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Abstract: The causes and consequences of individual variation in the anti-predator behaviour of Thomson's Gazelles (*Gazella thomsoni*) in the Serengeti National Park, Tanzania were investigated. Adult gazelles showed considerable variation in the level of antipredator behaviour, particularly in the extent to which they associated with both conspecifics and Grant's Gazelles (*Gazella granti*), the positions they maintained in groups, their vigilance levels in the absence of predators, and the rates at which they stotted when fleeing from coursing predators. All these factors were also shown to influence their risk of predation. Causes of variation included sex, reproductive status, and physical condition. In addition, immature gazelles, particularly fawns, differed considerably from adults in the anti-predator strategies they adopted. Unable to outrun the majority of predators in direct chases, they reduced encounters with predators by spending most of their time in hiding and dropping down, adopting a prone position, when chased.

Cheetahs and Gazelles: A Study of Individual Variation in Antipredator Behaviour and Predation Risk

by

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The causes and consequences of individual variation in the antipredator behaviour of Thomson's Gazelles *Gazella thomsoni* in the Serengeti National Park, Tanzania were investigated. Adult gazelles showed considerable variation in the level of antipredator behaviour, particularly in the extent to which they associated with both conspecifics and Grant's Gazelles *Gazella granti*, the positions they maintained in groups, their vigilance levels in the absence of predators, and the rates at which they stotted when fleeing from coursing predators. All these factors were also shown to influence their risk of predation. Causes of variation included sex, reproductive status, and physical condition. In addition, immature gazelles, particularly fawns, differed considerably from adults in the antipredator strategies they adopted. Unable to outrun the majority of predators in direct chases, they reduced encounters with predators by spending most of their time in hiding and dropping down, adopting a prone position, when chased.

Introduction

Early studies of antipredator behaviour described the wide range of behaviour patterns exhibited by prey animals in response to predators and discussed the means by which such behaviour might reduce predation risk. More recently, the extent of individual variation in the type and level of particular antipredator strategies has become the focus of attention (for example predator harassment: Owings & Loughry 1985, Curio *et al.* 1985). In part, this interest has arisen from the fact that determining the influence of factors such as age, sex, and reproductive status frequently helps to elucidate the functional significance of a particular behaviour (for example stotting, Caro 1986). In addition, the need to explain why individuals are not always observed to minimise their vulnerability to predators, even though avoiding predation is clearly important and failure to do so precludes any further contributions to reproductive success, has promoted interest (Ydenberg & Dill 1986).

It has now become clear that reducing the risk of predation frequently conflicts with maximising other components of fitness, such as feeding and reproduction (Sih 1980, Werner *et al.* 1983, Lima 1985, Godin & Smith 1988). Individuals are forced to trade-off the time and energy spent in antipredator behaviour with that required for other essential activities. Thus, to understand the causes and consequences of variation in antipredator behaviour, a cost-benefit analysis at the level of the individual is required to take into account these conflicting demands. However, because predation is generally so difficult to observe in the wild, the data required for these studies, namely the extent to which individuals vary in their vulnerability to predation and the influence of antipredator behaviour on vulnerability, is often unobtainable.

In this paper, I outline the results of a study carried out on Thomson's Gazelles *Gazella thomsoni* in the Serengeti National Park, Tanzania, aiming to determine the causes of individual

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differences in antipredator behaviour in this species, focusing on the influence of age, sex and reproductive status. I will also examine the consequences of this variation, in terms of determining a gazelle's vulnerability to Cheetahs *Acinonyx jubatus*, one of the main predators of Thomson's Gazelles in the park (Borner *et al.* 1987).

