Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*)

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(With 6 figures in the text)

Hunting group size, hunting rates and hunting success were monitored over a seven-year period among members of one large clan of spotted hyenas (*Crocuta crocuta*) inhabiting the Masai Mara National Reserve, in south-west Kenya. Prey availability varied seasonally in this study area, and hyenas tended to hunt whichever prey species were most abundant during each month of the year. Over 75% of 272 hunting attempts were made by lone hyenas, even when they hunted antelope three times their own body mass, such as wildebeest and topi. Of all prey that were commonly hunted, only zebra were usually hunted in groups. Approximately one-third of all hunting attempts resulted in prey capture. Although no significant sex differences were observed in juvenile or adult hunting rates, low-ranking adult females hunted at significantly higher hourly rates than did higher-ranking females. Hunting success was not influenced by the social rank of hunters, but hunting group size and hunter's age strongly influenced success. Young hyenas were poor hunters, and did not achieve adult competency levels until they were 5–6 years old.

Introduction

In his classic study, Hans Kruuk (1972) surprised us with his demonstration that hunting is more important than scavenging in the feeding ecology of the spotted hyena (*Crocuta crocuta*). Many subsequent workers have now replicated Kruuk's finding that *Crocuta* are significant predators (Bearder, 1977; Smuts, 1979; Tilson, von Blottnitz & Henschel, 1980; Henschel, 1986; Mills, 1990; Cooper, 1990; Hofer & East, 1993). In contrast to the other members of the family Hyaenidae, *Crocuta* regularly prey on medium- and large-sized ungulates, which they hunt either alone or with other members of their social units (Kruuk, 1972; Tilson & Hamilton, 1984; Mills, 1985, 1990; Cooper, 1990; Hofer & East, 1993). *Crocuta* tend to prey on whatever ungulate species are locally most abundant, and hunting group size varies with prey type (Kruuk, 1972; Cooper, 1990). Kruuk (1972) found that hunts of gazelles and wildebeest were most frequently initiated by lone hyenas, whereas zebra were hunted by groups containing an average of 11 hyenas. Approximately 25 to 35% of hunting attempts result in the capture of ungulate prey (Kruuk, 1972; Mills, 1990). Group hunts of some prey types, for example wildebeest calves, are significantly more successful than are hunts performed by lone hyenas (Kruuk, 1972, 1975). Several authors have suggested that group hunting is the norm among *Crocuta* (e.g. Deane, 1962; Schaller, 1972; Tilson & Hamilton, 1984), and Kruuk (1972, 1975)

and Tilson & Hamilton (1984) hypothesized that sociality in this species might represent an adaptation to capturing large prey.

In the current study, we examined hunting behaviour exhibited by *Crocuta* inhabiting the northern part of the Serengeti ecosystem. We obtained some of the same types of data on prey selection and hunting group size as those collected by Kruuk (1972) and Mills (1990), and replicated some of their results. However, our primary objectives were to elucidate new dimensions of the hunting behaviour of spotted hyenas by examining effects of social rank, sex and age on hunting rates in our study population. We also sought to identify the variables influencing hunting success among our study animals.

Methods

The study site was the Talek area of the Masai Mara National Reserve, in south-west Kenya. This is an area of open, rolling grasslands grazed year round by several different ungulate species, the most numerous of which are Thompson's gazelles (*Gazella thomsonii*), topi (*Damaliscus korrigum*) and impala (*Aepyceros melampus*). Each year the resident ungulate populations are joined for 3 or 4 months by large migratory herds of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*). The migratory herds typically arrive in the Talek area in July or August, and depart in October or November.

Our subject population was one large *Crocuta* clan of approximately 65 hyenas, inhabiting a home range of approximately 60 km^2. All hyenas in the study clan were known individually by their unique spots, and sex was determined from the dimorphic glans morphology of the erect phallus (Frank, Glickman & Powch, 1990). Except during 2 weeks in April, 1991, observers were continuously present in the study area from June 1988 to the present. Mother-offspring relations were established on the basis of regular nursing associations, and other genealogical relationships were as described in Holekamp *et al.* (1993). Because male *Crocuta* have viable sperm in their testes by 24 months of age (Matthews, 1939), and females generally bear their first young at around 36 months of age, we considered juvenile hyenas to be those less than 3 years old, and adults to be those 3 years or older. For analyses involving age as an independent variable, we divided natal Talek animals into 7 age groups: 1–2 yrs, 3–4 yrs, 5–6 yrs, 7–8 yrs, 9–10 yrs, 11–12 yrs, and animals older than 12 yrs.

Female *Crocuta* generally spend their entire lives in their natal clans, but all males leave their natal clans between the ages of 2 and 5 yrs. We divided adult immigrant males to Talek into 2 categories. Resident adult immigrant males remained in the study clan's home range for at least 6 months, whereas transient adult immigrant males were present for shorter periods, ranging from 1 day to a few weeks.

Crocuta clans are structured by rigid, linear dominance hierarchies (Kruuk, 1972; Tilson & Hamilton, 1984; Frank, 1986; Mills, 1990). Although the hierarchical dominance relationships among *Crocuta* clan members closely resemble those characteristic of many Old World primate societies, they are unique among social carnivores (Ewer, 1973; Gittleman, 1989). In the current study, intrasexual social ranks of individuals were established on the basis of outcomes of dyadic agonistic interactions, as described previously (Holekamp & Smale, 1990; Smale, Frank & Holekamp, 1993). One comprehensive dominance matrix was constructed for adult members of each sex, covering the entire study period, and intrasexual ranks were determined from these matrices even though all individuals were not present concurrently as adult clan members. Thus, if individual A outranked B, and B outranked C in our matrix, then A was considered to outrank C even if A and C were not present

concurrently as adults. During the study period, members of 14 different matrilines (including sisters, mothers, grandmothers and great-grandmothers) were present in the clan.

