

# Determinants of asociality in felids

T.M. CARO

*Evolution and Human Behavior Program, Rackham Building, University of Michigan,  
Ann Arbor, Michigan 48109-1070, USA*

## SUMMARY

**1** Despite a number of benefits that could accrue from living in groups, adult members of most felid species live alone, which suggests that there are considerable costs to living together for members of this family.

**2** The reasons why male felids of most species live alone, but why male cheetahs and lions live in groups are first discussed. I then address the more problematic question of why the great majority of adult female cats do not live together.

**3** The idea that females actually live alone for most of their lives is dismissed. Using data from free-living cheetahs, it is shown that their companions (dependent cubs) consume a large share of the food that females acquire, but help their mothers little in catching prey.

**4** Data are presented on the time that cheetah mothers spend hunting with litters of different sizes. They show that the amount of extra time necessary to sustain members of a social group would be prohibitively high.

**5** For cheetahs, hunting larger prey in order to feed group members would be no more profitable than hunting smaller prey because of the difficulties in capturing large prey items. Then data from males are presented to show that increasing group size does not result in significant increases in hunting success.

**6** These results suggest that in becoming social, cheetah mothers would have to spend too much time hunting unless there were sufficient numbers of large or vulnerable prey in the habitat.

**7** The implications of these findings are then extended to other species of felid. Prey larger than that normally taken by females, necessary to sustain two families living together, is relatively scarce in nearly all the habitats that have been studied. The review suggests that conditions necessary for sociality to evolve are absent for virtually all extant felids.

## INTRODUCTION

In most of the thirty-seven species of felids, males and females are asocial. Only in cheetahs (*Acinonyx jubatus*) (Frame & Frame 1981) and lions (*Panthera leo*) (Schaller 1972) do males live in groups, and females live communally only in the latter species (van Orsdol, Hanby & Bygott 1985). A number of hypotheses have been advanced to explain why carnivores, including lions (see, for example, Caraco & Wolf 1975; Clark 1987), live in groups. For example, increased group

size might benefit individuals of both sexes because it might increase the chances of detecting predators (Rood 1986), it could reduce the risk of losing carcasses to other predators (Lamprecht 1978, 1981), or it might lower risks of injury during prey capture (see, for example, Gashwiler & Robinette 1957). For females in particular, the probability of infanticide by males is likely to be reduced if they defend their cubs together (Packer & Pusey 1983), while for males, group living might enhance access to females through advantages in contests with single males (Bygott, Bertram & Hanby 1979; Caro & Collins 1986). However, advantages that predators might gain through hunting cooperatively, previously thought to be an important evolutionary cause of sociality in many carnivores (Kruuk 1972, 1975; Curio 1976), have now been convincingly dismissed across a wide range of species, including lions (Packer 1986), especially when large or single prey times are hunted and when individual hunting success is reasonably high (Packer, in press; Packer & Ruttan 1988).

In the Felidae, both sexes could, in theory, benefit from group living in a number of different ways in so far as small cats suffer from predation (for example, servals *Leptailurus serval* by leopards *Panthera pardus*: Schaller 1972), felids lose carcasses to other predators (such as servals and cheetahs to spotted hyaenas, *Crocuta crocuta*: Geertsema 1985; Schaller 1972 respectively), cubs of several species are subject to infanticide by males (tigers *Panthera tigris*: Schaller 1967; cougars, *Felis concolor*: Seidensticker *et al.* 1973; possibly cheetahs: Burney 1980; see also Packer & Pusey 1984), and all male Felidae compete over access to females (for example, lions: Owens & Owens 1984; caracals, *Felis caracal*: Pringle & Pringle 1979). Indeed, in situations where domestic cats *Felis catus* are provisioned on farms and live socially, several females appear to guard and defend kittens from visiting males (MacDonald & Apps 1978). Therefore, considering the theoretical benefits of group living, it seems probable that there must also be considerable costs to explain why most members of this family are not social, yet to date these costs have not been examined.

This chapter focuses particularly on the costs of sociality rather than discussing its possible benefits. Packer (1986) also addresses the topic of felid sociality arguing that in those species where female felids live at high population densities, in open habitats, and which capture large prey, it would pay females to share their visible carcasses with female relatives rather than inevitably relinquish parts of them to unrelated conspecifics (see also Waser & Waser 1985). This reasoning may explain why female lions living in savannah regions could minimize foraging costs by living amongst groups of female relatives that do not disperse from their natal home range.

Three sets of observations question the generality of this explanation. First, lionesses should be solitary, in situations where prey carcasses would not be found by conspecifics, for example, in habitats where visibility is poor, such as thick woodlands, or where lionesses live at low densities. At present, there are insufficient data to test this proposition critically, but it is known that pride size does remain relatively constant across a wide range of lion populations living in

different habitats (Eloff 1973; van Orsdol 1981). Moreover, lionesses living at reduced densities in many areas where human hunting pressure is high should now live alone, but there is no strong evidence in support of this.

Second, in palaeartic and subarctic regions both predators and the carcasses of their prey can sometimes be seen from long distances, especially if snow is lying. Moreover, carcasses in these regions often last longer than in the tropics because of freezing temperatures. In some of these areas, felids such as lynxes, *Lynx canadensis*, and bobcats, *Lynx rufus*, live at high densities and often feed on large prey (see below), so females of these species would also be expected to be social in some regions if Packer's suggestion is applicable to species other than lions.

Third, it is known that nearly all felids scavenge (see, for example, Konecny 1987), including the morphologically specialized ones (Skinner 1979; Caro 1982), and there is growing evidence as studies accumulate that solitary, and presumably unrelated, individuals form temporary aggregations at kills in species other than lions (tigers: Schaller 1967; cougars: Scidensticker *et al.* 1973; cheetahs: personal observations). Thus, females in these species would also be expected to reduce foraging costs by sharing their kills with related adult females, as argued for lions.

Most troubling perhaps, are the tigresses living in the dry deciduous habitat of Ranthambore National Park, where visibility is good, at population densities higher (10/100 km<sup>2</sup>) than savannah lions (7.9/100 km<sup>2</sup>). Adult females sometimes take large sambar, *Cervus unicolor*, are attracted to each other's kills by vultures, and have been seen to compete over carcasses (Thapar 1986). According to the hypothesis, these tigresses should live in groups but they do not.

In short, this combination of ecological factors may allow lions to be social in savannah regions, but it seems somewhat surprising that more felids would not be following Packer's suggestion in other habitats, unless there were considerable costs to group living. Here, the time costs incurred by cheetah mothers feeding litters of different size and the difficulty they experience in capturing prey of different weight are examined, in order to estimate the costs of group living. There then follows a discussion on the extent to which conditions necessary for sociality are absent in the other felids, but I start with a brief review of sociality in males.

## MALES

As a consequence of internal fertilization and gestation, parental investment by female mammals is usually considerably greater than that of males, and reproductive success of females is restricted by access to resources (Trivers 1972). Male reproductive success is usually limited by access to females. Thus the distribution of females will be of major importance in determining male social organization in most species (Bradbury & Vehrencamp 1977; Emlen & Oring 1977; Wrangham 1979). In all but one of the felid species, females are characterized as living alone or with their dependent cubs, and either have exclusive home ranges which they

defend against other females (for example, bobcats: Bailey 1974; European wildcats, *Felis sylvestris*: Corbett 1979; tigers; Sunquist 1981; leopards: Bertram 1982) (see Fig. 1), or have home ranges with a considerable degree of overlap (e.g. cougars: Seidensticker *et al.* 1973; jaguars, *Panthera onca*: Schaller & Crawshaw 1980; North American lynxes: Carbyn & Patriquin 1983; ocelots *Felis pardalis*: Ludlow & Sunquist 1987). In both cases solitary males defend ranges that overlap those of several females.

In cheetahs, females have extremely large home ranges, 800 km<sup>2</sup> in the Serengeti (Frame 1984), compared to only 16 km<sup>2</sup> for similar-sized leopards living in the same ecosystem (Bertram 1978) (Fig. 1), because female cheetahs annually follow the migratory movements of their principal prey species, Thomson's gazelles *Gazella thomsoni* (Frame 1984; Durant *et al.* in press). Females do not defend their ranges against other females, and even one female range would probably be too large to be defended by a male. However, female cheetahs appear to collect in localities affording localized cover when Thomson's gazelles move into the area (Caro & Collins 1987a). By monopolizing such an area, only a fraction of a female's home range, a male cheetah may encounter many transient females. Males that join others have a much better chance of obtaining and maintaining exclusive access to these areas than do single males because they can oust residents and repel intruders of smaller coalition size (Caro & Collins 1986, 1987b).

In lions, females live in stable prides of two to eighteen related females with their dependent offspring (Schaller 1972; Bertram 1975). Male lions accrue reproductive benefits from living in groups because they have enhanced competitive ability to take over prides, they have extended pride tenure and they can occupy more than one pride; indeed per capita reproductive success is higher in larger

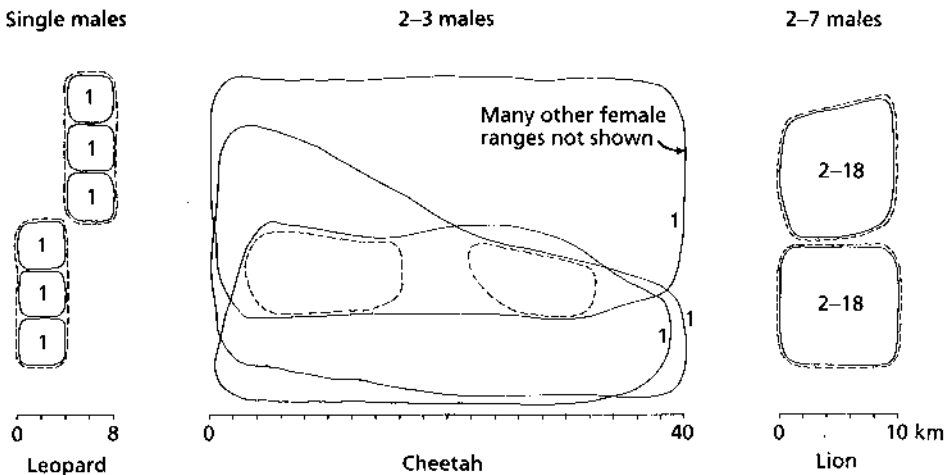


FIG. 1. Schematic representation of male territories (dashed lines) relative to female territories or home ranges (solid lines) in three species of felid. Numerals denote number of females that would typically occupy the ranges. Scale in kilometres shown below.

coalitions (Bygott, Bertram & Hanby 1979; Packer & Pusey 1982; Packer *et al.* 1988 (see Fig. 1). Thus, for different reasons, male cheetahs and male lions gain access to more females by living as coalitions because the costs of sharing matings are probably outweighed by the ability of coalitions to monopolize large numbers of females.

In the other Felidae where females' ranges overlap far less and females do not collect in small areas, or in species where female home ranges are exclusive, a pair of males would have to range over more than twice as many female ranges as would a single male in order to gain sufficient reproductive benefits to outweigh the costs of shared matings (Fig. 2). Assuming that, in these species, single males are currently occupying the maximum size of range they can defend successfully, it seems improbable that a pair of males could range over and defend effectively an area that was nearly twice this size. Only if they split up could they cover such an enlarged circuit, but in so doing, would lose their advantage in fights with single males. Hence, under current female distributions, the most successful reproductive option for males may be to remain single and attempt to limit range incursions by all other males.

In summary, males will form groups only if they can increase individual access to females. Larger coalitions of male lions can exclude smaller groups of males from prides of females, while coalitions of male cheetahs can monopolize areas where females collect. In other felid species, where females are more dispersed, a male's reproductive interests will be served best by excluding all other males from the greatest number of female ranges he can encompass.

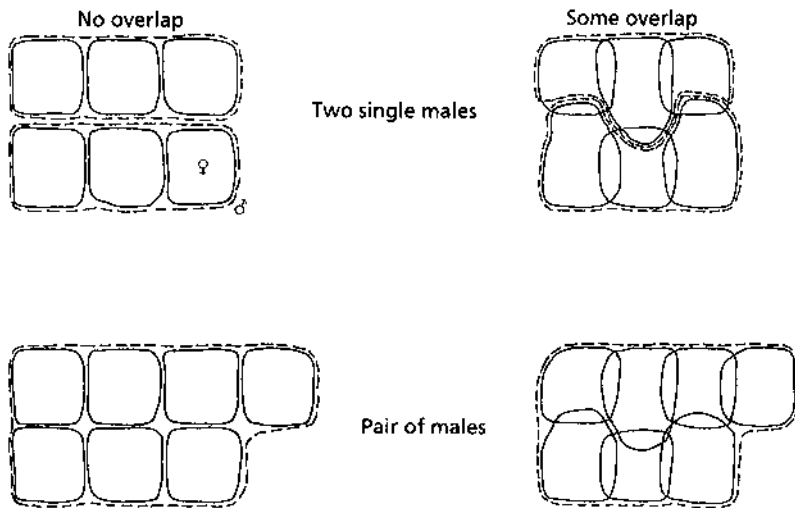


FIG. 2. Schematic representation of singleton male territories (dashed lines) relative to female territories or home ranges (solid lines) where no overlap occurs (left) or where some occurs (right). Diagrams below show the male territory size necessary to allow a hypothetical pair of males to gain reproductive advantages over a singleton.