In the Serengeti National Park, Thomson's Gazelles are vulnerable to a wide range of predator species, including Lions *Panthera leo*, Wild Dogs *Lycaon pictus*, Leopards *Panthera pardus*, and Spotted Hyaenas *Crocuta crocuta*, as well as Cheetahs (Kruuk & Turner 1967, Schaller 1967, Walther 1969, Kruuk 1972, Schaller 1972). Together these predators kill around 40,000 adult gazelles and a greater number of immatures each year from a population of approximately 250,000 (Borner *et al.* 1987). Thus predation constitutes a strong selection pressure and is likely to influence dramatically the morphology and behaviour of the gazelle population. Gazelles face the problem of developing antipredator strategies that will be effective against the varied hunting techniques of their wide range of predator species (Bertram 1979). Behavioural strategies which are either effective against a wide range of predator species or can be adjusted to the type of predator species and the particular situation a gazelle faces are an important complement to the gazelle's high speed, rapid acceleration and agility. The behavioural strategies which appear to be most important are grouping and vigilance (FitzGibbon 1988) and it is on these strategies that I will focus in this paper.

Methods

Thomson's Gazelles and their predators were observed on the short-, intermediate- and long-grass plains of the Serengeti National Park, Tanzania between March 1985 and April 1987. I spent 1,752 hr following hunting Cheetahs and collected data on 155 hunts of adult Thomson's Gazelles and 102 hunts of immatures. Over 1,000 hours were also spent observing Wild Dogs, during which time an additional 229 hunts were observed. Data on gazelles responding to other predator species were collected opportunistically.

When a predator hunted a gazelle (defined as stalking, trotting towards or running at a group) the following information was recorded: the size of the prey group (individuals were defined as group members if they were within 50m of each other), the sex and age of the selected prey animal (immature gazelles were categorised into four age classes: fawns, half-grown individuals, adolescents, and subadults, based on physical characteristics (see Walther 1973 for more details)); the position of the selected gazelle (edge versus centre of the group); and the outcome of the hunt (a hunt was deemed successful if the Cheetah killed the gazelle). If the prey animal selected was an immature gazelle, it was noted whether the gazelle was hidden or active when found by the cheetah, whether it dropped down, adopting a prone position, during the hunt and whether the mother attempted to attack or distract the predator. Towards the ends of chases, gazelles sometimes performed a series of sharp turns, moving in a zig-zag pattern (Walther 1969). I quantified the effectiveness of this zig-zagging behaviour in terms of increasing the predator-prey distance by estimating this distance before and after a period of zig-zagging. I could then calculate the distance lost or gained by the cheetah. More detailed description of the measures recorded are given in previous papers (FitzGibbon & Fanshawe 1988, FitzGibbon 1989, 1990a, b).

Time Budgets

In order to compare the vigilance level of different age/sex classes, I chose adult gazelles at random from feeding groups and recorded their vigilance behaviour for five minutes. A scan started when the focal gazelle lifted its head above shoulder height and finished when the gazelle lowered its head to feed. At the end of five minutes the percentage of time spent scanning was calculated. The sex, reproductive status, and group size was also recorded for each gazelle as was the height of the vegetation around it.

To assess the amount of time spent in hiding by infants of different ages, I chose a gazelle in the required age class at random from a group containing fewer than 11 gazelles and recorded the amount of time it spent hidden during a four-hour watch.

Adult Gazelles: Individual Differences in Antipredator Behaviour and Predation Risk

Differences between adult gazelles in their vulnerability to predation will depend in part on individual variation in physical characteristics such as morphology and condition. However, in this section, I want to review briefly how differences in the level of antipredator behaviour can also influence an adult gazelle's risk of predation, focusing on grouping, vigilance, and stotting as examples; and I examine how variation between individuals can arise.

Grouping

Thomson's Gazelles are generally gregarious, forming groups of anything from two to over 1,000 gazelles. As a result of Cheetahs' preference for attacking smaller groups, and the dilution effect, grouping clearly reduced a gazelle's individual risk of predation, through reduced attack rates (Table 1). Larger groups also appeared to detect approaching predators further away (FitzGibbon

Table 1. The effect of prey group size and composition (number of Thomson's and Grant's Gazelles) on the probability of capture for a particular Thomson's Gazelle in a group that comes within 1km of a hunting Cheetah.

Group size	Probability group hunted	Probability particular gazelle selected	Probability a gazelle killed	Probability particular gazelle killed
1TG	0.59	1.0	0.23	0.14
3TG	0.56	0.3	0.07	0.01
10TG	0.55	0.1	0.10	0.006
10TG 10GG	0.25	0.09	0.06	0.001
36TG	0.28	0.03	0.25	0.002
203TG	0.28	0.005	0.25	0.0004

TG: Thomson's Gazelle; GG: Grant's Gazelle.

