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Abstract: The social patterns of South African cheetah are compared to those of East African cheetah. The data analyzed suggest that in the absence of large interspecific competitors grouping of cheetah occurs, prey size expands and litter size increases. No evidence of allo-parenting was found although both females and males exhibited social tendencies.

Changes in the social behaviour of South West African cheetah

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ABSTRACT

The social patterns of South West African cheetah are compared to those of East African cheetah. The data analysed suggest that in the absence of large interspecific competitors grouping of cheetah occurs, prey size expands and litter size increases. No evidence of allo-parenting was found although both females and males exhibited social tendencies.

1 INTRODUCTION

Ecological disturbances have occurred in South West Africa which may have had significant impact on the cheetah population of that country. This study aims to verify the reported differences in social groupings, compared to those observed in E. Africa and to explore theoretical reasons for such alterations as may exist.

Among the large African carnivores, the cheetah, *Acinonyx jubatus* is considered a diurnal courser which is relatively solitary in its social behaviour. While the literature abounds with anecdotal comments from game preserves all over Africa, published field studies have been primarily on the East African cheetah. Field studies by Eaton (1970, 1974) Frame and Frame (1976, 1977) McLaughlin (in Schaller, 1972, Wrogemann, 1975) and Schaller (1972) as well as observations on a pet cheetah returned to the wild by Adamson (1969, 1972) have provided some information on mother-offspring relations, sibling groups, hunting techniques and preferred prey. The difficulty of observations in the wild, especially bushed areas, and the secretive nature of most cheetahs result in little information about overall population size, dynamics, and social structure in the parks. Using questionnaires and interviews, Myers (1975), Graham and Parket (1965), and Graham, (1966) have attempted to assess the status of the cheetah in East Africa within and beyond park boundaries. The present work attempts to make some similar assessments of the cheetah on privately held land in the northern portion of South West Africa.

While Myers (1975) considers the cheetah to be a declining species throughout its range, there are indications that in South West Africa the cheetah population may be increasing, and that unusually large groupings, as compared to East African cheetah, may exist (Joubert and Mostert, 1975; Gaerdes, 1974). Because no accurate population count has been made in the past, it is impossible to establish if the cheetah numbers are actually increasing. Even today, estimates for all of South West Africa vary from 1 500 (Myers, 1975) to 5 000 (Joubert and Mostert, 1975). Assuming that the population is not declining, it is important to consider what factors may be responsible for such relative success and what bearing these might have on the cheetah's social structure.

At least three factors can be identified as contributing to the survival of the cheetah on privately held land in South West Africa: a) bush encroachment, b) avail-

ability of food and water, c) decrease of competitive pressure. All of these are associated with the expansion of European settlers into the area.

a) Overstocking of domestic sheep, cattle, and goats led to overgrazing. Sensitive wild grazing species as well as the grasses of the savanna suffered, to be replaced by brush and browsers (Joubert and Mostert, 1975). Myers (1975) and Frame and Frame (1977) consider such a deterioration of the habitat to be detrimental to cheetahs, in that hunting efficiency is reduced. Most field studies have indirectly supported this view: since extensive observation in brushed areas remains impossible with techniques used to date, hunting there has been insufficiently observed. South West African cheetahs apparently do well in spite of the altered environment (Joubert and Mostert, 1975; Gaerdes, 1974). Possibly the accessibility of domestic stock together with concealment from the farmer-hunter offsets the suggested disadvantage or poorer hunting.

b) The European brought the technology for drilling, thereby vastly increasing the access to open water. Also in recent years the presence of wild ungulates has been encouraged by many farmers, rather than systematically eliminated as in the past. The increased availability of wild prey as well as the easily obtainable domestic stock must facilitate existence for the South West African cheetah as compared to one in an East African park. The resultant superior health should lead to decreased mortality in adults as well as young. The former is not testable until longitudinal field studies reveal adult mortality; the latter should be detected as larger litter sizes.

c) In an attempt to protect his flocks (and sometimes his family), the European farmer has virtually eliminated those animals which compete with him for the livestock. The lion (*Panthera leo*), hyena (mainly *Hyaena brunnea; Crocuta crocuta* was never common in most of the area) and wild dog (*Lycaon pictus*) have been extirpated. Of the large carnivores, only the leopard (*Panthera pardus*) and cheetah remain. The leopard, even more secretive than the cheetah, is also more modest in its requirements (Schaller, 1972) and seems to have responded to strong pressures to avoid humans. The cheetah, because it seldom returns to its kill, has not been susceptible to poisoning. Hunting is not cost effective, and trapping has been perfected only in the last decade.

The lion, leopard, hyena, even possibly the wild dog, all rank above the cheetah in the hierarchy of the normal African carnivore guild (Schaller, 1972). Of these only the leopard remains in the ranch-lands. In most areas of South West Africa, there appears to be little overlap and less interaction between leopard and cheetah. The freedom of the competition from other species is probably the over-riding factor in the success of the cheetah. It is interwoven with the two aforementioned influences and would exert a strong effect even alone.

Interference competition, defined by Pianka as "competition by way of direct interaction, such as aggressive encounters" (1974, p. 134), is important in the cheetah's life in East Africa (Adamson, 1969, 1972; Eaton, 1974; Frame, 1976, 1977; Kruuk, 1972; Schaller, 1972; Wrogemann, 1975). Lion and hyena predation is probably an important component of the high cub mortality. Lions and leopards occasionally kill an adult cheetah. Adamson (1972) relates the strong avoidance reaction a naive cheetah exhibits in the presence of lions. Such a response would be of selective advantage if lions even occasionally inflict injury on cheetahs. Strong evidence indicates that lions, hyenas, leopards, and groups of wild dogs steal fresh kills from cheetahs. The latter may lose as much as 9 % (Frame, 1976) to 14 % (Schaller, 1972) of its kills to these carnivores and other scavengers.

Exploitive competition ("more indirect inhibiting effects arising from a reduced availability of a common resource", Pianka, 1974, p. 134) is more difficult to assess. Contrary to the often quoted generalization by Bourliere (1963) that predators limit themselves to prey of approximately their own size, Eaton (in prep.), Schaller (1972), and Foster and Kearney (1967) have shown that there is a considerable overlap in prey size between such animals as the lion and cheetah. In the absence of large prey, lions turn to what is available. In the Serengeti, the Thomson's gazelle (*Gazella thomsoni*) is a prey item of lions in certain seasons; it is also the favoured prey of the cheetah. When the gazelle becomes scarce, as it sometimes does in the dry period, cheetahs suffer at the expense of lions. Frame and Frame (1976) document the current excellent status of the cheetah in the Serengeti, but they predict that in the next periodic decline of prey, the cheetah will be affected promptly.

Decreasing competition may have effects in addition to promoting healthier, better nourished cheetahs and thus raising survivorship. Eaton (1978) hypothesized that the presence of dominant competitors suppresses grouping in cheetahs, and conversely, that decreased competitive pressure should release tendencies toward sociality, if any exist.

