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# Why do hunting cheetahs prefer male gazelles?

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Abstract. Cheetahs, *Acinonyx jubatus*, in the Serengeti National Park kill more male Thomson's gazelles, *Gazella thomsoni*, than expected from the sex ratio of the local population. This paper examines whether behavioural differences between male and female gazelles predispose males to higher rates of predation. Cheetahs hunting groups of Thomson's gazelles preferentially selected individuals that were positioned on the periphery of groups, were further from their nearest neighbours, were in areas of high vegetation, were less vigilant and were either in small groups or on their own. As a result, male Thomson's gazelles, which tended to concentrate on the periphery of groups, had greater nearest-neighbour distances, were less vigilant and were found in smaller groups, were more vulnerable than females and were preferentially selected from groups. There was no evidence that males were more vulnerable because they tended to concentrate in areas of high vegetation. Overall, gazelles in groups were far less vulnerable to predation than solitary individuals and the fact that males spent so much more time alone than females was another factor contributing to their high risk of predation; although solitary males were actually better at escaping when chased by cheetahs than solitary females, the difference in escape ability was not sufficient to offset the greater number of attacks experienced by males as a result of their more solitary behaviour.

Increased male mortality, relative to that of females, has been observed in many studies of ungulate populations, including mule deer (*Odocoileus hemionus*; Robinette et al. 1957; Klein & Olson 1960), wildebeest (*Connochaetes taurinus*; Talbot & Talbot 1963), tsessebe (*Damaliscus lunatus*; Child et al. 1972) and hartebeest (*Alcelaphus buselaphus*; Kodnai 1974). Several reasons for the differential survival of the two sexes have been suggested (reviewed in Clutton-Brock et al. 1982), one of which is that males experience higher predation rates than females as a result of their reproductive activities.

While there is some evidence that males are more likely to be preyed upon than females (Robinette et al. 1957; Estes & Goddard 1967; Hornocker 1970; Kruuk 1972; Schaller 1972), the reasons for such a bias have not been thoroughly investigated. Hornocker (1970), for example, suggested that male mule deer are more vulnerable to predation than females because they are often on their own and tend to be in poor condition, particularly after the rut, while Robinette et al. (1959) concluded that they are more vulnerable because they are less wary than females and tend to occur around the periphery of herds. It is generally assumed that territorial males are most at risk in territory-holding species (Bradley 1977; Estes & Goddard 1967), although non-territorial bachelor males may in fact be more vulnerable since they tend to be in high vegetation, usually in unfamiliar habitat and are often injured during fights (Walther 1969; Gosling 1986). Because of the difficulty of observing predation attempts on ungulates in the wild, few quantitative data are available to resolve these issues.

The Thomson's gazelle, *Gazella thomsoni*, population in the Serengeti National Park, Tanzania is strongly female biased. In the early 1970s, only 36·8% of the adult population were males (Bradley 1977), although the sex ratios at birth and adolescence (approximately 4–8 months) did not appear to differ from unity (Hvidberg-Hansen 1970; Bradley 1977). Several studies have concluded that the bias results from differential predation, because a preponderance of adult males is found in the prey of a number of predator species, in particular wild dogs (*Lycaon pictus*; Estes & Goddard 1967; FitzGibbon & Fanshawe 1989) and spotted hyaenas (*Crocuta crocuta*; Kruuk 1972).

In common with many other ungulate species, the social system of Thomson's gazelles is a form of resource-defence polygyny (Gosling 1986). Although male and female gazelles may form mixed herds while migrating, during stationary

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periods females remain in groups with other females and their offspring while males compete for territories in areas that females visit (Brooks 1961; Estes 1967; Hvidberg-Hansen & de Vos 1971; Walther 1978). My aim in this paper is to determine whether differences in the behaviour and ecology of males and females predispose gazelles of one sex to higher rates of predation by cheetahs, *Acinonyx jubatus*, one of the main predators of Thomson's gazelles in the study area (Kruuk & Turner 1967; Borner et al. 1987). To do this, I first consider what factors influence the selection of prey by these predators. Only then can the significance of behavioural and ecological differences between the two sexes, in terms of influencing predation risk, be determined.