1990a). This is particularly effective at reducing vulnerability to stalking predators such as Cheetahs which, in order to be successful, have to approach undetected to within 20-30m of their prey before starting the final high-speed chase. Not all group members were equally vulnerable to predation; Cheetahs tended to hunt individuals positioned on the edge of the group, particularly those furthest from other gazelles, in preference to more centrally placed group members (FitzGibbon 1990b). Small groups, with a large edge: area ratio, therefore expose a higher proportion of their members to this risk of attack.

While the evidence shows that grouping is an effective antipredator strategy, there are clearly constraints on the formation of groups since individuals are regularly found on their own and in small groups (Bradley 1977). These constraints include individual factors such as the need for males to defend territories (see below) and females to remain near hidden young, preventing them from following the movements of the group, as well as environmental factors such as the distribution of food resources and the thickness of surrounding vegetation. It is commonly observed that ungulate groups tend to be larger in more open habitats than in areas with dense vegetation. This may arise from differences in food item distribution (Jarman 1974) or the difficulty of maintaining contact when visibility is restricted (LaGory 1986).

As well as associating with conspecifics, Thomson's Gazelles in the Serengeti often formed mixed-species groups (Sinclair 1985), particularly with Grant's Gazelle *Gazella granti* (Estes 1964). Compared with remaining on its own, a Thomson's Gazelle associating with Grant's Gazelles was less vulnerable to Cheetahs, as a result of improved predator detection, reduced success rate of

Cheetah hunts and the tendency for Cheetahs to avoid hunting larger groups (Table 1, FitzGibbon 1990a). However, compared with joining conspecifics, joining Grant's Gazelles to form mixed-species groups had few additional advantages (FitzGibbon 1990a).

Male gazelles were more likely to associate with the Grant's Gazelles than females; mixed-species groups contained a higher percentage of males than single species groups (35.4% versus 27.4%, $n = 137,346$) while the percentage of females was lower in the mixed-species groups (49.0% versus 42.0%). This probably resulted from the fact that males were often prevented from joining conspecifics because of the need to defend territories. Thus associating with Grant's Gazelles conferred greater benefits on males than on females. Gosling (1980) also noted that hetero-specific ungulate groups commonly consisted of a territorial male of one species associated with males or females of another species.

Vigilance

The vigilance behaviour of ungulates is generally believed to facilitate predator detection (Wilson 1975, Berger 1978), although it may have other functions, such as food location (Krebs & Partridge 1973) and searching for conspecifics (Dimond & Lazarus 1974). In this study, evidence that increased levels of vigilance improved predator detection came from data showing that more vigilant gazelles detected approaching Cheetahs at greater distances (FitzGibbon 1988). However, even when the gazelle did not detect an approaching Cheetah, a high level of vigilance still reduced its probability of being selected as the focus of the attack. Cheetahs hunting groups of gazelles selected group members scanning at lower rates in preference to their more alert associates (Table 2). How does this variation in vigilance levels even within the members of one group arise?

Table 2. The vigilance level (percentage of time spent scanning) and sex of 16 adult gazelles which were chosen by Cheetahs, compared with their nearest neighbour in the group (from FitzGibbon 1989; *denotes individuals which started to ruminate, maintaining the head up posture during the rest of the stalk).

Gazelle chased		Gazelle ignored		Gazelle chased		Gazelle ignored	
Vigilance	Sex	Vigilance	Sex	Vigilance	Sex	Vigilance	Sex
8.0	M	17.5	M	10.0	F	65.0	F
31.4	M	63.0	M	78.7	F	84.2	F
40.0	M	70.2	M	52.0	F	50.0	F
15.7	M	38.8	M	23.9	F	20.5	F
40.0	M	45.0	M	81.0	M	96.3	M*
35.3	M	39.1	M	49.7	M	90.1	M*
31.7	M	65.2	M	62.0	M	88.3	M*
68.5	M	72.5	M	72.6	M	89.9	M*