We adopted Kruuk's (1972) definitions of hunting attempts and successful hunts. Thus a hunt, or hunting attempt, was a chase by one or more hyenas of a selected prey animal that covered at least 50 m, and a successful hunt was one in which the prey was killed by the pursuing hyenas. A chase was usually preceded by one or more hyenas rushing a group of ungulates, then standing and watching to select a particular prey animal. However, these rushes alone were not considered to be hunts. A rush could be distinguished from a chase as follows. Following a rush, the hyena stopped to watch prey, whereas a chase was not followed by this period of prey observation. In addition, a rush was usually directed at a group of antelope, whereas a chase was directed at a single prey animal.

Kruuk (1972) observed that there are often different numbers of hyenas participating at the beginning and end of a chase. Therefore, we defined hunting group size as the number of hyenas participating at the end of a chase. A solo hunt was one conducted from start to finish by a single hyena, and a group hunt ended with 2 or more participating hyenas.

The data set utilized here contained information on 272 hunts observed in their entirety between June 1988 and May 1995. Although approximately 10% of these were observed at night with the aid of night vision binoculars, most hunts were observed between 06:00 and 09:00 h, or between 17:00 and 19:30 h. At these times, ambient light was adequate for individual identification of all hyenas participating in each hunt. During all 272 hunts, we recorded the prey species hunted, and the number of hyenas participating at the end of the chase, and in 244 of these hunts we were able to record the exact identities of all participating hunters. For 208 hunts we also knew the exact ages and social ranks of all participating hyenas.

We estimated local abundance of each different ungulate prey species by counting all prey animals found within 100 m of 4-km transect lines in 2 different areas of the study clan's home range. Both transects were run at biweekly intervals, between 08:00 and 10:00 h. Proportional representation of any given ungulate species in the total prey population was calculated as [(number of that species counted)/(total prey animals counted) × 100]. All biweekly ungulate census estimates were averaged by month over the 7 yrs of our study, with a mean number of 13 ungulate census counts per month for all months of the year. For purposes of the logistic regressions described below, overall prey abundance during each biweekly interval was assigned to 1 of 6 categories, based on census increments of 200 prey animals. Thus, in the first prey abundance category, fewer than 200 prey animals were counted along our transects, and in the last category more than 1000 prey animals were counted.

Three dependent measures were calculated for the analyses presented below. We calculated the hourly hunting rate for each individual hyena as the [(number of hunting attempts in which it participated)/(number of minutes the animal was observed away from natal or communal den sites) × 60]. We calculated each animal's hourly rate of successful hunts as the [(number of successful hunts in which it participated)/(number of minutes it was observed away from den sites) × 60]. Rate data were normally distributed, and rate differences between groups were evaluated with Student's *t*-tests or analysis of variance (ANOVA). Finally, each hunt observed could be classified as either successful or unsuccessful, but data documenting hunting success were not normally distributed. Therefore, we used logistic regression to evaluate the influence of hunting group size, prey type, prey abundance, hunter's age, and hunter's social rank on the dependent variable of hunting success. Mean values were presented ± S.E., and differences between groups were considered to be significant when $P < 0.05$.

Results

Ecology of hunting behaviour

The prey animals pursued most frequently by our study animals are listed in Table I. The five prey species listed in the table were pursued in 93% of the hunts observed. In addition, we observed 20 hunts of 'other' prey species, including three hunts of giraffe (*Giraffa camelopardalis*), four of Grant's gazelles (*Gazella granti*), one of kongoni (*Alcelaphus buselaphus*), one of dikdik (*Madoqua kirkii*), one of warthog (*Phacochoerus aethiopicus*), one of buffalo (*Syncerus caffer*), one of baboon (*Papio anubis*), two of hare (*Lepus capensis*), one of ostrich (*Struthio camelus*), two of passerine birds, and three of invertebrates.

For 244 hunts, we identified all participating hyenas. The 100 hyenas who participated in these hunts included 29 adult females, 23 juvenile females, 22 juvenile males, 17 adult resident immigrant males, and 9 adult transient immigrant males. Solo hunts were observed three times more frequently than were group hunts. Of the prey types commonly pursued by our study animals, only zebra were hunted by groups more often than by solitary hyenas. Mean hunting group sizes were 1.2 ± 0.1 for topi, 1.7 ± 0.3 for impala, 2.08 ± 0.1 for Thompson's gazelles, 2.92 ± 0.3 for wildebeest, and 9.1 ± 0.5 for zebra.

The hunting methods utilized by our study animals matched those described previously by Kruuk (1972), Mills (1990) and Cooper (1990). That is, our study animals typically first rushed a group of prey animals, stood briefly to observe the prey animals' locomotor behaviour, selected one target individual, then chased that individual down over distances ranging from 75 m to 4 km. Prey were then grabbed and disembowelled, taking 0.5 to 13 min to die. The scramble competition characteristic of this species (Kruuk, 1972) then usually followed as more hyenas arrived at the kill site.

