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Abstract: The condition and age of Thomson's gazelles *(Gazella thomsoni)* killed by two species of predators were compared. The wild dog, a coursing predator, was predicted to take a greater proportion of young, old and sick animals than the cheetah, a stalker. As measured by the narrow fat content of limb bones, wild dogs captured more Thomson's gazelles in poor condition than cheetah. This appeared to be a consequence of their preference for male gazelles, which were in worse condition than females. Cheetah did not capture fewer young and old gazelles than wild dogs.

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The condition and age of Thomson's gazelles killed by cheetahs and wild dogs

predation Africa

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(With 4 figures in the text)

The condition and age of Thomson's gazelles (*Gazella thomsoni*) killed by two species of predators were compared. The wild dog, a coursing predator, was predicted to take a greater proportion of young, old and sick animals than the cheetah, a stalker. As measured by the marrow fat content of limb bones, wild dogs captured more Thomson's gazelles in poor condition than cheetahs. This appeared to be a consequence of their preference for male gazelles, which were in worse condition than females. Cheetahs did not capture fewer young and old gazelles than wild dogs.

Contents

Introduction

It has long been assumed that predators select the old, weak and sick members of prey populations (Mech, 1970; Curio, 1976) and that the degree of selection depends on the predator's hunting technique (Schaller, 1972; Kruuk, 1972). Coursing predators, such as the African wild dog *Lycaon pictus*, which chase over long distances and do not usually select a particular individual until after the chase has been initiated (Estes & Goddard, 1967), might have time to survey a prey group and pick out a vulnerable animal. In contrast, stalkers, such as the cheetah *Acinonyx jubatus*, which tend to rely on surprise and short pursuits (Schaller, 1967), should have less time for prey selection during the chase and as a result should kill a more random sample of individuals.

Little empirical evidence has been presented, however, to confirm such a dichotomy. In North America, neither the puma *Felis concolor*, a stalking predator, nor the wolf *Canis lupus*, a courser,

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ge proportion of prey in poor condition as measured by marrow fat content (Hornocker, ch, 1970).

dence from African predators is also contradictory. In Kruger National Park, impalas *melampus* killed by wild dogs had both low and high marrow fat levels, indicating on animals in both poor and good condition (Reich, 1981*a*). Low visibility, a nce of dense cover, meant that the dogs encountered prey at short distances and that their re short. As a result, the dogs were probably unable to assess groups and pick out e animals. Wild dogs on the open Serengeti plains, however, have also been reported to kill Thomson's gazelles *Gazella thomsoni* in good condition, in common with the ons *Panthera leo* and cheetahs (Schaller, 1972). In contrast, both wild dogs and spotted *Crocuta crocuta*, another coursing predator, appeared to select wildebeests in poor (Kruuk, 1972; Schaller, 1972). Thus the extent of selection may also vary with the species on.

ollected on the age of prey taken by predators have been more conclusive and there be no evidence for a courser/stalker dichotomy. Both wolves and pumas have been take mainly young and old animals (Pimlott, Shannon & Kolenosky, 1969; Mech, 1970; r, 1970). Further, a comparison between the age of Thomson's gazelles killed by lions ahs and those killed by hyaenas and wild dogs, and of both, with a random sample shot opulation, suggested that all the predators were taking gazelles roughly in proportion to ation at large (Schaller, 1972).

paper, we extend Schaller's analysis using additional data from the same Serengeti n of Thomson's gazelles. The condition and age of gazelles taken as prey by one coursing the wild dog, and one stalking predator, the cheetah, are compared.

Methods

s and cheetahs were followed on the Serengeti Plains, Tanzania, between January 1985 and March ge and condition of Thomson's gazelles observed killed by the predators were recorded. Samples llected from carcasses found in the field as this can lead to underestimation of the number of young en. They are rapidly eaten and few remains are left to be found. Further, both wild dogs and casionally scavenge from other predators (pers. obs.).