Various authors have proposed numerous possible selective advantages to sociality: increased grazing and/or hunting efficiency, division of labour, interspecific hierarchy domination, defense against predation, greater success in either inter- or intra-specific competition for critically limiting resources (Alexander, 1974; Eaton, 1978; Schaller, 1972). These advantages must, of course, be weighed against the costs involved. For the cheetah, the disadvantages hinge on its morphology. Its structure has been determined by its role as a chaser rather than stalker-pouncer of prey. Light bones, long limbs, retracting claws, and lack of massive jaw musculature are forms matching function. These same forms, however, make the cheetah vulner-

able in confrontation with other carnivores sharing the environment. Eaton suggests that precisely because of its unique morphology, sociality for cheetahs would incur greater costs, in the form of risk of bodily harm, than benefits. The major competitors – the lion, hyena, and wild dog are dominant to the cheetah (Schaller, 1972; Kruuk, 1972; Eaton, 1978). Because of their vulnerability, even grouping by cheetahs would be unlikely to alter the dominance hierarchy; they would still be unable to defend their (larger) kill from or adequately resist predation on their young by lions or hyenas. However, should these predators be absent, the various advantages of sociality will be selectively reassessed. Increased hunting efficiency and more efficient division of labour in the form of allo-parenting would represent relatively minor changes in behaviour which could bring rapid increases in reproductive success.

Cheetahs in East Africa have been shown to take a rather narrow size-weight spectrum of prey (Schaller, 1972; Frame, 1976). This could be due either to an incapability of bringing down larger prey, to an excessive risk in handling such kills, to a poor cost-benefit energy ratio because one cheetah cannot consume a large kill (or is very likely to have it stolen), or because the dominant carnivores pre-empt the readily available (sick, old, etc.) game in the larger range. Should the last be a relatively important reason, absence of competition could produce intensive changes in the cheetah's prey pattern. It should then take as large a prey as it is capable of bringing down. This, in turn, may encourage co-operative hunting, which would presumably allow large game to be killed with less risk and greater efficiency (Schaller, 1972). Sharing the quarry, always a drawback to sociality, becomes profitable in terms of energy expenditure if the kill is large enough (Curaco and Wolf, 1975), and if there is little risk that it will be stolen.

Some social cohesiveness among cheetahs is known. All observers have noted the existence of relatively stable 2 to 4 male groups. There is some evidence that these are litter mates (Eaton, 1974). The proposed explanation of the advantages of such grouping is based on kin selection (Hamilton, 1964). If siblings gain more in inclusive fitness by not mating but supporting a mating brother than each would gain by attempting to mate singly, grouping of males should be favoured. Such grouping would foster success in intraspecific competition for a limited resource, in this case females. As such, the benefits to the males involved must offset the risks incurred by grouping since it is seen throughout cheetah populations.

However, this aspect of sociality applies only to males. If Eaton's proposed suppression of grouping by competitors is released, females, as well as males, should exhibit sociality.

To date, cheetah mothers have been observed to be solitary in raising their litters (Eaton, 1974; Frame and Frame, 1976; Schaller, 1972). Female offspring often occupy adjoining "home ranges" when rearing their own young (Lowry, personal communication). It is possible that there is a premium on solitary nesting in that it allows superior concealment from inter-specific dominants which threaten the young (Adamson, 1969; Eaton, 1974).

Felid cubs grow at an incredible rate. The calorie expenditure of a lactating mother is enormous. (McVittie, in prep.). The high infant mortality – 43 to 50 % according to Schaller (1972) and McLaughlin (in Schaller, 1972) – may be in part due to the female's inability to meet the demands of a litter whose normal size may be 4 to 6 (Eaton, 1970; Schaller, 1972; Wrogemann, 1975). If the necessity for secrecy is removed, it is conceivable in an area of high cheetah density that allo-parenting on the part of an older female sibling is beneficial to all parties involved. If the elder sibling assists her mother before having any young of her own, the gain must be a fourfold increase in survivorship of the young, since she is postponing her own reproductive effort on behalf of others related by, probably, only ¼ (assuming different fathers). The experience she gains in attending the young may affect the survival of her first litter, thus lowering the cost-benefit ratio somewhat. If, however, the mother and daughter have litters at approximately the same time, each may serve as an "aunt" to the other's litter. The benefits of group hunting will accrue while no large costs are involved. In lions it has been shown (Bertram, 1975) that litters born in synchrony in prides have higher survival rates than those born asynchronously. Female lions with similarly aged litters seem to share some of the responsibilities of motherhood. Since the danger of predation on cheetah cubs and thus the need for solitary nesting sites must be much lower in South West Africa than elsewhere, such allo-parenting could conceivably be beneficial to cheetahs in the ranch-lands.

The altered environment of South West Africa offers ideal conditions in which to assess the foregoing hypothesis. A survey conducted in the brief time available set out to evaluate aspects which could be assessed without a field study. The primary aim was to substantiate, if possible, the fact that grouping of cheetahs in South West Africa does occur. Information pertinent to Eaton's hypothesis (1978) was also sought. Specifically those predictions which could be challenged or supported by data from the survey include: due to diminished competition the cheetah of South West Africa a) has expanded its prey in comparison to East African cheetah, b) demonstrates more social cohesion than the East African cheetah. Specific examples in addition to group size should be manifest in evidence of group hunting and allo-parenting.

Various correlations and additional information which came to light will also be discussed.

2 METHODS

Direct field observations are, of course, preferable to second-hand information gained through surveys. An extended field study was not possible in this instance because of budget limitations. I therefore gathered data through interviews and questionnaires in the two months available to me, August and September, 1976. The survey covered selected ranches located within approximately 100 000 km² between 19 and 23°S and 15 and 19°E in South West Africa. In the interviews direct observations by the rancher on cheetah sightings, number of animals seen, sex and age of each animal, number of animals which escaped, and prey items were noted. In addition, the ecological conditions were assessed in terms of the availability of water, bush encroachment and wild ungulates. The number of years since the extirpation of each of the competing carnivores and current abundance of cheetahs were also determined. While the last involved a subjective frequency scale (See Table 2), it facilitated a comparison not possible with numerical data alone. In addition, the results of a questionnaire by Gaerdes (1974) were reviewed with Mr Gaerdes' assistance. These questions emphasized the relative occurrence of cheetah and thus were readily transformed into the same frequency index used in the interviews. Occasional respondees to this questionnaire offered information dating back to 1920, but most referred to sightings within 10 years of the correspondence.

The data were compiled in three sub-files for computer analysis.

a) 20 sites surveyed by personal interview. Data spans 1966 – 1977 unless supported by written records. Also included are 43 sites covered by monthly reports from a local government animal inspector from 10/76 to 3/77. These were transmitted to the author by Mr Gaerdes.
b) From one site, daily written data in the form of a farm diary, covering 20 years.
c) 90 sites surveyed by questionnaire from J. Gaerdes (1974, 1975a, b).

The SPSS Computer Program (Nie, *et al*, 1975) was utilised to present frequency and cross tabulation analysis, both on sub-files and the cumulative file. The first edit run offered a compact listing from which it was possible to determine which groups were probably repeated sightings. If a similar size group (original group ± 2) was sighted within 50 km and within 10 days of a previous sighting, the individuals were assumed to be the same and the smaller group was dropped. Thus 72 animals were removed from further computations. The results of the analysis are compared with those of previous cheetah studies in other areas wherever feasible.

It was not possible to assess accurately the population of cheetahs in the ranch-lands. In some areas, ranchers claim to trap 12 to 15 cheetahs per year from one 75 sq. km ranch. When this is the case, several other ranches in the vicinity often sustain the same yield, but it is not known from how large an area such a population actually draws. Only a few kilometres away cheetahs may be non-existent. Without careful study of the intervening terrain, reasons for these seemingly sharp demarcations remain obscure. Good topographical maps would offer some clues to changing ecology, but such maps are closely held by the government. The only guidelines presently available are the property owner's assessment of the status of the cheetah on his land and if that status has changed over a period of time.