When group hunts occurred, several clan members typically assembled at a den or other resting place in late afternoon or early evening. Such groups usually travelled without stopping through herds of gazelle or impala, until they reached a group of the ungulates (usually zebra) selected as prey. This behaviour pattern, also described by Kruuk (1972), suggested that the target prey species was selected in advance of the start of the hunt.

Absolute numbers of prey animals counted in biweekly ungulate censuses varied significantly throughout the year (Fig. 1: $F = 3.848$; $d.f. = 11, 138$; $P < 0.001$). Numbers of hunts observed each

TABLE I

Total hunts observed by Talek hyenas pursuing various prey types

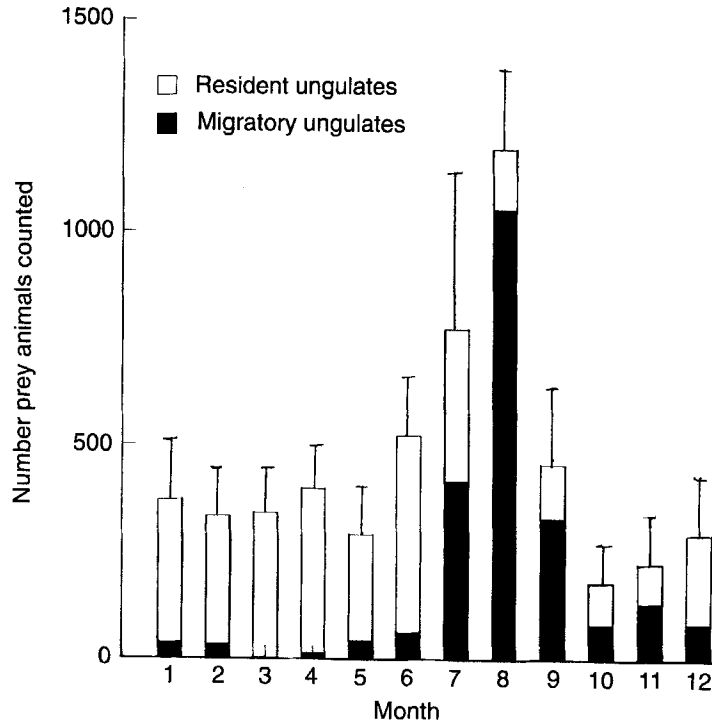| Prey	# Solo hunts			# Group hunts			Total hunts
	Attempts	Success	% Successful	Attempts	Success	% Successful	
Thompson's gazelle	102	32	31.4	26	13	50.0	128
Wildebeest	48	16	33.3	17	5	29.4	65
Topi	30	5	16.7	2	1	50.0	32
Zebra	6	0	0	13	1	7.7	19
Impala	6	2	33.3	2	1	50.0	8
Other species	16	6	37.5	4	1	25.0	20
Total	208	61		64	22		272

FIG. 1. Mean numbers of prey animals counted each month during biweekly ungulate censuses conducted from 1988 to 1995.

month varied inversely with prey abundance ($R_p = -0.591$; $P = 0.043$), suggesting that hyenas needed to engage in the fewest hunts when game was most abundant. Hyenas in our study clan exhibited seasonal changes in prey selection, and generally appeared to target whichever prey species were most abundant at any given time. Trends in percentage total hunts observed for specific types of prey closely tracked relative abundances of those prey species throughout the year. For example, the percentage of total hunts involving Thompson's gazelle was significantly correlated with gazelle abundance throughout the year (Fig. 2a: $R_p = 0.819$; $P < 0.001$). The discrepancy apparent in this figure between the two curves in the month of February can be accounted for by data from 1994, when large numbers of wildebeest briefly reappeared in the study area, and our study animals hunted them. The percentage of total hunts involving wildebeest was similarly highly correlated with wildebeest abundance throughout the year (Fig. 2b: $R_p = 0.945$; $P < 0.001$).