Condition measurement

ethods are available for assessing the condition of ungulates, for example, by estimating the level ubcutaneous or marrow fat (Smith, 1970). In general, since the long bones of the legs remain after ue required for other measures has been consumed, the fat content of bone marrow (Anderson, chs, 1969) appears to be the most suitable in predation studies. The dry weight of bone marrow, s a percentage of its fresh weight, is a good indicator of its fat content in a variety of East African Sinclair & Duncan, 1972; Bradley, 1977). The fat reserves in bone marrow are only mobilized after perinephric fat has been utilized (Bear, 1971; Brooks, Hanks & Ludbrook, 1977). As a result, l only be seen when animals are in relatively poor condition.

2 g and 5 g of bone marrow were removed from the central white portion of the femur and tibia of g of 44 adult gazelle carcasses, avoiding the hemopoietic end portions of bones (Bradley, 1977). s were weighed to the nearest 0·1 g, oven-dried at 65 °C and reweighed. The dry weight was then s a percentage of the fresh weight, enabling the percentage of marrow fat to be estimated using an ggested by Sinclair & Duncan (1972):

$$\% \text{ marrow fat} = \% \text{ dry weight} - 6$$

The constant represents the non-fat residue in the marrow after drying. The percentage marrow fat was greater in the tibia than in the femur of each animal (Wilcoxon matched pairs, $z = 2{\cdot}210$, $n = 44$, $P < 0{\cdot}05$, Fig. 1). Mobilization is thought to be sequential, with fat being removed from proximal leg bones before more distal ones (Brooks *et al.*, 1977). The average of the 2 values from each animal was used in this analysis.

Ageing criteria

Carcasses. By examining the lower mandible, 130 gazelle carcasses were divided into 10 age classes based on the number of molars and premolars erupted and the number of infundibuli present, according to the criteria of Schaller (1972, see Table I).

Live gazelles. In addition, all gazelles seen being killed ($n = 171$), including those from which the lower mandible could not be obtained ($n = 41$), were aged using Walther's (1973) method which relies on external physical characteristics of live gazelles. While the ages of adults could not be distinguished in this way, immatures could be separated into 4 classes:

(i) Fawns (corresponds approximately to Schaller's class I). Standing beside the mother, the fawn's back line is below the mother's belly or level with it.

(ii) Half-growns (corresponds approximately to Schaller's class II). Beside an adult gazelle, the back line of a half-grown is approximately at the same level as the adult's black flank stripe.

(iii) Adolescents (corresponds approximately to Schaller's classes II & IV). This is the first age class at which the sex of the young can be distinguished. Males have horns which may be up to 12 cm long (approximately at the tip of the ears). The adolescents are still smaller than adults and are of slighter build.

(iv) Sub-adults (corresponds approximately to Schaller's class V). Males in this age class are fully grown but their horns are 'C' shaped without the lower curve which gives rise to the characteristic 'S' shape of the adult males. Sub-adult females are almost fully grown and usually have short, thin horns which are not broken

Age class composition of the population

The age class composition of the population, based on Walther's (1973) categories, was also estimated using the sampling method employed by Bradley (1977). Each month a transect was driven through the main

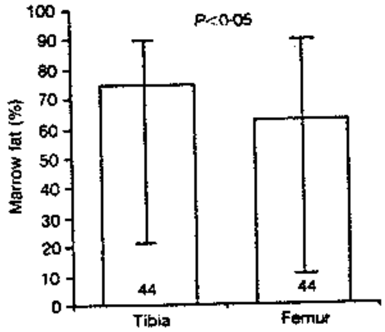


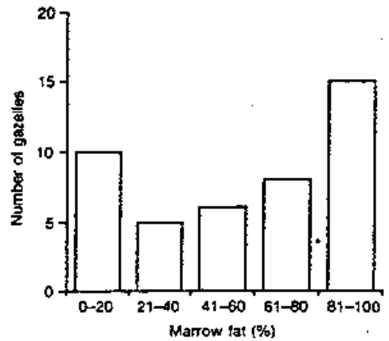
FIG. 1. Median percentage marrow fat values for the tibia and femur of Thomson's gazelles killed by both wild dogs and cheetahs. The numbers in the columns are the sample sizes and the bars represent interquartile ranges.

