1970
S.W.A. ranchlands	0	3.9+	9-14	1.9	2:1	3:1	Gaerdes, 1973-74 J. Gaerdes, pers. comm., 1974-76

* during predator control
** after predator control

cheetahs incur relatively little interspecific competition.) Kruger Park cheetahs may have had a higher sex-ratio because of control of larger predators until 1960, followed by a less favorable period.

The low-sex ratio, and puzzling scarcity, of cheetahs in the Serengeti can probably be explained by the combined effects of: 1) fractionating the ecosystem, which, among other things, places the cheetahs that follow migrating prey out of the park at a severe disadvantage due to human pressures; 2) cheetahs that remain in the park face the greatest degree of competition and predation during their limiting season. Thus, productivity, group-size and sex-ratio have declined. The scarcity and small group-size of wild dogs in the Serengeti are probably also caused by these interacting factors.

More advanced social evolution is indicated in SWA cheetahs imported the past decade to zoos in the U.S. Compared with previously imported East African cheetahs, the cheetahs from SWA have shown greater social and interspecific tolerance, which may explain their much higher breeding performance in captivity (Eaton, in press, b). SWA cheetahs are larger than cheetahs of other populations, which could result from removal of interspecific competition and a broader fundamental niche. The cheetah exhibits the least sexual dimorphism in body size of any larger felid except the presumably monogamous snow leopard. Sexual dimorphism appears most pronounced in cheetahs from Nairobi Park and SWA, possibly a result of a reduction in interspecific competition. Intrasexual competition should favor increased sexual dimorphism in the absence of counter-selection for ecotypic body size where a narrower niche is imposed by dominants.

Larger body-size and greater sexual dimorphism of SWA cheetahs does not appear to be related to a larger size of prey, but data are scarce on exact sizes of kills (Gaerdes, 1973-74). However, observation of group hunting (J. Gaerdes, pers. comm.; H. Theron, pers. comm.) suggests successful, cooperative tactics (H-2) as described elsewhere only in Nairobi Park (Eaton, 1974a).

Summary - The Cheetah

However efficient grouping is for capturing prey, in areas with abundant dominants the costs of theft may be too great for grouping to be favored. The conspicuousness of several adults should increase the frequency of theft by dominants. With few or no dominants, hunting efficiency should be sufficient to favor grouping (H-2). Thus, in some areas where dominants abound, males must benefit from grouping because of intrasexual competition (H-3), the advantages of which are probably sufficient to override the costs of interspecific competition (H-4). Grouping by females could be favored because it reduces predation on infants by numerous, smaller predators (H-1), by males (H-3), and/or because foraging efficiency is enhanced (H-2).

Intrasexual competition (H-3), predation by species subordinate to adults (H-1) and increased efficiency of foraging (H-2) could account for increased grouping. All of these benefits would be enhanced by removal of interspecific competition from dominants. For example, with removal of the cheetah's dominants, numerous subordinate species should be favored and have higher densities. Species such as ratels, jackals, servals and caracals, etc., could all threaten younger cheetahs (Eaton, in press, c). Grouping could be favored because of H-1, as in the lion in which females can divide labor and provide full-time protection for offspring against predators dominated by a single adult but vulnerable if left alone. (Whether or not the smaller predators significantly increase with the removal of the cheetah's dominants, defense against smaller predators could favor grouping by females.)

The Lion

The lion of 350 to 400 pounds is subordinate to groups of hyenas of 100 to 130 pounds (Kruuk, 1972; Pienaar, 1969) and hunting dogs weighing only 35 to 50 pounds each (in East Africa). Not only do these species win in competition for carcasses, groups can kill single lions. Thus, it is possible that lions evolved grouping to defend their kills against smaller, social predators. The presence of grouped competitors would cause evolution of grouping in lions. The following observation are consistent with H-4.

1. In terms of biomass or number of predators or biomass of prey, the ecologically dominant predator or African mammalian predator guilds is the lion (Schaller, 1972; Smuts, 1976), with the next most dominant species being the spotted hyena[2]. These species are the greatest competitors in an ecological sense, as they overlap most in food resources (see Schaller, 1972; Kruuk, 1972). They also exert the greatest level of competition on each other for carcasses. Schaller (1972) found that one lion could not defend a kill against a pack of hyenas, but two or more could. Perhaps equally important, grouped lions successfully steal food from packs of hyenas, but one lion cannot. Food

[2] However, until human alteration of ecosystems, the wild dog may have ranked as high as or higher than the hyena.

stolen from hyenas is a significant portion of the lion's diet; in some areas, groups of lions acquire the majority of their food by stealing from hyenas (Kruuk, 1972).

