

FitzGibbon CD. 1990. Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. *Animal Behaviour* 40(5):846-55.

Keywords: 1TZ/Acinonyx jubatus/anti-predator behavior/cheetah/fawn/Gazella thomsoni/mortality/predator/Serengeti/Thomson's gazelle

Abstract: The use of hiding and the prone response as anti-predator strategies by immature Thomson's gazelle, *Gazella thomsoni*, was investigated. Hiding, a behaviour restricted almost entirely to a decreased probability that infants would be found by cheetahs, *Acinonyx jubatus*, at a time when the ability to outrun predators was poor. The period of transition from hiding to active appeared to be a phase of high mortality; although no increase in the ability of fawns to outrun predators with age could be detected, older fawns still spent more time out of hiding, increasing the probability that they would be spotted by predators. Once chased, dropping down out of sight and adopting the prone response associated with a decreased probability of capture. Fawns that dropped down further from approach cheetahs were less likely to be found than those that dropped down when the predator was closer. Since fawns that dropped down had mothers that detected approaching predators further away and more vigilant mothers detected approaching cheetahs at greater distances, increased maternal vigilance had direct payoff in terms of increased infant survivorship.

# Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response

CLARE D. FITZGIBBON

Sub-department of Animal Behaviour, Madingley, Cambridge CB3 8AA, U.K.\*

**Abstract.** The use of hiding and the prone response as anti-predator strategies by immature Thomson's gazelles, *Gazella thomsoni*, was investigated. Hiding, a behaviour restricted almost entirely to fawns, decreased the probability that infants would be found by cheetahs, *Acinonyx jubatus*, at a time when the ability to outrun predators was poor. The period of transition from hiding to active appeared to be a time of high mortality; although no increase in the ability of fawns to outrun predators with age could be detected, older fawns still spent more time out of hiding, increasing the probability that they would be spotted by predators. Once chased, dropping down out of sight and adopting the prone response were associated with a decreased probability of capture. Fawns that dropped down further from approaching cheetahs were less likely to be found than those that dropped down when the predator was closer. Spotted fawns that dropped down had mothers that detected approaching predators further away and more vigilant mothers detected approaching cheetahs at greater distances, increased maternal vigilance had a direct payoff in terms of increased infant survivorship.

Ungulates are most vulnerable to predation during their first few weeks of life (Geist 1971; Lent 1974). Not only can they not run as fast or for so long as adults, but in addition they are vulnerable to a greater range of predators as a result of their smaller size. In wild ungulate populations, predation is frequently the major source of mortality for infants (Cook et al. 1971; Huegel et al. 1985; Smith 1986; Borner et al. 1987). The anti-predator strategies of ungulates can be broadly categorized into two groups, hiding and following (Walther 1965; Lent 1974; Leuthold 1977). In follower species, the young accompany the mother soon after birth whereas in hider species the young lie hidden at some distance from the mother for the first few days of life (see photograph in Gosling 1969). They rely mainly on cryptic coloration and minimal activity to avoid detection by predators. The mother and infant are in contact for only brief periods when the fawn suckles and the mother cleans it and ingests the faeces (Walther 1965, 1968). Thomson's gazelles, *Gazella thomsoni*, along with the majority of gazelles, the cervids and many antelopes are hidiers (Lent 1974; Ralls et al. 1986). In the majority of species hiding behaviour has begun to decline by the third week but there is much interspecific variation (Ralls et al. 1987).

Once predators have spotted fawns out of hiding the fawns may drop down out of sight, adopting the prone position which may make them less visible and more difficult for the predator to locate (Walther 1964; Lent 1974). This posture differs from the normal hiding position in that the head is kept low on the ground and the animal remains almost motionless. Although this tactic is common among hidiers, it is also found in several follower species (for example, caribou, *Rangifer tarandus*; Lent 1966). While both hiding and the prone response are generally considered to be effective anti-predator strategies, particularly for those species using forested habitat or for small species which can lie out of sight even in open habitats (Lent 1974; Estes & Estes 1979), their effectiveness in reducing infant predation has never been thoroughly investigated. Alternative hypotheses concerning the adaptive significance of hiding include protecting the young from intraspecific aggression (Lent 1974) or competition (Murdoch et al. 1983) and helping them to conserve energy and body water (Langman 1977).

Immature Thomson's gazelles in the Serengeti National Park, Tanzania are vulnerable to a wide range of predator species, including cheetahs, *Acinonyx jubatus*, lions, *Panthera leo*, wild dogs, *Lycaon pictus*, and spotted hyaenas, *Crocuta crocuta*. Schaller (1972) estimated that predators kill over 27 000 fawns per year. Since female

gazelles are rarely successful in actively deterring their young, except sometimes from jackals (Langman 1967), hiding and the prone response appear to be the main means of defence for infants (Walther 1969). My aims in this paper are to examine the effectiveness of the two behaviour patterns, hiding and the prone response, in reducing predation on immature Thomson's gazelles and to investigate how the use of the two behaviour patterns varies according to the age of the gazelle and its ability to outrun predators. I concentrated on predation by cheetahs, one of the most important predators of gazelles in the study area (Borner et al. 1987). Immature gazelles, in particular fawns, form a large part of the diet of these predators (Schaller 1968; FitzGibbon & Fanshawe 1989).