Again, precision in terms of numerical data is difficult. For example, in one area a recent average of 5 cheetahs seen per year may represent a 500 % increase over previous years, while in other areas it may mean a dramatic decrease. To this end the frequency index formulated in the interviews and questionnaires was used. (See Appendix). Correlations were sought between cheetah frequencies and the absence of competitive carnivores.

3 RESULTS AND DISCUSSION

Analyses of prey known [illegible] by specific cheetah groups in the ranch-lands are given (Table 1). This tabulation does not purport to be the average diet; it demonstrates only extremes at the upper size range. Ranchers can usually identify large kills with a specific cheetah group, because of time or space patterns and occasionally by distinctive spoor. One particular group (G), composed apparently of 2 males, survived for three years by drinking only the blood of its prey (or at least of the prey which was subsequently found). This suggests there may be some traditional behaviours associated with prey selection and/or consumption.

The findings of Table 1 suggest that prey taken by cheetah in South West Africa covers a very much wider size range than in East Africa. The data can be compared with that of Schaller (1972) who indicates cheetah kills exceed 40 kg. only 3 % of the time; the only instances in which the prey is larger are kills made by a group of 2 to 4 males (Table 2). Frame and Frame's data (1976) is less specific with reference to weights, but also appears to show very few kills exceeding 40 kg. (probably 12 of 106 kills, though neither prey weight nor number of animals participating in the hunt are given. (see Table 3.) In East Africa, the larger prey are hunted by lions and hyenas. In their absence it is not surprising that a cheetah would seize an opportunity of a meal offered by perhaps an ailing larger animal. Even if frequencies are not known, the fact that larger animals than usual are sometimes taken is relevant to the cheetah's response to lessened competitive pressure. These findings support the prediction that cheetah prey size increases in the absence of dominant competitors.

TABLE 1: Prey analysis: South West Africa. Unusually large prey taken by some cheetah groups.

Group	Number of adults ♂	♀	?	Number of prey items	Estimated weight (l) in kg. (each)
A	2			2 adult kudu	180
				1 calf eland	40
				1 adult blesbok	80
B	1			1 adult kudu bull	250
C			4	1 adult oryx	180
				1 adult kudu	220
D			1 +	large cubs	
				1 adult kudu	220
E	2			2 adult wildebeest	170
F	2			6 adult kudu (both sexes)	220
				14 adult hartebeest	125
				2 juvenile eland bulls	220
				3 adult ostrich	85
				2 juvenile oxen	100
G	2			1 adult kudu bull	250
				1 adult hartebeest cow	125
H	1	1		2 juvenile oxen	100
I		4 +	3	20 juvenile kudu	150
J		3		5 calf eland	50
				4 juvenile hartebeest	45
K	2			1 sub-adult ox	200

1) Weights from Dorst & Dandelot (1969) and Zaloumis and Cross (1974): adult weights based on female unless male specified.

TABLE 2: Prey analysis: Serengeti National Park data from Schaller (1972)

Species	Weight in kg.	Number	Percent
Thomson's gazelle	12	238	91.2
Grant's gazelle	32	6	2.3
Reedbuck	37	2	.8
Wildebeest	108	5	1.9
Topi	82	2	.8
Hartebeest	95	1	.4
Dik-dik	5	1	.4
Impala	32	3	1.1
Hare	3	3	1.1

TABLE 3: Prey analysis: Serengeti Plains. Data expanded from Frame and Frame (1976[1]).

Species	Weight in kg.	Number	Percent
Thomson's gazelle	12	66	62
Hares	3	13	12
Wildebeest	108	9	8
Grant's gazelle	32	6	6
Impala	32	6	6
Reedbuck	37	2	2
Hartebeest, juv.	54	1	1
Kongoni, juv.	63	1	1
Waterbuck, juv.	85	1	1
Dik-dik	5	1	1

[1] Weights not given by Frame and Frame. Weight estimates supplied from Schaller (1972) and Dorst and Dandelot (1969).

Table 1 also supports the premise that 2 or more cheetah may handle larger prey more readily than one. When there is no competition for the larger game, it may be advantageous for cheetah to start hunting in groups. This outcome would be particularly true where large game is common. Most ranchers interviewed claim to have more kudu and oryx than springbok on their land. Since the former can negotiate fences more readily than springbok, and since other small game is not easily censused, such claims may be misleading, but there is no doubt that large ungulates are readily available.

To establish if cheetahs could readily support themselves in social groups, analysis was made of the estimated biomass killed by a number of cheetahs in a small area (420 sq. km.) over 30 days (Table 4). When cheetahs are held in a confined area, at least one prey and often more falls per predator because the livestock cannot escape. Since a moving animal is probably a stimulus to hunt even when the predator is not hungry, the assumption is made that approximately half of the total sheep and goats killed by this group could not have been consumed (due to satiation) and is therefore excess slaughter. Schaller (1972) calculates that an average of about 10 kg. of prey weight/day is taken by an adult cheetah. His estimate was based on kills made by one female with cubs kept under constant observation for 26 days. Other observers (Pienaar, 1969) have assumed much lower figures, but agree that kill estimates based on found carcasses must be low since smaller game (fawns, hares, etc.) are consumed entirely and therefore not included. If no smaller game had been taken as well, the size of the group, using Schaller's figures, is deduced to be approximately 14 animals. Two weeks later, further reports indicated about 3 900 kg. of meat brought down, with perhaps 1 900 kg. in excess of caloric requirements. On a 15 day, 10 kg./day basis, this is approximately 13 cheetahs. Cheetahs were sighted four times along the path of destruction: first 9 were seen, of which 2 were shot. Next 6 large cats, 2 shot; then a group of 2 large males, 3 adult females and 8 large cubs (13 total). Finally 8 cheetahs were trapped: one small male and 7 females. At least 2 and perhaps 5 escaped, including one large male and one cub. Without photographs, it cannot be established whether only 1 or up to 4 separate groups were involved. Even though the assigned prey weights of Table 4 are "order of magnitude" estimates, the sightings together with the quantity of kills indicate that large groups can and do exist in South West Africa.

The limitations inherent in interview data must be considered in inspecting the results shown in the following figures and tables. Over a period of time, the rancher is more likely to remember and report group sightings than those of individual animals. Also, groups, especially large ones, are more easily sighted. Therefore, the percentage of sightings is biased in favour of groups. Graham's study in 1966, covering a large area of East Africa, was done in a manner very similar

TABLE 4: Prey killed by one cheetah group in 30 days, South West Africa

Number	Item	Approx. average weight per item in kg.	Total weight in kg.
85	calves	20	1700
11	lambs	6	66
49	sheep	35	1715
9	kid	6	54
58	goats	30	1740
11	kudu calves	20	220
9	duiker	10	90
16	steenbok	10	160
6	oryx calves	20	120
		Total:	5865
		Less excess slaughter	1730
		30 day total	4135
		Single day average	138

Sheep and goat kills include 3 instances in which the group entered a kraal (fenced enclosure). In confined areas cheetahs invariably kill more than they can consume; thus the estimated excess slaughter has been deducted. Data from Serengeti National Park indicate 138 kg. would feed approximately 14 cats (Schaller, 1972).

to this one. His results are likely to show the same bias and therefore the two are compared wherever possible.

In South West Africa another possibility of bias exists; its effect on Graham's data is unknown. Males are known to congregate periodically at marking trees, at which times they are more readily visible and often trapped. It is not clear whether such male gatherings occur elsewhere. The ramifications of this bias are discussed below.