## FEMALES

*Female life histories*

Although adult female felids usually live apart and avoid contact with each other (for example African wildcats, *Felis lybica*: Smithers 1971), they spend a considerable proportion of their lives with dependent cubs. Table 1 shows that the percentage of time adult females have cubs in their charge is normally over 80% for the ten species for which data are available. Moreover, adult females in each species had weaned cubs accompanying them for an average of nearly 60% of their lives, assuming an unbroken reproductive career. In practice, loss of cubs at birth and post-natal mortality caused by factors such as disease (for example cheetahs: O'Brien *et al.* 1985) or infanticide (lions: Packer & Pusey 1983) would reduce the total amount of time that adult females had cubs accompanying them. However, an example from the first 4 years of my field study of cheetahs shows that mothers were usually accompanied by offspring. Of the 173, 298, 254 and 208 sightings of independent female cheetahs seen in each year, 54.3%, 65.4%, 64.2% and 58.7% of these sightings respectively were of females with cubs accompanying them.

During the period of post-weaning dependence, cubs consume large quantities of food. In cheetahs, cubs leave the den in which they have been hidden by their mother at about 6 weeks and accompany her on hunting expeditions, remaining with her for between 13 and 20 months (Frame 1980). Thus mothers have to share a proportion of their food with offspring for between 46 and 74 weeks, or 71–80% of the time between pregnancies (Frame 1984). By 8 months, cheetah cubs' jaw size has reached that of adult females' (personal observations) suggesting they consume as much food as their mothers per unit time. Thus mothers with only a single cub may have to share carcasses approximately equally for 31–52% of their reproductive careers. Given that two or three cubs (the most common

TABLE 1. Reproductive parameters of ten species of felid (calculated from Gittleman 1986)

	% of life female has cubs*	% of life female has attendant cubs <sup>†</sup>
<i>Acinonyx jubatus</i>	83.6	64.0
<i>Panthera pardus</i>	86.0	66.0
<i>Panthera leo</i>	91.1	78.4
<i>Felis caracal</i>	83.2	55.2
<i>Panthera tigris</i>	84.6	60.1
<i>Lynx lynx</i>	78.0	41.3
<i>Lynx rufus</i>	85.3	71.3
<i>Puma concolor</i>	82.4	—
<i>Felis lybica</i>	71.1	—
<i>Felis sylvestris</i>	67.6	27.1

\* Age at independence/(length of gestation + age at independence).

<sup>†</sup> (Age at independence - age at weaning)/(length of gestation + age at independence).

litter size at this older age in the Serengeti) are feeding for an average of 73% of the time that all family members are feeding (Table 2), adult female cheetahs may relinquish two-thirds of the meat they catch to other individuals for half their lives.

Cubs are not only a drain on the food that mothers capture, they are of little help in acquiring food. The percentage of the family's successful hunts made by cheetah cubs alone was very low compared to those made by their mother (Fig. 3). Indeed, of the 178 successful hunts that fifty-four cheetah families were seen to make during 2773 hours of observation, only eleven were actually made by cubs alone, and these were usually of easy-to-catch hares.

Although cubs began to initiate hunts from 5½ months of age onwards, they would usually hang back after their mother started to hunt, and rarely contacted prey until their mother had captured it. Mothers' hunting success rates did not increase with cub age despite cubs' participation in hunts (Fig. 4), nor was there any indication that mothers attempted to capture large prey when they had older cubs (Table 3). These results indicate that in the one felid species where quantitative data are available on hunting behaviour of both offspring and mothers, cubs are essentially parasitic on adult females for food.

#### *Time costs to sociality*

If adult female felids did live together (were social) and bred seasonally, then on average, the minimum size of a social group would reach two adult females plus twice the mean litter size. Even if breeding lacked seasonality, mothers might nevertheless live in groups of this size during some periods of their lives. If two females lived together, their individual rates of food intake would decrease unless

TABLE 2. Total numbers of minutes mothers and individual cubs from different litters ate from carcasses during the period they were observed

Cub age in months	Number of days observed	Mother	Time spent eating by:			Total % of time cubs ate
			First cub	Second cub	Third cub	
8	7	238.2	221.3	253.1		66.6
8	6	95.4	146.3	128.2		74.2
8	7	189.5	285.1	256.5		74.1
8	3	0	7.9	3.8		100.0
8	6	76.4	87.0	107.1		71.8
8	4	28.9	52.8	27.7	15.5	76.9
10	6	97.1	68.3	90.4		62.0
10	5	36.7	49.1	55.5	71.8	82.8
≥12	1	37.7	33.7	37.3		65.3
≥12	1	11.0	9.5	6.9		59.9
≥12	6	105.6	75.7	92.3		61.4
≥12	7	79.9	86.7	79.0		67.5
≥12	5	46.8	70.6	79.4	72.2	82.6

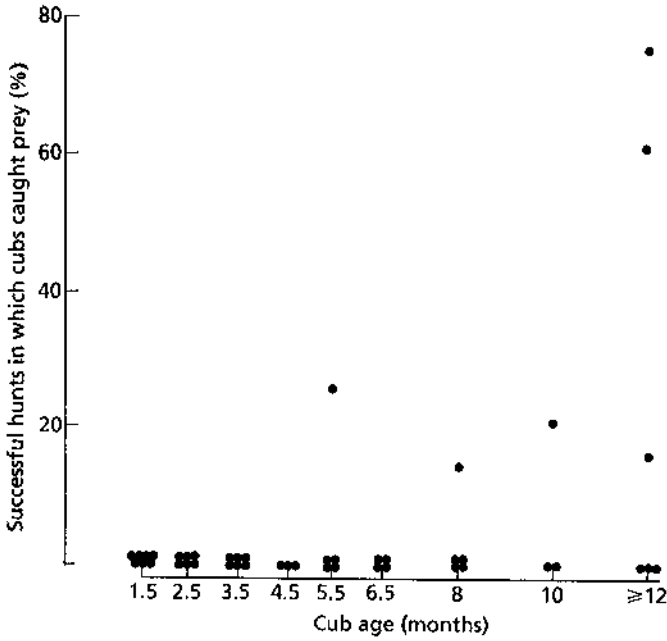


FIG. 3. Percentage of families' successful hunts that were made by dependent cubs without the aid of their mothers, separated by cub age ( $n=45$ ,  $r_s=0.440$ ,  $P<0.002$ ).

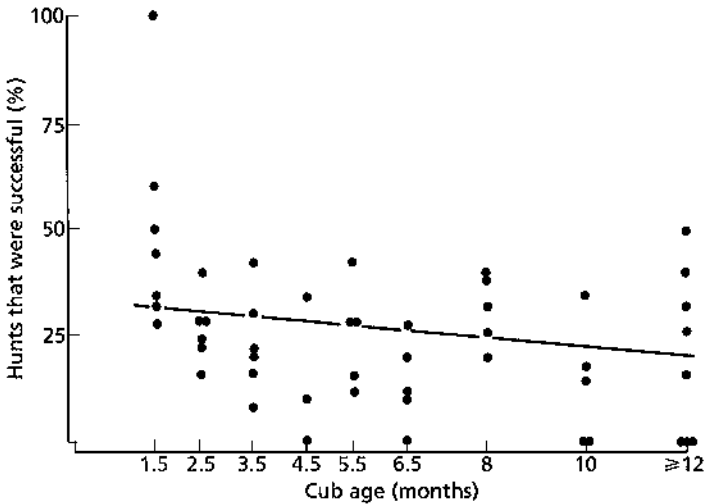


FIG. 4. Mothers' successful hunts expressed as a percentage of all mothers' hunts, separated by cub age ( $n=51$  mothers,  $r=-0.207$ , N.S.;  $y=0.333-0.011x$ ).



TABLE 3. Attempts on known prey larger than an adult male Thomson's gazelle by cheetah mothers with cubs of different age. Prey were subadult male, adult female and adult male Grant's gazelles; neonate, yearling and 2 year old wildebeests, an adult male topi, neonate zebra, a subadult and adult female reedbeek, and a hartebeest of unknown age or sex.

	Cub age in months								
	1½	2½	3½	4½	5½	6½	8	10	≥12
Grant's gazelle	3	1	2*	2	7	1	3	4	0
Wildebeest	3*	1	2	0	0	0	1	0	4
Other	0	1	0	0	1	0	2*	4	1
Total	6	3	4	2	8	1	6	8	5

\* Denotes that one of the attempts was successful.

compensation could be made for loss of food. Additional food could be provided effectively in only two ways: either by hunting more often per group, or by capturing larger prey per hunt, or some combination of the two.

A third way of increasing food intake without increasing hunting rates or size of prey might be for the two mothers to take alternate turns in hunting. However, in this situation all other non-hunting group members (cubs) would have to double the amount of time and energy spent in accompanying the huntresses so as to be able to consume prey every time it was caught by each of the two mothers. It is argued below that the pooled dependent cubs would suffer prohibitive costs under this new regime.

A fourth possibility might be for mothers to bring food back to a common den where cubs spent a large proportion of their time, in order to free cubs of travel costs spent in accompanying them on hunts. This sometimes occurs in spotted hyaenas (Kruuk 1972). In this situation, however, food intake provided by a mother per unit time would be reduced unless mothers increased their hunting rates, because they would have difficulty in carrying all but the smallest prey back to the den, especially since felids have relatively small heads (Van Valkenburgh & Ruff 1987) lacking the musculature required to carry large pieces of meat. Moreover, cubs that spent a large proportion of their time in a den might have little opportunity to learn hunting skills before independence.

Only in one scenario would hunting habits not need to change, that is if females lived together but if they and their own cubs travelled, hunted and ate separately. Yet in these circumstances it is unlikely they could capitalize on the benefits of sociality derived from early detection of predators, cooperative defence of carcasses, or protection of cubs.

Could mothers then hunt twice as often as they do when they are asocial, in order to feed a social group as argued above? The mean number of minutes that cheetah mothers hunted per hour (defined as stalking, trotting towards, crouching at, rushing or chasing a group of prey animals; see Caro 1987a) decreased with age of their cubs from 2.47 min/h when cubs were young (1½–3½ months old) to

1.24 min/h when cubs were 8–18 months old ( $F_{2,51}=2.895$ ,  $P=0.064$ ; see Caro 1987b for methods). This measure is an underestimate of the time spent hunting, however, because many of the prey caught by mothers were neonate Thomson's gazelles, and hares *Lepus crayshawi* and *Lepus capensis* (mean percentage representation in prey killed by forty-three mothers; 30.4% S.D.=33.0; 14.9%, S.D.=25.2 respectively). These prey items were not caught using a concealed approach, but were located and briefly pursued only when they had been disturbed by mothers walking through vegetation in which they were hiding. Maternal effort to acquire prey is therefore better measured as the percentage of time mothers hunted, moved and sat up observing their surroundings (searched for prey) during the course of the day; the last behaviour was strongly associated with prey capture (Caro 1987b).

Figure 5 shows the percentage of time that mothers searched for prey when cubs were young (when they spent most time hunting), separated by litter size. Mothers spent an average of 41.9% of the time searching for prey when they had three young cubs. By fitting a regression to these data, one can estimate the percentage of time mothers would have to search for prey to support increasing numbers of cubs of this age, assuming search time increases linearly with litter size. With litters of six young cubs, which have been seen in the Serengeti (G. Frame, personal communication; personal observations), mothers would have to search for prey for 57.0% of daylight hours. For groups of seven or eight (two litters of the normal three or four young cubs, Schaller 1972), mothers would have to search for between 63.4 and 70.0% of the day.

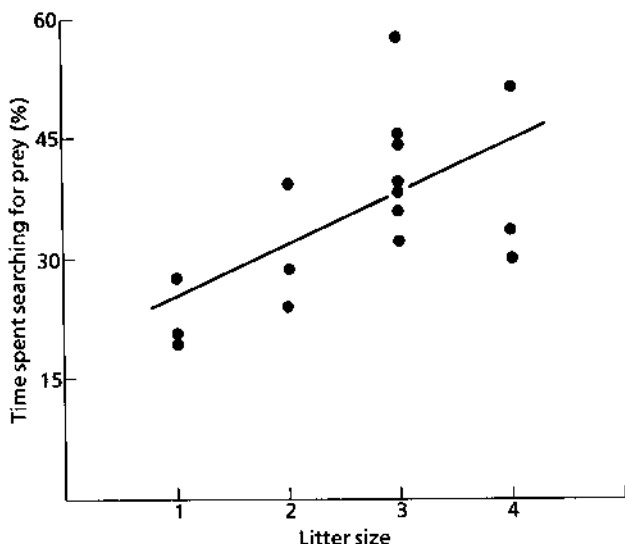


FIG. 5. Percentage of instantaneous scans taken every 15 minutes that mothers with young cubs ( $1\frac{1}{2}$ – $3\frac{1}{2}$  months old) searched for prey (hunted, moved or sat up observing), separated by litter size ( $n=16$ ,  $r=0.612$ ,  $P=0.012$ ;  $y=18.583+6.409x$ ).