## METHODS

I carried out the study 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 102 hunts of immature Thomson's gazelles and 155 hunts of adult gazelles. Observations were made from a Landrover during daylight hours, using 10 x 50 binoculars, and were recorded onto tape for later transcription to data sheets.

I initially categorized immature Thomson's gazelles into three age classes, fawns (1-8 weeks), half-grown individuals (2-4 months) and adolescents (4-8 months), based on physical characteristics, in particular the gazelle's size relative to its mother (see Walther 1973a). In addition, I could sometimes distinguish three ages of fawns. The youngest fawns, aged between 1 and 2 weeks (called neonates by Walther 1973a) were very small and dark. The intermediate-aged fawns, thought to be between 3 and 4 weeks old, were small but had lost their dark coloration, while the oldest fawns, about 6-8 weeks old, almost reached the belly of their mother. If I could not distinguish the three classes of fawns, for example because I could not get close enough, I just described the infant as a fawn.

## Hunting Data

To calculate the success of cheetahs hunting Thomson's gazelles of different ages, I recorded the success of any hunts seen (abandoned or resulting in a kill) and the age of the gazelle chased (a hunt

trotted towards, or ran at a gazelle). I also noted whether the predator found fawns when they were hidden or active (out of hiding) and, if the fawns were active, whether or not they dropped down in response to the predator's approach and the distance from the predator at which this occurred. In addition, I calculated the vigilance level (the percentage of time spent scanning, defined as standing with head above shoulder level) of the mother before she detected the predator, from a continuous record of her scanning behaviour that lasted for at least 5 min prior to detection of the predator, but usually far longer. The distance from the predator at which the mother first detected it (as distinguished by the stare posture, Walther 1969) was also noted. I regularly checked estimated distances against known distances.

Towards the ends of chases, infants often 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 counting the number of zig-zags/sharp turns and estimating the predator-prey distance before and after a period of zig-zagging. I could then calculate the distance lost or gained by the cheetah. Distances were normally estimated to the nearest 10 m unless the distance was less than 20 m in which case I estimated it to the nearest 1 m.

## Time Budgets of Infants

Instantaneous sampling of focal animals (Altmann 1974) was used to sample the behaviour of infants of different ages. I chose a gazelle in the required age class from a group containing fewer than 11 gazelles and recorded its behaviour, categorized as feeding, vigilant (if the head was above shoulder height), walking or lying down, at 5-min intervals. I also recorded the distance of the infant from its mother every 5 min. Half-grown individuals and adolescents were watched for periods of 4 h and the watches were distributed over the day, giving approximately equal numbers of morning (0700-1100 hours), afternoon (1100-1500 hours) and evening (1500-1900 hours) watches. This removed any bias due to the time of sampling since behaviour patterns vary through the day (Walther 1973b). The system for fawn watches had to be different because mothers of fawns could be reliably identified only when the fawn was out of hiding, making them more difficult to find and, in

\*Present address: Large Animal Research Group, Department of Zoology, Downing Street, Cambridge CB2 3EJ, U.K.

**Table I.** The effect of fawn age on the percentage of time spent hiding, the mean duration of hiding period, percentage of time spent feeding on vegetation and the amount of time spent suckling

	Age of fawn			
	1-2 weeks	3-4 weeks	5-8 weeks	
% of time spent hiding	75.1 ± 7.2 (N=8)	61.4 ± 10.3 (N=8)	44.6 ± 5.4 (N=8)	ANOVA $F=6.03^*$
Mean duration of hiding periods (min)	135.6 ± 29.0 (N=8)	153.1 ± 55.2 (N=8)	32.5 ± 8.1 (N=8)	ANOVA $F=3.28$
% of time spent feeding on vegetation	5.3 ± 2.0 (N=8)	22.7 ± 10.3 (N=8)	32.3 ± 6.7 (N=8)	ANOVA $F=3.42$
Suckling time (s/h)	39.8 ± 9.6 (N=7)	21.2 ± 7.8 (N=5)	5.4 ± 5.0 (N=8)	Kruskal-Wallis $H=9.71^{**}$

\* $P < 0.05$ ; \*\* $P < 0.01$ .

In addition, data were required on the duration of lying out periods. I therefore started watches when I found a mother with a fawn out of hiding and continued recording when the fawn lay down, ending only when the fawn stood up for the next activity bout. In certain cases the fawns had very short lying out periods and if the watch lasted less than 1 h when the fawn got up for its next activity bout, I continued the watch until the fawn had been watched for a total of 4 h. The fawn watches were approximately equally distributed through the day. When fawns were out of hiding, I watched them continuously and recorded the total time (in s) spent suckling. These data could not be collected on all fawns because in some cases the mothers and fawns moved too far away for me to get a good view of the suckling behaviour. I kept disturbance of mothers and infants to a minimum by keeping the car 200-300 m away and by moving it as little as possible (in the majority of watches, the car was not moved at all).