Effects of social rank, sex, and age on hunting rates

On average, each adult hyena in the study clan was observed away from dens for 113.7 ± 16.9 h, was seen hunting once every 13.3 h of observation, and was successful in $26.33 \pm 5.26\%$ of its total hunts. Among adult females and their offspring, mean hunting group size varied significantly with social rank: high-ranking hyenas tended to hunt in larger groups than did lower-ranking individuals (Fig. 3: $F = 23.412$; $d.f. = 1,185$; $P < 0.001$). Furthermore, the composition of hunting groups varied with social rank. Group hunts in which high-ranking natal animals participated were significantly more likely to contain close kin (mothers, offspring and siblings) than were those in which low-ranking natal
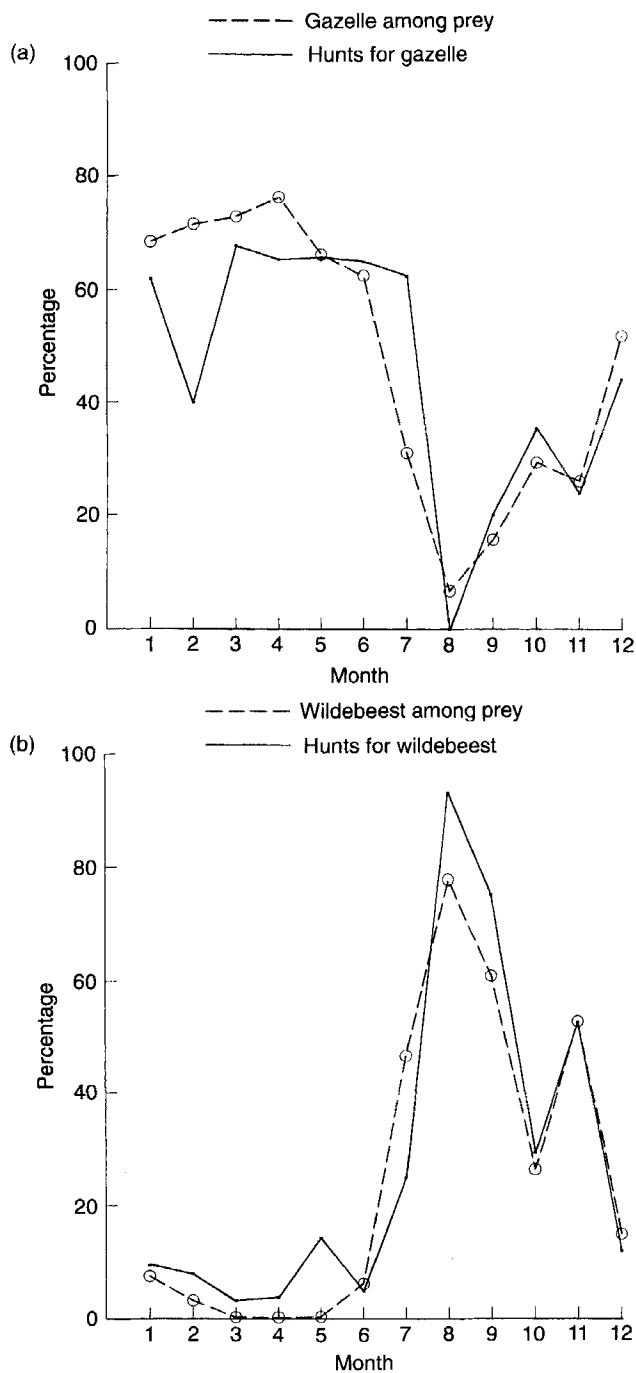
FIG. 2. (a) Dashed line is the percentage of all hunts observed during each month of the year that involved chases of Thompson's gazelles. Solid line is the percentage of all animals counted each month that were Thompson's gazelles. (b) Same values for wildebeest.

animals participated (F = 11.411; $d.f.$ = 1, 58; $P < 0.01$). These effects were apparently due, at least in part, to the fact that high-ranking matrilines have more members than do lower-ranking matrilines (Frank, 1986; Mills, 1990) so more kin are available as hunting partners to high- than low-ranking animals.

Adult immigrant males hunting in groups tended to hunt more frequently with other immigrant males than with adult females or natal juveniles (F = 4.738; $d.f.$ = 3, 73; P = 0.004). We found no significant relationship between intrasexual rank of adult immigrant males and their individual hourly hunting rates (F = 2.269; $d.f.$ = 1, 15; P = 0.153). We found no significant differences between adult resident males and adult females with respect to either hourly hunting rates (t = −1.275; $d.f.$ = 43; P = 0.213) or hunting success. When all adult males were considered together, hourly hunting rates were significantly higher among male than female adults (t = 2.440; $d.f.$ = 43; P = 0.021). However, transient adult immigrant males tended to hunt at significantly higher hourly rates than did resident immigrant adult males or any other age-sex group of resident hyenas (Fig. 4: F = 37.89; $d.f.$ = 4, 188; $P < 0.001$).

Among adult females, social rank influenced individual hourly hunting rates. Low-ranking females hunted at higher overall rates than did higher-ranking ones (Fig. 5: F = 6.538; $d.f.$ = 1, 27; P = 0.016), and also engaged in higher hourly rates of solo hunting (F = 6.719; $d.f.$ = 1, 27; P = 0.015). However, hourly rates of successful hunting (F = 1.283; $d.f.$ = 1, 27; P = 0.267) did not vary with female rank.

Juvenile hyenas were observed to hunt passerine birds and invertebrates while they were still living at the clan's communal den. The youngest age at which we saw juveniles capture mammalian prey was 9 months, when a sibling pair killed a hare. Overall, juvenile hyenas joined larger hunting groups than did adults (juveniles; x̄ = 4.99 ± 0.37 hyenas per group; adults: x̄ = 3.20 ± 0.22; t = −4.12, $d.f.$ = 397, $P < 0.001$). The youngest age at which we observed a hyena hunting antelope alone was 6 months, but the youngest age at which a solo antelope hunt was successful was 1.4 yrs. We found no sex difference among juvenile hyenas in their hourly hunting rates (t = 0.405; $d.f.$ = 131; P = 0.697) or hourly success rates (t = 0.300; $d.f.$ = 131; P = 0.764). When juveniles and adults were considered in the same analysis, hourly hunting rates did not vary between age groups (F = 0.945; $d.f.$ = 1, 158; P = 0.332), but hourly rates of successful hunting were significantly higher among older than younger hyenas (F = 16.02; $d.f.$ = 1, 158; $P < 0.001$).

Determinants of hunting success

Hunting success varied with hunting group size for a variety of prey types (Table II). We used logistic regression to evaluate concurrently the effects of several independent variables on the dependent measure of whether or not a given hunt was successful. These variables included the hunter's age in years, its social rank, concurrent prey abundance, month of the year, prey type, and hunting group size. To evaluate the possibility of a non-linear relationship between number of hunters and hunting success, we also included the square of the hunting group size as an independent measure.