Given that mothers nurse litters of one to four young cubs for an average of 11.5% ( $n=19$ , S.D.=11.0) of the day (18.9% in 1½ month old cubs) and that they spend an average of 5.8% ( $n=14$ , S.D.=2.8) of the day eating during this period, only 12.7% of the day would be available, on average, for other activities if mothers were with eight group members. Mothers only caught prey on an average of a quarter of all the hunts they embarked on; moreover, there was considerable variability in hunting success ( $n=51$ ,  $\bar{X}=27\%$ , S.D.=21%; see Fig. 4), some mothers having runs of up to ten hunts without success. Thus, having only approximately 7.5 minutes 'free' in each hour might be risky in terms of securing prey, energetic costs aside. If pooled cubs continuously accompanied two mothers that hunted alternately, as argued in the third scenario, they would spend 80–90% of the day involved in searching for prey (double that shown for three or four cubs in Fig. 5).

#### *Prey size, ease of procurement and sociality*

If female cheetahs were social they might be able to feed group members by regularly catching large prey. Serengeti cheetah mothers were less successful at capturing prey, however, as the carcass weight of the prey they attempted increased in size (Fig. 6a), and there was no indication that success rates levelled off as prey size increased. Also, the total time spent in hunting necessary to capture different sorts of prey items did not level off as prey size increased (Fig. 6b). In effect, cheetah mothers could not improve on their food intake per unit time by concentrating on large prey because these took too long to hunt successfully. Only by focusing on very small prey (hares) could they marginally increase food intake. In fact, hungry cheetahs tried to minimize the risk of starvation by walking long distances searching for hares and neonate Thomson's gazelles in vegetation, and not by hunting medium or large-sized prey (personal observations).

Moreover, the larger the prey item, the more likely it is to be an adult member of a species rather than a neonate or juvenile which is usually less vigilant and less competent at escaping predators. Indeed, mothers attempted to capture the youngest age classes of Thomson's gazelles disproportionately relative to their abundance (relative abundance of adult males was 27.9%, adult females 58.2%, subadult males and females 9.3%, and half-grown and fawns 4.7% ( $n=30642$  counted, Borner *et al.* 1987), whereas these classes were attempted in respectively 33.2%, 20.4%, 6.8% and 39.6% of the 265 hunts where the age sex class of this quarry was known ( $\chi^2=754.07$ ,  $df=3$ ,  $P<0.001$ ).

It is also possible to estimate the amount of prey that a female cheetah living socially might need to capture. Figure 7 shows the number of kilograms of edible flesh that mothers made available to cubs per hour separated according to litter size. Mothers made an average of 0.14 kg of flesh available to single cub litters per hour, 0.22 kg/h to two cubs, 0.29 kg/h to three cubs, and 0.24 kg/h to four cubs ( $F_{3,50}=1.132$ , N.S.). Being conservative, extrapolation suggests mothers with seven or eight cubs would have to procure approximately 0.30 kg of flesh/h, but assuming

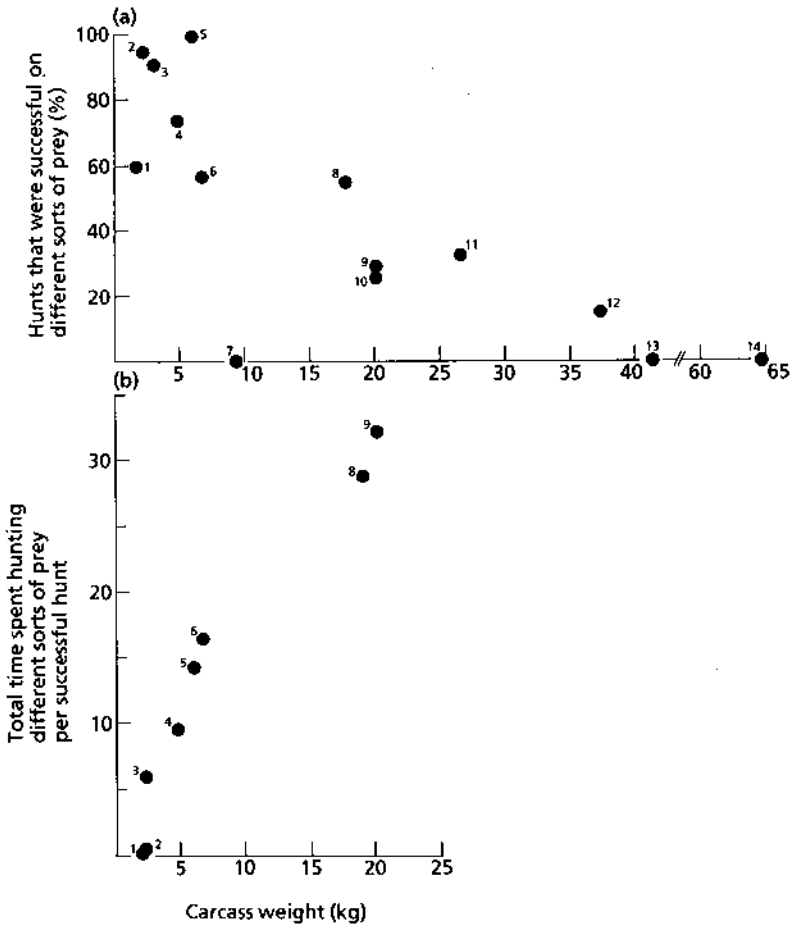


FIG. 6. (a) Hunting success rates of cheetah mothers on prey of different body weights for prey that were hunted more than once, calculated by dividing the total number of successful hunts made by mothers of fifty-five litters by the number of hunts attempted on each sort of prey item.  $n=14$ ,  $r_s=-0.822$ ,  $P<0.002$ . (b) Time expended by cheetah mothers in capturing prey of different body size that were hunted more than once, calculated by dividing the total time spent in successful and unsuccessful hunts by the number of successful hunts made by mothers of fifty-five litters on each sort of prey item.  $n=8$ ,  $r_s=1.000$ ,  $P<0.002$ . 1. Subadult hare; 2. Adult hare; 3. Neonate (N) Thomson's gazelle; 4. Halfgrown Thomson's gazelle; 5. N Grant's gazelle; 6. Subadult female (SF) Thomson's gazelle; 7. Subadult male (SM) Thomson's gazelle; 8. Adult female (AF) Thomson's gazelle; 9. Adult male (AM) Thomson's gazelle; 10. N wildebeest; 11. SM Grant's gazelle; 12. AF reedbuck; 13. AF Grant's gazelle; 14. AM Grant's gazelle.

a linear increase, they might have to capture 0.44–0.49 kg/h for groups of this size.

If, for the sake of argument, mothers exclusively fed on neonate Thomson's gazelles (edible flesh weight 1.7 kg; Blumenschine & Caro 1986), those with one cub would need to kill once every 10 daylight hours, but make one hunting

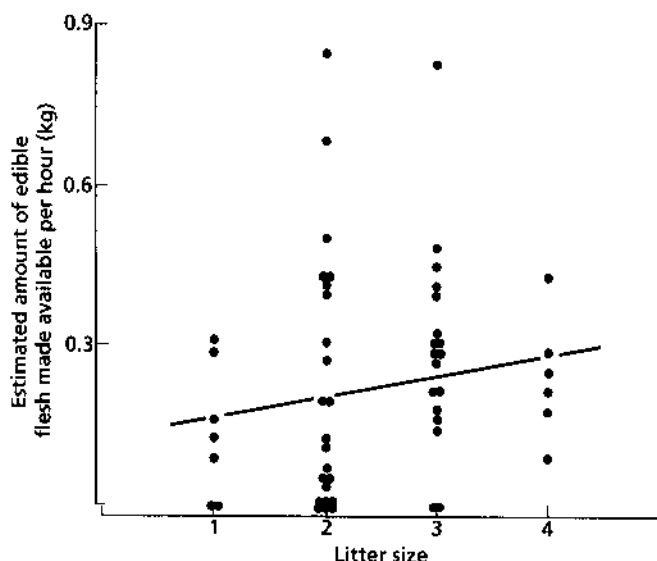


FIG. 7. Estimated number of kilograms of edible flesh that mothers of fifty-four litters made available to their cubs per hour, separated by litter size ( $r=0.189$ , N.S.;  $y=0.129+0.044x$ ).

attempt every 9 hours when failed hunts are taken into account (see Fig. 6a). Mothers with eight group members would need to attempt this prey every 3.2–5.1 hours, depending on whether they needed to capture 0.30 or 0.49 kg/h. If however, mothers sought larger prey such as 20 kg adult male Thomson's gazelles then mothers with eight mouths to feed would have to procure the 10 kg of edible flesh once every 20.4–33.3 daylight hours. But to realize this intake, they would need to attempt to capture adult males every 5.8–9.5 hours, nearly twice a day, using hunting success rates from Fig. 6a. If mothers switched to larger prey still, they would need to hunt almost continuously to have a chance of securing prey because success rate is extremely low on prey of large body size (Fig. 6a). These arguments hold whether the burden of hunting fell on one, or on two mothers, because the pooled cubs would still suffer the same failure rates and have to hunt for these lengths of time in order to be present when each kill was made.

#### *Two caveats*

Although these arguments suggest that social cheetah mothers would face considerable difficulties in finding either enough time to catch prey, or in being able to catch sufficient large prey items necessary to feed dependent cubs, they make two assumptions: that the amount of food cubs consume does not decline appreciably with litter size, and that hunting efficiency is not appreciably greater with increasing numbers of adult females.

Amount of food each cub ate per unit time was estimated by dividing the proportion of time a cub fed from each carcass compared to other family members and multiplying by the estimated weight of edible flesh consumed on that carcass; these amounts were then summed across carcasses and divided by the total time a family was observed. When cubs were young ( $1\frac{1}{2}$ – $3\frac{1}{2}$  months) and had small mouths, I estimated mothers ate three times as much meat per unit time as each cub; when  $4\frac{1}{2}$ – $6\frac{1}{2}$  months old, twice as much; but when 8 months or older, equal amounts per unit time as each cub. Of those families that were seen eating, the estimated average amount of food cubs actually ate per hour, rather than that made available to them, was unaffected by litter size ( $n=44$ ,  $\bar{X}=0.05$  kg/h, S.D.=0.05,  $F_{3,39}=0.542$ , N.S.). Furthermore, when litters were separated by age group, food ingested per cub was not significantly affected by litter size (one and two vs. three and four cubs respectively,  $1\frac{1}{2}$ – $3\frac{1}{2}$  months,  $\bar{X}s=0.05$ ,  $0.04$  kg/h,  $t_{6,13}=1.12$ , N.S.;  $4\frac{1}{2}$ – $6\frac{1}{2}$  months,  $\bar{X}s=0.04$ ,  $0.05$ ,  $t_{6,6}=-0.59$ , N.S.; 8–18 months,  $\bar{X}s=0.09$ ,  $0.06$ ,  $t_{10,3}=0.68$ , N.S.). Thus, cubs in my sample of large litters did not consume markedly less flesh than those in small litters because mothers made somewhat more kilograms available to them per unit time (see Fig. 7).

The second assumption, that groups of adult females would not hunt more effectively than singletons, cannot be tested directly in cheetahs because females are solitary. However, some male cheetahs do live in groups, providing a comparison for examining the effects of group size on hunting success. Differences in food intake in different sized male groups could not be used as an analogy for females because males are up to 25% heavier (Smithers 1983) and, in the Serengeti, attempt to capture different sorts of prey. Whereas only forty-three out of 641 hunts by mothers were attempts to capture prey larger than an adult male Thomson's gazelle (20 kg), single males attempted such prey items on a total of thirty-two out of 163 occasions ( $X^2=24.16$ ,  $df=1$ ,  $P<0.001$ ). These differences notwithstanding, Table 4 shows that there were no significant differences in the number of hunts made per hour, hunting success per group, or number of successful hunts per hour in male groups of differing size.

In sum, cheetah cubs did not get significantly less food in large litters, and hunting success of male cheetahs did not change appreciably with increasing number of males (see also Eaton 1974; Packer & Rutman, in press), suggesting female hunting success would not increase appreciably if females lived in groups. Indeed, it is difficult to imagine how felid hunting methods, a concealed approach followed by a short chase, could benefit substantially by the participation of several individuals.

### *Conclusions*

Female felids do not live alone because mothers live with cubs of varying sizes for much of their lives. Cubs in all felid species appear to require extensive practice to hunt efficiently (see also Caro 1980) and they help their mothers little in catching food, but mothers have to share the food they capture with their cubs.