Only the most experienced observers can distinguish the sexes and ages of the cheetahs. It is very likely that offspring more than 15 months old were considered adult when seen in the field. However, a large percentage of given ages and sexes is based on animals that were actually captured, in which case identification was certain. Most ranchers were aware of this limitation: animals not positively identified were tallied as unaged or unsexed or both. In compiling the charts, some extrapolations were made from known to unknown animals, but always in the most conservative manner.

Assessing litter size (Table 5) presents great difficulties. Field work is subject to small samples, but litter size at different ages is available. Surveys are hampered by lack of precise aging and almost no sighting of black or new-born cubs. The latter may result in an inflated mean litter size, as shown with Adamson's cheetah (1969, 1972, Table 5).

As discussed above, uncontested access to prey may lead to larger litters and probably to less infant loss. Elimination of infant mortality due to lion or hyena predation may also be a factor in apparent increased litter size over that in the East African parks. While samples are too small for statistic results, a trend to more surviving cubs can be seen.

It is tempting to ascribe the increase in group size, (Tables 6, 7, 8, Figures 1, 2) to the dual factors of increased litter size and difficulty of distinguishing older juveniles from adults. It can be argued that the large groups are mothers with 14 to 18 month old offspring, or are as yet undivided sibling groups. Cheetahs have been known to have 8 cubs (in captivity, Thompson and Vestal, 1974; reported by survey,

TABLE 5: Mean litter size.
Number in parenthesis indicates number of litters determining the mean. Note that litters lost entirely at or near birth have the effect of raising the observed mean. Adamson's semi-wild cheetah lost 2 litters within a week of birth. A field observer unless studying that particular animal would have seen only the remaining litters, thus deducing the mean litter size at 10 months to be 3 (6 young surviving in 2 litters).

Location	Age				Source
	1 Month	1–3 Months	3–10 Months	10 Months	
Nairobi	4.3(6)[a]				McLaughlin in Schaller 1972
Serengeti	4(1)[a]	3(14)	1.9(14)[b]	2.1(21)[c]	Schaller 1972
Serengeti	4.2(12)	2.8(33)	2.5(61)	2.6(32)	Frame & Frame 1976
Kenya	3.75(4)[a]	2(4)	1.75(4)	1.5(4)	Adamson, 1969, 1972
E. Africa	3.7[e]	3.1[e]	2.9[e]	2[e]	Graham, 1966
S.W. Africa		4.2(5)		4(9)	McVittie, this survey
Captive Births	3.27(55)[a, d]				Wrogemann 1975, Eaton, pers. comm.

a) New-born;
b) 3 to 6 months;
c) 12 months;
d) Includes still-born cubs;
e) Number of litters not given.

Graham, 1966) although 6 is the most ever seen by field workers. In South West Africa of 89 positively identified litters, only 2 were litters of 6, 14 were of 5 and 13 were of 4. Frame and Frame's data (1976) indicate at least one but no more than 3 litters of 6 in 54. Thus an explanation for the relatively high number of South West African cheetah occurring in groups of 7 and more must be found elsewhere. It would seem that the increased group size reflects a change in the social habits of at least some of the cheetah, lending some support to Eaton's contention (1978) that interspecific carnivore competition suppresses grouping in cheetah and its corollary, that decreased competition allows grouping.

TABLE 6: Groups of adults unaccompanied by young: South West African data, McVittie, this survey.

Group size	Absolute frequency	Relative frequency (Percent)	Cumulative frequency (Percent)	Number of individuals/group	Relative frequency individuals (Percent)	Cumulative frequency individuals (Percent)
1	89	42.7	42.7	89	15.2	15.2
2	36	17.3	60.1	72	12.3	27.6
3	30	14.4	74.5	90	15.4	43.0
4	17	8.2	82.7	68	11.6	54.6
5	7	3.4	86.1	35	6	60.6
6	9	4.3	90.4	54	9.2	69.9
7	10	4.8	95.2	70	12	81.9
8	1	0.5	95.7	8	1.4	83.2
9	2	1.0	96.6	18	3.1	86.3
10	2	1.0	97.6	20	3.4	89.7
11	2	1.0	98.6	22	3.8	93.5
12	2	1.0	99.5	24	4.1	97.6
14	1	0.5	100	14	2.4	100
	208			584		

Mean group size 2.81
Variance = 5.32
SD = 2.31

TABLE 7: Groups of adults unaccompanied by young, East African data (Graham, 1966)

Group size	Absolute frequency	Relative frequency (Percent)	Cumulative frequency (Percent)	Number of individuals/group	Relative frequency individuals (Percent)	Cumulative frequency individuals (Percent)
1	475	48.9	48.9	475	26.5	26.5
2	307	31.5	80.5	614	34.2	60.7
3	115	11.8	92.3	345	19.2	79.9
4	46	4.7	97.0	184	10.3	90.2
5	15	1.5	98.6	75	4.2	94.4
6	5	.5	99.1	30	1.7	96
7	5	.5	99.6	35	2.0	97.9
8	3	.3	99.9	24	1.3	99.3
9	–	–	–	–	–	–
10	–	–	–	–	–	–
11	–	–	–	–	–	–
12	1	0.1	100	12	.7	100
13	–	–	–	–	–	
	972			1794		

Mean group size = 1.85
Variance = 1.34
SD = 1.16

TABLE 8: Groups of adults unaccompanied by young, Serengeti National Park data (Schaller, 1972).

Group size	Absolute frequency	Relative frequency (Percent)	Cumulative frequency (Percent)
1	Not given	52	52
2		31	83
3		14	97
4		3	100

As described above, the hypothesis predicts that females or males and females group as well as males. Of the 102 positively identified adult females, 16 % were observed in groups of two or more. The percentage is not large, but is significant when compared to Schaller's 0 %. 43 % of the positively identified males were living in groups. In addition 22 animals whose sex was unknown were thought to be adults. 84 % of these were in groups. In the latter especially, but in the other two also, the possibility remains that sub-adult siblings were identified as adults. In a less easily biased observation, 28 % of all litters were accompanied by more than one adult, which compares favourably with Graham's 26 % (1966). (Table 9). An adult female with two differently aged litters was seen once. All these phenomena are important in that they have not been previously recorded by field observers (Foster and Kearney, 1967, mention one male accompanying a female with 22-month old cubs, which suggests the female was probably in estrus).

Allo-parenting is not well substantiated by these figures, as only 3 definite cases of adult females accompanying mothers with cubs were reported. The 14 cases in which an unsexed adult accompanied the mother and litter leave the possibility open, however. (Table 10). Schaller (1972) assumed temporary absence of the adult female when he found unaccompanied cubs. In this study, the high proportion of litters accompanied by more than one adult, makes such an assumption untenable.