An individual's vigilance level reflects, in part, its assessment of its own vulnerability to predation (Lendrem 1983); thus individual vigilance levels tend to be higher in smaller groups (Lazarus 1979, Barnard 1980, Table 3) and in individuals positioned in higher vegetation (which provides cover for stalking predators, Underwood 1982, Table 3) or towards the edge of groups (Jennings & Evans 1980). In the case of mothers, vigilance levels also reflect the vulnerability of their offspring. In Thomson's Gazelles, the level of maternal vigilance declined with increasing offspring age and mothers of fawns were particularly vigilant when their fawns were out of hiding (Table 3), and consequently more vulnerable to predators (see below). The increased vigilance of mothers with young had a direct payoff in terms of improved predator detection, with mothers of fawns and half-grown detecting approaching Cheetahs at significantly greater distances than other adult females in the same group (Fig. 1). This allowed the infants to flee at greater distances from the predator, an action which significantly increased their chances of escaping (FitzGibbon 1990c).

Since vigilance behaviour is mutually exclusive of essential activities such as feeding, time spent vigilant must also be traded off against the time required for other activities. Animals in poor

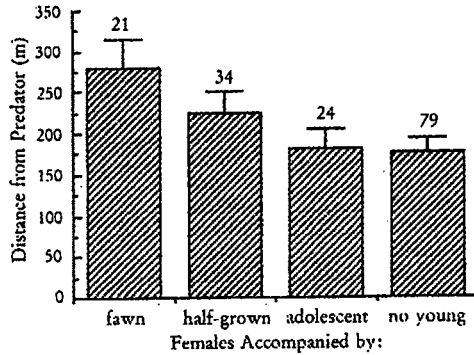


Figure 1. The influence of infant's age on the mean distance at which mothers detected approaching Cheetahs, compared with an adult female without young in the same group. Vertical lines indicate SE. Sample sizes are given above the bars.

condition or on a particularly poor food resource may spend less time vigilant, leaving more time for feeding. Finally, a gazelle's optimal vigilance level will also depend on the relative levels of other group members, since by increasing its level above that of others, a gazelle reduces its chances of being selected by a hunting Cheetah (FitzGibbon 1989). Thus, considering the large

Table 3. The influence of sex, group size and vegetation height on the mean percentage time spent vigilant by adult Thomson's Gazelles. In addition, the influence of infant's age and whether the fawn is hidden or active (three fawn age classes combined) on the vigilance level of females is given. Male gazelles were used to consider the influence of group size since females were never found on their own unless they had fawns hidden nearby, which might have confounded the results.

Sex	Male	Female			
% time vigilant	8.4 ± 0.8	11.4 ± 1.3			
Group size (males only)	1	2-5	6-10	11-20	>20
% time vigilant	15.1 ± 5.0	13.0 ± 2.5	5.2 ± 2.4	7.8 ± 3.7	3.1 ± 1.6
Vegetation height	<10cms	10-30cms	>30cms		
% time vigilant	7.4 ± 1.7	9.9 ± 2.6	16.7 ± 3.3		
Infant's age	1-2 weeks	3-4 weeks	5-8 weeks	half-grown	adolescent
% time vigilant	50.0 ± 4.9	36.3 ± 9.4	28.8 ± 6.3	17.9 ± 3.0	21.8 ± 3.1
Behaviour of fawn	hidden	active			
% time vigilant	31.8 ± 3.2	56 ± 4.0			

number of factors that influence an individual's decision to adopt a particular vigilance level, it is not surprising that so much variation, even within a single group, is recorded.

Distraction/Attack Behaviour

While adults without attendant young were never seen to defend themselves actively, gazelle mothers sometimes attempted to move predators away from their young, either by actively attacking the predators or by trying to distract them (Walther 1969, Kruuk 1972, Caro 1986). This they did by running to and fro, often stotting, between the predator and their offspring. Although the risks associated with such predator harassment have been disputed (Hennessy 1986), I saw one female being killed while attempting to distract a Cheetah during this study. The level of defence depended on the threat posed by the predator to the offspring, the risk the mothers incurred in responding and the effectiveness of the behaviour in promoting infant survivorship (Table 4).