In order to restrict our analysis to those variables having important effects on hunting success, we first ran a preliminary regression that included 11 monthly dummy variables, and seven prey type dummy variables, along with the measures of hunting group size, and hunter's age and social rank, listed above. None of the monthly dummy variables had even marginally significant effects on hunting success when controlled for prey abundance. Thus, although the proportion of hunts that were successful was higher in some months than others, this variation was due to variation in prey abundance.

Our next regression (Table III) was the same as the first except for deletion of the monthly dummy variables. The only variable generating a significant one-tailed t-value here was the hunter's age,
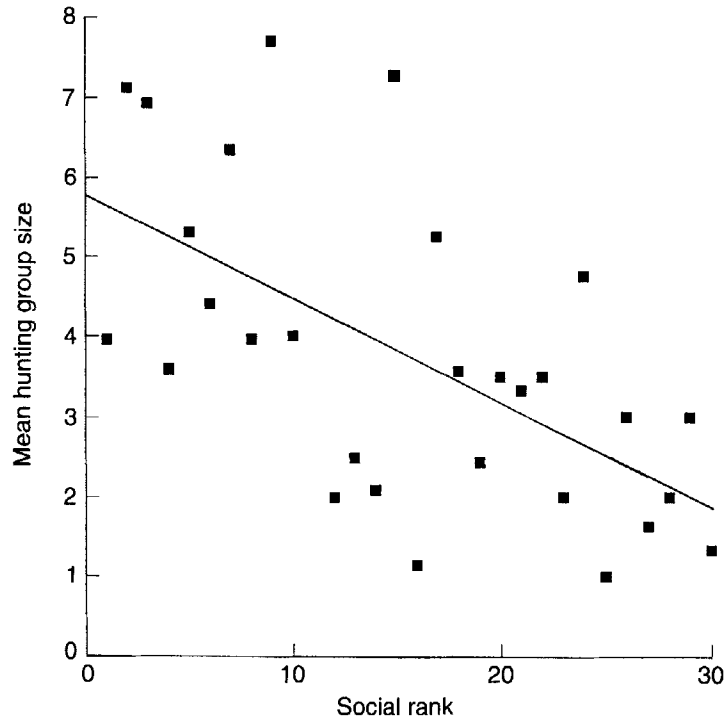
FIG. 3. Mean number of hyenas seen chasing the same prey animal, plotted against social rank of the participating hunters, when hunting groups contained adult females and/or their offspring. By convention, the animal with the highest rank is ranked number 1.

TABLE II

Percentage successful hunts by prey type and number of hyenas participating in 264 hunts. Prey types are: (1) Thompson's gazelle; (2) wildebeest; (3) topi; (4) zebra; (5) impala; (6) Grant's gazelle and warthog; (7) dikdik, baboon, hare; and (8) buffalo and giraffe

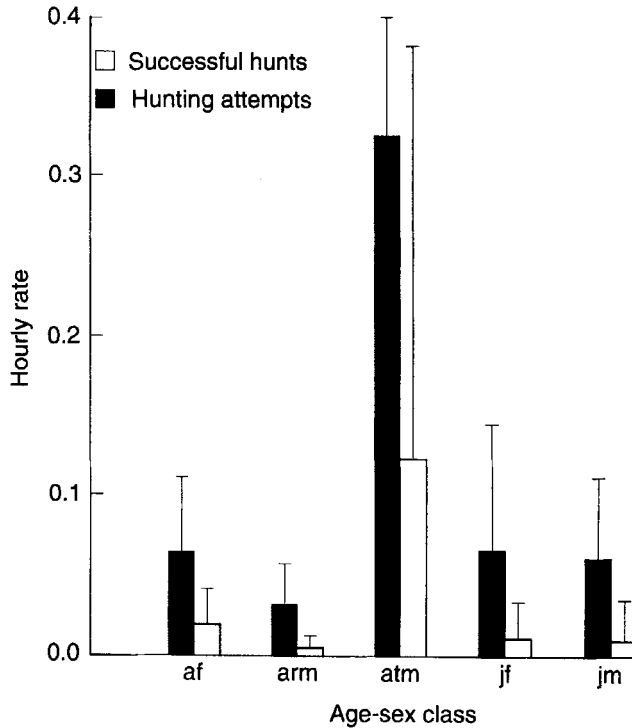| Number hyenas	Prey type								Overall percentage	Hunts seen
	1	2	3	4	5	6	7	8		
1	31	33	19	0	33	0	40	0	28	201
2	56	50	0	0	100		100		52	29
3	60	0	100	0	100			100	36	14
4	0	0		0					0	4
5	0	0							0	2
6						0			0	1
7	50	100			0				33	6
8				50				0	33	3
9		0							0	1
11				0					0	1
14				0					0	1
15				0					0	1

FIG. 4. Hourly rates of hunting attempts (■) and successful hunts (□) made by members of each age-sex class in the study population. Key: af = adult females, arm = adult resident males, atm = adult transient males, jf = juvenile females, jm = juvenile males.

although hunting group size, prey abundance, and the dummy variable for zebra (prey type dummy 4) all yielded t-values for which $P < 0.10$. In subsequent regressions, the only dummy prey type variable retained was that for zebra. The results from this regression indicated that the hunter's social rank had no significant effect on hunting success, so rank was not retained as an independent variable in subsequent analyses.