Although the postulate concerning cheetahs and competitive pressures from dominant carnivores did not

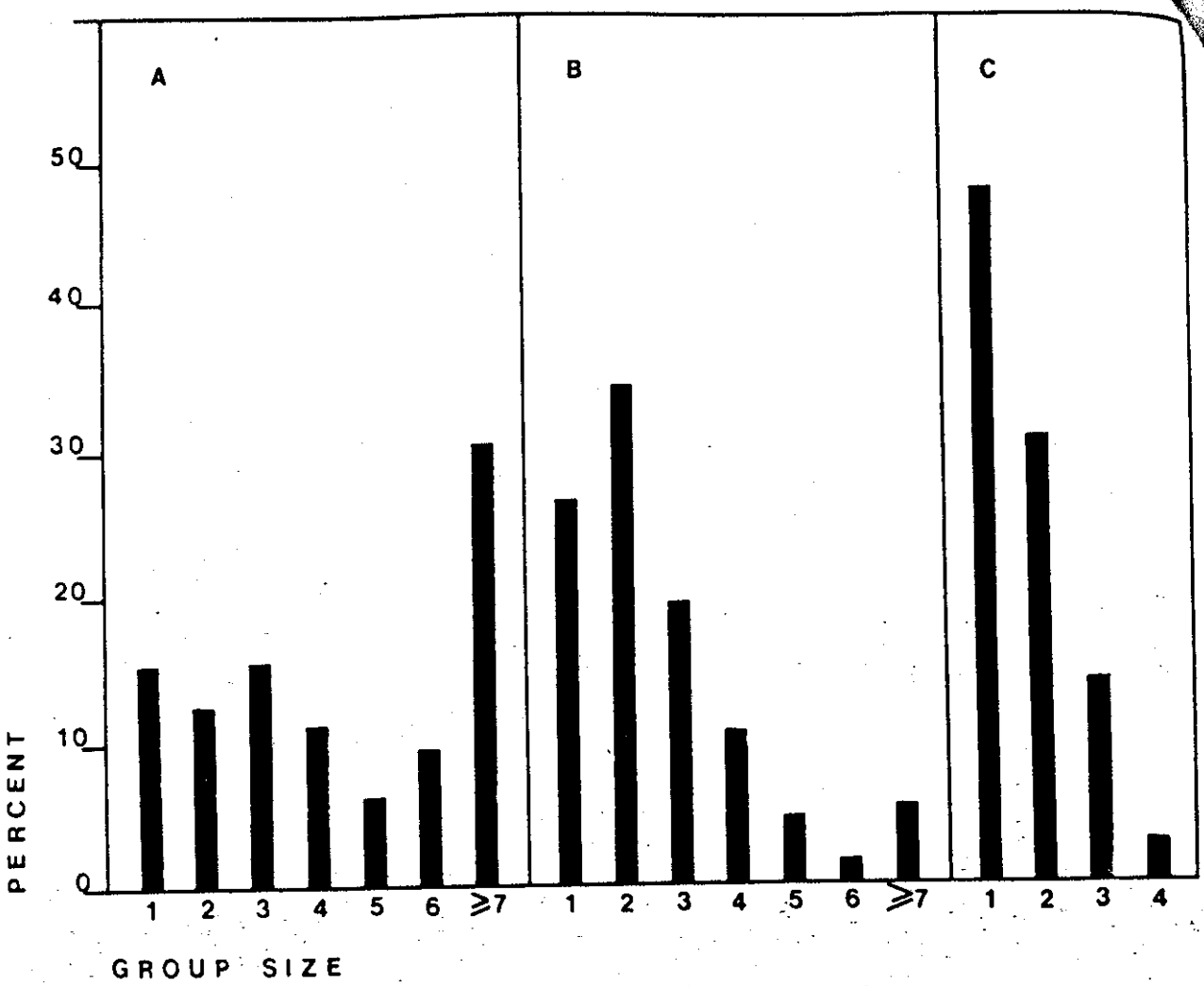

FIGURE 1: Percentage of unaccompanied adult cheetahs as a function of group size. a) South West Africa, McVittie, this survey. b) East Africa, expanded from Graham (1966). c) Serengeti, expanded from Schaller (1972).

generate a prediction of sex ratios, the sex ratios which appeared from the data as "fall out" is highly interesting as well as unexpected. Juvenile sex ratios are especially sketchy statistics, as even the best of field studies are plagued by inaccessibility to newly-born infants, repeated sightings included in different age groups, small samples, or lumping of age groups. All the data in Figure 3 are subject to one or more such restrictions. It is informative, however, to include these numbers as they suggest an imbalanced sex ratio favouring females.

The adult sex ratios (Figure 4) offer another set of problems. Schaller (1974) and Frame and Frame (1976) found females had a greater degree of visibility in the area which they were studying. A field study will naturally focus on areas in which the animals can reliably be found. If the home range of one male includes that of several females, a bias toward females is bound to occur. Also, as noted by Frame and Frame (1976) males which travel in and out of the park are more secretive than females living exclusively in the park, due probably to greater hunting pressure by humans outside the park. Information gathered by survey introduces a different set of biases. Males may be more visible than females on non-park land for several reasons. First, in parks the family group must beware particularly of lions and hyenas; humans may be a nuisance but have proven to be not dangerous. On farm-lands the reverse is true and females undoubtedly are more reclusive. There is also evidence that many males are widely nomadic. Thus they may be counted repeatedly at various widely separated ranches. (These contrasting biases are apparent in Table 11). In South West Africa, one rancher, apparently more interested in natural history than in cattle, has trapped cheetahs and leopards, marked them and released them. Of 62 cheetahs so marked, 9, all males, were subsequently trapped more than 200 km from the release site. The same rancher contributed 14 cheetahs to the Etosha National Game Park. So far, two of these have returned to the original capture site, a 450 km distance. Other ranchers keep track of specific cheetah groups by the trail of carcasses they leave behind. There is agreement that groups are