Only individuals in groups of fewer than 11 gazelles were chosen since this reduced any differences in behaviour caused by variation in group size and, in addition, it proved difficult to keep track of both focal animals in large groups. Data on a total of 64 mother-infant pairs were collected, 24 with fawns, 19 with half-grown individuals and 21 with adolescents.

## RESULTS

### Hiding Behaviour

The percentage of time that fawns spent in hiding declined with age (Table I), and by the half-grown

stage, infants did not appear to spend any time in hiding, although they tended to spend more time lying down than adults ( $\bar{X} \pm SE = 35.7 \pm 5.5\%$  versus  $17.0 \pm 6.5\%$ ; matched pairs  $t$ -test,  $t = 2.00$ ,  $N = 12$ ,  $P = 0.06$ ). Unlike hiding, lying down did not appear to be an anti-predator strategy; individuals that lay down usually kept their heads up and rarely selected areas of high vegetation to lie in as hiding individuals did. In addition, individuals lying down stood up in preparation for flight if a predator approached, whereas fawns in hiding remained motionless.

The decrease in hiding with age resulted from a decline in the duration of lying out periods rather than an increase in the duration of activity bouts. Thus, there was no significant change in the duration of activity bouts with age ( $\bar{X} \pm SE = 28.1 \pm 4.1$  min,  $N = 24$ ;  $t = 0.98$ , NS), but the older fawns (5-8 weeks) stayed hidden for shorter periods than younger fawns (1-4 weeks,  $t = 3.21$ ,  $P < 0.05$ ; Table I). There was, however, no difference in the duration of lying out periods between the two youngest age classes (1-2 weeks versus 3-4 weeks,  $t = 0.26$ , NS). The younger fawns usually waited until their mothers approached them before getting up and trying to suckle while older fawns often left the hiding place and ran to the mother without her coming to collect them. As the fawns grew older and spent more time out of hiding, it also spent an increasing percentage of its time feeding on vegetation (Table I) while the time spent suckling per hour watched declined (Table I). On average, 8% of the fawn's time out of hiding was spent suckling while 56% was spent feeding on vegetation.

How long fawns spent out of hiding depended on the season; they spent a greater percentage of time

**Table II.** 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

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%)	25
	Predicted	19 (56%)	15 (44%)	34

$\chi^2 = 22.00$ ,  $df = 1$ ,  $P < 0.001$  for 1-2 weeks and  $\chi^2 = 23.42$ ,  $df = 1$ ,  $P < 0.001$  for 3-8 weeks; the two older fawn age classes were lumped for this comparison because of the small number of fawn hunts that were observed.

of hiding, controlling for the effect of age, in the wet season than in the wet season ( $\bar{X} \pm SE = 55.3 \pm 5.3\%$ ,  $N = 12$  versus  $22.9 \pm 4.7\%$ ,  $N = 12$ , ANOVA,  $F = 11.36$ ,  $df = 1$ ,  $P < 0.005$ ). This difference may have been related to the food supply since fawns spent a greater percentage of their time feeding on vegetation in the dry season than in the wet season; again controlling for the effect of age ( $\bar{X} \pm SE = 22.7 \pm 7.5\%$ ,  $N = 12$  versus  $5.5 \pm 2.7\%$ ,  $N = 12$ , ANOVA,  $F = 11.41$ ,  $df = 1$ ,  $P < 0.005$ ).

### Hiding as an Anti-predator Strategy

If hiding reduces predation on fawns, fewer fawns should be hunted by cheetahs than predicted from the percentage of time that fawns spend hidden. For example, 1-2 week fawns spend an average of 75% of their time in hiding. If hiding does not reduce the risk of predation, one would predict that 75% of the fawns hunted by cheetahs would be found when they were hidden. Although cheetahs killed a greater proportion of younger fawns (1-2 weeks) that were hidden than older ones (3-8 weeks, two older age classes were lumped due to small sample sizes;  $\chi^2 = 5.1$ ,  $df = 1$ ,  $P = 0.06$ ; Table II), at both ages fewer hidden fawns were hunted than expected from the percentage of time that the two age classes spent hidden (Table II). Thus, compared with remaining active, hiding was associated with a reduced probability of being hunted by cheetahs.

### The Prone Response

The incidence of the prone response declines with age and appears to have disappeared completely by the half-grown stage. 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. Instead of adopting the prone position, older gazelles responded to predators with flight and, considering fawns only, older fawns were more likely to respond to cheetahs by fleeing than younger ones (percentage of chased fawns using prone response: 1-2 weeks, 34.8%; 3-4 weeks, 45.8%; 5-8 weeks, 0%;  $\chi^2 = 10.55$ ,  $df = 2$ ,  $N = 57$ ,  $P < 0.005$ ).