## METHODS

Thomson's gazelles and cheetahs were observed on the long-, intermediate- and short-grass plains of the Serengeti National Park, Tanzania between March 1985 and April 1987. I spent 1752 h following hunting cheetahs, when I collected data on 155 hunts of adult Thomson's gazelles in single-species groups. In 102 of these hunts I could determine the sex of the gazelle selected by the cheetah. Observations were made from a Landrover during daylight hours, using 10 × 50 binoculars, and were recorded onto tape for later transcription to data sheets.

### Measures Recorded

When a cheetah hunted a gazelle group (defined as stalking, trotting towards or running at the group), I recorded the following measures: the height of the vegetation in which the hunt took place, the number of gazelles in the prey group (individuals were defined as group members if they were within 50 m of each other), the time (in s) from the cheetah initiating its chase to the first gazelle in the prey group fleeing (termed the 'flight delay'), the distance (in m) from the cheetah to the nearest gazelle in the prey group when it flees (termed the 'flight distance'), the distance from the prey at the end of the chase (either when the prey is killed, in which case it is zero, or when the chase is abandoned) and finally the duration of the chase timed to the nearest 1 s from the point at which the prey fled to the point at which the cheetah killed the prey or else abandoned the chase. Obtaining the last three measures enabled me to calculate the rate at which the cheetah gained on the prey during the chase (in m/s; flight distance minus predator–prey distance at end of chase, divided by the chase duration).

In addition to these measures, I recorded the position and nearest-neighbour distance of any gazelle selected by the cheetah. Individuals occurred on the periphery of the group if they had no group members within a semi-circle on one side of them; otherwise they occurred in the centre. Gazelles in small groups of fewer than five individuals could not usually be assigned such position categories. I normally estimated all distances to the nearest 5 m (except those less than 20 m which I estimated to the nearest 1 m) and regularly checked them by comparing the estimated distance between two objects with the same distance measured with a tape measure.

### Prey Selection Index and Sex Ratio

To determine whether cheetahs were preferentially selecting to hunt male or female gazelles, I had to take into account the sex ratio of the population from which the selection was made. To do this I calculated a selection index $(H-A)/(H+A)$ where $H$ is the percentage of gazelles of that sex in the sample of hunted animals and $A$ is the proportion of gazelles of that sex available to be hunted. A negative value for the selection index reflects an avoidance of gazelles of that sex while a positive one reflects a preference. A similar index, the predation risk index, was calculated to compare the sex ratio of gazelles killed by the cheetahs with the sex ratio expected if males and females were equally vulnerable.

To calculate the proportion of males and females in the gazelle population, I drove a transect through the main gazelle concentrations each month, stopped the car at 500-m intervals and classified all adult gazelles that were (1) within a 180° arc in front of the car and (2) within 200 m according to their age, sex, the size of the group and the height of the vegetation they were in (categorized as ≤30 cm or >30 cm). The transect was continued until at least 1000 adult gazelles had been sampled. By taking the transect through the main gazelle concentrations, the count may have been biased towards females. Groups were often large in these areas and the proportion of males in a group decreases with increasing group size (see below). This is also true of Bradley's estimate of the sex ratio as he used the same method: However, Robinette & Archer (1971), sampling a nearby population using a different method, found that only 19·6% of the adult population was male, far lower than Bradley's estimate for the Serengeti population of 36·8%. As a result, the female-biased sex ratio is unlikely to result from the sampling technique alone.

### Selection of Prey Groups by Cheetahs

To compare the sizes of groups that cheetahs chose to hunt with those available to them, I followed hunting cheetahs and noted both the size of any group within 1 km every 15 min and the height of the vegetation. If a group that had already been noted was still within 1 km after 15 min, it was not recorded again or on subsequent scans. I also recorded the size of any groups that the cheetah hunted.

### Position Survey

To assess whether male and female gazelles differed in the position they maintained in groups, I surveyed 1589 adult gazelles in 50 groups of various sizes and noted the position of each individual (periphery versus centre and distance from nearest neighbour).