We next ran a regression (Table IV) examining effects on hunting success of hunting group size, hunter's age, prey abundance, and the zebra dummy variable. Here hunting group size was divided into four categories: 1) solo hunts, 2) hunting pairs, 3) trios, and 4) hunts involving more than three hyenas, and dummy variables were assigned to these categories. With these variables included in the regression, over 76% of hunt outcomes could be successfully predicted. All indicators (e.g. log likelihood, and percentage successful predictions) in Table IV show that this regression fits the data better than did the regression presented in Table III. Here it is clear that hunting group size significantly influenced hunting success. The dP/dX values reflect the incremental effect of each new hunter, and indicate that addition of a second hunter increased the probability of hunting success by 19%. Although the t-value for the trios dummy variable was not significant, the dP/dX value indicates that adding a third hunter increased the probability of success by another 20%. These regression results, and the data presented in Table II, clearly indicate that the relationship between hunting group size and hunting success was not linear.
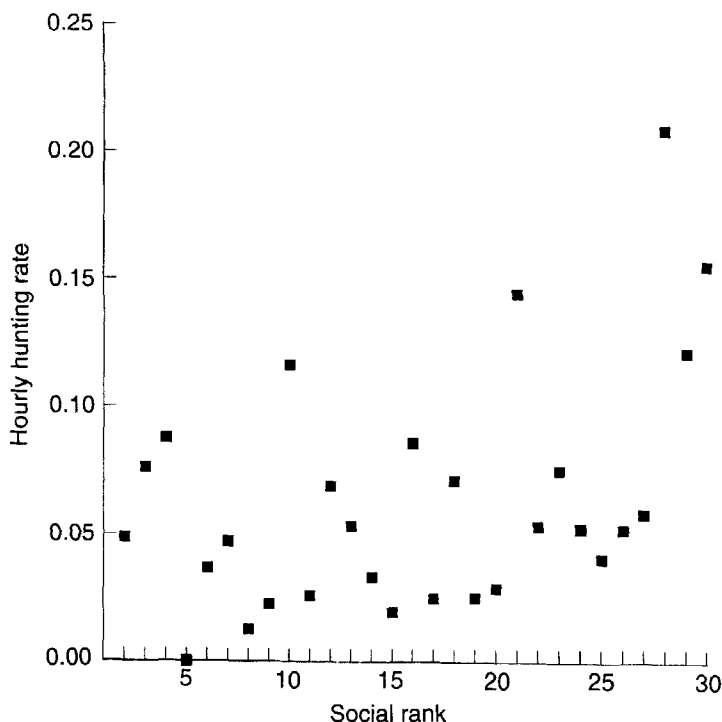
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F1G. 5. Hourly hunting rates observed in 29 adult females, plotted against their intrasexual social rank.

These regression results also show that having zebra as the prey type lowered hunting success by approximately 29%. However, because the influence of the zebra dummy variable was marginal, we ran a new regression that excluded the zebra dummy, and another that excluded all observations of hunts for zebras. The only successful zebra hunt in our sample occurred with a hunting group size of eight hyenas, and only 5% of all hunts included more than four hyenas. The coefficients yielded by these new regressions were nearly identical to those shown in Table IV, reflecting the robustness of the basic specifications.

Finally, our results showed that hunting success increased significantly with age (Fig. 6: $F = 4.096$; $d.f. = 6, 153$; $P < 0.001$). The dP/dX values shown in Tables III and IV indicate that each additional year of age increased a hunter's probability of success by 3%. However, the data shown in Fig. 6 reveal that this relationship was non-linear, and that there was a large increase in hunting success after 4 years of age. Thus young hyenas did not appear to reach mean adult competency levels at hunting until they were 5–6 years old. These data suggest that successful hunting in this species is an acquired skill demanding a great deal of practice.

Discussion

Like spotted hyenas elsewhere in Africa, members of the Talek study population were efficient hunters who preyed upon a wide variety of animal species. The relationship between numbers of hunts observed for each prey species, and the relative abundance of each prey species in the study area at that time, revealed striking functional responses (Holling, 1966). Talek hyenas mainly hunted gazelles and

TABLE III

Results of logistic regression examining effects of independent variables on whether or not hunts were successful

Parameter	Estimate	S.E.	t	dP/dX
Constant	−3.166	0.821	−3.859	−0.517
Hunting group size	0.843	0.496	1.701	0.138
Group size squared	−0.082	0.061	−1.329	−0.013
Hunter's age	0.188	0.049	3.779*	0.031
Hunter's rank	−0.025	0.029	−0.868	−0.004
Prey abundance	0.153	0.113	1.347	0.025
Prey type dummy2	0.101	0.435	0.233	0.017
Prey type dummy3	−0.893	0.677	−1.320	−0.146
Prey type dummy4	−1.890	1.175	−1.609	−0.308
Prey type dummy5	−20.361	17268	−0.118	−3.321
Prey type dummy6	−19.755	19758	−0.999	−3.222
Prey type dummy7	1.448	0.991	1.462	0.236
Prey type dummy8	−19.949	22342	−0.893	−3.253

*$P < 0.05$

Log of likelihood function $= -101.581$
Number of cases $= 208$
Sum of squared residuals $= 33.957$
$R^2 = 0.179$
Percentage correct predictions $= 75.00\%$

topis until the annual migration inundated the clan's home range with wildebeest and zebra. When the migratory ungulates arrived, the hyenas switched to hunting them, and continued to do so until the wildebeest and zebra left the study area. Similar results were obtained by Cooper (1990) for a Botswana hyena clan feeding on both sedentary and migratory prey. Our findings were consistent with Kruuk's (1972) hypothesis that seasonal fluctuations in *Crocuta*'s diet directly reflect changes in relative availability of various ungulate species.