Only 50% of fawns that dropped down ( $N = 14$ ) were caught by cheetahs while 77% of fawns that ran away ( $N = 47$ ) were killed. Therefore, compared with running away, dropping down was associated with a decreased probability of capture ( $\chi^2 = 4.10$ ,  $df = 1$ ,  $P < 0.05$ ). Cheetahs were more likely to find and kill fawns that dropped down close to them than those that dropped down further away (Mann-Whitney  $U$ -test,  $U = 6.0$ ,  $P < 0.05$ ). The distance at which fawns that were killed dropped down was  $81 \pm 28$  m ( $\bar{X} \pm SE$ ,  $N = 7$ ) and of those that escaped was  $138 \pm 23$  m ( $N = 5$ ).

Whether a fawn dropped down or not was influenced by the behaviour of its mother. Fawns that dropped down had mothers that detected predators further away ( $\bar{X} \pm SE = 126 \pm 29$  m,  $N = 12$ ) than those that fled ( $62 \pm 12$  m,  $N = 18$ ; Mann-Whitney  $U$ -test,  $z = -2.49$ ,  $P = 0.01$ , using only 1-4-week fawns since older fawns rarely drop down, see above). The distance at which a mother detects predators will depend on several factors such as the height of the surrounding vegetation, her group size (FitzGibbon 1988) and vigilance level. Mothers that remained vigilant all the time their fawns were out of hiding detected approaching cheetahs further away ( $\bar{X} \pm SE = 171.9 \pm 34.3$  m,  $N = 14$ ) than females that spent at least some of the time feeding ( $75.8 \pm 14.7$  m,  $N = 12$ ; Mann-Whitney

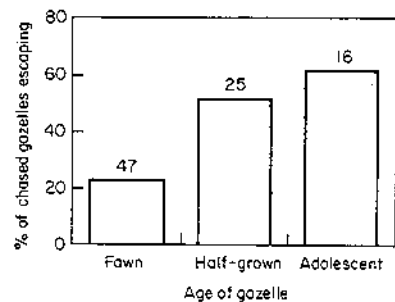


Figure 1. The effect of gazelle's age on the probability of escaping once chased by cheetahs ( $\chi^2 = 7.20$ ,  $df = 2$ ,  $P = 0.05$ ). Sample sizes are given above the bars.

*U*-test,  $U = 62.0$ ,  $P > 0.05$ ). Mothers remained far closer to their fawns when they were out of hiding ( $6.3 \pm 1.2$  m,  $N = 24$ ) than when the fawns were hidden ( $52.6 \pm 8.3$  m,  $N = 24$ ). Consequently they could quickly warn their offspring of approaching predators.

#### Speed and Agility

Across the three main age classes (fawn, half-grown individual and adolescent), the probability of an infant escaping capture (excluding fawns that dropped down) increased with age (Fig. 1). However, when the three age classes of fawn were considered, there was no effect of age on this variable (using only those cases in which the fawn was found already standing and did not drop down;  $\chi^2 = 0.33$ ,  $df = 2$ ,  $N = 47$ , NS). There must therefore be a dramatic improvement in escape ability during the half-grown stage, although it is also possible that all the 'poor runners' had been killed by predators by this stage. While the main factor influencing escape ability is likely to be the running speed of the infant, this could not be estimated accurately in the field. Nevertheless, improved agility might also be a contributory factor because gazelles often perform sharp turns and zig-zag movements at the end of chases when the cheetahs are very close. The total number of zig-zags and sharp turns performed during a chase did not vary between fawns, half-grown individuals/adolescents (combined due to low sample sizes) and adults (Fig. 2a). The average distance lost by the cheetahs during zig-zagging, however, increased with age (Fig. 2b). Since cheetahs lost less distance when the gazelles started the sharp turns/zig-zags further away (there was a significant negative correlation between the aver-

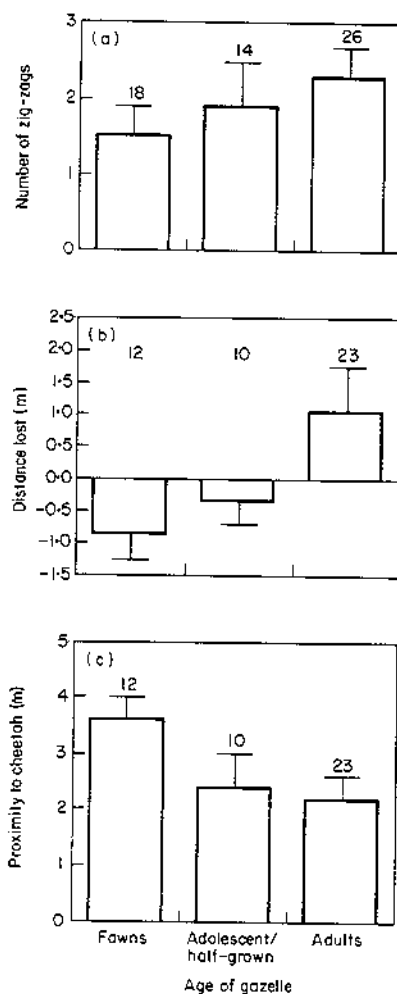


Figure 2. (a) Variation in the mean number of zig-zags performed by gazelles in three age categories (Kruskal-Wallis one-way ANOVA,  $H = 1.68$ ,  $N = 58$ , NS). (b) The effect of gazelle's age on the mean distance lost by cheetahs during zig-zagging of prey (Kruskal-Wallis one-way ANOVA,  $H = 9.80$ ,  $N = 58$ ,  $P < 0.005$ ). A positive value represents distance gained by the gazelle and a negative value represents distance gained by the cheetah. (c) The effect of gazelle's age on the mean distance from cheetahs at which gazelles start to zig-zag (Kruskal-Wallis one-way ANOVA,  $H = 2.83$ ,  $N = 45$ , NS). Sample sizes are given above the bars. Vertical lines indicate SE.

age distance lost by the cheetah during the period of zig-zagging and the distance that the gazelle started to zig-zag;  $r_s = -0.461$ ,  $N = 45$ ,  $P < 0.001$ ; Fig. 3).