TABLE 4. Effects of male group size on measures of hunting in male cheetahs. Data refer to group hunts because coalition members nearly always hunted together; analysis is restricted to groups observed for 12 or more hours. Mean values, and standard deviations in brackets

Measure	Male group size			F-test	P value
	1	2	3		
Hours watched	491.1	464.4	305.5		
Number of hunts per hour*	0.15 (0.11)	0.22 (0.14)	0.15 (0.05)	$F_{2,24}=1.039$	N.S.
% hunting success†	22.6 (26.6)	24.8 (20.9)	47.1 (33.0)	$F_{2,22}=1.659$	N.S.
Number of successful hunts per hour*	0.04 (0.04)	0.06 (0.08)	0.07 (0.05)	$F_{2,24}=0.500$	N.S.

\*  $n=11$ , 11 and 5 groups respectively for male group sizes of 1, 2 and 3.

†  $n=10$ , 10 and 5 groups respectively.

Thus if females were to live with other females and benefit from some of the advantages that sociality is known to bring in other carnivores, mothers would either have to hunt more often or catch larger prey to feed an increased number of group members.

Cheetah mothers spent a large proportion of each day searching and hunting for food and appeared to be near the upper limit of the time that they were able to spend in this activity. By extrapolation, it would be difficult for mothers to feed additional group members by hunting more often. If cheetah mothers were to live in groups, mothers would also find it difficult to feed group members by capturing larger prey because hunting success decreased and time spent hunting increased with prey size attempted. To realize an increased food intake through taking large prey, the family would again be forced to be almost continuously involved in hunting. Female cheetahs in groups would be unlikely to enjoy enhanced hunting success; hunting success in males did not increase significantly with group size.

In short, if female felids were to live socially, they would need to catch large prey that were easy to capture because most felids are likely to be at the upper limit of the time they can spend hunting with normal litter sizes. However, more information is needed on the proportion of time that mothers of different felid species allocate to hunting and food acquisition.

### COMPARATIVE EVIDENCE

These data have shown that the only real means by which mothers could support a group of cheetah cubs would be to concentrate on large prey that were easy to catch. The working hypothesis is that this would also hold for other species of felid because it is assumed that each species gives birth to the maximum number of cubs it can usually raise successfully. Some prey species are more

vulnerable than others because they are less vigilant, live in smaller groups, or run slowly, but unfortunately very little is known about species' differences in anti-predator behaviour (but see Johnsingh 1983) and the problems predators must overcome in capturing different sorts of prey (Hornocker 1970). At present, a first broad approximation of how easily prey can be caught is the relative frequency with which they might be encountered (but see Bertram 1973). If prey species relatively large to a female's body weight were numerous in the habitat then, other things being equal, the opportunity to increase food intake necessary to sustain sociality would be open. Here I examine different-sized prey available to free-living felids in the habitats where these data have been collected.

### Cheetahs

For cheetahs, modal prey size across different studies is approximately 30 kg or 80% of an adult female's body weight (38 kg, Caro *et al.* 1987) (Table 5). In order to take large prey that were easy to catch, as measured by abundance (necessary to sustain a group of animals as argued above), female cheetahs in the Serengeti would have to feed regularly on subadult and adult wildebeests, *Connochaetes taurinus*, (32, 39, 40 in Fig. 8), but these animals are three to seven times the size of prey cheetahs normally take, or 200–400% of their own body weight. The most numerous prey closest to their own body weight are small Thomson's gazelles (11, 12) and neonate wildebeests (13) which may effectively preclude living in permanent groups in this habitat. Similarly, Fig. 9 shows that in Kruger National Park, cheetahs would have to switch from impalas, *Aepyceros melampus* (12, 20, 24), about their own body weight, to female greater kudu, *Tragelaphus strepsiceros* (36), zebras, *Equus burchelli* (35, 47, 48) and wildebeests (37, 39), up to ten times their modal prey size, to take advantage of large prey that were abundant and so be able to feed as a group; there are relatively few prey in the 60–120 kg range.

Presence of abundant domestic livestock, usually poor in detecting predators, means that felids can have an increased opportunity to catch large prey easily, if livestock are not well protected by people. In south-west Africa, where farms carry high concentrations of domestic sheep and goats, McVittie (1979) reported that twenty-three out of 123 sightings of adult female cheetahs consisted of two females associating together, with or without cubs. In Serengeti, only one out of 390 female sightings was of this sort (Frame & Frame 1976)  $\chi^2=67.25$ ,  $df=1$ ,  $P<0.001$ ). McVittie's data came from information provided by farmers, some of whom caught cheetahs in box traps, so it is possible that different individuals that had never met before were caught together over a period of time using this method (D. Morsbach, personal communication). Nevertheless, the data do suggest that under certain conditions where prey are easy to catch, cheetahs can be social. Further information on cheetahs' prey capture and feeding rates is clearly needed from this region.



TABLE 5. Identity of the most frequently eaten prey species by some of the felids described in the text (some studies reported two species); data could not be separated by sex of felid. Prey weights (kg) are given as 75% female body weight because the proportion of adults of both sexes and juveniles eaten was unknown. K=kills, S=scats, St=stomach contents

Prey species	Weight	K	S	St	Location	Source
<b>Cheetah</b>						
Impala	31.6	X			Nairobi N.P.	1
Puku	45.9	X			Kafue N.P.	2
Thomson's gazelle	13.3	X			Serengeti N.P.	3, 4
Impala	31.6	X			Kruger N.P.	5
<b>Leopard</b>						
Reedbuck	28.1	X			Kafue N.P.	2
Thomson's gazelle	13.3	X			Serengeti N.P.	3
Impala	31.6	X			Kruger N.P.	5
Impala	31.6	X			Serengeti N.P.	6
Thomson's gazelle	13.3	X			Serengeti N.P.	6
Impala	31.6		X		Tsavo N.P.	7
Procyonidae	2.3		X		Matopos N.P.	8, 9
<b>Lion</b>						
Buffalo	562.5	X			Kafue N.P.	2
Wildebeest	122.3	X			Serengeti N.P.	3, 4
Bluc wildebeest	135.0	X			Kruger N.P.	5
Zebra	226.7	X			Serengeti N.P.	6
Hartebeest	94.5	X			Nairobi N.P.	10
Zebra	226.7	X			Nairobi N.P.	11
Wildebeest	122.3	X			Nairobi N.P.	11
<b>Tiger</b>						
Chital	42.6	X	X		Kahna N.P.	12
Chital	42.6		X		Bandipur	13
Sambar	122.7	X			Chitawan N.P.	14
Chital	42.6		X		Chitawan N.P.	14
Wapiti	152.3		X		Primorje	15
Wapiti	152.3		X		Lazorski reserve	16
Wild pig	42.0		X		Sikhote Alin reserve	17
Wapiti	152.3		X		Sikhote Alin reserve	18
<b>Cougar</b>						
Elk calves	109.3	X			Idaho Primitive area	19
Mule deer	48.8			X	Western USA	20
Varying hare	1.1		X		Washington State	20
Mule deer	48.8			X	Utah & Nevada	21
Mule deer	48.8			X	British Columbia	22
European hare	2.8		X		Torres del Paine N.P.	23
Agouti	4.0		X		Cocha Cashu N.P.	24

1. Eaton 1974; 2. Mitchell, Shenton & Uys 1965; 3. Kruuk & Turner 1967; 4. Schaller 1972; 5. Pienaar 1969; 6. Bertram 1982; 7. Hamilton 1976; 8. Grobler & Wilson 1972; 9. Smith 1978; 10. Rudnai 1973; 11. Foster & Kearney 1967; 12. Schaller 1967; 13. Jonhsingh 1983; 14. Sunquist 1981; 15. Abramov 1962; 16. Matjushkin, Zhivotchenko & Smirnov 1980; 17. Yudakov 1973; 18. Gromov & Matjushkin 1974; 19. Hornocker 1970; 20. Young & Goldman 1946; 21. Robinette, Gashwiler & Morris 1959; 22. Spalding & Lcsowski 1971; 23. Yancz *et al.* 1986; 24. Emmons 1987a.

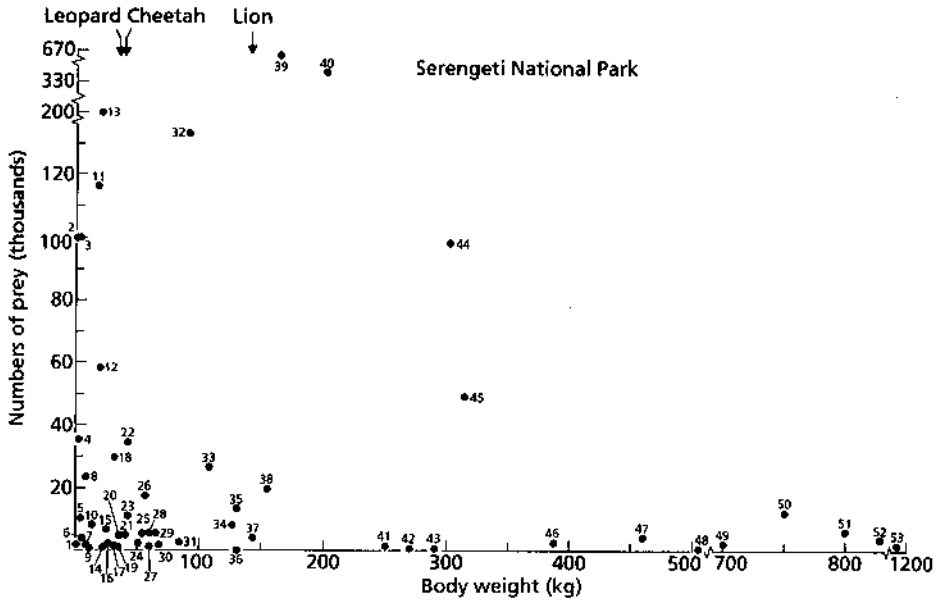


FIG. 8. Estimated abundance (in 1000s) and body weights (kg) of prey in the Serengeti National Park, Tanzania (after several sources). Also shown are weights of an adult female leopard, female cheetah and lioness. 1. Neonate (N) warthog; 2. Subadult (S) hare; 3. Adult hare; 4. N Thomson's gazelle; 5. N impala; 6. N Grant's gazelle; 7. N 'other' (average of roan, oryx, reedbuck, bushbuck, etc., from Schaller (1972)); 8. S Thomson's gazelle; 9. N waterbuck; 10. N topi; 11. Adult female (AF) Thomson's gazelle; 12. Adult male (AM) Thomson's gazelle; 13. N wildebeest; 14. S 'other'; 15. S impala; 16. S Grant's gazelle; 17. N eland; 18. N zebra; 19. S warthog; 20. N buffalo; 21. AF 'other'; 22. AF impala; 23. AF Grant's gazelle; 24. AM 'other'; 25. AF warthog; 26. AM impala; 27. N giraffe; 28. S topi; 29. AM Grant's gazelle; 30. S hartebeest; 31. AM warthog; 32. S wildebeest; 33. AF topi; 34. AF hartebeest; 35. AM topi; 36. S waterbuck; 37. AM hartebeest; 38. S zebra; 39. AF wildebeest; 40. AM wildebeest; 41. AF waterbuck; 42. AM waterbuck; 43. S eland; 44. AF zebra; 45. AM zebra; 46. S buffalo; 47. AF eland; 48. S giraffe; 49. AM eland; 50. AF buffalo; 51. AM buffalo; 52. AF giraffe; 53. AM giraffe. Weights from Schaller (1972), Smithers (1983), Georgiadis (1985), Blumenschine & Caro (1986), while subadult weights were estimated as half mean adult male and female weights. A few age classes of uncommon species were omitted from the figure where weights were unobtainable. Abundance for each species calculated from Schaller (1972), Frame & Wagner (1981), Borner *et al.* (1987), K. Campbell, personal communication; age classes were calculated as AM 25%, AF 50%, S 10% and N 15% of each population.