### Vigilance Behaviour

To compare the vigilance levels maintained by male and female gazelles, I chose adult gazelles at random from feeding groups and recorded their vigilance behaviour on a continuously running tape-recorder for 5 min. I later transcribed the data using a stopwatch to measure durations to the nearest 1 s. A scan started when the focal gazelle lifted its head above shoulder height and finished when the gazelle lowered its head and resumed feeding. Time spent walking, grooming or interacting socially was not counted as time spent vigilant. A sample was terminated if the focal animal changed position in the group (i.e. from periphery to centre or vice versa), left the group (leaving was defined as moving more than 50 m away from the closest group member), lay down or started to ruminate.

At the start of recording, I noted the number of Thomson's gazelles in the group and estimated the height of the vegetation around the group (< 10 cm, 10–30 cm or > 30 cm). In addition, I categorized individuals as being on the periphery or in the centre of the group. Every 30 s during the 5-min watch, the distance from the focal gazelle to its nearest neighbour was estimated and the 11 records were later averaged to give a mean nearest-neighbour distance for the watch.



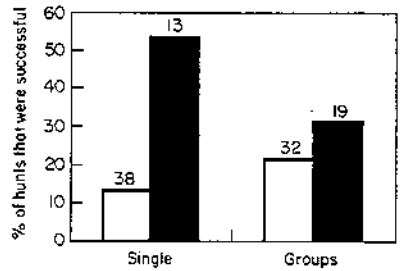



**Figure 1.** The success of cheetahs hunting adult male (□) and female (■) Thomson's gazelles when the gazelles are alone and in groups. Sample sizes are given above the histogram.

## RESULTS

Cheetahs hunted more adult male gazelles (68·6% of total) than females (31·3% of total). However, only 17·1% of chases against males resulted in a kill compared with 40·6% of those against females, so cheetah were, in fact, more successful when hunting females than males ($\chi^2 = 6{\cdot}55$, $df = 1$, $P = 0{\cdot}01$). As a result, the sex ratio of animals killed approximated to unity (12 males:13 females). The increased success of cheetahs hunting females was, however, restricted to solitary females; cheetahs were more successful hunting solitary females than solitary males ($\chi^2 = 8{\cdot}91$, $df = 1$, $P < 0{\cdot}01$), but there was no difference in the success of hunts against male and female gazelles in groups ($\chi^2 = 0{\cdot}59$, $df = 1$, NS; Fig. 1).

The cheetahs' preference for males and females also appeared to depend on the gazelles' group size. When hunting solitary gazelles, the cheetahs selected females in preference to males but when hunting groups they preferred males (Fig. 2, Table I). Overall, considering gazelles in all group sizes, more males were killed than expected from the sex ratio of the local population ($\chi^2 = 5{\cdot}02$, $df = 1$, $P < 0{\cdot}05$; Table II).

Approximately half the gazelles killed by cheetahs were solitary individuals (Table II). Since the majority of gazelles in the Serengeti (98·4%) are found in groups, this suggests that solitary animals

**Table I.** The sex ratio of gazelles hunted by cheetahs when alone and in groups compared with the sex ratio of gaz… the local population in that group size category and the selection indices, representing the cheetahs' preference for… and females when alone and in groups

| | | Sex ratio of gazelles, male:female | | Selection inde… | |
|---|---|---|---|---|---|
| | | | | Male | Fema… |
| Single gazelles | Hunted | 2·9:1 | ($N$=51) | −0·07 | +0·3… |
| | In population | 6·3:1 | ($N$=760) | | |
| Gazelles in groups | Hunted | 1·7:1 | ($N$=51) | +0·37 | −0·3… |
| | In population | 0·4:1 | ($N$=47 149) | | |

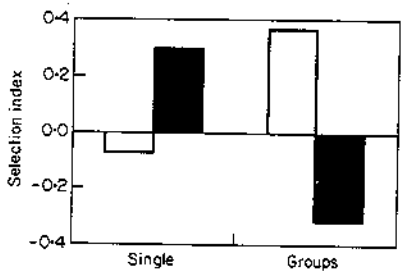



**Figure 2.** The selection indices of male (□) and female (■) gazelles hunted by cheetahs when alone and in groups.

experience far higher predation rates than group members. This was confirmed by the finding that more solitary animals (48% of kills) were killed than expected from the frequency of lone animals in the population (1·6% of gazelles encountered during transects were alone; $\chi^2=336{\cdot}43$, $df=1$, $P<0{\cdot}0001$). Consequently, the fact that males were so much more likely to be found on their own than females (nearly 16 times more) contributes to the relatively high predation rates they experience; although solitary males are better at escaping once chased by cheetahs than solitary females, the difference in escape ability is not sufficient to offset the high number of attacks experienced by males as a result of their more solitary behaviour (Table II).