Compared to the prey choices made by *Crocuta* living elsewhere in Africa, prey selection in the Talek study clan most closely resemble that described by Kruuk (1972) for his Serengeti hyenas. We

TABLE IV

Results of logistic regression examining effects of six independent variables on whether or not hunts were successful

Parameter	Estimate	S.E.	t	dP/dX
Constant	−2.813	0.481	−5.849	−0.475
Pairs dummy	1.145	0.528	2.169*	0.193
Trios dummy	1.189	0.783	1.519	0.201
Larger groups dummy	0.392	0.784	0.499	0.066
Hunters' age	0.176	0.043	4.070*	0.030
Prey abundance	0.184	0.108	1.698	0.030
Zebra dummy	−1.711	1.12	−1.533	−0.289

*$P < 0.05$

Log of likelihood function $= -106.346$
Number of cases $= 208$
Sum of squared residuals $= 35.097$
$R^2 = 0.152$
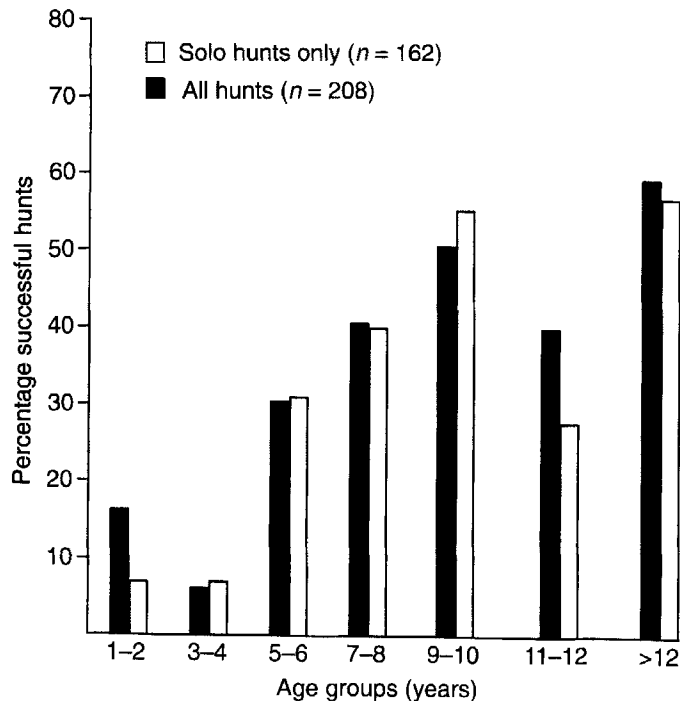Percentage correct predictions $= 76.64\%$

FIG. 6. Percentage successful hunts observed for members of each age group.

observed only two substantial differences between the hunting behaviour of our study animals and that of Kruuk's Serengeti hyenas. First, our hyenas did not prey on young wildebeest calves, since wildebeest calving does not usually occur in our study area. Second, Talek hyenas hunted more topi than did those in the Serengeti.

The hourly rates of hunting attempts and successful hunts we observed among Talek hyenas were substantially lower than were those observed by Cooper (1990) in her Botswana study population. This difference might reflect the fact that most of our observations were made during daylight hours, whereas Cooper (1990) mainly observed hunting behaviour at night. Thus our finding that high-ranking female hyenas hunted at lower rates than did lower-ranking females must be viewed with caution since the number of hunts we observed at night was too small to allow us to rule out the possibility that high-ranking females preferred to hunt at night.

As Kruuk (1972), Cooper (1990), Mills (1990), and Gasaway, Mossestad & Stander (1991) observed before us, we found that adult hyenas were generally successful in about one-third (overall mean = 30.5%) of their overall hunting attempts. Kruuk's (1972) study animals succeeded in 34% of their hunts for wildebeest and in 33% of their gazelle hunts. The Kalahari hyenas observed by Mills (1990) were successful in 39% of their wildebeest hunts, 31% of hunts for gemsbok (*Oryx gazella*), and 50% of hunts for eland calves (*Taurotragus oryx*). During the migration of wildebeest and zebra into our study area each year, when prey animals were superabundant, we observed higher proportions of successful hunts than at other times of year. When enormous numbers of migratory prey animals are available to choose from, it may be that sick or injured animals represent a larger proportion of the available prey population than at other times, thereby making it easier for hyenas to select and kill unfit individuals. Alternatively, since migratory ungulates generally occur in the Talek area only during the

dry season, shortage of water might weaken migrants and thus make them more vulnerable to hyena predation.