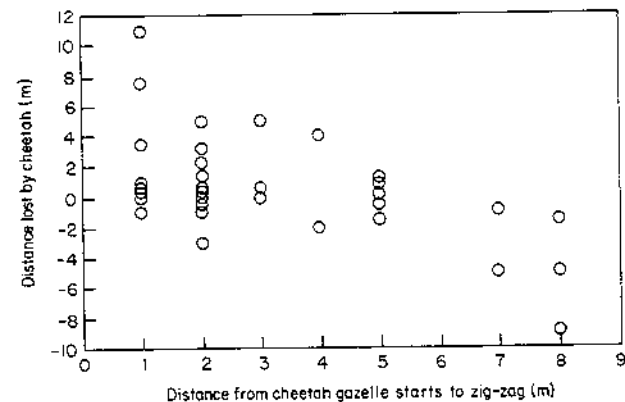


Figure 3. Distance lost by a cheetah during a period of zig-zagging plotted against the distance from the cheetah at which the gazelle first started to zig-zag ( $r_s = -0.461$ ,  $N = 45$ ,  $P < 0.001$ ).

this result could have been explained if younger animals started to zig-zag further away from cheetahs than older gazelles. However, no such tendency was found (Fig. 2c), suggesting that the gazelle's ability to turn sharply, and therefore cause the cheetah to overrun, increases with age.

## DISCUSSION

#### Hiding and the Prone Response as Anti-predator Behaviour

The success of cheetahs hunting Thomson's gazelles decreased as the age of the gazelle increased and this may explain why these predators selected immature gazelles in greater numbers than predicted on the basis of their numbers in the population, despite their smaller size (FitzGibbon & Fanshawe 1989). Much of the predation was concentrated on fawns and the main anti-predator strategy used by this age class was to hide. This was an effective means of passive defence, reducing the infant's probability of being found by cheetahs at a stage of development when its ability to outrun them was minimal. The effectiveness of the hider strategy in reducing predation depends, at least in part, on the mother's ability to reduce the amount of information she transmits to predators as to the position of her hidden fawn (Byers & Byers 1983) and Thomson's gazelle mothers succeed in keeping such information to a minimum (FitzGibbon 1988). If fawns are disturbed while hidden, they frequently run away stotting; this behaviour may

inform mothers that the fawns have been disturbed and are in need of defence (Caro 1986).

If a fawn was found by a cheetah while out of hiding, its principal means of defence was to drop down out of sight, adopting the prone position. This response appeared to reduce a fawn's chance of being caught by cheetahs, but it is also possible that fawns only dropped down in situations when their probability of survival was high, for example when there was lots of vegetation around to hide in. Predators had considerable difficulty in finding hidden fawns; cheetahs, hyaenas and jackals have all been observed to walk within 5 m of hidden fawns without detecting them (Walther 1969; Kruuk 1972; personal observation). The fawn's cryptic coloration and lack of scent, resulting from the inactivity of its scent glands (Gosling 1969; Walther 1969) and the ingestion of urine and faeces by the mother, which is typical of hider species (Gosling 1969; Lent 1974; Autenreith & Fichter 1975), will help to make the fawn difficult to find. In addition, fawns in the prone response have lower respiration and heart beat rates than fawns in the normal resting position (Jacobsen 1979).

Mothers whose fawns were out of hiding were far more vigilant than either adult females or mothers whose fawns were hidden (FitzGibbon 1988). This increased vigilance had a direct payoff, in terms of increased infant survivorship, because fawns that dropped down had more vigilant mothers that detected predators further away. Fawns were less likely to drop down if the predators were close, presumably because their chances of being found

were then so great that it was better to flee, in an attempt to outrun the cheetahs.

### Changes in Hiding with Age

In common with other hider species (for example, white-tailed deer, *Odocoileus virginianus*, Jackson et al. 1972), the proportion of time Thomson's gazelles spent in hiding declined gradually with age, and by the time they reached the half-grown stage at approximately 8 weeks of age, they had almost completely abandoned the hiding strategy. Walther (1968) considered that fawns were spending most of their time out of hiding by 6 weeks of age. The change from hiding to active was brought about by a decline in the duration of lying out periods rather than an increase in the duration of activity bouts (i.e. fawns got up more often as they got older rather than staying up for longer). Although it is typical in hider species for mothers to seek out fawns prior to nursing (Lent 1974; Autenreith & Fichter 1975), perhaps so that they can ensure that there are no predators nearby, older fawns may sometimes get up without their mothers approaching (also seen in white-tailed deer, Jackson et al. 1972 and fallow deer, *Dama dama*, Chapman & Chapman 1975). As a result, the fawns may be responsible for this decline in the duration of lying out periods. In other ungulate species (tsessebe, *Damaliscus lunatus*, Huntley 1972 and dorcas gazelle, *Gazella dorcas*, Baharav 1983, for example), the timing of the change from hiding to active varies between individuals. Two factors that are likely to influence the change are the infant's ability to outrun predators and its food supply.