### Factors Predisposing Males in Groups to Predation

In this section, I consider what factors influence the selection of adult gazelles by cheetahs and determine whether differences in the behaviour and ecology of males and females may predispose males in groups to selection by these predators.

#### *Group size*

Compared with the number of groups in each size category available (i.e. that came within 1 km of the hunting cheetah), cheetahs selected to hunt small groups of fewer than 11 gazelles in preference to larger ones ($\chi^2=12{\cdot}34$, $df=5$, $P<0{\cdot}05$; Fig… Even excluding solitary animals, cheetahs st… hunted small groups (2–10 gazelles) in preference… larger ones (>10 gazelles; $\chi^2=5{\cdot}86$, $df=$… $P<0{\cdot}05$). The proportion of males in a grou… decreased with increasing group size, while the pro… portion of females increased (Fig. 4). As a result, th… number of males available to the cheetahs may b… greater than expected from considering the popu… lation as a whole. This cannot, however, be th… main reason why cheetahs select more male… because even in the small groups there are mor… females than males (Fig. 4).

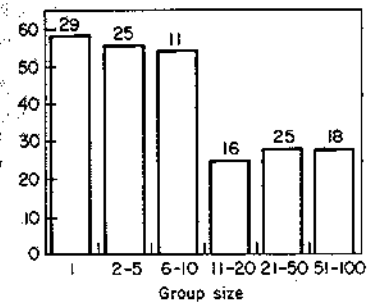
#### *Position*

Cheetahs usually hunted gazelles on the side of th… group from which they approached, only occasion… ally skirting round the group to get close to individ… uals on the far side. On the 43 occasions that I noted… the position of the prey, the individual chased wa… on the periphery of the group more often than in the… centre (83·7% versus 16·3%). Peripheral gazelle… were chased significantly more often than expected… by chance ($\chi^2=9{\cdot}70$, $df=1$, $P<0{\cdot}05$), compared… with the mean percentage of peripheral individuals… available in the hunted groups (59·6%). The… cheetahs also preferred gazelles that were further… from their nearest neighbours; when the nearest-… neighbour distances of hunted individuals were… compared with those recorded during the position… survey using analysis of variance techniques to… correct for the gazelle's position, sex and group size,… the distances of the hunted gazelles ($\bar{X}\pm$SE=… 19·8±3·1 m, $N=41$) were significantly greater than… those of the randomly sampled individuals… (5·0±0·2 m, $N=1589$; ANOVA, $F=17{\cdot}56$,



**…II.** The sex ratio of gazelles killed by cheetahs when alone and in groups compared with the overall sex ratio of …les in the local population (not the sex ratio of gazelles in that group size category as in Table I) and the predation …dices, for both solitary and grouped animals

| | | Sex ratio of gazelles, male:female | | Predation risk index | |
|---|---|---|---|---|---|
| | | | | Male | Female |
| …e gazelles | Killed | 0·7:1 | ($N$=12) | +0·18 | −0·10 |
| | In population | 0·4:1 | ($N$=47 909) | | |
| …elles in groups | Killed | 1·2:1 | ($N$=13) | +0·30 | −0·21 |
| | In population | 0·4:1 | ($N$=47 909) | | |
| …gazelles | Killed | 0·9:1 | ($N$=25) | +0·25 | −0·16 |
| | In population | 0·4:1 | ($N$=47 909) | | |




**…igure 3.** The effect of prey group size on the percentage of …homson's gazelle groups encountered by hunting …eetahs that the cheetahs chose to hunt (number of …unts=53). Numbers above the histograms refer to the …tal number of groups in each size category encountered.