2. Rudnai (1973) observed that lions drag the carcasses of multiple kills together, and in every case the lions remained nearby and fed until the carcasses were consumed. Schaller (1972) noted that some kills may be abandoned before consumed, but the important point is that grouped lions are able to multiply their resources through group defense of food against other predators and scavengers. When food is scarce, lions should remain near their kills and consume them entirely. Only group defense could allow realization of the benefits of group hunting.

3. The evolutionary result of interspecific competition of a direct, behavioral nature should be adaptations for interspecific aggression. Lions and hyenas expend time and energy attacking and killing one another without any direct benefit, for example, there is no competitive goal such as food, and normally the victim is not eaten (Schaller, 1972; Kruuk, 1972; Eloff, 1973). The expressive behavior of lions interacting with hyenas is not associated or apparently evolved from predatory behavior, but rather resembles offensive or defensive (depending on which species poses the greatest threat, which is dependent largely on numbers of each) aggressive patterns observed in the intraspecific realm (Eaton, 1973; Schaller, 1972; van Lawick-Goodall and van Lawick-Goodall, 1971). The lion's behavior manifests an evolved motivation of interspecific aggression, not predation, towards hyenas, the lion's greatest competito

If grouping by lions is caused by interspecific competition for food, then lions might be expected to forage in groups during the limiting season when competition with hyenas should be most intense. On the other hand, the large size of the lion usually makes grouping less economical than solitary hunting in the dry season (Schaller, 1972). While hyenas hunt, steal or scavenge individually, they also tend to group more on a year-round basis than lions (van Lawick-Goodall and van Lawick-Goodall, 1971; Kruuk, 1972). If single lions can support themselves with gazelles, it is not unlikely that groups of three hyenas would do about as well utilizing the same prey resource. Hyenas are able to use virtually 100% of a kill, while lions use about 75% (Schaller, 1972). But hunting of gazelles in open terrain must favor solitary larger predators whether they employ hyenid or felid tactics. Like lions, hyenas tend to break up during the same season to hunt migratory or small prey; both tend to singly hunt Thomson's gazelles. In fact single hyenas are most successful killing gazelles in the dry season (Kruuk, 1972). As most gazelles killed are solitary, food items are scarce and tend to be widely dispersed.

Regardless of group size, hyenas would not be able to gain by stealing, from lions; the size and denisty of dead but uneaten carcasses killed by lions would make group foraging (stealing) uneconomical. By the same token, especially considering that a small group of hyenas can consume a gazelle faster then a single lion of equal biomass, lions could not gain by grouping to steal from hyenas during the dry season.

If solitary hunting is the optimal mode for lions in the dry season of the Serengeti area, then why should lions always group in the Kalahari with such extremely low densitites of biomass and larger prey species? As Kalahari lions are highly mobile, individuals would have to remain close together to maintain their groups, but this does not explain why they group. If anything, a social system similar to the cheetah's should be expected. Perhaps interspecific competition with the hyena (and with man, below), may explain grouping by desert-living lions.

In such extremely open habitats, hyenas are probably more efficient predators of the largest ungulates. Lions kill larger herbivores only rarely in the Kalahari (Eloff, 1973). Without grouping, lions could not defend offspring against hyenas (H-1), especially when prides are constantly moving and the terrain is not conducive to escape and hiding. A single male with a female group may deter otherwise dominating hyenas. A male and females may gain from grouping because of interspecific competition (H-4) and protection of offspring (H-1).

Generally as the productivity of habitats increases, the size of groups of social predators increases. If interspecific competition is a factor in grouping then lions should have the largest groups where their competitors have the largest groups and vice-versa. In the Serengeti area, lion prides are larger on the average then anywhere (Schaller, 1972), and so are hyena packs (Kruuk, 1972). But this trend does not hold up in Kruger Park, where hyenas form small groups (G. Smuts, pers. comm.), or the opposite trend locally as in Ngorongoro Crater (Kruuk, 1972), for reasons not contradictory to the hypothesis (Eaton, in prep.). Lions are extremely dense in Nairobi Park, which lacks hyenas and wild dogs

(Eaton, 1974a; Rudnai, 1973). Females form only loose associations and only one group of males shares several prides (Rudani, 1973).