### Leopards

Leopards (female body weight, 34 kg: Wilson 1968) usually take prey of similar size to cheetahs (about 30 kg: Table 5), although a leopard is capable of taking prey several times its own body weight (e.g. sable antelope, *Hippotragus niger*: Pienaar 1969). In Serengeti and Kruger National Parks (Figs 8 and 9), abundant prey five to nine times an adult female's body weight are present, but these may be too large to catch on a regular basis. Prey two to four times female body weight are not particularly common in either of these habitats suggesting regular

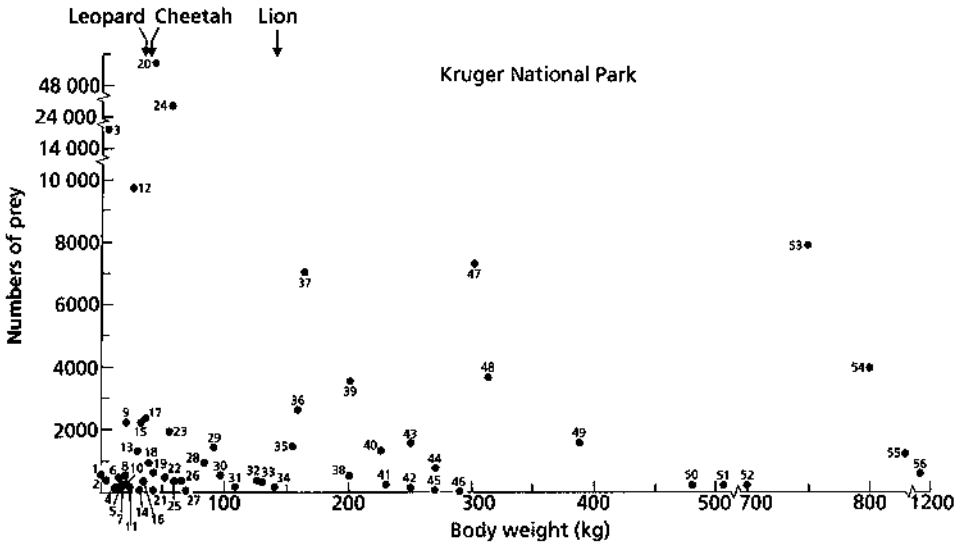


FIG. 9. Estimated abundance and body weights (kg) of prey in the Kruger National Park, South Africa (after Pienaar 1969). Also shown are weights of an adult female leopard, female cheetah and lioness. 1. Neonate (N) warthog; 2. N bushbuck; 3. N impala; 4. Subadult (S) 'other' (average of baboon, bushpig, klipspringer, steenbok, grysbok, suni, red duiker, grey duiker); 5. N sable antelope; 6. N waterbuck; 7. S bushbuck; 8. Adult female (AF) 'other'; 9. N wildebeest; 10. AM 'other'; 11. S reedbuck; 12. S impala; 13. AF bushbuck; 14. N eland; 15. N zebra; 16. S warthog; 17. N buffalo; 18. AF reedbuck; 19. AM bushbuck; 20. AF impala; 21. S nyala; 22. AM reedbuck; 23. AF warthog; 24. AM impala; 25. N giraffe; 26. AF nyala; 27. S tsessebe; 28. AM warthog; 29. S wildebeest; 30. S kudu; 31. AM nyala; 32. AF tsessebe; 33. S waterbuck; 34. AM tsessebe; 35. S zebra; 36. AF kudu; 37. AF wildebeest; 38. AF sable antelope; 39. AM wildebeest; 40. AM kudu; 41. AM sable antelope; 42. AF roan antelope; 43. AF waterbuck; 44. AM waterbuck; 45. AM roan antelope; 46. S eland; 47. AF zebra; 48. AM zebra; 49. N buffalo; 50. AF eland; 51. S giraffe; 52. AM eland; 53. AF buffalo; 54. AM buffalo; 55. AF giraffe; 56. AM giraffe. Weights from Sachs (1967), Eisenberg (1981), Smithers (1983), Georgiadis (1985), while subadult weights were estimated as described in legend, Fig. 8. A few uncommon age classes were omitted from the figure where weights were unobtainable; see Fig. 8 for calculation of age-class abundance.

acquisition of large prey items in these areas might also be difficult for this species as it is for cheetahs.

### Lions

Currently there are no quantitative data specifically on the hunting of single lionesses (weight 141 kg: Wilson 1968) although single females are known to have killed an adult zebra, an adult female topi, *Damaliscus korrigum*, an adult warthog, *Phacochoerus aethiopicus* and a warthog piglet on separate occasions (C. Packer & D. Scheel, personal communication); the data in Table 5 are mostly derived from kills made by groups of lions. Although cases of solitary lions attacking prey the size of an adult buffalo, *Syncerus caffer* do exist (Schaller 1972;

C. Packer, personal communication) usually several lions do so simultaneously (Schaller 1972); thus modal prey size for single lions, at least, is probably 155 kg, or just above a female's body weight. In both Serengeti and Kruger National Parks there is abundant prey of this body size and upwards to 300 kg (Figs 8 and 9). Thus the opportunities for lionesses and their cubs to live together in groups are far greater than they are for cheetahs and leopards because relatively large prey, greater and up to double the weight of a lioness, are numerous, will be encountered often and hence will be reasonably easy to capture, other things being equal. In both these ecosystems therefore, lionesses are the only large female felid that could afford to capitalize on any benefits that might result from group living. Similar arguments can be applied to the numerous buffalo in Lake Manyara National Park which constitute 62% of lions' diet there (Schaller 1972).

### Servals

There are few quantitative data on prey availability for other species of African felid. Servals (females 9.7 kg: Smithers 1983) can take prey as large as impala fawns (c. 5 kg: Pienaar 1969) but these are likely to be far less numerous than the rodents on which servals specialize. Geertsema (1985) argues that servals' hunting technique makes it difficult for them either to chase hares or catch bounding springhares, *Pedetes capensis*, which are 10–15 times the body weight of *Otomys*, *Mus* and *Arvicanthis*, the most common items in the diet. Thus servals may find it difficult to catch larger prey not only because they are less numerous than rodents (see Senzota 1978; Frame & Wagner 1981) but because the medium-sized species are difficult to capture.

### Caracals

Caracals (females 11.5 kg: Smithers 1983) take a wide range of prey from small birds to juvenile impalas but Pienaar (1969) and Pringle & Pringle (1979) report hyraxes, *Procavia capensis*, as the most frequent prey item. Certain individuals, however, specialize on sheep and goats in some areas (Pringle & Pringle 1979) and in the Mountain Zebra National Park, South Africa, fifteen out of twenty-one caracal kills were of mountain reedbuck, *Redunca fulvorufula*, representing 19.6% of items found in scats (Grobler 1981). Given that a tame subadult female caracal ate approximately 1 kg of meat per day, a pair of females each with two cubs (see Smithers 1971 for litter sizes) would require only 6 kg/day. The estimated 26.1 kg available on a mountain reedbuck carcass (Grobler 1981) would theoretically support a caracal group for 3 days providing the meat could be defended (Stoddart 1979) and would not putrify.

Although probable encounter rates of caracal with mountain reedbucks are unknown, it seems possible that female caracals could live socially in this area. In support of this, Grobler reported that over a 2-year period eleven out of fifty-seven sightings were of pairs of adults (which he was careful to separate from five

sightings of females with kittens). The possibility that these were pairs of females and not consorting male–female pairs clearly requires further investigation.

### Tigers

Tigers (females 147 kg, Sunquist 1981) eat comparatively small prey for their body weight in lower latitudes but larger prey in the USSR (see Table 5). In Kahna National Park, they feed primarily on chital *Axis axis*, the most abundant wild ungulate (Schaller 1967) (Fig. 10). Sambar, barasingha, *Cervus duvauceli* and gaur, *Bos gaurus*, are also eaten to a lesser degree; analysis of kills rather than scats suggests gaurs are eaten infrequently. Large prey are not particularly abundant: there are only one-third as many female sambar (22, Fig. 10) as female chital (13), and less than a fifth as many gaur (27, 28), which probably makes it difficult for tigresses to locate large prey sufficiently often to support a group. Tigers living outside Schaller's central study area would have encountered large herds of domestic cattle and buffalo (>200 kg, not shown in Fig. 10) which were probably easy to catch and might have allowed peripheral tigresses to live together with attendant cubs. Schaller observed tigresses occasionally feeding together at the same kills.

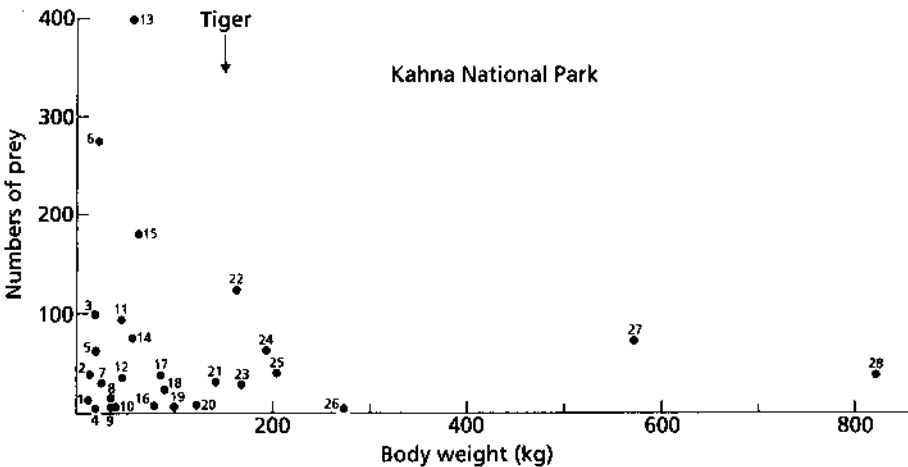


FIG. 10. Estimated abundance and body weights (kg) of prey in the Kahna National Park, India (after Schaller 1967). Also shown is weight of an adult female tiger. 1. Subadult (S) barking deer; 2. Neonate (N) sambar; 3. 4-horned antelope (average of all age classes); 4. S blackbuck; 5. Adult female (AF) barking deer; 6. N chital; 7. Adult male (AM) barking deer; 8. S wild pig; 9. AF blackbuck; 10. AM blackbuck; 11. S gaur; 12. N gaur; 13. AF chital; 14. AF wild pig; 15. AM chital; 16. S barasingha; 17. AM wild pig; 18. S sambar; 19. S nilgai; 20. AF nilgai; 21. AF barasingha; 22. AF sambar; 23. AM barasingha; 24. AM sambar; 25. S gaur; 26. AM nilgai; 27. AF gaur; 28. AM gaur. Weights from Schaller (1967), Eisenberg (1981), Sunquist (1981), while subadult classes were estimated (see legend, Fig. 8). A few uncommon age classes were omitted from the figure where weights were unobtainable. Abundance calculated as in Fig. 8.

In the Royal Chitawan National Park, absolute prey numbers are greater than in Kahna (Seidensticker 1976; Tamang 1979) (Fig. 11). Here chital are taken most frequently as measured by scat analysis but sambar are as measured from kills (Sunquist 1981) (Table 5). Sunquist suggests sambar (13, 14, 15, Fig. 11) are the preferred prey or are most vulnerable, although hogdeer, *Axis porcinus* (4, 7, 8) and chital (5, 9, 11) are more numerous (Sunquist & Sunquist, in press). There seems little reason why tigresses could not be social in this habitat given that adult sambar body weights are greater than that of tigresses, and that they occur at a moderately high density (2.3–2.6/km<sup>2</sup>), although they are not as common as other species. Larger prey still, adult and juvenile rhinoceroses, *Rhinoceros unicornis* (not shown in Fig. 11) are probably too dangerous to capture on a regular basis (Sunquist 1981).

#### Snow leopards

The scant data on snow leopards, *Panther uncia* (females 31.7 kg, Schaller 1977) suggests they feed primarily on bharals, *Pseudois nayaur* but also on much smaller marmots, *Marmota caudata* as determined by scat analysis (Schaller 1977; Schaller *et al.* 1987). Although bharals are large (males 60 kg, females 39 kg), they are probably sufficiently scarce to preclude regular capture required of group living: Schaller suggests snow leopards must move large distances to locate and catch wild ungulates. Thus, feeding almost exclusively on livestock without harassment probably represents the only possible way to sociality in this species.

#### European lynxes

European lynxes, *Lynx lynx* (females 16.8 kg, Haglund 1966) normally feed on hares, *Lepus timidus* in Sweden, but they take an increasing proportion of roe deer, *Capreolus capreolus* and reindeer, *Rangifer tarandus* as winter progresses (Haglund 1966). In some areas 50% of their kills consisted of these species as measured from stomach contents and these prey appear easy to capture: forty-five out of sixty-six hunts on reindeer and twenty-three out of thirty-five hunts on roe deer were successful. Similarly, lynxes reintroduced into the Swiss alps took large prey: of eighty-eight prey items found, forty-eight were of roe deer and thirty were of chamois, *Rupicapra rupicapra* (Breitenmoser & Haller 1987). Given that lynxes eat approximately 2 kg per meal and that Haglund saw three lynxes feeding on a medium-sized roe deer for 2 days, these large ungulates could have provided sufficient food for lynxes to live socially at least in the Renomraden and Radjuvsonraden districts of Sweden in the early 1960s. One situation in which two adults killed and fed together (on a hare) is described but, in general, female lynxes living in northern latitudes are thought to be solitary.

Spanish lynxes, *Lynx pardina* in the Coto Donana take only a small proportion of deer in their diet, and the annual availability of fallow deer fawns *Dama dama* there is probably too low to make it worthwhile switching from rabbits, *Oryctolagus cuniculus* to larger prey (Beltran *et al.* 1985).

