CHAPTER 8

VIGILANCE BEHAVIOUR IN UNGULATES IN RESPONSE TO FELID REINTRODUCTION: THE ROLE OF PREDATION PRESSURE.

Vigilance behaviour in ungulates has been attributed to a number of different reasons. It is widely accepted that one of the principal functions is to increase the probability of predator detection. However, many ungulates live in social groups where they may need to co-ordinate their movements with companions and where interactions between individuals are mediated by complex visual signals (Leuthold, 1977; Prins, 1996). Furthermore, herbivores potentially find food by eye so the reasons for being alert may be more complex than solely looking for danger. Nonetheless, most studies on ungulates have assumed the risk of being preyed upon is the primary influence on vigilance behaviour and have investigated its role in the detection of predators. Intuitively, this seems reasonable and there is extensive empirical evidence that predation risk is one of the main reasons animals are alert (see review in Elgar, 1989) and that less vigilant animals are more vulnerable to predation (Fitzgibbon, 1990b). However, few studies have been able to directly examine the role of predation pressure where all other factors are controlled. Comparisons in the field, particularly in large mammals, are complicated by problems such as the difficulty in quantifying predation levels, ecological differences between field sites and the logistical difficulties in performing the necessary manipulations to control for sources of variation.

Berger and Cunningham (1988) compared vigilance in bison where their major predator the wolf was present and where it was absent. Search times did not differ between the two sites. However in the wolf-present site, predation pressure varied on a seasonal basis and as the authors stress, their data was collected during a period when wolf predation was not likely: hence predation pressure between the two sites at the time of their study probably did not differ. Scheel (1993) related vigilance to the risk of predation for eight species of African ungulates in the Serengeti and counter-intuitively, discovered that species experiencing the most predation pressure from lions exhibited the lowest vigilance. However, these species employed other anti-predatory behaviours such as active self-defence and the formation of extremely large herds. Those species which displayed no other anti-predatory behaviours were the most vigilant. The differences between species in their reliance on vigilance for other reasons was not explored. Underwood (1982) suggested that even when the likelihood of being preyed upon

is low, vigilance in ungulates nonetheless appears to be affected by the possibility of predation. In his study where the risk of predation was apparently very low, animals in thick cover looked more than in open habitats, central animals in the herd looked less than their companions and head-up behaviour was negatively correlated with group size, attributes one would expect in animals watching for predators. While there is clearly a fundamental link between predation and vigilance, the degree to which predation pressure versus other factors affects vigilance remains unclear. Differences in the degree to which vigilance is influenced by the interplay of predation pressure and other factors may become more apparent in a situation where comparisons can be made among populations where the level of predation is the only source of variation.

In this chapter, I report on the vigilance response of a naïve prey population to the introduction of their historical felid predators and compare that to a population where those predators were absent. I examined vigilance behaviour in impalas and wildebeest following the re-introduction of lions and cheetahs after at least four decades of absence (Rautenbach *et al*, 1980). I concurrently monitored vigilance in these ungulates in an adjacent site where cats had not been released.

I postulated that:

1. The increase in predation pressure as a result of the re-introduction of lions and cheetahs would be reflected in increased vigilance, and

2. Vigilance should show an increase over time in the months immediately following an increase in predation pressure (i.e. following the re-introduction of lions and cheetahs).

I also examined the relationship of the following factors to vigilance behaviour where re-introduced cats were present and where they were absent:

    i: group size

    ii: location in herd.

    iii: presence of juveniles.

Many studies have reported a negative correlation between group size and levels of individual vigilance, widely attributed to the anti-predatory benefits of living in groups (see review by Elgar, 1989). Central to this hypothesis is the "many eyes" effect which suggests that as group size increases in socially foraging animals, there are more eyes watching for predators which increases the likelihood of their detection. Individuals can, therefore, devote more time to foraging without increasing their personal risk of being preyed upon (Lima, 1995). If this is the case, the relationship may be less compelling where predation is not a strong factor. Here I compare the relationship of group size to vigilance where lions and cheetahs were present and where they were absent. Position in the group also has an influence on vigilance in socially foraging species. Numerous studies on African ungulates (Underwood,