Summary: The Lion

All of the hypotheses can explain grouping by lions. Interspecific competition for clumped resources (H-4) and predation of offspring (H-1) are inseparable factors most likely to have caused the initial evolution of grouping in lions, probably among females. Between close competitiors, such as lions and hyenas, it is probably justified to consider what others have tended to label predation as interspecific aggression, which has evolved not for its advantages in directly acquiring food as competitors usually are not eaten. Rather, the investment, almost always entailing some risk when carnivores are involved, has a long-term gain in terms of reducing predation, theft of food and exploitive competition. However, for males, intrasexual competition would have been equally important as indicated by the cheetah (H-3), and certainly it became the paramount feature in the association of male groups with female groups. After separate male and female groups were evolving, cooperative hunting by members of groups is to be expected, as seen in male cheetahs and non-pride male groups in the Kalahari (Eloff, 1973). Then with association of males and females, cooperative hunting became even more pronounced among females but less important to prime males, which have become warriors and inseminators (H-3), but which also contribute to hunting success by killing large prey (H-2).

Reconstruction of Social Evolution

The Cheetah

Grouping because of intrasexual competition (H-3) would not have evolved until the cheetah had reached an extreme level of specialization on highly mobile, small prey, because this necessitates a temporal spacing system. If direct interspecific competition and predation have been as significant as indicated, then it is to expected that the spacing system used by cheetahs today evolved partly as an adaptation for avoiding dominants, which not only establish group territories, but which also exhibit nomadism, migration and solitary foraging within the same populations. Temporal spacing could evolve in subordinate guild members initially not because of specialization on highly mobile prey but because of interspecific competition, with advantages in intraspecific competition being secondary. It does benefit cheetahs to avoid congestions and to shift their location relative to movements of their prey, but were it not for interspecific competition and threat of predation (possibly aggression) from dominants, the optimal spacing system for a solitary or grouped mammalian predator would appear to be geographical, not temporal, territory.

The fact that solitary-hunting, territorial-resident lions and hyenas can utilize gazelles during the dry season indicates that cheetahs would gain more if they were territorial rather than highly mobile. Apparently, cheetahs migrate to reduce interspecific competition; and, especially females should benefit by reducing predation on offspring.

Grouping normally benefits males because of advantages in intrasexual competition, which is possible only because of temporal spacing. Thus, the ultimate cause of evolution of unisexual grouping is interspecific competition. Male cheetahs should not have grouped until after lions and hyenas had evolved socially to the point of group territoriality, which would have been advantageous to both in intraspecific and interspecific competition. This may have coincided and been causally related to extinction of large canids and evolution of the small and specialized hunting dog, resulting in added competition for the cheetah and further selection for temporal spacing. Thus, I would speculate that grouping by males did not evolve until the appearance of the wild dog.

The evolution of sociality or further social behavior in dominants should lead to a greater competitive impact and, thus, a narrower niche in subordinates. Temporal spacing by the cheetah seems to reduce its niche breadth. If temporal spacing favored grouping by males, what effect has this had on the cheetah's niche? Grouping by males does not appear to alter the cheetah's niche breath *except* where dominants are reduced. Interestingly, in the past century, it has been the selective predation by the dominant predator, man, on all other guild members higher in rank than the cheetah, which has indirectly led to greater grouping and probably a broader niche in the cheetah population of SWA, and locally in East Africa (e.g., Graham and Parker, 1965). All the species extirpated were social and ranked between the "dominant" and most subordinate in the guild. The lowest ranking species, the cheetah, has been able to evolve a higher level of social behavior only because the higher ranking guild members competed much more with man for prey resources. Oddly, this has favored greater sociality in the cheetah, which should result in greater impact on the "dominant's" resources, and, thus, counter-selection against grouping, which may be occurring now in SWA (P. Jonas, pers. comm.).

The Lion

It is reasonable that the ancestral lion occupied habitats and had a social organization comparable to the larger, asocial polygynous felids of today, such as the leopard, tiger and puma. In wooded savannas, lions would have found higher carrying capacity and an increased density and diversity of other carnivores. The lion would have faced a new kind of competitor in social canids and hominids, possibly social hyenids, or at least faced social competitors in a habitat more favorable to their success in direct confrontations, such as contests for food, interpsecific aggression and predation. Although smaller, grouped canids, hyenids and probably hominids would have dominated individual lions. In defense of food and offspring in open areas densely saturated with grouped predators, grouping would have favored a large felid. How would grouping most likely occur--between who and whom--and what causes would have been important at each stage? Social evolution is reconstructed from what has been described for the asocial species and the cheetah.