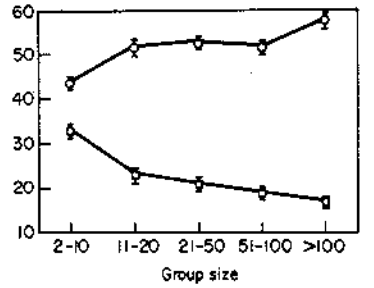



**Figure 4.** The percentage of adult males (□) and females (○) in groups of five different sizes. The percentage of males decreases with increasing group size (ANOVA, $F=12{\cdot}21$, $df=4{,}1298$, $P<0{\cdot}0001$), while the percentage of females increases (ANOVA, $F=9{\cdot}00$, $df=4{,}1298$, $P<0{\cdot}0001$). Vertical lines indicate SE.

$df=1{,}1622$, $P<0{\cdot}001$). Males had greater nearest-neighbour distances than females ($F=30{\cdot}51$, $df=$ 1,1622, $P<0{\cdot}001$) and peripheral individuals were further away from their neighbours than those in the centre ($F=49{\cdot}10$, $df=1{,}1622$, $P<0{\cdot}001$).

Since males surveyed during the position count were more likely to be on the periphery of groups (74·4% of 502 males) than females (52·7% of 1087 females; $\chi^2=66{\cdot}31$, $df=1$, $P<0{\cdot}001$), it is possible that males are chosen because they tend to congregate on the outside of groups. The greater nearest-neighbour distances of males than females ($\bar{X}\pm$SE=9·3±0·5 m versus 4·6±0·2 m) may also predispose them to attack.

#### *Vigilance level*

Faced with the choice of two adult gazelles similarly positioned within the group, cheetahs were more likely to choose the least vigilant one (FitzGibbon 1989). I compared the vigilance levels of males and females in non-hunt situations, using analysis of variance techniques to control for the effects of group size, vegetation height and position. Although the relative vigilance of male and female gazelles are likely to vary through the year, on average, females spent a greater percentage of their time vigilant ($\bar{X}\pm$SE=11·4±1·3% versus 8·4±0·8%) than males ($F=10{\cdot}60$, $df=1{,}239$, $P<0{\cdot}01$). Hence, cheetahs may select more males from groups because they tend to be less vigilant than females.

#### *Cover*

Cheetahs hunted a greater proportion of gazelle groups available to them (i.e. which came within 1 km) in high vegetation (>30 cm, 52·9%, $N=68$)

than in low vegetation ($\leqslant$30 cm, 30·4%, $N=56$; $\chi^2=5{\cdot}41$, $df=1$, $P<0{\cdot}05$). However, gazelle groups found in high vegetation (>30 cm) during the monthly transects did not contain a greater proportion of males than those found in low vegetation ($\leqslant$30 cm; ANOVA, $F=0{\cdot}09$, $df=1,1298$, NS) so this cannot be a reason why males were more likely to be hunted by cheetahs than females.

*Physical condition*

It was not possible to determine whether cheetahs were selecting gazelles on the basis of their physical condition, but on the two occasions that these predators were observed to hunt groups containing a gazelle with a broken leg, the injured individual was selected on both occasions.

**Factors Predisposing Solitary Females to Predation**

Although cheetahs preferentially selected males when hunting groups, they selected to hunt lone females in preference to lone males, suggesting that in this situation females were easier to catch; this is borne out by the finding that a greater proportion of hunts of female than of male gazelles resulted in a kill.

Why should females on their own be easier to catch than lone males? The three factors that are most likely to influence cheetahs' hunting success in this situation are the gazelle's vigilance level and physical condition, and the height of the vegetation in which the hunt took place (FitzGibbon 1988). Although lone females were no less vigilant than lone males (Mann–Whitney $U$-test, $z=-0{\cdot}19$, $N=20,13$, NS), they did tend to occur in higher vegetation (comparing the vegetation height in which lone male and female gazelles were found during the monthly transects, Mann–Whitney $U$-test, $z=-3{\cdot}79$, $N=42,102$, $P<0{\cdot}001$). This may have been one reason why they were easier to catch. It cannot have been the only one, however, because when the heights of the vegetation in which the hunts of male and female gazelles actually occurred were compared, there was no significant difference (Mann–Whitney $U$-test, $z=-1{\cdot}10$, $N=37,13$, NS).