### Ability to outrun predators

Since hiding reduces the probability of an infant being found by predators, the need for hiding declines as the gazelle's ability to outrun predators increases. We might, therefore, expect the decline in hiding to be linked to the gazelle's escape ability. However, Barrett (1978) considered that the period of transition from hiding to active was a time of high mortality for pronghorn fawns since they could not yet outrun predators but spent more time active so were more visible to predators. Similarly, the results of the present study showed that older Thomson's gazelle fawns were no more likely to

escape, once chased by cheetahs, than younger ones, but they still spent more time out of hiding and were therefore more likely to be found by cheetahs. These results suggest that the increase in the fawn's probability of being found and chased by predators, as it gets older and spends more time out of hiding, is not compensated for by an increase in its ability to escape once chased. A possible explanation is that, in order to develop the speed and agility and endurance required to escape predators, the fawn must exercise. As a result, reduced predation pressure by remaining hidden will conflict with developing the physical attributes needed to outrun predators that will be increasingly required as it spends more time out of hiding. Intense play bouts associated with the periods out of hiding (which took up approximately 8% of activity periods, also seen in Cuvier's gazelle, *Gazella cuvieri*, Gomendio 1988) may play an important role in this physical development (Byers 1977; Berger 1980). The need to exercise would explain why fawns spent more time out of hiding than was required to suckle and be cleaned by their mother, even though this increased their exposure to predators.

The period of transition from hiding to active may have been a period of increased vulnerability, but by the time fawns reached the half-grown stage, their ability to escape once chased was improved dramatically. Although increased running speed and stamina were probably the main factors contributing to this increase, greater agility may have been an additional factor. The cheetahs were able to follow the sharp turns of younger animals more closely than those of older animals and, as a result, the sharp turns of younger gazelles were less effective in gaining distance on the cheetahs. In a theoretical study, Howland (1974) showed that a gazelle could gain distance on a cheetah by executing a sharp turn if the gazelle was capable of (1) judging the distance of the predator with sufficient accuracy that it could execute the turn at the optimal time and (2) turning with a sufficiently small radius. Since the distance from the predator at which gazelles started to zigzag did not vary with age, it seems likely that younger gazelles were not as agile and could not turn as quickly as older ones. Howland (1974) also pointed out, however, that the cheetah's ability to follow the sharp turns of a gazelle depends on its running speed and it is possible that cheetahs were not running as fast when chasing younger gazelles, so were able to turn more quickly.

### Food supply

Although the time required for suckling is short, the mother's milk supply may be an important factor in determining the amount of time that a fawn spends out of hiding. Carl & Robbins (1988) noted that in mule deer, *Odocoileus hemionus*, fawns ingest smaller amounts of milk relative to conspecifics and frequently abandoned hiding to search for their mothers. In addition, if its milk intake is reduced, a fawn may have to spend more time feeding on vegetation to supplement its milk diet (Robbins & Owen 1975; Muller-Schwarze et al. 1982). This is possible in ungulates because forage intake is often initiated shortly after birth (Church et al. 1962; Nordan et al. 1970). Therefore, a decline in the amount of milk available to the fawn will increase the amount of time spent out of hiding. A decline is likely to occur with increasing age of the fawn (for examples, see Gauthier & Barrett 1985). In addition, several studies have shown that female ungulates reduce the quantity and/or the quality of milk they produce when their food supply is reduced (for example in domestic sheep, *Ovis aries*, Wallace 1948, domestic cows, *Bos primigenius*, Hafez & Lineweaver 1968; red deer, *Cervus elaphus*, Arman et al. 1974 and white-tailed deer, Vermeulen 1977). Such conditions of reduced food supply occur in the Serengeti in the dry season (when there is also a shortage of water, Sinclair 1982) and may explain why the fawns spent less time hiding and more time feeding on vegetation in the dry season than in the wet season. Since the infants are more vulnerable to cheetahs while they are active, fawns born in the dry season may experience greater predation rates than those born in the wet season.

### Changes in Prone Response with Age

The prone response appeared to have almost completely disappeared before the end of the hiding phase, although it has occasionally been observed in adults (Walther 1969; T. Caro, personal communication). The behaviour has been recorded to disappear as quickly as 24–48 h after birth in caribou (Lent 1966) but remains for approximately 14 days in dorcas gazelle (Walther 1968) and roe deer, *Capreolus capreolus* (Von Raesfeld 1957), similar to the Thomson's gazelle fawns seen in this study (although without fawns of known ages it is not possible to give exact ages). Kelly & Whately (1975) found a negative correlation between the

day of onset of the fleeing response and the birth weight of red deer fawns, suggesting that the timing of this change is adjusted to the physical development of the infant and its ability to outrun predators. However, in Thomson's gazelles, the prone response wanes long before there is a significant increase in escape ability (at the half-grown stage). Why this is so is unclear, but the prone response may become less effective as the fawn gets larger and loses its dark coloration.