Due to intense predation on offspring, as in the cheetah, as well as inability to utilize kills being stolen by grouped predators, females would have had higher success by grouping. The step from simple family to a grouped female unit involves a relatively simple adjustment in relationship. Mother and daughter ties would already by strong and lasting because of the evolution of site tenacity in mature, solitary-living daughters as in the puma, which apparently evolves for two reasons: a) by reserving space within their territories females could increase the probability that a daughter and not some unrelated or more distantly related female replaces her; and/or b) the female could gain by providing inclusive territorial space for daughters to breed.

In many carnivores it is usually the aggressive or secretive behavior of parents that leads to offspring dispersal. In the evolution of grouping in felids the only change would be one of not expelling female offspring. Kleiman and Eisenberg(1973) presented a model for the course of social evolution in felids. They argued that the change from asociality to sociality begins with a male remaining with one of the females he has been associated with only briefly for mating in the past. Such a transition is less probable than parent-offspring association in which the female lives with adult offspring.

It is much simpler to change directly to polygynous sociality than pass through monogamy in the process. A monogamous male could not have successfully competed with a male group. Females can gain from grouping first with other females rather than males for several reasons, for example, suckling young. Males would not have anything to gain from monogamy, but they could gain by grouping with several females. Monogamy would be selected against rapidly, if not from competition with grouped males, then because females in groups--which can dominate a single male lion--would be outcompeting monogamously mated females and therefore monogamous males would be at a disadvantage. By gains and losses to individuals there may never have been monogamy.

Less behavioral adjustment is required to change from asocial polygyny to sociality directly than by passing through monogamy. In changing from polygyny to monogamy, the following might be expected: a) increased tolerance of the female by the male when the female is not in mating condition. In the absence of released inhibitory mechanisms normally operative in courtship the male's aggression would have to become inhibited; b) the same would apply to the female when not in estrus; c) the male would have to become further inhibited, for example, predation or aggression towards offspring; and, d) when offspring and the male are together, the female's behavior would have to change from protectiveness to trustworthiness.

In a direct transition from asocial polygyny to sociality by extension of relationship between mother and daughter, only one behavioral modification would have been required over what we observe today in representative asocial species such as the puma. The female would simply tolerate her offspring as they entered adulthood. Either aggression would have to be inhibited or the female would cease using separative tactics, such as hiding and avoidance (Eaton, 1974a). A female and her nearly adult offspring normally have well established ordered relationships, which should be more conducive to grouping than the brief, rather aggressive mating bond between male and female. Moreover, a family group consists of highly related individuals which, everything else being the same, is more conducive to social behavior and cooperation. Felid families are adapted to sharing resources. In simple families "group" hunting suggests the potential for a higher efficiency of foraging; prior to the mother's normal separation from a litter the offspring are relatively efficient hunters. Where conditions permit, family members should benefit most from group hunting.

If all the behavioral changes described for evolution of grouping were in fact under genetic influence, the most probable course to sociality in felids would have been extension of family ties into adulthood, that is between mother and daughter, and between males which are siblings. The observations that: a) male cheetahs group and appear to be brothers; b) even in habitats where lion prides normally have one male, males group and they appear to be closely related; and, c) in cheetah populations with reduced interspecific competition females group (probably with daughters, possibly sisters) are consistant with the hypothesis that sociality in felids evolved from polygny, not monogamy.

The successive stages must have been this: grouping by females because of advantages in reduction of predation (H-1) and in interspecific competition for resources (H-4), coincident with grouping by males because of intrasexual competition (H-3), and then association of males and females for advantages in interspecific competition (H-3), and, for both sexes, enhanced benefits from defense against predation (H-1) and foraging(H-2).