The physical condition and running speed of the two sexes could not be measured, but there was a non-significant tendency for cheetahs to catch up more rapidly on females ($\bar{X}\pm$SE$=2{\cdot}5\pm0{\cdot}6$ m/s) than on males ($1{\cdot}1\pm0{\cdot}5$ m/s; Mann–Whitney $U$-test, $U=25{\cdot}53$, $N=7,14$, $P=0{\cdot}07$). In addition, males reacted more rapidly to the cheetah's attack (comparing the delay to flee; $1{\cdot}1\pm0{\cdot}4$ s versus $2{\cdot}5\pm0{\cdot}3$ s; Mann–Whitney $U$-test, $U=12{\cdot}0$, $N=14,7$, $P<0{\cdot}01$).

## DISCUSSION

When individuals are faced with a choice of prey, classical optimal foraging models predict that cheetahs should maximize their rate of energy intake by selecting the most profitable food item available. This will depend on both the size of the meal yielded by different prey animals and the probability of capture. By preferentially selecting gazelles that were on the periphery of groups, were further from their nearest neighbours, were less vigilant, and were either in small groups or on their own, cheetahs were presumed to improve their chances of making a successful kill. Even so, the observed success rates of cheetahs hunting gazelles of the two sexes are not expected to differ. Assuming it has a choice of prey, a cheetah selecting on the basis of vulnerability will simply select more males. Females are less likely to be the most vulnerable group member available.

The percentage of males in groups decreased with increasing group size and it is possible that cheetahs were hunting a higher proportion of small groups because of their preference for males. However, the results of a number of studies support the suggestion that predators can increase their hunting success by selecting to hunt smaller prey groups irrespective of the sex ratio of those groups (for example Neill & Cullen 1974; Kenward 1978; Morgan & Godin 1985). The observed decline in hunting success with increasing prey group size is thought to result from a number of factors (reviewed in Pulliam & Caraco 1984 and Pitcher 1986): these include the early-warning effect, the tendency for large groups to detect approaching predators further away, allowing more time for evasive action (Powell 1974; Siegfried & Underhill 1975; Lazarus 1979; FitzGibbon 1990) and the confusion effect, whereby a large number of individuals fleeing at the same time make it difficult for a predator to isolate or choose a single individual for attack (Neill & Cullen 1974; Milinski 1977; Pitcher 1986).

It has been argued that the preferential selection of prey individuals positioned towards the periphery of groups, such as that shown by cheetahs, may make it easier for the predator to concentrate on the chosen prey, without being confused by the movements of other group members (Milinski 1977). Whilst cheetahs may have preferred gazelles with greater nearest-neighbour distances for a similar reason, the effect of position and nearest-neighbour distance are confounded because gazelles on the periphery of groups have greater nearest-neighbour distances than those in the centre. In fact, both factors are likely to be important for another reason; cheetahs must stalk undetected to within 30–40 m of their prey in order to have a reasonable chance of success (Caro 1986) and individuals on the periphery with greater nearest-neighbour distances are likely to be closest to them.

By selecting the less vigilant individual in a group cheetahs are predicted to increase their hunting success for two reasons (FitzGibbon 1989). First, such animals are likely to react more slowly to the cheetah's final attack. Second, since animals facing starvation are expected to maximize energy intake by spending more time feeding at the expense of other activities, in particular vigilance, less vigilant animals may be in worst condition and therefore less able to outrun a predator.

As a result of the cheetahs' non-random selection of prey animals, male Thomson's gazelles, which tend to concentrate on the periphery of groups, to have greater nearest-neighbour distances, to be less vigilant, to be found in smaller groups and to spend more time on their own than females, were more vulnerable to selection by these predators. The suggestion that males were more vulnerable because they tended to be found in higher vegetation (Bradley 1977) was not confirmed by this study.

The poor physical condition of male gazelles relative to females may also increase their vulnerability to predation. In common with a number of other ungulate species (red deer, *Cervus elaphus*, for example, Clutton-Brock et al. 1982), male Thomson's gazelles maintain lower fat stores than females, particularly during peaks of breeding activity (Bradley 1977). In addition, Schaller (1972) noted that males were more susceptible to sarcoptic mange and he found a greater proportion of males dying or dead of disease. It is, however, still unclear whether stalking predators, such as cheetahs, which probably select their prey before starting the final attack are able to asses the relative condition of group members without the prey group fleeing (FitzGibbon & Fanshawe 1989). In addition to information provided by the physical appearance of prey animals, their vigilance levels may also provide some cues as to their physical condition (see above).