### ACKNOWLEDGMENTS

I thank David Babu, Director of Tanzania National Parks, and Bernard Maregesi, Chief Warden, for allowing me to work in Serengeti National Park and Professor Karim Hirji, Hassan Nkya, and other members of the Serengeti Wildlife Research Institute for their assistance and support. The research was funded by a studentship from the Science and Engineering Research Council. I am very grateful to P. Bateson, T. Caro, J. Fanshawe, M. Gomendio, L. M. Gosling, H. Kruuk and an anonymous referee for their helpful comments on earlier drafts of the manuscript.

### REFERENCES

- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–265.
- Arman, P., Kay, R. N. B., Goodall, E. D. & Sharman, G. M. 1974. The composition and yield of milk from captive red deer (*Cervus elaphus*). *J. Reprod. Fert.*, **37**, 67–84.
- Autenreith, R. E. & Fichter, E. 1975. On the behaviour and socialisation of pronghorn fawns. *Wildl. Monogr.*, **42**, 1–111.
- Baharav, D. 1983. Reproductive strategies in female mountain and Dorcas gazelle *Gasella gazella* and *Gazella dorcas*. *J. Zool., Lond.*, **200**, 445–453.
- Barrett, M. W. 1978. Pronghorn fawn mortality in Alberta. *Proc. Biennial Pronghorn Antelope Workshop*, **8**, 429–444.
- Berger, J. 1980. The ecology, structure and functions of social play in bighorn sheep (*Ovis canadensis*). *J. Zool., Lond.*, **192**, 531–542.
- Borner, M., FitzGibbon, C. D., Borner, M., Caro, T. M., Lindsay, W. K., Collins, D. A. & Holt, M. E. 1987. The decline in the Serengeti Thomson's gazelle population. *Oecologia (Berl.)*, **73**, 32–40.
- Byers, J. A. 1977. Terrain preferences in the play behaviour of Siberian ibex kids (*Capra ibex sibirica*). *Z. Tierpsychol.*, **45**, 199–209.
- Byers, J. A. & Byers, K. Z. 1983. Do pronghorn mothers reveal the locations of their hidden fawns? *Behav. Ecol. Sociobiol.*, **13**, 147–156.