The initial evolution of grouping in lions probably was at the transition between wooded savanna and forest, as the habitat of leopards tends to be in the Serengeti today. To progress from the asocial pattern to grouping would have involved the association of females within a resident male's territory. The females in a resident male's territory would have increased in number from about 2 or 3 to 4 or 6. Females would be favored which formed groups larger than two because of the disproportionately greater reproductive success which at least three females gain over two. When two females form a group, and one hunts while the other tends offspring, each faces high risks from grouped predators. With three or more females all femlaes should benefit because two could protect offspring against most groups of predators, or two could hunt together, if not initially cooperatively, then individually, followed by cooperative protection of food against grouped predators. Four females would do even better in division of labor. They could consort in a minimum of pairs, which would benefit them in terms of defense against predation and defense or theft of food. Without the association of a male, four females may have been an optimal group. With addition of a male, three would have been optimal, for example, as in the Kalahari.

As soon as female grouping became successful, it would have become increasingly difficult for a resident, dominant male to prevent other males from mating. Expelled males would be favored by grouping because of reduced risks from aggression by resident males, higher reproductive success and interspecific competition, the latter being more important in more productive, open habitats. By grouping males could better defend or steal food. The frequency of males dispersing in groups would increase as a consequence of grouping by females. The probability of two females producing two, related males which survive to adulthood is probably more than twice as great as one female producing two adult sons, and so on. Groups of two or more related males would displace single, resident males in territories containing small groups of females, as in Nairobi Park today (Rudnai, 1973).

As females grouped, the ability of a resident male or group of males to defend separate groups of females within one territory would markedly decline partly because of more females, but also because as female groups enlarged, division of labor and temporary splintering of individuals and subgroups would scatter females out over space and time, which would increase the probability of nonresident males achieving mating. If groups of resident males splintered to counter the proliferation of females, floating males including individuals and cohesive groups would be all the more favored. Thus, selection would favor males that remained as close as possible to a female group. Before long, resident males would have defended single groups of females and their territories. The size of male groups would have been affected by a number of factors, but ultimately by kin selection and the size of female groups, the latter being a reflection of the quality of a territory, and the ability of females to support males.

At the stage of males joining autonomous female groups, intrasexual competition between males would have favored increased sexual dimorphism in males: larger size and the mane. Greater conspicuousness would have reduced the hunting ability of males relative to females. With less selective pressure on hunting ability of prime-aged males, increased sexual dimorphism would have cost females for having to provision so much more food which could have gone to offspring and female relatives. Females may have gained overall because of reduced male turnover rate plus the fact that a male is far more effective than a female in defense against predation and theft or protection of food.

Group hunting by females and by males would already have evolved prior to males associating with prides. Thus, group hunting tactics between males and females would have been successful. Intraspecific competition would have favored a greater division of labor between males and females, so that males were favored which most effectively defended females, and females were favored which were most effective foragers. The increased demands placed on females with males in their groups would have favored greater foraging ability of females and thus cooperative hunting.

After intrasexual competition between males and between females favored association of males with females, a new selective force would have favored grouping between the sexes: the ability to acquire exceptionally large prey previously not "killable" by groups of females or males would have resulted from increased sexual dimorphism of males and *preceding* social evolution.

The only significant differences in size of prey of solitary and group hunting lions is due to the cooperation of males in dispatching the largest prey species. Groups could kill larger prey *after* the evolution of exaggerated sexual dimorphism. Pronounced sexual dimorphism is an *effect* of males grouping with females (H-3). The ability of grouped lions to kill much larger prey than individuals (H-2) is a product of social evolution, not the cause of it. The same principle applies to direct interspecific competition for food (H-4) and defense against predation (H-1). Thus, the association of males with females must have greatly benefitted lions relative to their competitors.

As lion prides expanded with association of males able to acquire territory and expand resources, still more females could be added, which enhances the males' and all females' fitnesses. Prides would produce still larger male groups, which in turn would cause increasing rate of male turnover, eventually acting to reduce productivity until at equilibrium in terms of the optimal sex-ratio and pride size in a habitat, a function of its carrying capacity.

In different habitats, modern lions chiefly differ in the extent and structure of grouping by males. Scaling of social behavior probably overrides phylogenetic inertia within wide tolerance limits set by fluctuating environments. The social system of the lion is intrinsically as or more adaptable than that of social canids and hyenids; where sympatric, this partly explains the lion's dominance as well as its relatively greater success in competition with man, the "super dominant".

Relationships to Hominids

Carnivore students except Ewer (1973) have not speculated on the effect of hominids on the social evolution of carnivores, although several have speculated on the impact of social carnivores in hominid evolution. Attempts at the latter, for example by Schaller and Lowther (1968) are presented as if the carnivore scene has been static since hominids appeared. However, fossils indicate sympatry for millions of years between hominids, many extinct carnivores and the ancestors of extant social carnivores.