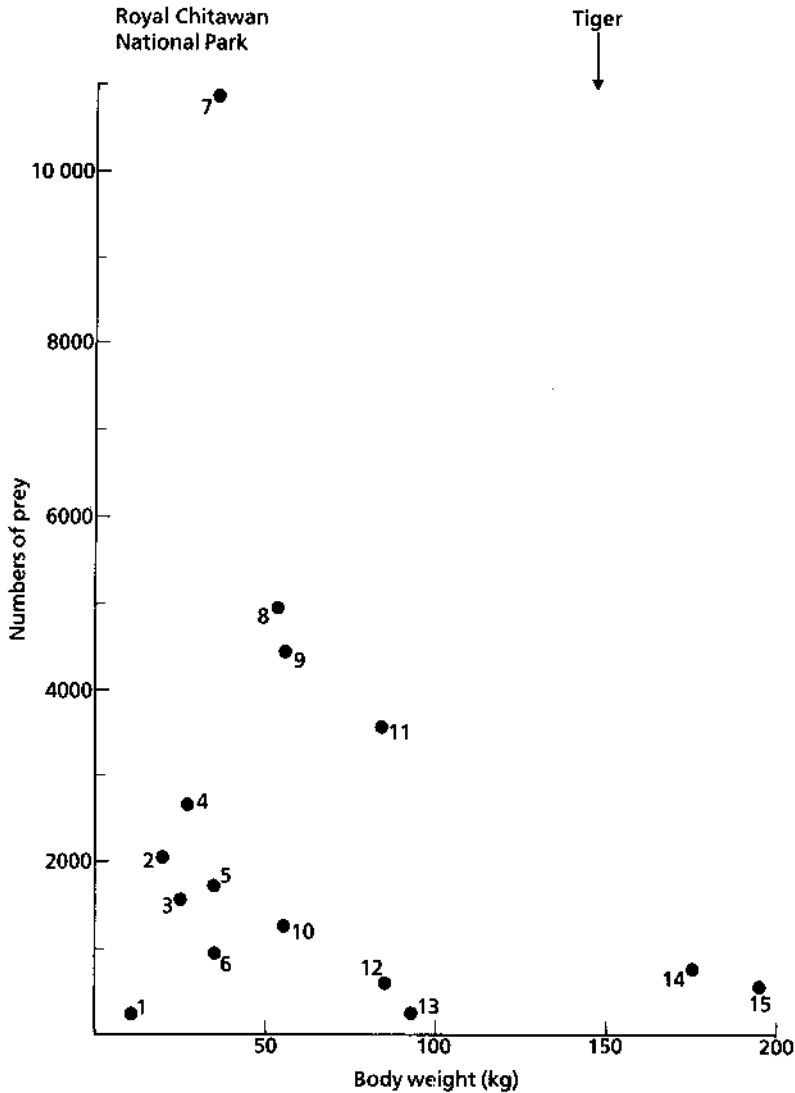


FIG. 11. Estimated abundance and body weights (kg) of prey in the Royal Chitawan National Park, Nepal (after Sunquist 1981). Also shown is weight of an adult female tiger. 1. Young (Y) barking deer; 2. Adult female (AF) barking deer; 3. Adult male (AM) barking deer; 4. Y hogdeer; 5. Y chital; 6. Y wild pig; 7. AF hogdeer; 8. AM hogdeer; 9. AF chital; 10. AF wild pig; 11. AM chital; 12. AM wild pig; 13. Y sambar; 14. AF sambar; 15. AM sambar. Weights from Schaller (1967), Eisenberg (1981), Sunquist (1981), abundance calculated as a mean of data from Seidensticker (1976) and Tamang (1979).

#### North American lynxes

North American lynxes, *Lynx canadensis* (females, 18.9 kg: Saunders 1964) consume snowshoe hares, *Lepus americanus* more than any other prey item in

each of the habitats they have been studied whether their populations are increasing or in decline (see, for example, Saunders 1963; van Zyll de Jong 1966; Nellis & Keith 1968; Brand & Keith 1979). In one study of lynxes on Cape Breton Island, Newfoundland, 160 hares and 155 red-backed voles, *Clethrionomys gapperi*, the most common small mammal, were caught on 1000 trapnights over the whole study area; grouse numbers were not estimated but were reported as common (Parker *et al.* 1983). Numbers of larger animals, white-tailed deer, *Odocoileus virginianus*, were said to be common when the ground was free of snow, but only ten to twelve moose, *Alces alces* were present. Lynxes can kill large ungulates, caribou, *Rangifer caribou* (c. 100 kg) (Saunders 1963) or mule deer, *Odocoileus hemionus* (57 kg) (Sheppard 1960), and also scavenge them (moose: Saunders 1963). However, snowshoe hares are likely to be far more numerous than these species in nearly every habitat, although quantitative data are difficult to find. As a lynx requires 0.6 kg of meat per day (Nellis *et al.* 1972) and hares weigh 1.4 kg, mothers with three or four kits would already have to kill hares more than once a day, and would thus be obliged to switch to larger but much less numerous ungulate prey to sustain group living.

#### Bobcats

Bobcat diet is extremely variable as determined by the numerous analyses of bobcat stomach contents (see, for example, Blum & Escherich 1979). In general, representation of large prey, white-tailed deer, in the diet increases in the north-east of the USA accounting for 16–35% occurrence in this region (summarized in Maehr & Brady 1986); unfortunately data on comparable densities of prey species available to bobcats are difficult to locate (Benson & Moore 1977). Although strong representation of deer in bobcat diet in high latitudes suggests females could live in groups, surveys that separate diet by sex show that males (body weight 12.3 kg) eat considerably greater proportions of deer than do females (body weight 7.2 kg: Litvaitis, Stevens & Mautz 1984): occurrence of deer in Arkansas bobcat stomachs was 10% in males, but 3% in females (Fritz & Selander 1978), and in Maine was 19% ( $n=72$ ) and 7% ( $n=95$ ) respectively ( $\chi^2=5.26$ ,  $P<0.05$ : Litvaitis, Clark & Hunt 1986). Also, larger bobcats ( $>12$  kg) eat more deer than smaller individuals (Litvaitis, Clark & Hunt 1986). It therefore seems probable that the majority of bobcat deer kills (up to 55 kg: Marston 1942; see also Pollack 1951; Petraborg & Gunvalson 1962) are made by males, although females might scavenge them. If the smaller females can only take deer fawns or juveniles, and those in low numbers, then the opportunities for sociality in this species appear limited.

#### Cougars

Cougars (females 42 kg: Young & Goldman 1946) have been studied most extensively in the northern part of their range where they capture large prey such



as elk *Cervus canadensis* and mule deer (Table 5). Cougars concentrated on these species because they were forced into terrain offering ideal hunting conditions during winter (Hornocker 1970). Abundance of smaller prey such as snowshoe hares, or even beavers or porcupines, known to be taken by cougars (Robinette, Gashwiler & Morris 1959) are not available for comparison with ungulate densities in this area (Fig. 12). Superficially, it appears that exploiting prey this size (even

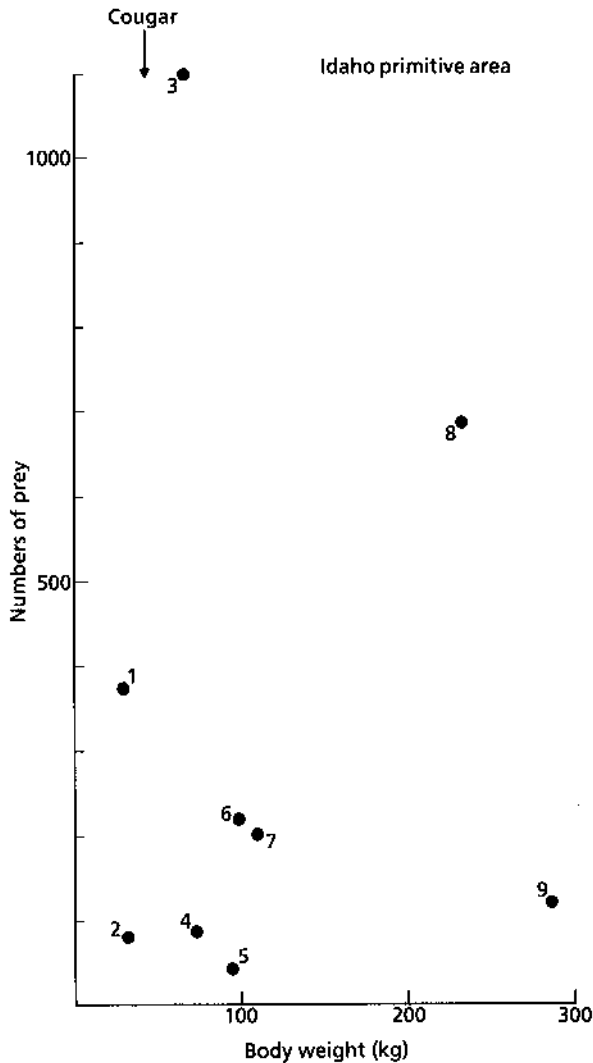


FIG. 12. Estimated abundance and body weights (kg) of prey in the Idaho Primitive Area, USA (after Hornocker 1970). Also shown is weight of a North American adult female cougar. 1. Mule deer calf; 2. Big horn sheep lamb; 3. Adult female (AF) mule deer; 4. AF big horn sheep; 5. Adult male (AM) big horn sheep; 6. AM mule deer; 7. Elk calf; 8. AF elk; 9. AM elk. Weights from Hornocker (1970), Schaller (1977).

though many mule deer were fawns) is sufficient to sustain a pair of female cougars with a total of four or five pooled cubs (see Robinette, Gashwiler & Morris 1961 for litter sizes), and temporary associations of cougars at large kills were seen (Seidensticker *et al.* 1973). Hornocker calculated that adults require 1.8–2.7 kg of meat per day, thus a group would need 10.8–18.9 kg. He also estimated that elk calves (7, Fig. 12), and adult male mule deer (6), 28% and 16% respectively of ungulate prey taken by Idaho cougars, would have 77 kg and 69 kg of edible flesh on them. This would mean that social mothers would have to kill large prey about once every 5 days. A mother with three 32 kg cubs did kill four deer in 18 days, so this estimated killing rate is within the range found in this habitat during this season. The key variable is whether these size categories of ungulates are encountered sufficiently often to sustain such a killing rate throughout the year. Densities of these species (elk: 0.2/km<sup>2</sup>, mule deer: 0.3/km<sup>2</sup>) suggest it might be difficult. Moreover, large prey disperse during summer resulting in much larger female cougar ranges (Seidensticker *et al.* 1973) which implies that catching such prey becomes problematic during this period.

In tropical regions, cougars feed on much smaller prey (Table 5). Although cougars are smaller in these regions (for example, females 23.6 kg: Sanborn 1954; 29 kg: Emmons 1987a) and might thus prefer smaller prey species, there are few large species on which to prey. In Cocha Cashu National Park, Peru, collared peccaries, *Tayassu tajacu* (7, Fig. 13), red brocket deer, *Mazama americana* (8) and capybara, *Hydrochaeris hydrochaeris* (9) were present in low numbers and were not found in the small number of cougar scats sampled by Emmons (1987a). Predation by jaguars on these species may have reduced the rate at which cougars could encounter these larger prey.

Finally, cougars living in Torres del Paine National Park, Chile, ate introduced hares, *Lepus capensis* most frequently but also caught guanacos, *Lama guanicoe* (males up to 130 kg: Yanez *et al.* 1986). Although 540 guanacos are estimated to live in the park, Wilson (1984) considers adult and subadult males, 39% of the population, to be relatively invulnerable to attack because they live in large groups. Nevertheless, adult female and young guanacos might be sufficiently numerous to enable cougars to live in groups.