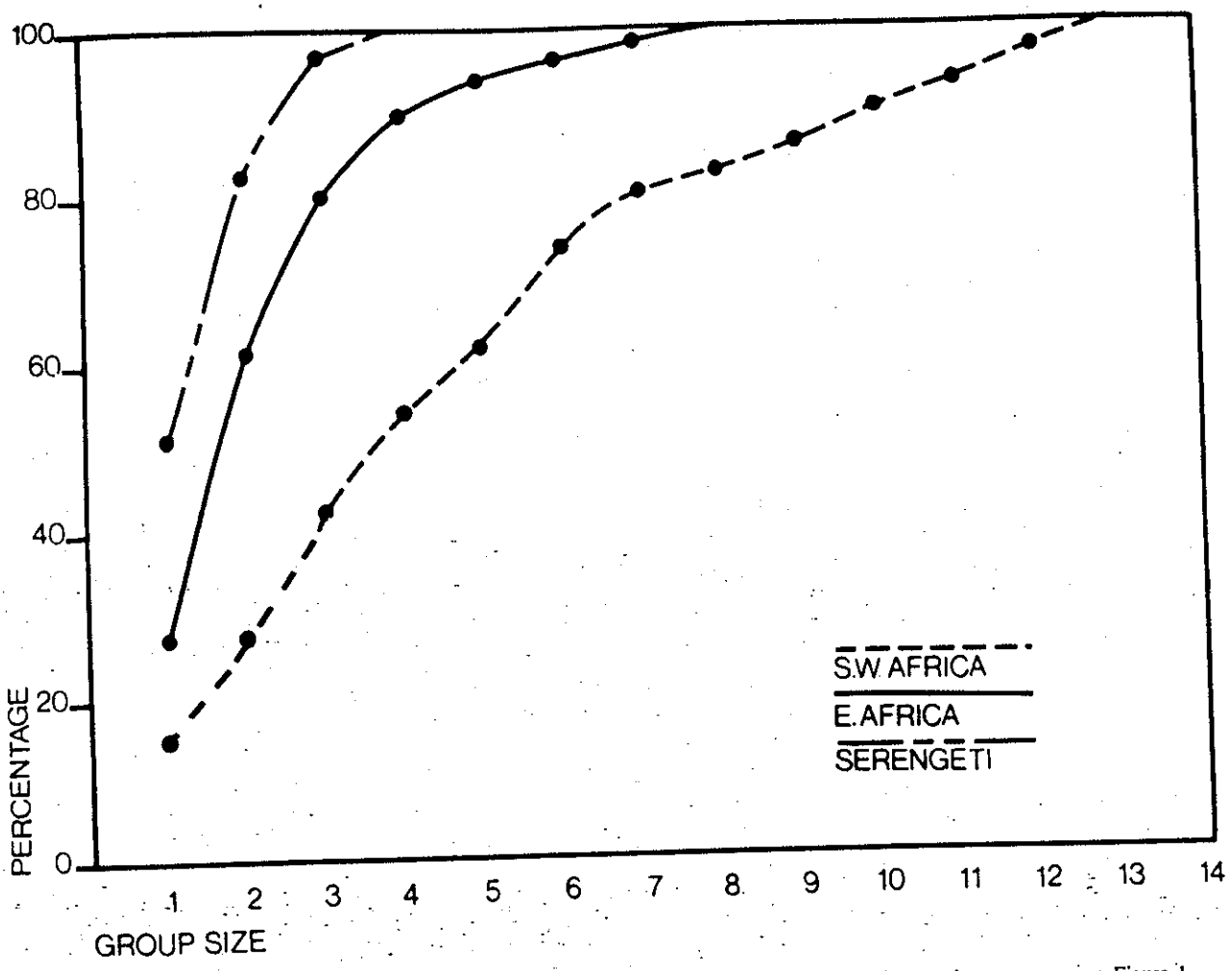

FIGURE 2: Cumulative percentages of unaccompanied adult cheetahs as a function of group size. Data and sources same as Figure 1.

stationary only when the mother has very small young. Otherwise even the so-called resident cheetahs hunt a range which varies from 300 to 1 000 sq. km. depending on terrain as well as availability of prey.

Another reason for male visibility concerns social gathering points. While Graham (1966) says nothing about where farmers commonly see cheetah in East Africa, in South West Africa males periodically are attracted to certain specific sites which are known as marking trees. By staking out a female for long periods of time and by using faeces of estrus females as bait, it has been determined that it is the estrus females which attract the males. Comparative kill records seem to indicate that more than local males are involved. There is some indication that the trees are located where several ranges overlap (A. Port, personal communication), but since no observations have been done on home ranges, such evidence can only serve as guidelines for future field-work.

Many ranchers prefer to set traps and look for the animals at marking trees. In this way, some have caught as many as 40 males and no females over a ten year period. A few ranchers, in a more serious attempt to control the local cheetah population, avoid marking trees, as young are seldom caught there. This takes diligence and constant trap moving; these ranchers are in the minority. Therefore, the sex ratio may be upset as a consequence of oversampling at marking trees. The shift to the almost 1:1 adult from the 1:2 juvenile sex ratio would be partially accounted for by the above considerations.

The incidence of marking trees in East Africa has not been reported. While Schaller makes no mention of such sites, he did on two separate occasions see large congregations of apparently mature males at the same place, the Gol Kojes. While it is probable that an estrus female was involved, it is possible that an ecological object like a marking tree attracted both sexes. If no marking trees are found in the parks, the reasons for such a difference in social systems must be considered. An extremely low cheetah density may be one reason, but begs the essential question: Is the cheetah population size perhaps inversely related to competitive predator presence?

TABLE 9: Groupings of adults with litter

S. W. Africa (McVittie, this survey)

Number of adults with litter	0	1	2	3	4	5	6
Number of litters	14	50	17	6	1	1	
Percentage of litters	15.6	55		28.1			

East Africa (Graham, 1966)

Number of adults with litter	0	1	2	3	4	5–8	9
Number of litters	31	160	52	8	1	–	1
Percentage of litters	12	63			26		

Serengeti (Frame & Frame, 1976)

Number of adults with litter	0	1	2 to 9
Number of litters	47	269	11
Percentage of litters	14.4	82	3

Serengeti (Schaller, 1972)

Number of adults with litter	0	1	2 to 9
Number of litters	–	68	–
Percentage of litters	0	100	0

TABLE 10: Cheetah associations. Serengeti data from Fra... Frame, (1976). South West African data, this survey.

Association	Serengeti No. of Sightings	Serengeti Percent	S.W. African No. of Sightings	S.W. African Percent
Adult female w/cubs	269	55.2	50	26.6
Lone adult female	93	19.1	19	10.1
Group of grown littermates separated from mother	47	9.7	–	–
Litters, various ages, seen without mother	–	–	14	7.4
Lone adult male	29	6.0	40	21.3
Group of adult males	29	4.1	11	5.9
Adult female with cubs and 1 or more adult male	11	2.2	6	3.2
Adult female with cubs and 1 or more unsexed adults	–	–	14	7.5
Adult female without cubs and 1 or more adult males	16	3.3	11	5.9
2 or more adult females with male(s)	–	–	19	10.1
2 adult females, each with cubs	1	.2	1	.5
2 adult females, one (apparent) litter	–	–	3	1.6
Lone adult male with grown littermates separated from mother	1	.2	–	–
	487		188	

Population size in the ranch-lands can probably never be precisely determined. An attempt was nevertheless made to investigate relationships between the presence of cheetah and the presence of the other large predators.

To this end, the frequency index formulated in the interviews and questionnaires was used. (Appendix). Viewed by itself, it showed only that cheetah numbers were not varying uniformly over the country. When compared to the number of years since lions, hyenas or wild dogs were present in the same location, the relationship became highly significant: X^2 values for lions = 50.1, d.f. = 8, $p<.001$; hyenas = 37.9, d.f. = 6, $p<.001$; wild dogs = 24.3, d.f. = 6, $p<.01$. Thus there is support for the suggestion that the presence of cheetahs is inversely related to the presence of competitive carnivores, though no conclusion can be drawn about actual population size.

Little has yet been said about the leopard, the other major carnivore of the area and one which is also potentially an interspecific competitor of the cheetah. (Kruuk, 1972; Schaller, 1972). While the leopard has not been extirpated from the South West African ranch-lands, there appears to be little overlap between leopards and cheetahs, with a few areas of exception. One of these is the ranch for which written records were available for 20 years. One hundred and sixty cheetahs were sighted in that time, of which 144 were trapped. While the leopard sightings are not strictly comparable, because repeated sightings have not been eliminated, it is worth noting that 42 leopards were shot or trapped and sightings and/or kills attributable to leopards were recorded 154 times. Clearly the area was sustaining both cheetah and leopard populations. Therefore a test was made of the null hypothesis that mean group size of cheetahs in the absence of competitors (from sub-file a) is the same as that of cheetahs coinhabiting an area with leopards (from sub-file b). Only adults unaccompanied by young were assessed. Such a test should reflect the effect the presence of a specific competitor on the cheetah's tendency toward grouping. As expected, the null hypothesis was rejected ($p<.0005$, T = 4.73, d.f. = 170, one tailed Student's T test). $\bar{x}_o = 3.3$, $\bar{x}_a = 2.8$.

A further test was made comparing the litter size of the two study areas. (H_o: $\bar{x}a = b$). The results, again significant (H_o rejected, $p<.01$, T = 2.424 d.f. = 64 one tailed Student's T test $\bar{x}_o = 3.4$. $\bar{x}_a = 2.6$), indicate that cheetah litter sizes tend to be larger in the absence of a substantial leopard population. The cause can likewise be attributed to diminished competition, either directly (decreased infant mortality due to predation by leopards) or indirectly (better nutritional base available to mother and offspring).