The cheetah was headed on its specialized course before hominids became part of the predator community, but lions may not have evolved until well after hominids were living in savannas and/or their edges. What role if any did hominids play in the social evolution of cheetahs and lions?

The addition of a large, dominant predator to the community, plus the increasing competitive influence of hominids as predators and stealing scavengers probably favored further specialization by the cheetah to open savannas and swifter prey. As the lion and hominids codominated wooded savannas, larger canids became extinct, giving rise to a smaller canid specializing in the same direction as the cheetah, culminating in the wild dog.

It seems not unlikely that stone-age man was at best codominant with the lion, and that the lion and man held a relationship similar in some respects to that of the lion and hyena today, in which interspecific rank is governed by numbers of each species engaged in encounters. Both would represent risks to the other in terms of predation, theft of food and interspecific aggression.

The Kalahari Bushmen of 20 years ago would not challenge lions for their kill, but readily dominated groups of cheetahs and hyenas (Marshall, 1957). The Kalahari lion offensively threatens humans that approach, and charges readily compared to lions which have been subject to selection by man with firearms, as in East Africa, where lions often run away at the sight of humans (Schaller and Lowther, 1968). It has not been recognized that human-caused selection has favored avoidance of man by lions in most regions, and probably only since just prior to the advent of agricultural and pastoralist societies, which have: sufficient numbers of males; time and energy to invest in interspecific combat; and, relatively advanced weaponry. I believe that it is only in the past few thousand years that man achieved fully dominant status over the lion in most of its range, and this may have been due as much to size of male human groups as to weaponry as the Kalahari Bushmen have long used bows and arrows with lethal poisons, and they are able in groups as small as four to kill species as large as giraffe (Marshall, 1957). If size of competing groups of hominids and lions has played a significant role in the evolution of grouping and dominance, then male lions may have originally gained from grouping because of interspecific competition with hominids in groups. Perhaps Kalahari male lions group because of the risks of theft and/or aggression by the Bushmen. In short, it strikes me as quite plausible that were it not for hominid influences on carnivores the lion may not have evolved or at least not have evolved socially as we know it today.

The hypothesis that dominant status over the lion was achieved by man fairly recently would explain the *unparalleled* symbolic status of the lion to so many African and southern Eurasian peoples (Eaton, in prep.). It would require numerous well-armed males to achieve dominance over the larger prides of lions. Larger prides often with three or more males happen to occur in the most productive habitats, also preferred by hunter-gatherer or pastoralist societies. Males of human warring societies have used the lion as a worthy adversary for demonstration of skills as a means of gaining status within groups as well as for training for intraspecific warfare. The dominant pastoralist societies of Africa, such as the large and powerful Masai went in groups of several well-armed and shielded individuals to attempt killing a *single* male lion. It should be appreciated that female lions might have joined males in interspecific competition with solely male groups of hominids.

It was only when man could dominate competing grouped predators that intraspecific competition between groups of hominids would have accelerated the evolution of technology and warfare. Perhaps reciprocity between unrelated groups --the keystone of hominid evolution--was initially favored because of its advantages in competition with grouped predators. If so, interspecific competition between our ancestors and lions may have been the last and most important obstacle to the evolution of civilization.

The insight of Aldo Leopold (1948) as to man's relationship with predators amounts to this: humility is necessary to preserve them. I believe he recognized that man still instinctively hates those species which have most threatened him

(H-1) or his success (H-4). The larger social carnivores have been until very recently the greatest nonhuman threat to man. Rather than exterminate them, we may grow by understanding them as mirrors and molders of our making. Perhaps this necessitates an acceptance of the lion within our being before we can realize the full potential of our differences.

Recommendations

A grand naturalistic experiment in social evolution could be undertaken in SWA if a cheetah population were permitted to continue *without* dominants, but in a suitable preserve. With the return of larger prey, cheetahs might quickly increase in size and, eventually, form multimale prides as in the lion. An equally illuminating project would consist of a few courageous men going to the Kalahari and following the same fundamental procedures used by Schaller and Lowther (1968) in East Africa. We already know that the Kung avoid lions, and that men on foot in East Africa normally dominate lions without overt threat or use of weaponry. The question is: would crudely armed human males, behaving in a cooperative manner, be able to steal food from Kalahari lions? How many would be required relative to the number of lions? Any interested volunteers should contact the author.