### Ocelots

At Cocha Cashu, 31% of ocelot scats contained *Proechimys* sp. (1, Fig. 13), and 21% *Oryzomys* sp. (2) while a smaller number contained opossum and bird remains (Emmons 1987a). Ocelots (9.3 kg) fulfilled their food requirements of 0.6–0.8 kg/day by capturing prey usually weighing less than 5% of their body weight, which agrees with studies in Belize (Konecny, in press) and Venezuela (Ludlow & Sunquist 1982). Although ocelots did take prey between 1 kg and 8 kg (4.5% representation in scats), these prey were far less numerous than small rodents (Fig. 13) and may have been difficult to find sufficiently often. Feeding on rodents 'required spending many hours foraging to catch several prey each day'

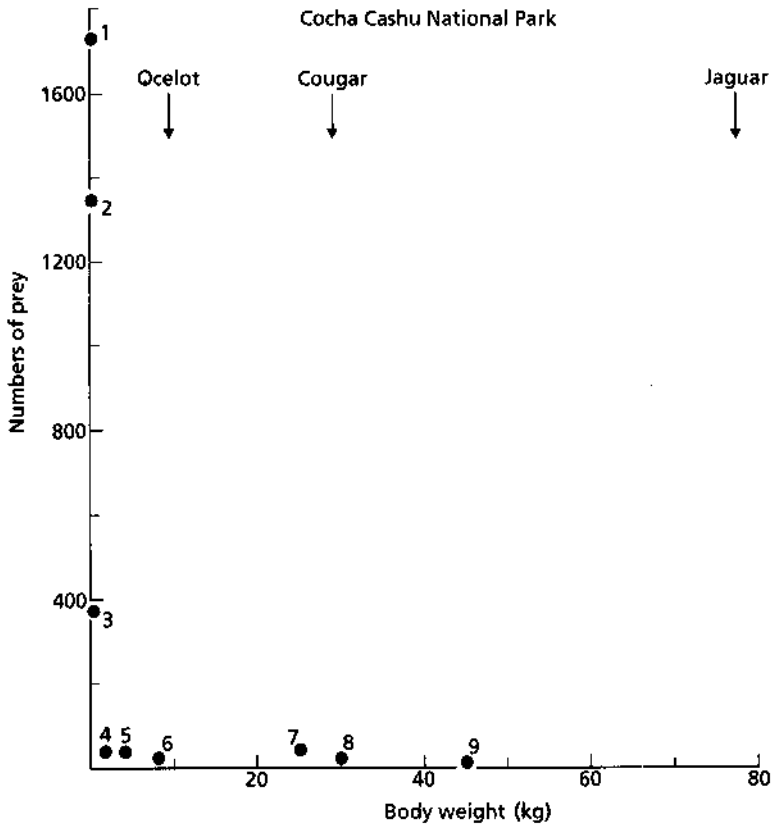


FIG. 13. Estimated abundance and body weights (kg) of prey in the Cocha Cashu National Park, Peru (after Emmons 1987a). Also shown are weights of an adult female ocelot, female cougar and female jaguar in this habitat. 1. *Proechimys* sp.; 2. *Oryzomys* spp.; 3. Opposum sp.; 4. *Myoprocta pratti*; 5. *Dasyprocta variegata*; 6. *Agouti paca*; 7. *Tayassu tajacu*; 8. *Mazama americana*; 9. *Hydrochaeris hydrochaeris*. Weights from Emmons (1987a).

(Emmons 1987a, see also Emmons 1987b), thus it appeared difficult for a hypothetical group-living female to increase food intake through taking small prey because of time limitations, and through taking large prey because of lack of availability.

### Jaguars

The bulk of jaguar scats in Cocha Cashu contained medium-sized mammals, collared peccaries (7, Fig. 13), agoutis, *Dasyprocta variegata* (5), pacas, *Agouti paca* (6) and brocket deer (8), as well as tortoises, *Geochelone denticulata* (7 kg). These represented the largest prey that were reasonably abundant in the park; tapirs *Tapirus terrestris* (150 kg), are reportedly difficult to bring down (Emmons

1987a) and were rarely seen in the study area (M. Symington, personal communication). This suggested that female jaguars (78 kg; Schaller & Vasconcelos 1978) would have little opportunity to exploit prey larger than 60% of their own body weight in this habitat.

In Belize, prey most commonly found in scats was of similar body weight, nine-banded armadillos *Dasypus novemcinctus* (3 kg), paca (8 kg) and red brocket deer (30 kg) (Rabinowitz & Nottingham 1986); larger domestic livestock were not taken (Rabinowitz 1986). Nevertheless, in Acurizal, Brazil, jaguars readily take 250 kg cattle, although they prefer to take calves (Schaller 1983). Such observations suggest jaguars, and even cougars, could become social in Acurizal. However, calves are poorly represented in the area owing to bad management, and cattle reportedly have a tendency to bunch at nights (Schaller 1983), so in practice there might be limited opportunity for exploiting large prey in this habitat.

## CONCLUSIONS

A review of felids living in twenty-one situations suggests females of most species have little opportunity to be social because large prey are not usually abundant. However, further data are required on the abundance, age structure and sizes of prey available to felids in many of these and other habitats. Only in a few situations might there be opportunities for sociality. Tigers in the Royal Chitawan National Park, European lynxes in northern Sweden, cougars in the Torres del Paine National Park, and jaguars on the Acurizal ranch are all reported to live in areas with fairly high densities of large prey. Given the flexibility of carnivore social organization in this (MacDonald & Apps 1978) and other families (Kruuk 1972; MacDonald 1983), felids might be expected to respond to these favourable conditions and have taken advantage of some of the benefits of sociality. That they have not, suggests that prey in these regions are still difficult to catch despite their abundance, perhaps because of grouping patterns, vigilance, or difficulty in subduing them. Further work on anti-predator behaviour of prey in response to felid predation is needed in these areas. Alternatively, there may be no benefits to sociality in these habitats; however, known cases of infanticide by cougar males in other areas, for example, suggests females could repel males if they lived together, as argued for lions (Packer & Pusey 1983). In one species, caracals in the Mountain Zebra National Park, some females may now live in groups as a consequence of catching large prey.

Lionesses have abundant prey available to them that is slightly larger than themselves, which enables them to catch relatively big prey frequently and without much difficulty. The costs of feeding additional group members are thereby greatly reduced compared to other felids, allowing lionesses to capitalize on advantages that group living provides. This explanation emphasizes that availability of abundant prey, somewhat larger than a lioness, is the factor that allows lions to feed additional group members, whereas Packer (1986) argues that open habitat,

high female density and the relatively large size of their observed kills forces lions to share carcasses with relatives.

In summary, this review shows that in most situations where adequate data are available, prey larger than that normally taken by females and up to double that of an adult female's body weight, necessary to sustain two families living together, are relatively scarce. At present then, the hypothesis that sociality in felids is limited by the costs rather than by the benefits needs serious consideration.

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### REFERENCES

- Abramov, V.K. (1962). K. biologii amurskogo tigra (On the biology of the Amur tiger). *Panthera tigris longipilis* Fitzinger 1868. *Acta Zoologica Societie Bohemoslovenicae*, 26(2), 189-202.
- Bailey, T.N. (1974). Social organization in a bobcat population. *Journal of Wildlife Management*, 38, 435-46.
- Beltran, J.F., Sanjose, C., Delibes, M. & Braza, F. (1985). An analysis of the Iberian lynx predation upon fallow deer in the Coto Donana, SW Spain. *XVIIth Congress of the International Union of Game Biologists*, pp. 961-7. Brussels, September 17-21.
- Benson, S.L. & Moore, R.A. (1977). Bobcat food habit response to a change in prey abundance. *Southwest Naturalist*, 21, 451-7.
- Bertram, B.C.R. (1973). Lion population regulation. *East African Wildlife Journal*, 11, 215-25.
- Bertram, B.C.R. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology*, 177, 463-82.
- Bertram, B.C.R. (1978). *Pride of Lions*. Dent, London.
- Bertram, B.C.R. (1982). Leopard ecology as studied by radio tracking. *Telemetric Studies of Vertebrates* (Ed. by C.L. Cheeseman). Symposium of the Zoological Society of London, 49, pp. 341-52. Academic Press, London.
- Blum, L.G. & Escherich, P.C. (1979). *Bobcat Research Conference Proceedings: Current Research on Biology and Management of Lynx rufus*. Smithsonian Institution, Front Royal, Virginia.
- Blumenschine, R.J. & Caro, T.M. (1986). Unit flesh weights of some East African bovids. *African Journal of Ecology*, 24, 273-86.
- Borner, M., FitzGibbon, C.D., Borner, Mo., Caro, T.M., Lindsay, W.K., Collins, D.A. & Holt, M.E. (1987). The decline in the Serengeti Thomson's gazelle population. *Oecologia*, 73, 32-40.
- Bradbury, J.W. & Vehrencamp, S.L. (1977). Social organization and foraging in emballonurid bats. III. Mating systems. *Behavioral Ecology and Sociobiology*, 2, 1-17.
- Brand, C.J. & Keith, L.B. (1979). Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management*, 43, 827-49.
- Brettenmoser, von U. & Haller, H. (1987). Zur Nahrungsökologie des Luchses *Lynx lynx* in den schweizerischen Nordalpen. *Zeitschrift für Säugetierkunde*, 52 (special issue), 168-91.

- Burney, D.A. (1980). *The effects of human activities on cheetahs (Acinonyx jubatus Schr.) in the Mara Region of Kenya*. M.Sc. thesis, University of Nairobi.
- Bygott, J.D., Bertram, B.C.R. & Hanby, J.P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature*, **282**, 839–41.
- Caraco, T. & Wolf, L.L. (1975). Ecological determinants of group sizes of foraging lions. *American Naturalist*, **109**, 343–52.
- Carbyn, L.N. & Patriquin, D. (1983). Observations on home range sizes, movements and social organization of lynx, *Lynx canadensis*, in Riding Mountain National Park, Manitoba. *Canadian Field Naturalist*, **97**, 262–7.
- Caro, T.M. (1980). The effects of experience on the predatory patterns of cats. *Behavioral and Neural Biology*, **23**, 1–28.
- Caro, T.M. (1982). A record of cheetah scavenging in the Serengeti. *African Journal of Ecology*, **20**, 213–14.
- Caro, T.M. (1987a). Indirect costs of play: cheetah cubs reduce maternal hunting success. *Animal Behaviour*, **35**, 295–7.
- Caro, T.M. (1987b). Cheetah mothers' vigilance: looking out for prey or for predators? *Behavioral Ecology and Sociobiology*, **20**, 351–61.
- Caro, T.M. & Collins, D.A. (1986). Male cheetahs of the Serengeti. *National Geographic Research*, **2**, 75–86.
- Caro, T.M. & Collins, D.A. (1987a). Ecological characteristics of territories of male cheetahs (*Acinonyx jubatus*). *Journal of Zoology*, **211**, 89–105.
- Caro, T.M. & Collins, D.A. (1987b). Male cheetah social organization and territoriality. *Ethology*, **74**, 52–64.
- Caro, T.M., Holt, M.E., FitzGibbon, C.D., Bush, M., Hawkey, C.M. & Kock, R.A. (1987). Health of adult free-living cheetahs. *Journal of Zoology*, **212**, 573–84.
- Clark, C.W. (1987). The lazy, adaptable lions: a Markovian model of group foraging. *Animal Behaviour*, **35**, 361–8.
- Corbett, L.K. (1979). *Feeding ecology and social organization of wildcats (Felis sylvestrus) and domestic cats (Felis catus) in Scotland*. Ph.D. thesis, Aberdeen University.
- Curio, E.B. (1976). *The Ethology of Predation*. Springer-Verlag, Berlin.
- Durant, S.M., Caro, T.M., Collins, D.A., Alawi, R.M. & FitzGibbon, C.D. (in press). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology*.
- Eaton, R.L. (1974). *The Cheetah: The Biology, Ecology, and Behavior of an Endangered Species*. Van Nostrand Reinhold, New York.
- Eisenberg, J.F. (1981). *The Mammalian Radiations*. Athlone Press, London.
- Eloff, F.C. (1973). Ecology and behavior of the Kalahari lion. *The World's Cats, Vol 1* (Ed. by R.L. Eaton), pp. 90–126. World Wildlife Safari, Winston, Oregon.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science*, **197**, 215–23.
- Emmons, L.H. (1987a). Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, **20**, 271–83.
- Emmons, L.H. (1987b). Jungle cruisers. *Animal Kingdom*, **90**(1), 22–30.
- Foster, J. & Kearney, D. (1967). Nairobi National Park game census, 1966. *East African Wildlife Journal*, **5**, 112–20.
- Frame, G. & Frame, L. (1976). Interim cheetah report for the Serengeti Research Institute, annual report, mimeographed.
- Frame, G. & Frame, L. (1981). *Swift and Enduring: Cheetahs and Wild Dogs of the Serengeti*. E.P. Dutton, New York.
- Frame, G.W. (1980). *Cheetah Social Organisation in the Serengeti Ecosystem of Tanzania*. Paper presented at the Animal Behavior Society, Fort Collins, Colorado.
- Frame, G.W. (1984). Cheetah. *The Encyclopedia of Mammals, Vol 1*. (Ed. by D.W. MacDonald), pp. 40–3. Allen & Unwin, London.
- Frame, G.W. & Wagner, F.H. (1981). Hares on the Serengeti Plains, Tanzania. *Proceedings of the World Lagomorph Conference* (Ed. K. Myers & C.D. MacInnes), pp. 790–802. IUCN, Morges, Switzerland.