TABLE I

Age scale for Thomson's gazelles based on tooth eruption and wear in the lower jaw (from Schaller 1972: table 48)

Class	Approx. age at beginning of class (months)	Character
I	0	Only premolars present
II	2	M1 erupting to erupted
III	6	M1 present; m2 erupting to erupted
IV	9	Deciduous pm4 still present; m3 erupting
V	18	Full permanent dentition; 3rd cusp of 3rd molar not worn; posterior infundibulum of pm4 open
VI	24	Posterior infundibulum of pm4 present and usually closed. Anterior infundibulum of m1 very small, round or oval, or just worn off; posterior infundibulum of m1 present; 3rd cusp of m3 worn
VII		Both infundibuli off ml; posterior infundibulum of pm4 small and round, or gone
VIII		Both infundibuli off m1 and off anterior part of m2; posterior infundibulum of pm4 gone
		All infundibuli off m1 and m2
X		Infundibuli off m1 and m2 and one or more off m3; some incisors non-functional

oncentrations, the car was stopped at 500 m intervals and all individuals that were: (a) within a 180° ont of the car; and (b) within 200 m, were classified according to their age and sex. The average on that each age class represented in the population over the 2 years could then be calculated. Since end much of the first 4–6 weeks of their lives lying out (Walther, 1968) and only those which were ; could be seen on the transects, fawn numbers were severely underestimated. To compensate, the nber of fawns counted on the transects was increased by a factor representing the proportion of time end hidden (62%, FitzGibbon, 1988).



The distribution of percentage marrow fat values (average of tibia and femur) for gazelles killed by both wild cheetahs.

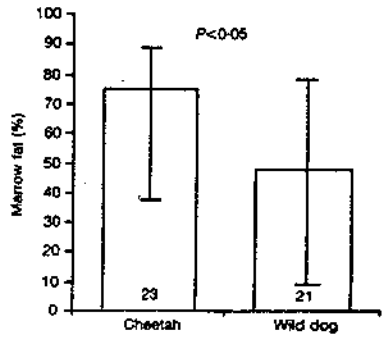


FIG. 3. Median percentage marrow fat values for Thomson's gazelles killed by cheetahs and wild dogs. The numbers in the columns are the sample sizes and the bars represent interquartile ranges.

Results

The condition of kills

Gazelles killed by the two species of predators had a wide range, from 0% and 93%, of percentage marrow fat values (Fig. 2). The marrow fat reserves of gazelles killed by wild dogs were, however, lower than those killed by cheetahs (Mann-Whitney U test, $z = 1{\cdot}195$, $n = 21, 23$, $P < 0{\cdot}05$, Fig. 3).

The marrow fat levels of male gazelles killed by both predator species were lower than those of females (Mann-Whitney U test, $z = -2{\cdot}59$, $n = 11, 33$, $P < 0{\cdot}01$, Fig. 4). Analysis of all adult kills ($n = 67$), including those which did not yield marrow samples, revealed that wild dogs took a greater proportion of adult male gazelles than cheetahs ($\chi^2 = 5{\cdot}07$, $d.f. = 1$, $P < 0{\cdot}05$). There was no difference in the marrow fat levels of the male gazelles taken by the two predator species (Mann-

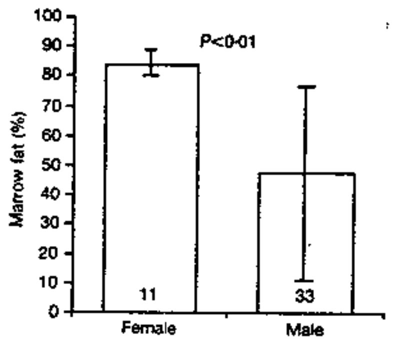


FIG. 4. Median percentage marrow fat values for male and female Thomson's gazelles killed by both cheetahs and wild dogs. The numbers in the columns are the sample sizes and the bars represent interquartile ranges.