While the ease with which different individuals can be caught is one factor determining the selection of prey by predators, another is the size of the meal yielded. Male Thomson's gazelles are larger than females (by approximately 20% by weight, Ledger 1968; Robinette & Archer 1971) and, consequently, even in the absence of any differences in vulnerability, males should be the preferred prey of cheetahs. They would be predicted to hunt females only if their probability of success was at least 1·2 times that of hunting a male (i.e. to compensate for the fact that females provide 20% less energy if caught). Since cheetahs were almost four times as successful at hunting solitary females as they were solitary males, this would explain why they showed such a strong preference for solitary females: although they provided a smaller meal, they were far easier to catch and were therefore more profitable.

So why were cheetahs so successful when hunting solitary females? Female Thomson's gazelles are rarely on their own unless they have hidden fawns (Walther 1969). Such females would have been lactating, the costs of which are high and can result in loss of physical condition (Dunham & Murray 1982; Johns et al. 1984). This could be one reason why solitary females were, on average, easier to catch than solitary males; the females were slower to react once the cheetahs started their chases and cheetahs gained on them more rapidly. In addition, the fawns' requirement for cover in which to conceal themselves (Walther 1964) may have been one reason why solitary females were found in higher vegetation than solitary males, increasing their vulnerability to predation by stalking predators, such as cheetahs. It seems strange that the cheetahs should ever hunt solitary males considering their probability of success, compared with hunting solitary females, is so low. However, for cheetahs hunting in the Serengeti, prey are often widely dispersed and consequently it is necessary to take into account the time and energy required to search for other prey, which may be considerable.

Despite the cheetahs' preference for solitary females over solitary males, overall these predators killed more males than expected when the female-biased sex ratio of the population was taken into account. As a result, cheetahs, which kill approximately 8% of the adult population per year (calculated from Borner et al. 1987), contribute to the

female bias in the gazelle population. Wild dogs and hyaenas, however, concentrate to a greater extent on males than cheetahs do (Estes & Goddard 1967; Kruuk 1972). Since these two predators together kill between 3 and 9% of the adult gazelle population each year (calculated from Borner et al. 1987), they will have a greater influence on the adult sex ratio. The poor physical condition of males relative to females (except for lactating females, Schaller 1972; Bradley 1977) is likely to be one of the main reasons why coursing predators tend to kill more males. As a result of their long chases and their tendency to select particular prey animals after the chase has been initiated, coursing predators have more opportunity to select animals in poor condition than stalking predators (Kruuk 1972; FitzGibbon & Fanshawe 1988).

Thus, there are a variety of differences between males and females in their behaviour and ecology that predispose males to predation. The ultimate cause of many of these differences is the competition between males for mates. The increased body size, early growth rates and levels of competitive interactions that result (Clutton-Brock et al. 1982) have energetic costs, the consequences of which are loss of physical condition and increased time required for feeding (leaving less time for vigilance). In addition, the high levels of aggressive interactions result in males tending to concentrate on the periphery of groups, often at some distance from their nearest neighbours (Walther 1977).

For male Thomson's gazelles, the result of competing successfully is the acquisition and defence of territories and access to females which move through those territories. However, having to defend territories in the absence of females is extremely risky since males will tend to be alone and these solitary individuals are so much more vulnerable to predation by cheetahs than gazelles in groups (FitzGibbon 1990). Nevertheless, the large number of solitary males killed by cheetahs is not evidence that territorial Thomson's gazelle males experience greater predation than bachelor males as has been suggested (Bradley 1977). In this species bachelor males spend time on their own and cannot be distinguished from territorial males except by examination of their behaviour prior to flight (Walther 1969, 1978). Even so, it can be concluded that the results of this study do support earlier suggestions that one of the costs of competition between males is increased vulnerability to predation (Trivers 1972; Daly & Wilson 1983).

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