- Carl, G. R. & Robbins, C. T. 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Can. J. Zool.*, **66**, 239–246.
- Caro, T. M. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Anim. Behav.*, **34**, 663–684.
- Chapman, D. & Chapman, D. 1975. *Fallow Deer: their History, Distribution and Biology*. Lavenham, Suffolk; Terence Dalton.
- Church, D. C., Jessup, G. L. & Bogart, R. 1962. Stomach development in the suckling lamb. *Am. J. Vet. Res.*, **23**, 220–225.
- Cook, R., White, S., Trainer, D. O. & Glazener, W. C. 1971. Mortality of young white-tailed deer fawns in south Texas. *J. Wildl. Mgmt*, **35**, 47–56.
- Estes, R. D. & Estes, R. K. 1979. The birth and survival of wildebeest calves. *Z. Tierpsychol.*, **50**, 45–95.
- FitzGibbon, C. D. 1988. The antipredator behaviour of Thomson's gazelles. Ph.D. thesis, University of Cambridge.
- FitzGibbon, C. D. & Fanshawe, J. H. 1989. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *J. Zool., Lond.*, **218**, 99–107.
- Gauthier, D. & Barrett, C. 1985. Suckling and weaning in captive white-tailed and fallow deer. *Behaviour*, **94**, 128–149.
- Geist, V. 1971. *Mountain Sheep: a Study in Behavior and Evolution*. Chicago: University of Chicago Press.
- Gomendio, M. 1988. The development of different types of play in gazelles: implications for the nature and functions of play. *Anim. Behav.*, **36**, 825–836.
- Gosling, L. M. 1969. Parturition and related behaviour in Coke's hartebeest, *Alcephalus buselaphus cokei* Gunther. *J. Reprod. Fert. Suppl.*, **6**, 265–286.
- Hafez, E. S. E. & Lineweaver, J. A. 1968. Suckling behaviour in naturally and artificially fed neonate calves. *Z. Tierpsychol.*, **25**, 187–198.
- Howland, H. C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. theor. Biol.*, **47**, 333–350.
- Huegel, C. N., Dahlgren, R. B. & Gladfelter, H. L. 1985. Mortality of white-tailed deer fawns in south-central Iowa. *J. Wildl. Mgmt*, **49**, 377–380.
- Huntley, B. J. 1972. Observations on the Percy Fyfe Nature Reserve tsessebe population. *Ann. Transvaal. Mus.*, **27**, 225–239.
- Jackson, R. M., White, M. & Knowlton, F. F. 1972. Activity patterns of young white-tailed deer fawns in South Texas. *Ecology*, **53**, 262–270.
- Jacobsen, N. K. 1979. Alarm bradycardia in white-tailed deer fawns (*Odocoileus virginianus*). *J. Mammal.*, **60**, 343–349.
- Kelly, R. W. & Whately, R. 1975. Observations on the calving of red deer (*Cervus elaphus*) run in confined areas. *Appl. Anim. Ethol.*, **1**, 293–300.
- Kruuk, H. 1972. *The Spotted Hyena: a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.
- Langman, V. 1977. Cow-calf relationships in giraffe (*Giraffa camelopardalis giraffa*). *Z. Tierpsychol.*, **43**, 264–286.
- Lent, P. C. 1966. Calving and related social behaviour in the barren-ground caribou. *Z. Tierpsychol.*, **23**, 702–756.
- Lent, P. C. 1974. Mother-infant relationships in ungulates. In: *The Behaviour of Ungulates and its Relevance to Management* (Ed. by V. Geist & F. Walther), pp. 14–55. Morges, Switzerland: International Union for the Conservation of Nature and Natural Resources.
- Leuthold, W. 1977. *African Ungulates: a Comparative Review of their Ethology and Behavioral Ecology*. New York: Springer-Verlag.
- Muller-Schwarze, D., Stagge, D. & Muller-Schwarze, H. 1982. Play behavior: persistence, decrease and genetic compensation during food shortage in deer. *J. Science*, **215**, 85–87.
- Murdoch, G. K., Stine, W. W. & Maple, T. L. 1978. Observations of maternal-infant interactions in a captive herd of sable antelope (*Hippotragus niger*). *Biol.*, **2**, 215–224.
- Nordan, H. C. I., McCowan, T. & Wood, A. J. 1970. Feed intake and heat production of the young white-tailed deer (*Odocoileus hemionus columbianus*). *Can. Zool.*, **48**, 275–282.
- Ralls, K. B., Kranz, K. & Lundrigan, B. 1986. Mother-young relationships in captive ungulates: variability and clustering. *Anim. Behav.*, **34**, 134–145.
- Ralls, K. B., Kranz, K. & Lundrigan, B. 1987. Mother-young relationships in captive ungulates: behavioural changes over time. *Ethology*, **75**, 1–14.
- Robbins, C. T. & Moen, A. N. 1975. Milk composition and weight gain of white-tailed deer. *J. Wildl. Mgmt*, **39**, 355–360.
- Schaller, G. B. 1968. Hunting behaviour of the cheetah in the Serengeti National Park. *E. Afr. Wildl. J.*, **6**, 95–100.
- Schaller, G. B. 1972. *The Serengeti Lion: a Study of Predator-Prey Relationships*. Chicago: University of Chicago Press.
- Short, H. L. 1964. Postnatal stomach development in white-tailed deer. *J. Wildl. Mgmt*, **28**, 445–458.
- Sinclair, A. R. E. 1982. The Serengeti environment. In: *The Serengeti: Dynamics of an Ecosystem* (Ed. by A. R. E. Sinclair & M. Norton-Griffiths), pp. 31–45. Chicago: University of Chicago Press.
- Smith, C. A. 1986. Rates and causes of mortality in mountain goats in southeast Alaska. *J. Wildl. Mgmt*, **50**, 743–746.
- Verme, L. J. 1977. Assessment of natal mortality in upper Michigan deer. *J. Wildl. Mgmt*, **41**, 700–708.
- Von Raesfeld, F. 1957. *Das Rotwild*. Berlin: P. Parey Verlag.
- Wallace, L. R. 1948. The growth of lambs before and after birth in relation to the level of nutrition. *J. agric. Sci. Camb.*, **38**, 93–153.
- Walther, F. 1964. Einige Verhaltensbeobachtungen an Thomsongazellen (*Gazella thomsoni* Gunther 1884) im Ngorongoro-Krater. *Z. Tierpsychol.*, **22**, 167–208.
- Walther, F. 1965. Verhaltensstudien an der Grantsgazelle (*Gazella granti* Brocke, 1872) im Ngorongoro-Krater. *Z. Tierpsychol.*, **22**, 167–208.
- Walther, F. 1968. *Verhalten der Gazellen*. Wittenberg-Lutherstadt: A. Ziemsen Verlag.
- Walther, F. 1969. Flight and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, **34**, 184–221.
- Walther, F. R. 1973a. On age class recognition and individual identification of Thomson's gazelle in the field. *E. Afr. Wild. Mgmt. Ass.*, **2**, 9–15.
- Walther, F. R. 1973b. Round the clock activity of Thomson's gazelles (*Gazella thomsoni* Gunther 1884) in the Serengeti National Park. *Z. Tierpsychol.*, **32**, 105–110.
- Wyman, J. 1967. The jackals of the Serengeti. *Animals*, **10**, 79–83.

(Received 26 July 1989; initial acceptance  
16 October 1989; final acceptance 21 November 1989;  
MS. number: 3438)