Three-quarters of the hunts we saw were made by solitary hyenas. Thus, like scavenging (Kruuk, 1972; Cooper, 1990), hunting by spotted hyenas is largely a solitary occupation. Solo hunts were commonly undertaken for most of the prey species in our study area. Only hunts for zebra, buffalo, and giraffe were more commonly undertaken by groups of hyenas than by lone hunters. Kruuk (1972) reported that gazelle hunts were usually performed by lone hyenas in his Tanzanian study areas, despite the fact that two hyenas were likelier to catch gazelle than were solo hunters. Kruuk also noted that groups of hyenas were no more likely to catch a wildebeest there than were solitary hunters. Similarly, Mills (1990) found that springbok (*Antidorcas marsupialis*) were usually hunted by lone hyenas in the Kalahari. Mills (1990) found that there was no relationship between hunting success and hunting group size among Kalahari hyenas chasing eland calves, wildebeest, or gemsbok. By contrast, results from our logistic regressions suggest that hunting group size was an important determinant of hunting success among Talek hyenas. Specifically, adding second and third hunters increased the probability of a hunt being successful by 19% and 20%, respectively.

We found that high-ranking female *Crocuta* tend to hunt in larger groups, and in groups containing more kin, than do lower-ranking females. Mills (1985, 1990) also found that closely related *Crocuta* tend to forage together. Effects of social dominance upon individuals' decisions to feed alone or in groups have been examined in recent laboratory studies of avian foraging (Caraco *et al.*, 1989; Krebs & Inman, 1994). Dominant birds initiated bouts of social foraging, whereas subordinates terminated them, suggesting that dominant animals have more to gain and less to lose by social foraging than do subordinate individuals (Caraco *et al.*, 1989). Among social carnivores, each individual must be able to harvest some threshold food yield from participation in a hunt, and hunting group size should be influenced by the effects of other hunters on individuals' food intake (Caraco & Wolf, 1975; Zimen, 1975; Nudds, 1978; Krebs & Inman, 1994).

Quantity and quality of food ingested by *Crocuta* competing at a fresh ungulate carcass appear to depend importantly on four variables: 1) the number of hyenas attempting to feed from the carcass; 2) the timing of the individual's arrival at the kill; 3) the individual's ability to ingest food rapidly; and 4) its social rank. Like many other aspects of hyena behaviour, hunting rates are profoundly affected by the individual's social rank. High-ranking resident females tend to hunt less often than do lower-ranking females. Interestingly, however, we found that hunting success does not vary with female social rank. If low-ranking females hunt more frequently than do high-ranking females, and if hunting success does not vary with social status, then low-ranking females should theoretically be able to ingest more food than can higher-ranking females. However, low-ranking hyenas are typically displaced from carcasses by socially dominant animals as soon as the latter arrive at a kill, and dominant animals generally obtain more food during group feeding at carcasses (Kruuk, 1972; Tilson & Hamilton, 1984; Frank, 1986). It seems reasonable to expect that hungrier hyenas should hunt at higher rates than others, as apparently also occurs in lions (Packer, Scheel & Pusey, 1990). Furthermore, if a low-ranking hyena can succeed in capturing an ungulate alone, then it often enjoys 1–15 minutes of competition-free feeding before other hyenas arrive at the kill. During that time, an adult hyena can ingest 2–20 kg of flesh, and this mass of food would equal or exceeds its required daily food yield (Kruuk, 1972; Tilson & Hamilton, 1984; Henschel & Tilson, 1988; Cooper, 1990). The fission-fusion society characteristic of this species permits individual hyenas, particularly low-ranking ones, to forage alone, yet still benefit from participation in group defence of food and territory.

Although social rank influenced hunting rates among Talek hyenas, rank did not affect hunting success. Furthermore, we found no sex differences among adult hyenas with respect to hunting

success. These results suggest that perhaps, in order to survive and reproduce in *Crocuta* society, every individual needs to attain some basic level of competence in securing its own food via predation. The mean hourly hunting rate we observed for adult resident males did not differ significantly from that of adult females, but adult transient males hunted at a mean hourly rate five times higher than that of adult females. Similarly, Mills (1990) noted that adult immigrant males led foraging parties disporportionately often in his Kalahari study area. Most of the transient Talek males represented in the current study were only observed in our study clan's home range for a few days, suggesting that perhaps these males visited the food-rich Talek area specifically to hunt and feed. Another possibility is that, following successful hunts, transient males frequently lost their kills to resident hyenas, and were therefore obliged to hunt more frequently.

Young hyenas proved to be ineffective predators, and appeared to reach adult competency levels only after years of practice hunting. In addition to being relatively slow to detect and arrive at ungulate kills, immature hyenas are clumsy feeders who are severely handicapped during scramble competition with adults at carcasses by their inability to swiftly remove and ingest flesh from the carcass (Holekamp & Smale, unpubl. obs.). Hunting behaviour of juvenile hyenas differed in several respects from that of adults. Juveniles stalked proportionately more non-mammalian prey and small mammals than did adults, who mainly hunted ungulates. Similarly, Mills (1990) observed juvenile Kalahari hyenas hunting mice, whereas adult hyenas preyed on ungulates. When Talek youngsters hunted ungulates, they often selected inappropriate prey, or attempted to use inappropriate methods for prey capture. For example, only juvenile hyenas ever attempted solo hunts to catch zebra, a strategy which inevitably failed. Hyenas younger than 5 years old enjoyed significantly less hunting success than did animals 5 years and older. A great deal of learning is apparently involved in the shaping of an efficient hunter during *Crocuta*'s ontogeny. Caro's (1994) observations of cheetahs (*Acinonyx jubatus*) suggest this is also true of other large carnivores. Juvenile hyenas seldom hunted ungulates alone, although solo hunting was commonly observed among older hyenas. Thus juveniles may more frequently require assistance in securing prey than do older animals.

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