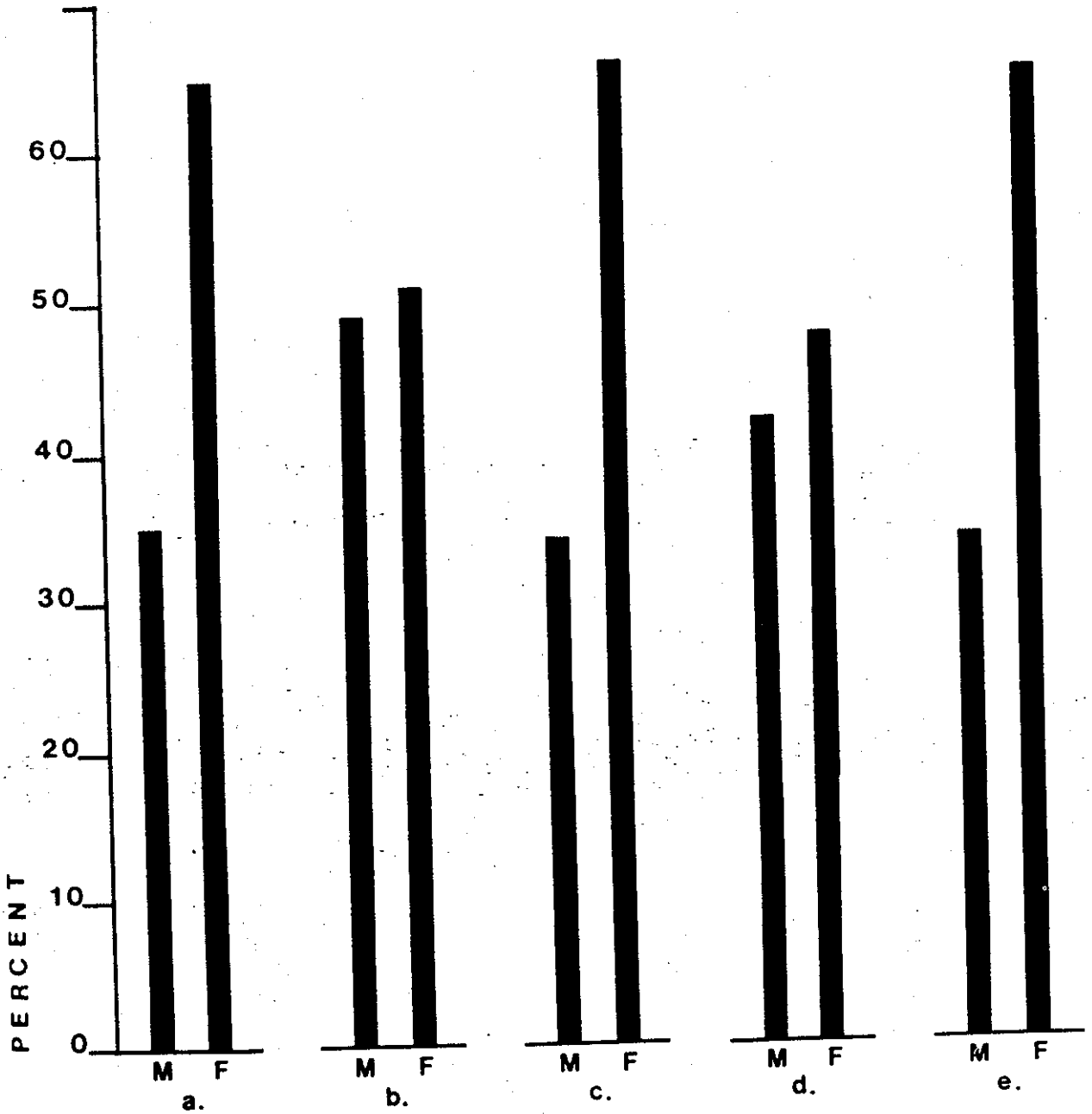

FIGURE 3: Sex ratios of young. Histogram depicts remarkable agreement in sex ratios from various parts of the world in various circumstances. a) Serengeti, from Schaller (1972). N = 39 cubs, all ages. b) Serengeti from Frame & Frame (1976). N = 57, all ages. c) S. W. Africa from McVittie, this survey. N = 113, all ages. d) Captive births, East African and unknown parentage, from Eaton (personal communication) and Wrogemann (1975). N = 70, newborn. e) Captive births, South West African parentage, from Eaton (personal communication) and Wrogemann (1975). N = 61, newborn. Because his Serengeti data were taken after some mortality may have already occurred, Schaller (1972) reasons the actual birth ratio may be more nearly 1:1, implying a disproportionate mortality of infant males. While the similarities depicted may be coincidental, they may point to an imbalance in the new-born ratio.Graham (1966) presents no sex ratios for comparison because at the time of his survey live trapping was not generally practised.