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LITERATURE CITED

Abbot, S. and T. Fuller. 1973. (Article on cheetahs in Serengeti.) *Smithsonian.*

Alexander, R. 1974. The evolution of social behavior. *Ann. Rev. of Ecology and Systematics* 5:325-383.

Adamson, J. 1971. *Pippa's Challenge.* Ballantine Books.

Asdell, S. A. 1964. *Patterns of Mammalian Reproduction.* 2nd Ed. Cornell University Press, Ithaca, New York.

Ansell, W. F. H. 1969. A multiple kill by lions, and a stolen kill. *Puka* 5:214-215.

Bertram, B. 1973. Lion population regulation. *East Africa Wildlife J.* 11:215-225.

Brown, J. and G. H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecology and Systematics* 1:239-262.

Eaton, R. L. 1970a. Hunting behavior of the cheetah. *J. Wildl. Mgmt* 34(1):56-67.

Eaton, R. L. 1970b. Group interactions, spacing and territoriality in the cheetah. *Zeit. f. Tierpsychologie* 27(4):481-491.

Eaton, R. L. 1970c. The predatory sequence with emphasis on killing behavior and its ontogeny in the cheetah. *Zeit F. Tierpsychologie* 24(4):492-504.

Eaton, R. L. 1973. Aggressive behavior in the lion. Ph.D. Dissertation, Purdue, University, W. Lafayette, Indiana.

Eaton, R. L. 1974a. *The Cheetah.* Van Nostrand Reinhold, New York.

Eaton, R. L. 1974b. The biology and social behavior of reproduction in the lion. In: R. Eaton (Ed.), *The World's Cats*, II. Feline Research Group, Woodland Park Zoo, Seattle, Washington.

Eaton, R. L. 1975. Sociality, niche breadth and social dominance in African carnivore guilds. (Abstract.) Ann. Meeting Am. Soc. of Mammalogists, June, 1975, Missoula, Montana.

Eaton, R. L. 1976. Reproductive biology of the leopard. *Der Zoologishche Garten.*

Eaton, R. L. In press. The brown hyena: a review of biology and status. *Mammalia.*

Eaton, R. L. In press, b. Propagation of the cheetah in captivity, a review and analysis. In: R. Eaton (Ed.), *The World's Cats*, III(3).

Eaton, R. L. In press, c. Mimicry of the ratel by the cheetah. *Evolution.*

Eaton, R. L. In preparation. The evolution of trophy hunting.

Eaton, R. L. and S. J. Craig. 1973. Captive management and mating behavior of the cheetah. In: R. Eaton (Ed.), *The World's Cats*, I. World Wildlife Safari and Institute for the Study and Conservation of Endangered Species, Winston, Oregon.

Eaton, R. L. and M. Hutchins. In press. Socio-ecology of carnivores: a model for hominid evolution. In: R. Harding and G. Teleki, (Ed.'s), *Diet and Hominid Evolution.* Columbia University Press.

Eaton, R. L. and K. Velander. In press. Reproduction in the puma: biology, behavior and ontogeny. In: R. Eaton (Ed.), *The World's Cats*, III(3).

Eloff, F. 1973. The ecology and social behavior of the Kalahari lion. In: R. Eaton (Ed.), *The World's Cats*, I. World Wildlife Safari, Winston, Oregon.

Eloff, F. 1973. Lion predation in the Kalahari Gemsbock National Park. *J. South African Wildl. Mgm't.*

Erickson, A. 1955. An ecological study of the bobcat. M.S. Thesis, Michigan State University, East Lansing, Michigan.

Ewer, R. F. 1973. *The Carnivores.* Cornell University Press, Ithaca, New York.

Ewer, R. F. 1974. The evolution of mating systems in the Felidae. Pp 110-120. In: R. Eaton (Ed.), *The World's Cats*, II. Feline Research Group, Woodland Park Zoo, Seattle, Washington.

Gaerdes, J. 1973-74. Geparden in Seudwest Afrika. *Southwest Africa Scientific Newsletter.* 14(9-12):31 pp.

Graham. A. 1966. Cheetah survey. *East Africa Wildlife J.* 4:50-55.

Graham A. and I. Parker. 1965. Cheetah survey. East Africa Wildlife Society, Nairobi (mimeo).