Mothers of fawns regularly attacked jackals, which posed little threat to them, but never Wild Dogs or Cheetahs (Table 4). Mothers attempted to distract Cheetahs and hyaenas which pose little danger to adults alert to their presence, but rarely attempted to distract Wild Dogs, always effective hunters of adult gazelles. All the predator species were a great threat to gazelle offspring at this age (see below). A mother's probability of using both distraction and attack be-

Table 4. The percentage of hunts against immature gazelles in which the mother attempts to distract the predator. No data were available for the incidence of distraction or attack behaviour in response to jackals *Canis* spp. by mothers of half-grown and adolescents because jackals were not seen to hunt infants in these age classes. The last line of the table shows the incidence of attacks directed towards the three predator species by mothers of fawns (mothers of older age classes were never seen to attack predators).

Prey age	Predator species		
	Cheetah	Wild Dog	Jackal
Distraction behaviour			
Fawn	30.5 (n=56)	7.0 (n=14)	0.0 (n=13)
Half-grown	8.0 (n=25)	0.0 (n=7)	— —
Adolescent	0.0 (n=16)	0.0 (n=8)	— —
Attack behaviour			
Fawn	0.0 (n=56)	0.0 (n=14)	76.9 (n=13)

haviours decreases with increasing age of her infant. As the infant's ability to outrun predators develops, the extra benefits to be gained by the mother distracting or attacking the predator no longer outweigh the costs.

Stotting

Stotting is a display performed by a number of species of Bovidae, Antilocapra, and Cervidae (Byers 1984). It is defined as leaping off the ground with all four legs held stiff and straight (Walther 1969). Stots are generally performed by adults when fleeing from coursing predators, such as Wild Dogs and hyaenas which chase over long distances and rely on stamina to outrun their prey (FitzGibbon & Fanshawe 1988). It is rarely performed in response to stalking predators. During chases by Wild Dogs there was considerable variation in the incidence of stotting; some gazelles did not stot at all, some at high rates, others more slowly (range 1.1-2.0 stots/s). There also seemed to be variation in the height of stots, although this was impossible to quantify. Gazelles that Wild Dogs selected stotted at lower rates than those they did not select (means = 1.64 stots/s and 1.86 stots/s respectively). In addition, those which were chased but which outran the predators were more likely to stot (89% of escapees stotted while only 74% of those captured did) and stotted for longer durations than those which were chased and killed (means = 53s and 19s, respectively). The data suggested that one function of stotting was as an honest signal of a gazelle's ability to outrun predators (FitzGibbon & Fanshawe 1988). Individuals in better physical condition were able to stot at higher rates and/or to maintain stotting for longer period of time. Thus individual differences in physical condition gave rise to variation in stot rates and coursing predators took account of this variation when selecting their prey.

Male versus Female Gazelles: An Example

The way in which individual differences in antipredator behaviour can result in differential predation rates is well illustrated by comparing the predation risk and behaviour of male and female gazelles. Five main differences in the behaviour of male and female gazelles appear to predispose males to higher rates of predation (FitzGibbon 1990b).

- (1) Male gazelles spend far more time on their own than females (nearly 16 times more). Since grouping significantly reduces a gazelle's risk of predation, this may increase the vulnerability of males to a wide range of predator species.
- (2) When male gazelles are in mixed-sex groups, they tend to be on the outside where they are more at risk from stalking predators (FitzGibbon 1990b).
- (3) Although the relative vigilance levels of male and female gazelles vary through the year, on average males spend a smaller percentage of their time vigilant than females (means = 8.4% versus 11.4%). Since Cheetahs, and probably other stalking predators, tend to select less vigilant individuals

rather than their more vigilant associates, the reduced vigilance of males contributes to their increased predation risk.

(4) When fleeing from approaching Wild Dogs, females tended to flee from approaching dogs at greater distances than males which frequently delayed their flights until the dogs were much closer (mean flight distance = 169m, SE = 12, n = 73 and 119m, SE = 9, n = 98 respectively). The reduced flight distance of males, perhaps resulting from a reluctance to leave their territories (Estes & Goddard 1967), meant that when the dogs caught up with the prey group, males were frequently at the back and were more likely to be selected as a result.