TABLE II

Age classes, as determined from tooth wear, of Thomson's gazelles killed by cheetahs and wild dogs, from this study and from Schaller (1972)

	Cheetah				Wild dog			
Age	This study	Schaller	Total	(%)	This study	Schaller	Total	(%)
I	22	42	64	(22·7)	13	23	36	(34·0)
II	14	37	51	(21·4)	6	6	12	(11·3)
III	10	16	26	(10·9)	2	1	3	(2·8)
IV	3	2	5	(2·1)	1	2	3	(2·8)
V	5	2	7	(2·9)	1	2	3	(2·8)
VI	3	10	13	(5·5)	1	3	4	(3·8)
VII	6	24	30	(12·6)	8	14	22	(20·8)
VIII	10	8	18	(7·6)	5	2	7	(6·6)
IX	3	9	12	(5·0)	2	3	5	(4·7)
X	9	13	22	(9·2)	6	5	11	(10·3)

ey *U* test, $z = -1{\cdot}185$, $n = 14, 19$, N.S.). The marrow fat levels of the females could not be ıred for only two samples were available from wild dog kills.

The age of kills

:e there was no difference in the age distribution of kills between this study and that of er (1972) for kills made by cheetahs ($\chi^2 = 15{\cdot}1$, $d.f. = 9$, N.S.) or wild dogs ($\chi^2 = 9{\cdot}2$, $d.f. = 9$, the data from both studies are combined (Table II).

age structure of gazelles killed by the two predators, as estimated from tooth wear of ses, did not differ when all age classes were considered ($\chi^2 = 14{\cdot}76$, $d.f. = 9$, N.S.), nor when dults of class V and above were compared ($\chi^2 = 2{\cdot}91$, $d.f. = 5$, N.S.). Both species took a ely high number of gazelles in the oldest age class (X) but wild dogs did not take a greater rtion of these.

sample of gazelles aged, using Walther's (1973) method, revealed that cheetahs appeared to greater proportion of immature animals, particularly fawns, than wild dogs ($\chi^2 = 14{\cdot}6$, 4, $P < 0{\cdot}01$, Table III). Why the two methods of ageing should give different results is unclear. lection of adult age classes cannot be compared for this sample since Walther's method does stinguish between adults of different ages.

TABLE III

Age classes, as determined from external physical characteristics, of Thomson's gazelles killed by cheetahs and wild dogs compared with the overall population

Age class	No. killed by cheetahs	(%)	No. killed by wild dogs	(%)	Proportion in population
Fawns (class I)	44	(40·7)	13	(20·3)	3·0
Half-growns (class II)	14	(13·0)	6	(9·4)	2·9
Adolescents (class III–IV)	13	(12·0)	4	(6·3)	9·2
Sub-adults (class V)	5	(4·6)	4	(6·3)	10·7
Adults (class VI–X)	32	(29·6)	37	(57·9)	74·2

Comparing the age classes of kills made by the two predators with the age class distribution of the population revealed that both species appeared to select more immature animals, particularly fawns (class I) and half-growns (class II), than might be expected from the proportions that these age classes represented in the population (for cheetahs, $\chi^2 = 634{\cdot}8$, $d.f. = 4$, $P < 0{\cdot}0001$; for wild dogs, $\chi^2 = 72{\cdot}6$, $d.f. = 4$, $P < 0{\cdot}0001$, Table III).

Discussion

The condition of prey

A greater proportion of gazelles killed by coursing predators were predicted to be in poor condition than those killed by stalkers. While both wild dogs and cheetahs took gazelles with high and low marrow fat reserves, the gazelles taken by wild dogs were, on average, in worse condition. This result must be interpreted cautiously, however, for wild dogs, when compared with cheetahs, selected a greater proportion of adult male gazelles. Alone, this can explain the observed difference in the condition of prey, since male gazelles killed were found to have lower fat reserves than females. Moreover, there was no difference in the condition of male gazelles killed by the two predator species. Bradley (1977) found that males in a shot sample had lower kidney fat indices than females so this may be a feature of the gazelle population. In addition, Schaller (1972) noted that male Thomson's gazelles in the Serengeti were more prone to sarcoptic mange than females and he found a greater proportion of males dying or dead from disease.