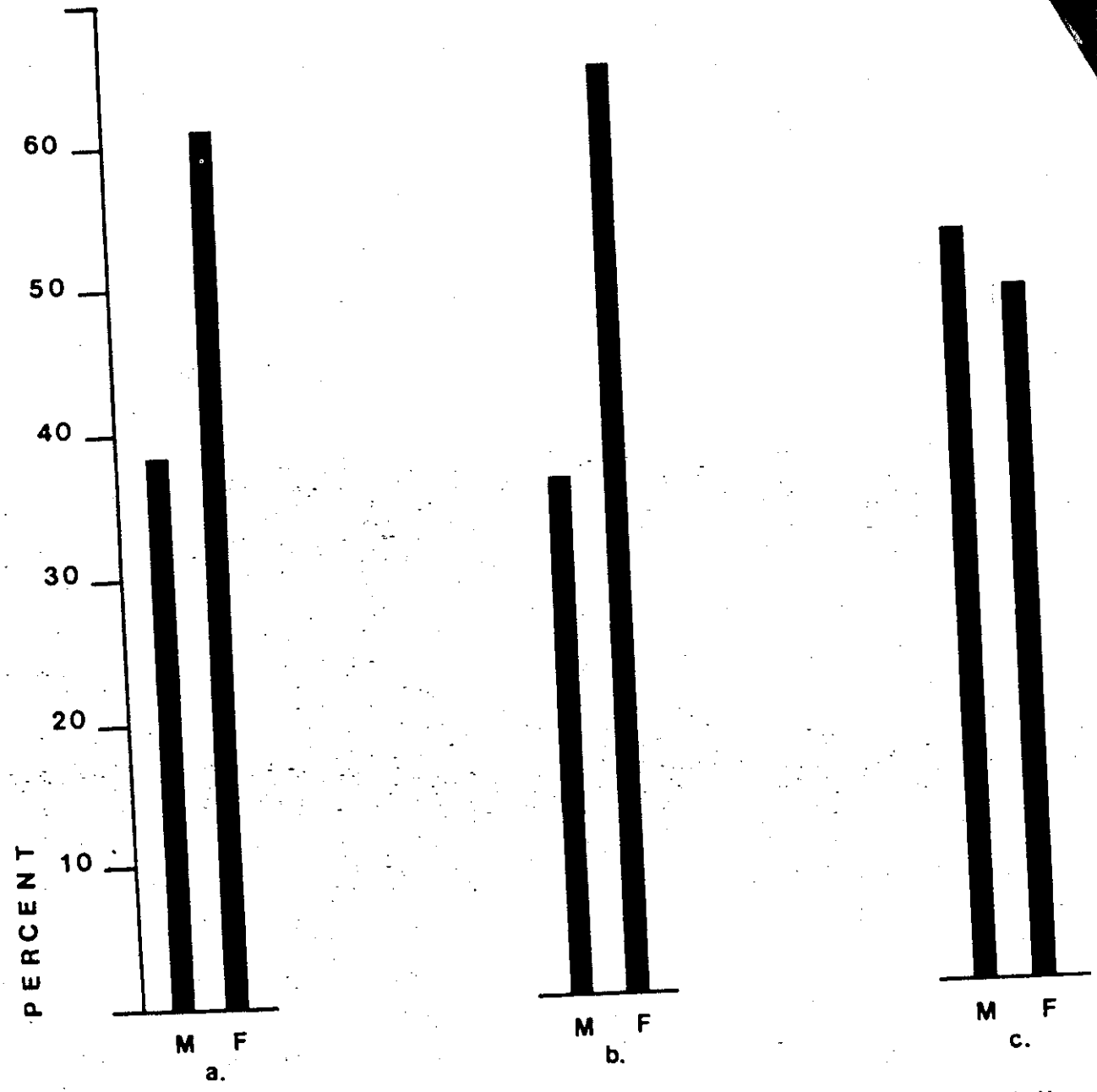

FIGURE 4: Sex ratios of adults. a) Serengeti, from Schaller (1972). N = 150. b) Serengeti, from Frame & Frame (1976). N not given. c) S. W. Africa, from McVittie, this survey. N = 212. Graham's data (1966) on adult sex ratios are not comparable. In this case the Serengeti data of two field workers agree and are in contrast with the South West African data. Possible reasons for this are discussed in the text.

4 SUMMARY

The object of this study was to present information concerning some of the social patterns of South West African cheetah which appear to be in contrast with those of East African cheetah. The data were analysed to focus on an hypotheses originally set forth by Eaton (1978): that the presence of large interspecific competitors inhibits grouping by cheetahs, whereas the absence of such competitors may allow social tendencies of the cheetahs to develop. The hypothesis led to predictions that because of the general absence of interspecific predators, cheetah in South West Africa would be found in groups more often than cheetah in national parks where competitive carnivores are still present. It was also predicted that prey size would be expanded and litter size would be greater for South West Africa cheetah. The data supported these predictions. The expectation that females as well as males should exhibit social tendencies was fulfilled, but firm evidence for allo-parenting was absent. Correlations between the absence of lions, hyenas or wild dog, and the presence of cheetah were found. Finally, cheetah which lived in an area where leopard were still common were found to exhibit smaller (adult) group size and smaller litter sizes than cheetah which were entirely free of interspecific competition. Further field work to substantiate the survey data would appear to be worthwhile, as the implications of Eaton's hypothesis could have vital importance in the ultimate survival of the cheetah.

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6 REFERENCES

ALEXANDER, R.
1974: The Evolution of Social Behaviour. *Ann. Rev. of Ec. & Syst.* 5: 325–383

ADAMSON, Joy
1969: *The Spotted Sphinx*. Harcourt Brace & World. N.Y.

ADAMSON, Joy
1972: *Pippa's Challenge*. Harcourt Brace Jovanovich. N.Y.

BERTRAM, B. C. R.
1975: Social factors influencing reproduction in wild lions. *J. of Zool.* 177: 463–482.

BOURLIERE, F.
1963: Specific feeding habits of African carnivores. *African Wildlife* 17: 21–27.

CARACO, T. and WOLF, L.
1975: Ecological determinants of group sizes of foraging lions. *American Naturalist* 109: 343–352.

DORST, J. and DANDELOT, P.
1969: *A Field Guide to Larger Mammals of Africa*. Houghton Miflin. Boston.

EATON, R.
1970: Hunting behaviour of the cheetah. *J. Wildl. Manag.* 34(1): 56–67.

EATON, R.
1974: *The Cheetah*. van Nostrand Rheinold Co., N.Y.

EATON, R.
1978: The Evolution of Sociality in the Felidae. in *The World's Cats Vol. III* 2. Second Edition. R. L. Eaton, ed., Carnivore Research Institute, Seattle.

FOSTER, J. and KEARNEY, D.
1967: Nairobi National Park census, *E. Afr. Wildl. J.* 6: 152–154.

FRAME, G. and FRAME, L.
1976: Interim cheetah report for the Serengeti Research Institute, annual report, mimeographed.

FRAME, G. and FRAME, L.
1977: Our Three Years with Cheetahs, *Intl. Wildl.* Jan. – Feb.: 4–11.

GAERDES, J. H.
1974: Geparden in Südwestafrika, *Mitteilungen der SWA Wissenschaftliche Gesellschaft* XIV (9, 10).

GAERDES, J. H.
1975a: Leoparden in Südwestafrika, *Mitteilungen der SWA Wissenschaftliche Gesellschaft* XVI (2).

GAERDES, J. H.
1975b: Löwen in Südwestafrika, *Mitteilungen der SWA Wissenschaftliche Gesellschaft* XVII (5, 6).

GRAHAM, A.
1966: East African Wild Life Society cheetah survey: extracts from the report by wildlife services, *E. Afr. Wildl. J.* 4: 50–55.

GRAHAM, A. and PARKER, I. S. C.
1965: East African Wildlife Cheetah Survey: report by wildlife services, East African Wildlife Society, Nairobi, mimeographed.

HAMILTON, W. D.
1964: The genetical theory of social behaviour, I, II. *J. Theor. Biol.* 7(1): 1–52.

JOUBERT, E.
1974: The development of wildlife utilization in South West Africa, *J. Sth. Afr. Wildl. Mgmt. Assoc.* 4(1): 35–42.

JOUBERT, E. and MOSTERT, P. K. N.
1975: Distribution patterns and status of some mammals in South West Africa. *Madoqua* 9(1): 6–44.

KRUUK, H.
1972: *The Spotted Hyena*. Univ. of Chicago. Chicago.

MYERS, N.
1975: *The Cheetah*, Acinonyx jubatus, *in Africa*, I.U.C.N. Monograph № 4, International. Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. and BENT, D. H.
1975: *SPSS, Statistical Package for the Social Sciences*. Second Ed. McGraw Hill, New York.

PIANKA, E. R.
1974: *Evolutionary Ecology*. Harper & Row, N.Y.

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

SCHALLER, G.
1972: *The Serengeti Lion*, University of Chicago, Chicago.

THOMPSON, R. and VESTAL, B.
1974: Survey of conditions associated with breeding cheetah in captivity, *Okla. Zoo. J.* 2(3).

WROGEMANN, N.
1975: *Cheetah Under the Sun*, McGraw-Hill, Johannesburg.

ZALOUMIS, E. A. and CROSS, R.
1974: *A Field Guide to the Antelope of Southern Africa*, Wildlife Society of Southern Africa, Natal Branch, Durban.

7 APPENDIX: QUESTIONNAIRE

Name
Ranch name
Location
Date
Size of ranch in hectares
Number of wells
Estimated number of domestic stock
Cattle Sheep Goats
Estimated number of wild stock
Kudu Oryx Springbok Other
Bush encroachment[1]
Heavy Moderate Light or none
Number of years since carnivores common
Lion
Hyena
Wild dog
Leopard
Cheetah
Current abundance of cheetah:
Estimated number on ranch/year
Subjective Scale
Scale
0 = None
1 = Decreasing (as compared to past years)
2 = Increasing to occasional
3 = Occasional (1 to 5/year)
4 = Increasing to common
5 = Common (5/year)
Sighting
Date
Location
Near house Near water
Near domestic stock By tree
Other
Number of animals
Adult males
Adult females
Unsexed adult
Young male estimated age
Young female estimated age
Young, unsexed estimated age
Neither sexed nor aged
Number caught
Prey
Prey killed by unobserved cheetah
Proof of kill

[1] Bush encroachment often varied over the extent of the ranch.