(5) On the basis of bone marrow fat and kidney fat indices, male gazelles tend to be in poorer condition than females (Bradley 1977, FitzGibbon & Fanshawe 1989) and as a result are probably more vulnerable to predation. Their poor condition, compared to females, is reflected in their reduced stot rates and the fact that they are more likely to be selected by hunting Wild Dogs as a result (FitzGibbon & Fanshawe 1993).

Do these differences in the behaviour and ecology of male and female gazelles actually res-

Table 5. The sex ratio of adult gazelles killed by predators in the Serengeti compared with the sex ratio of the population.

	Sex ratio of gazelles male: female	(n)	Source
Population	0.4: 1	(47 909)	FitzGibbon 1988
Cheetahs	0.9: 1	(25)	FitzGibbon 1990b
Wild Dogs	2.1: 1	(44)	Fanshawe & FitzGibbon 1993
Leopards	2.7: 1	(58)	Schaller 1972
Lions	1.2: 1	(145)	Schaller 1972
Hyaenas	3.2: 1	(54)	Kruuk 1972

ult in an observable increase in male predation rates? Data from both Cheetahs and Wild Dogs suggest that they do (Table 5), particularly when the female bias in the population is taken into account.

The Influence of Age on Vulnerability to Predation and the Level of Antipredator Behaviour

Ungulates are most vulnerable to predation during their first few weeks of life (Geist 1971, Lent 1974), and for Thomson's Gazelles their probability of outrunning predators increased dramati-

Table 6. Percentage hunting success of Cheetahs, Wild Dogs, Spotted Hyaenas, and Golden Jackals against gazelles of different ages. The data on hunting success of hyaenas are from Kruuk (1972).

	Adult	(n)	Ado- lescent	(n)	Half- grown	(n)	Fawn	(n)
Cheetahs	20.6	(141)	37.5	(16)	48.0	(25)	70.5	(61)
Wild Dogs	42.7	(131)	50.0	(8)	85.7	(7)	100.0	(14)
Hyaenas	20.0	(10)	—	—	—	—	36.0	(33)
Jackals	—	—	—	—	—	—	50.0	(14)

ically with age (Table 6). For example, Wild Dogs were always successful when hunting fawns, but were only successful on 50% of occasions when hunting adolescents. Not only can infants not run as fast or for so long as adults, but in addition they appear to be less agile. Gazelles often perform sharp turns and zig-zag movements at the end of chases when predators are very close. When chased by Cheetahs, the average distance lost by a the predator during a period of zig-zagging increased with the gazelle's age (Fig. 2), suggesting that the gazelle's ability to turn sharply and therefore cause the Cheetah to overrun increased. Immature gazelles, particularly fawns, faced an additional problem; they were vulnerable to a greater range of predators as a res-

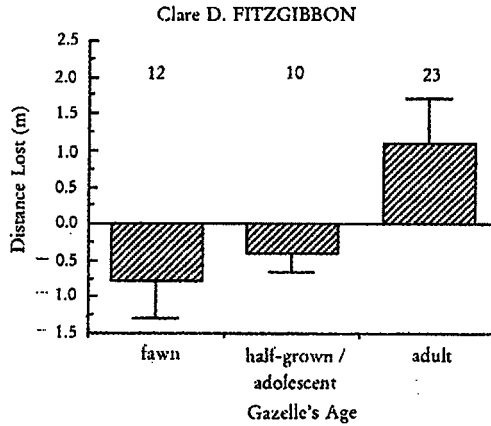


Figure. 2. The influence of gazelle's age on the mean distance lost by cheetahs during a period of zig-zagging by the prey (from FitzGibbon 1990c). A positive value represents distance gained by the gazelle and a negative value represents distance gained by the cheetah. The data from adolescents and half-grown individuals had to be lumped because of the small amount of data available. Vertical lines indicate SE. Sample sizes are given above the bars.

ult of their smaller size. For example, jackals sometimes attacked fawns but never older gazelles (Table 6).

These differences in vulnerability and ability to outrun predators have resulted in the evolution of two behaviour patterns specific to younger animals, hiding and prone response, and the use of another behaviour, stotting, for a different function to that it performs in adults. In addition, immature gazelles appear to make more effort to gather information from predators they encounter, particularly through inspection behaviour.