- Fritz, S.H. & Selander, J.A. (1978). Diets of bobcats in Arkansas with special reference to age and sex differences. *Journal of Wildlife Management*, **42**, 533-9.
- Gashwiler, J.S. & Robinette, W.L. (1957). Accidental fatalities of the Utah cougar. *Journal of Mammalogy*, **38**, 123-6.
- Geertsema, A.A. (1985). Aspects of the ecology of the serval *Leptailurus serval* in the Ngorongoro crater, Tanzania. *Netherlands Journal of Zoology*, **35**, 527-610.
- Georgiadis, N. (1985). Growth patterns, sexual dimorphism and reproduction in African ruminants. *African Journal of Ecology*, **23**, 75-87.
- Gittleman, J.L. (1986). Carnivore life history patterns: allometric, phylogenetic, and ecological associations. *American Naturalist*, **127**, 744-71.
- Grobler, J.H. (1981). Feeding behaviour of the caracal *Felis caracal* Schreber 1776 in the Mountain Zebra National Park. *South African Journal of Zoology*, **16**, 259-62.
- Grobler, J.H. & Wilson, V.J. (1972). Food of the leopard *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, Rhodesia, as determined by faecal analysis. *Arnoldia*, **35**(5) 1-10.
- Gromov, E.N. & Matjuschkin, E.N. (1974). K analizu konkurentnih otnoshenii tigr i volka v Sikhote-Aline (Analysis of the competing relations of the tiger and wolf in Sikhote-Alin). "Biologich. Nauki", **N2**, 20-5.
- Haglund, B. (1966). Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Summary in English. *Viltrevy*, **4**, 245-83.
- Hamilton, P.H. (1976). *The movements of leopards in Tsavo National Park, Kenya, as determined by radio-tracking*. M.Sc. thesis, University of Nairobi.
- Hornocker, M.G. (1970). An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs*, **21**, 1-39.
- Johnsingh, A.J.T. (1983). Large mammalian prey - predators in Bandipur. *Journal of the Bombay Natural History Society*, **80**, 1-57.
- Konecny, M.J. (1987). Food habits and energetics of feral house cats in the Galapagos Islands. *Oikos*, **50**, 24-32.
- Konecny, M.J. (in press). Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. *Mammals of the Americas: Essays in Honor of Ralph M. Wetzel* (Ed. by J.F. Eisenberg).
- Kruuk, H. (1972). *The Spotted Hyaena: A Study of Predation and Social Behavior*. University of Chicago Press, Chicago, Illinois.
- Kruuk, H. (1975). Functional aspects of social hunting in carnivores. *Function and Evolution in Behaviour* (Ed. by G. Baerends, C. Beer & A. Manning), pp. 119-41. Oxford University Press, Oxford.
- Kruuk, H. & Turner, M. (1967). Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia*, **31**, 1-27.
- Lamprecht, J. (1978). The relationship between food competition and foraging group size in some larger carnivores. A hypothesis. *Zeitschrift für Tierpsychologie*, **46**, 337-43.
- Lamprecht, J. (1981). The function of social hunting in larger terrestrial carnivores. *Mammal Review*, **11**, 169-79.
- Litvaitis, J.A., Clark, A.G. & Hunt, J.H. (1986). Prey selection and fat deposits of bobcats (*Felis rufus*) during autumn and winter in Maine. *Journal of Mammalogy*, **67**, 389-92.
- Livaitis, J.A., Stevens, C.L. & Mautz, W.W. (1984). Age, sex, and weight of bobcats in relation to winter diet. *Journal of Wildlife Management*, **48**, 632-5.
- Ludlow, M.E. & Sunquist, M.E. (1987). Ecology and behavior of ocelots in Venezuela. *National Geographic Research* **3**, 444-61.
- MacDonald, D.W. (1983). The ecology of carnivore social behaviour. *Nature*, **301**, 379-84.
- MacDonald, D.W. & Apps, P.J. (1978). The behaviour of a group of semi-dependent farm cats, *Felis catus*: a progress report. *Carnivore Genetics Newsletter*, **3**, 256-86.
- Macher, D.S. & Brady, J.R. (1986). Food habits of bobcats in Florida. *Journal of Mammalogy*, **67**, 133-8.
- Marston, M.A. (1942). Winter relations of bobcats to white-tailed deer in Maine. *Journal of Wildlife Management*, **6**, 328-37.
- Matjushkin, E.N., Zhivotchenko, V.I. & Smlrnov, E.N. (1980). *The Amur Tiger in the USSR*. IUCN, Gland, Switzerland.

- McVittie, R. (1979). Changes in the social behaviour of South West African cheetah. *Madoqua*, **11**, 171-84.
- Mitchell, B.L., Shenton, J.B. & Uys, C.M. (1965). Predation on large mammals in the Kafue National Park, Zambia. *Zoologica Africana*, **1**, 297-318.
- Nellis, C.H. & Keith, L.B. (1968). Hunting activities and success of lynxes in Alberta. *Journal of Wildlife Management*, **32**, 718-22.
- Nellis, C.N., Wetmore, S.P. & Keith, L.B. (1972). Lynx-prey interactions in central Alberta. *Journal of Wildlife Management*, **36**, 320-9.
- O'Brien, S.J., Roelke, M.E., Marker, L., Newman, A., Winkler, C.A., Meltzer, D., Colly, L., Evermann, J.F., Bush, M., & Wildt, D.E. (1985). Genetic basis for species vulnerability in the cheetah. *Science*, **227**, 1428-34.
- Orsdol, K.G. van, (1981). *Lion predation in Rwenzori National Park, Uganda*. Ph.D. thesis, University of Cambridge.
- Orsdol, K.G. van, Hanby, J.P. & Bygott, J.D. (1985). Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology*, **206**, 97-112.
- Owens, M. & Owens, D. (1984). *Cry of the Kalahari*. Houghton Muffin Co., Boston.
- Packer, C. (1986). The ecology of sociality in felids. *Ecological Aspects of Social Evolution: Birds and Mammals* (Ed. by D.I. Rubenstein & R.W. Wrangham), pp. 429-51. Princeton University Press, Princeton, New Jersey.
- Packer, C. (1988). Constraints on the evolution of reciprocity: lessons from cooperative hunting. *Ethology and Sociobiology*, **9**, 137-47.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, D., Hanby, J.P., Cairns, S.J. & Borgerhoff Mulder, M. (1988). Reproductive success of lions. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T.H. Clutton-Brock), pp. 363-83. University of Chicago Press, Chicago, Illinois.
- Packer, C. & Pusey, A.E. (1982). Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature*, **296**, 740-2.
- Packer, C. & Pusey, A.E. (1983). Adaptations of female lions to infanticide by incoming males. *American Naturalist*, **121**, 716-28.
- Packer, C. & Pusey, A.E. (1984). Infanticide in carnivores. *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by G. Hauslater & S.B. Hrdy), pp. 31-42. Aldine, New York.
- Packer, C. & Rutlan, L. (in press). The evolution of cooperative hunting. *American Naturalist*.
- Parker, G.R., Maxwell, J.W., Morton, L.D. & Smith, G.E.J. (1983). The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. *Canadian Journal of Zoology*, **61**, 770-86.
- Petraborg, W.H. & Gunvalson, V.E. (1962). Observations on bobcat mortality and bobcat predation on deer. *Journal of Mammalogy*, **43**, 430-1.
- Pienaar, U. de (1969). Predator-prey relations amongst the larger mammals of Kruger National Park. *Koedoe*, **12**, 108-76.
- Pollack, M.E. (1951). Food habits of the bobcat in the New England states. *Journal of Wildlife Management*, **15**, 209-13.
- Pringle, J.A. & Pringle, V.L. (1979). Observations on the lynx *Felis caracal* in the Bedford District. *South African Journal of Zoology*, **14**, 1-4.
- Rabinowitz, A.R. (1986). Jaguar predation on domestic livestock in Belize. *Wildlife Society Bulletin*, **14**, 170-4.
- Rabinowitz, A.R. & Nottingham, B.G. (1986). Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology*, **210**, 149-59.
- Robinette, W.L., Gashwiler, J.S. & Morris, O.W. (1959). Food habits of the cougar in Utah and Nevada. *Journal of Wildlife Management*, **23**, 261-73.
- Robinette, W.L., Gashwiler, J.S. & Morris, O.W. (1961). Notes on cougar productivity and life history. *Journal of Mammalogy*, **42**, 204-17.
- Rood, J.P. (1986). Ecology and social evolution in the mongooses. *Ecological Aspects of Social Evolution: Birds and Mammals*. (Ed. by D.I. Rubenstein & R.W. Wrangham), pp. 131-52. Princeton University Press, Princeton, New Jersey.
- Rudnai, J.A. (1973) *The Social Life of the Lion*. Medical and Technical Publishing Co., Lancaster.



- Sachs, R. (1967). Live weights and body measurements of Serengeti game animals. *East African Wildlife Journal*, 5, 24-36.
- Sanborn, C.C. (1954). Weights, measurements, and color of the Chilean forest puma. *Journal of Mammalogy*, 35, 126-8.
- Saunders, J.K. Jr. (1963). Food habits of the lynx in Newfoundland. *Journal of Wildlife Management*, 27, 384-90.
- Saunders, J.K. Jr. (1964). Physical characteristics of the Newfoundland lynx. *Journal of Mammalogy*, 45, 36-47.
- Schaller, G.B. (1967). *The Deer and the Tiger: A Study of Wildlife in India*. University of Chicago Press, Chicago, Illinois.
- Schaller, G.B. (1972). *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago, Illinois.
- Schaller, G.B. (1977). *Mountain Monarchs: Wild Sheep and Goats of the Himalaya*. University of Chicago Press, Chicago, Illinois.
- Schaller, G.B. (1983). Mammals and their biomass on a Brazilian Ranch. *Arquivos de Zoologia*, 31(1), 1-36.
- Schaller, G.B. & Crawshaw, P.G. Jr. (1980). Movement patterns of jaguar. *Biotropica*, 12, 161-8.
- Schaller, G.B., Talipu, L.H., Hua, L., Junrang, R., Mingjiang, Q. & Halbin, W. (1987). Status of large mammals in the Taxkorgan Reserve, Xinjiang, China. *Biological Conservation*, 42, 53-71.
- Schaller, G.B. & Vasconcelos, J.M.C. (1978). Jaguar predation on capybara. *Zeitschrift für Säugetierkunde*, 43, 296-301.
- Seidensticker, J. (1976). Ungulate populations in the Chitawan valley, Nepal. *Biological Conservation*, 10, 183-210.
- Seidensticker, J., Hornocker, M.G., Wiles, W.V. & Messick, J.P. (1973). Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs*, 35, 1-60.
- Senzota, R.B.M. (1978). *Some aspects of the ecology of two dominant rodents in the Serengeti Ecosystem*. M.Sc. thesis, University of Dar es Salaam.
- Sheppard, D.H. (1960). *The ecology of the mule deer of the Sheep River region*. M.Sc. thesis, University of Alberta.
- Skinner, J.D. (1979). Feeding behaviour in caracal (*Felis caracal*). *Journal of Zoology*, 189, 523-55.
- Smith, R.M. (1978). Movement patterns and feeding behavior of the leopard in the Rhodes Matopos National Park, Rhodesia. *Carnivore*, 1(3), 58-69.
- Smithers, R.H.N. (1971). *The Mammals of Botswana*. Museum memoir No. 4, National Museums of Rhodesia, Salisbury.
- Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria, South Africa.
- Spalding, D.J. & Lesowski, J. (1971). Winter food of the cougar in south-central British Columbia. *Journal of Wildlife Management*, 35, 378-81.
- Stoddart, D.M. (1979). Feeding behaviour in caracal *Felis caracal*. *Journal of Zoology*, 189, 523-57.
- Sunquist, M.E. (1981). The social organization of tigers (*Panthera tigris*) in Royal Chitawan National Park. *Smithsonian Contributions to Zoology*, 336, 1-98.
- Sunquist, M.E. & Sunquist, F.C. (in press). Ecological constraints on predation in large felids. *Carnivore Behavior, Ecology and Evolution* (Ed. by J.L. Gittleman). Cornell University Press, Ithaca, New York.
- Tamang, K.M. (1979). Population characteristics of the tiger and its prey. Unpublished paper presented at the International Symposium on the Tiger. New Delhi, India.
- Thapar, V. (1986). *Tiger: Portrait of a Predator*. Fact on File Publications, New York.
- Trivers, R.L. (1972). Parental investment and sexual selection. *Sexual Selection and the Descent of Man, 1871-1971*. (Ed. by B. Campbell), pp. 136-79. Aldine Press, Chicago, Illinois.
- Valkenburgh, B. van & Ruff, C.B. (1987). Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology*, 212, 379-97.
- Waser, P.M. & Waser, M.S. (1985). *Ichneumia albicanda* and the evolution of viverrid gregariousness. *Zeitschrift für Tierpsychologie*, 68, 137-51.
- Wilson, P. (1984). Puma predation on guanacos in Torres del Paine National Park, Chile. *Mammalia*, 48, 515-22.

- Wilson, V.J. (1968). Weights of some mammals from eastern Zambia. *Arnoldia*, 32(3) 1-20.
- Wrangham, R.W. (1979). On the evolution of ape social systems. *Social Science Information*, 18, 335-68.
- Yanez, J.L., Cardenas, J.C., Gezelle, P. & Jaksic, F.M. (1986). Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy*, 67, 604-6.
- Young, S.P. & Goldman, E.A. (1946). *The Puma: Mysterious American Cat*. American Wildlife Institute, Washington, D.C.
- Yudakov, A.G. (1973). O vlijanii tigra na chislennost kopitnih (On the influence of the tiger upon the ungulate population). *Redkie vidi mlekopitajuschih fauni SSR i ih ohrana*, Sbornik materialov, str. 93-94. Izd. 'Nauka', Moskva.
- Zyll de Jong, C.G. van (1966). Food habits of the lynx in Alberta and the Macenzie District, N.W.T. *Canadian Field-Naturalist*, 80, 18-23.