Herdman, R. 1972. Captive cheetah reproduction. *Zoonooz* 45(10):4-12.

Hornocker, M. 1969. Winter territoriality in mountain lions. *J. Wildl. Mgmt.* 33:457-464.

Hornocker, M. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* No. 21. The Wildlife Society, Washington, D.C.

Kleiman, D. G. 1974. The estrous cycle in the tiger. In: R. Eaton (Ed.), *The World's Cats*, II. Feline Research Group, Woodland Park Zoo, Seattle, Washington.

Kleiman, D. G. and J. F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behavior.* 21(4):637-659.

Kruuk, H. 1972. *The Spotted Hyena.* University Chicago Press, Chicago, Illinois.

Leopold, A. 1948. *A Sand County Almanac*, Oxford University Press.

Leyhausen, P. 1965. The communal organization of solitary mammals. *Symposia of the Zool. Soc. London* 14:249-263.

Leyhausen, P. and B. Tonkin. 1966. Breeding the black-footed cat, *Felis nigripes*, in captivity. *Int. Zoo Yb.* 6:178-182.

Lowry A. 1975. quoted in "Appeal for wildlife in danger.", *The Windhoek Advertiser* p. 13, 26 June.

Marshall, J. 1957. "The Hunters." McGraw Hill, New York.

McCord, C. M. 1974. Courtship behavior in free-ranging bobcats. In: R. Eaton (Ed.), *The World's Cats*, II. Feline Research Group, Woodland Park Zoo, Seattle, Washington.

McLaughlin, R. T. 1970. Aspects of the biology of cheetahs in Nairobi National Park. M.S. Thesis, University of Nairobi.

Mech, D. L. 1970. *The Wolf.* Natural History Press, New York.

Mills, G. 1973. The brown hyaena. *African Wildlife* 27(4):150-153.

Muckenhirn, N. and J. F. Eisenberg. 1973. The home ranges and predation of the Ceylon leopard. In: R. Eaton (Ed.), *The World's Cats*, I. World Wildlife Safari, Winston, Oregon.

Myers, N. 1976. Status of the cheetah and leopard in Africa. In: R. Eaton (Ed.), *The World's Cats*, III(1). Department of Zoology, University of Washington, Seattle, Washington.

Pienaar, U. de V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12:108-176.

Robinette, W., J. Gashwiler and O. Morris. 1961. Notes on cougar productivity and life history. *J. Mammal* 42(2):204-217.

Rudnai, J. 1973. Reproductive biology of lions in Nairobi National Park. *East African Wildlife J.* 11:241-253.

Schaller, G. B. 1967. *The Deer and the Tiger.* University Chicago Press, Chicago, Illinois.

Schaller, G. B. 1972. *The Serengeti Lion.* University of Chicago Press, Chicago, Illinois.

Schaller, G. H. and G. R. Lowther. 1969. The relevance of carnivore behavior to the study of early hominids. *Southwest J. Anthropology* 25:307-341.

Schenkel, R. 1968. *Toten Lowen ihre Artgenossen? Umschau* 6:172-174.

Seidensticker, J., M. Hornocker, W. Wiles and J. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* No. 35. The Wildlife Society, Washington, D.C.

Shorey, D. and R. L. Eaton. 1974. The management and behavior of the Bengal tiger under semi-natural conditions. In: R. Eaton (Ed.), *The World's Cats*, II. Feline Research Group, Woodland Park Zoo, Seattle, Washington.

Smuts, G. L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe*. 19.

van Lawick Goodall, H. and J. van Lawick Goodall. 1970. *Innocent Killers*. Collins, London.

Visser, J. 1976. Status and conservation of the smaller cats of southern Africa. In: R. Eaton (Ed.), *The World's Cats*, III(1), Department of Zoology, University of Washington, Seattle, Washington.

Walther, F. R. 1969. Flight behavior and avoidance of predators in Thomson's gazelle. *Behaviour* 34:184-221.

Wilson, E. O. 1975. *Sociobiology*. Harvard University Press, Cambridge, Mass.

Wrogemann, N. 1976. *Cheetah Under the Sun*. McGraw-Hill, Johannesburg.

Young, S. P. and E. A. Goldman. 1946. *The Puma*. Dover, New York.

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Dedicated to Our Memory of the Holistic Perception of Griff Ewer

Griff Ewer at Second Cat Conference, Winston, Oregon, 1973. Photo: K. Eaton.