Hiding and the Prone Response

Thomson's Gazelles, along with the majority of gazelles, the cervids, and many antelopes, are hidiers (Walther 1968, Lent 1974, Ralls *et al.* 1986, FitzGibbon 1990c). The young lie hidden at some distance from the mother for the first few days of life, relying on cryptic colouration and minimal activity to avoid detection by predators. The mother and infant are only in contact for brief periods when the fawn suckles. In Thomson's Gazelles, this behaviour is almost entirely restricted to fawns (Fig. 3) and has generally disappeared by the half-grown stage. Considering the proportions of time they spend hidden and out of hiding, unexpectedly few hidden fawns are hunted by cheetahs (Table 7). Thus hiding appears to be an effective means of passive defence, reducing a fawn's probability of being detected by cheetahs when its ability to outrun them is

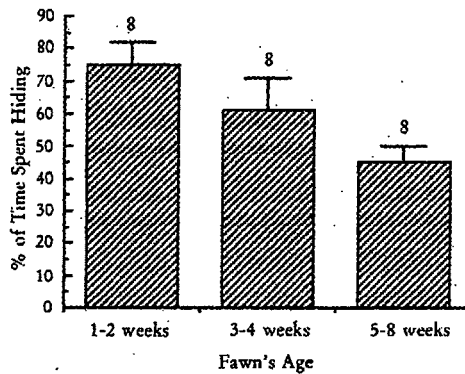


Figure. 3. The influence of fawn's age on the percentage of time spent in hiding. Infants older than 8 weeks were never observed to hide (data from FitzGibbon 1990c). Vertical lines indicate SE. Sample sizes are given above the bars.

minimal (FitzGibbon 1990c). If fawns are disturbed while hidden, they frequently run away stotting; at this age, the behaviour probably informs mothers that the fawns have been disturbed and are in need of defence (Caro 1986).

Table 7. The number of fawns found by Cheetahs when in hiding and when active compared with the number predicted from the proportion of time fawns of each age class spent in hiding. The two older fawn age classes were lumped because of the small number of fawn hunts that were observed.

Age		In hiding	Active	Total
1-2 weeks	Observed	9 (36%)	16 (64%)	25
	Predicted	19 (76%)	6 (24%)	25
3-8 weeks	Observed	5 (15%)	29 (85%)	34
	Predicted	19 (56%)	15 (44%)	34

Once predators have spotted a fawn out of hiding, the gazelle may drop down out of sight, adopting a prone position (Walther 1964, Lent 1974, FitzGibbon 1990c). While 23.0% of fawns ($n = 61$) dropped down when chased by Cheetahs, no cases of gazelles dropping down and adopting the prone response were recorded in 41 hunts of half-grown individuals and adolescents (FitzGibbon 1990c). The behaviour reduces the fawn's chance of being caught by Cheetahs, making it less visible and more difficult for the predator to locate. Only 50% of fawns that dropped down ($n = 14$) were caught by Cheetahs while 77% of fawns that ran away ($n = 47$) were killed. However, whether a fawn dropped down or not depended on the vigilance level of its mother (FitzGibbon 1990c). Fawns were less likely to drop down if their mothers did not detect an approaching predator until it was quite close; their chances of being found were then so great that it was better to flee, in an attempt to outrun the Cheetahs.

Timing of Births

Although there is a peak in the number of fawns born during the wet season, fawns continue to be born throughout the year (Bradley 1977). In contrast to follower species, swamping predators, by the majority of females giving birth within a short period of time, is less common in hider species (Rutberg 1987). Thomson's Gazelles in the Serengeti ecosystem are migratory, tending to spend the drier parts of the year in the woodlands to the north and west of the park, while concentrating on the short-grass plains to the south east during the wet season. Fawns born in the wet and dry seasons therefore experience very different conditions. While the nutritional advantages of giving birth during the wet season are obvious, could there be antipredator advantages that also make this period more favourable?