While these results suggest that wild dogs are selecting males because their poor condition results in a reduced ability to outrun predators, this conclusion may, for two reasons, be invalid. First, the fat indices for the two sexes may not be comparable, particularly since fat reserves vary during the year, depending on reproductive state as well as energy intake. Males are likely to lose condition during peaks of breeding activity, females during the early months of lactation (Hanks *et al.*, 1976; Bradley, 1977; Dunham & Murray, 1982). Secondly, the sex bias in the sample of kills may result from factors unrelated to condition such as the reduced flight distance of males, which are reluctant to leave their territories (Estes & Goddard, 1967).

The distribution of the marrow fat values of Thomson's gazelles killed by the two predators, with most of them below 30% or above 60%, and few intermediate values, is similar to the marrow fat distribution of impalas killed by wild dogs in South Africa (Reich, 1981*a*). The implication is that the animals taken are either in relatively good or very poor condition and shows that this is not solely a feature of low visibility habitats, as Reich (1981*a*) has suggested. Even in open habitats, where the dogs can assess available prey, they will be forced to chase gazelles in good condition, as measured by marrow fat content, if no gazelles in poor condition are available. Furthermore, it may be the case that these gazelles have weaknesses which do not affect their bone marrow fat content but which reduce their ability to outrun predators. Mech & Frenzel (1971) found that, although few of the wolf-killed deer investigated had severely depleted bone marrow, they did exhibit more abnormalities, such as dental problems and jaw necrosis, than a randomly shot sample.

The age of prey

When compared with cheetahs, wild dogs were predicted to kill more young and old gazelles. The additional age class data presented here, however, confirmed Schaller's finding that this is not he case and that wild dogs do not take a greater proportion of gazelles in these age classes. If ınything, cheetahs captured more immature gazelles, particularly fawns (class I), although this nay be a result of sampling bias as found in a similar study (Reich, 1981*b*). Wild dog packs often plit up during hunts and individuals may capture and consume fawns without their kills being ecorded. Both species of predator captured immature gazelles at a higher frequency than they ›ccur in the population. It is perhaps not surprising that, in contrast to the prediction, cheetahs ake a large proportion of young animals (both classes I and II)—they are relatively easy to catch Schaller, 1967) and can be selected on the basis of their size before a chase has been initiated.

Cheetahs also captured as many gazelles in the oldest age class as wild dogs. One possible reason s that both predators were selecting old gazelles and that cheetahs were able to distinguish these ınimals without chasing them. An alternative is that neither predator is selecting old gazelles. Since the distribution of adult age classes in the population could not be determined in this study, it vas not possible to distinguish these two possibilities. Schaller was able to compare the listribution of adult age classes in a small random sample from the population ($n = 27$), collected by A. de Vos & H. Hvidberg Hanson (in Schaller, 1972), with the age class distributions of the wild log and cheetah kills. There was no difference in either case, suggesting that neither predator elects older animals. In a similar study, however, where a random sample from the population vas available, Pimlott *et al.* (1969) found that wolves killed a greater proportion of fawns and older age classes of white-tailed deer than were present in the population. Additional studies of volves preying on other ungulate species have confirmed this (Murie, 1944; Kuyt, 1972).

Summary

When compared with cheetahs, it appears that wild dogs take a greater proportion of Thomson's gazelles in poor condition. The difference is due to wild dogs selecting more male gazelles, which appear to have lower fat reserves than females. If wild dogs are selecting males because their lower fat reserves reduce their ability to outrun predators, the result supports the talker/courser dichotomy. It is possible, however, that the preponderance of males among the vild dog kills results from their flight distances which are lower than those of females. Wild dogs, vhen compared with cheetahs, do not take a greater proportion of young and old gazelles; if ınything cheetahs take a greater proportion of very young animals, although this may result from ι sampling bias. Both predators are selecting more immature gazelles than expected from the proportion they represent in the population.

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