On the short-grass plains, the even distribution of food items and the short vegetation result in the formation of huge flocks of gazelles. In addition, the short vegetation makes vigilance more effective and provides less cover for stalking predators. As a result, predation risk is reduced. Predator densities may also be lower as a result of the low density of resident prey to support predators in the absence of migratory game. Fawns born during the wet season may therefore have a higher chance of survival than those born in the woodlands when groups are smaller and predators more difficult to spot. The antipredator advantages of breeding while out on the short-grass plains may therefore contribute to the peak in births during the wet season. However, females do give birth at other times of the year, perhaps because they lose fawns born at more optimal times or because they are able to give birth to more than one fawn each year.

Inspection Behaviour

When gazelle first encounter predators, their initial reaction is to cease foraging, to form a more compact group and in some cases to approach the predator (FitzGibbon 1994). This inspection (or fascination behaviour, Walther 1969) may continue for 20 minutes or more, with

part or all of the gazelle group following the predator, running towards it and then, when the predator gets too close, fleeing to the back of the group. Although the behaviour is common in both young and adult gazelles (Walther 1969), a higher proportion of young animals in a group will inspect than older ones. For example, once a group detected an approaching Cheetah, approximately 52% of males proceeded to inspect it, the rest returning to feed, while over 65% of young (subadults and adolescents) did so. In addition, younger gazelles followed the Cheetah for longer, before returning to feed. Inspection behaviour probably has a number of functions, but this difference between young and old in their tendency to inspect suggests that one function may be to gather information about the predator so that it can be easily recognised at a later stage (FitzGibbon in press).

Discussion

This chapter has outlined some of the causes and consequences of individual variation in the antipredator behaviour of Thomson's Gazelles. As far as possible the consequences have been measured directly in terms of differences in predation risk. Adult gazelles showed considerable variation in the extent of grouping either with conspecifics or with Grant's Gazelles, the positions they maintained in groups, vigilance levels in the absence of predators, and the incidence of stotting when fleeing from coursing predators. All these factors were also shown to influence their risk of predation. Immature gazelles, particularly fawns, differed markedly from adults in the antipredator strategies they adopted. Unable to outrun the majority of predators, they reduced their risk of being chased by spending much of their first few weeks hidden out of sight, and if they were chased, dropped down, adopting a low, prone position to try and avoid being refound. These strategies appeared to be effective at reducing the fawns' chances of being located by hunting predators.

Since avoiding predation is obviously so important, it is sometimes difficult to understand why individuals do not always adopt the most effective antipredator strategy. In order to do so, it is necessary to appreciate the full range of conflicting requirements that compete for an individual's time and energy, such as feeding, obtaining mates and caring for young. Differences in both predation risk (which depends on an individual's physical capabilities, its surroundings, and the type and number of predators around) and the relative importance of conflicting activities will determine an individual's level of antipredator behaviour in a particular situation. The latter was well illustrated by the comparison of antipredator behaviour and vulnerability to predation in male and female gazelles.

There were a variety of differences between males and females in their behaviour and ecology which predisposed males to predation, including differences in group size, vigilance and physical condition (FitzGibbon 1990b). The ultimate cause of these differences is the competition between males for females. 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. For male gazelles, the result of competing successfully is the acquisition and defence of territories (Walther 1978, Hvidberg-Hansen & de Vos 1971). However, having to defend these territories in the absence of females is extremely risky since males will be alone and this is probably the most important factor contributing to the high predation rate, at least by Cheetahs, on male gazelles. Thus male Thomson's Gazelles regularly find that they cannot reduce their risk of predation without concurrently reducing their probability of obtaining access to females.

Although a number of conflicting requirements, such as obtaining mates and caring for young, were considered in this study, it was not possible without known individuals, and thus more exact information on factors such as age, reproductive condition and social status, to invest-

igate these requirements in depth. This also meant that it was not possible to determine whether there were consistent differences between individuals in terms of the strategies they adopted. Such consistent differences have been observed, for example, in the level of inspection behaviour shown by Minnows (*Phoxinus phoxinus*) in response to a stalking Pike *Esox lucius* (Magurran 1986). Certain individuals appear to act selfishly, spending little time on inspection behaviour but benefiting from the information gathered by more diligent inspectors. It is hoped that future studies will focus on identifying individuals within the population, and reveal the more subtle differences in antipredator strategies between individuals.

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