1982; Prins & Iason, 1989; Bednekoff & Ritter, 1994; Burger & Gochfield, 1994) have demonstrated that animals on the edge of herds devoted more time to vigilance than individuals in central locations, presumably because they were more exposed to attack. If predation is non-existent or at very low levels, one would expect that location in the group becomes less of an influencing factor in vigilance behaviour. Similarly, mothers with juveniles are generally more alert than females without young (Burger & Gochfield, 1994), presumably because juveniles are exposed to greater levels of predation as a result of predator naïveté, reduced ability to escape an attack and vulnerability to a greater variety of predators due to their small size. If risk of predation is low, the disparity between mothers' vigilance and that of females without young should be reduced. To assess these questions, I compared the effect of position in the herd and the presence of juveniles on vigilance where re-introduced cats were present and where they were absent.

METHODS.

This study was carried out between August and December, 1992. During that time, an internal fence divided Phinda into two approximately-equal sized halves and release of lions and cheetahs was restricted to the northern half of the reserve (refer Fig. 2, Chapter 2). Leopards, spotted hyaenas and smaller carnivores such as jackals *Canis mesomelas* and *C. adustas,* were present throughout the reserve, though at very low densities as a result of heavy persecution prior to the establishment of Phinda. I assumed that the presence of re-introduced cats in one half of the reserve gave rise to an increase in predation pressure and have termed that condition "high predation pressure". I refer to "low predation pressure" where re-introduced cats were absent.

Impala and wildebeest herds were located by and observed from a 4WD vehicle. Animals at Phinda are continually exposed to vehicles and mostly ignore them. Nonetheless, in an effort to eliminate any vehicle effect, herds were allowed to 'settle down' for a minimum of 5 min before beginning observations and my vehicle was the only one present during observations in case a build-up of cars stimulated increased interest from ungulates. Observations were usually conducted at distances greater than 70m.

Data was recorded within 3h of sunrise or within 3h before sunset, periods in which predators were typically active and ungulates were alert. In the high predation treatment, all observations were made in areas known to be used by re-introduced cats (which were radio-monitored) but at times when they were not closer than 1000m to observed herds. Observations were restricted to open grassland (maximum grass height 60cm) to eliminate variations due to cover and observed herds were monospecific to eliminate variation

resulting from the presence of heterospecifics. Herds were observed for 906 sessions lasting 5min each (a total of 75.5 h: Table 36). During each session, a focal animal was defined as vigilant when it lifted its head away from the ground and paid attention to its surroundings, indicated by the head held high, either with or without a scan of its environment (Walther, 1969). All animals were standing when observed and were usually stationary: I did not score the 'nodding head' posture of walking ungulates as vigilance. I did not attempt to discriminate between possible levels of vigilance (eg 'active' versus 'weak', see Alados, 1985) or if vigilance was directed to specific objects (see LaGory, 1986). Finally, although ungulates may display subtle postural differences between looking for predators and looking for other reasons (eg decision-making concerning movement between foraging patches in buffalo; Prins 1996), I did not attempt to define these differences in impala and wildebeest. I assumed animals in both levels of predation were potentially using the alert head-up posture to gather information on all possible factors. The number of times an animal looked and the duration of each look was timed for each session. Other data recorded for each focal animal included sex, position in herd (front, side, centre, rear), herd size, and parenthood (adult with or without juvenile).

Species	Predation	Total	Aug	Sept	Oct	Nov	Dec
Impala	High	223	43	43	45	55	37
	Low	214	43	46	36	47	42
Wildebeest	High	226	42	40	41	52	51
	Low	243	48	47	51	50	47

Table 36. Number of observation sessions conducted per month on herbivore vigilance.

Data were not normally distributed and transformations did not achieve normality, primarily because in many sessions the subject did not look at all, hence the zero class for vigilance parameters was the mode for some months. Accordingly, non-parametric analyses were employed. Differences as a function of predation conditions, and position in herd were examined with a Wilcoxon Rank Sum test. The effect of sex and the presence of juveniles was examined with a Kruskal-Wallis one way ANOVA which calculates a Z-statistic to determine where differences lie. Differences in vigilance behaviour over time under different predation conditions were analysed with a Kruskal-Wallis H-test. Spearman correlation coefficients were used to examine the relationship between herd size and vigilance behaviour.
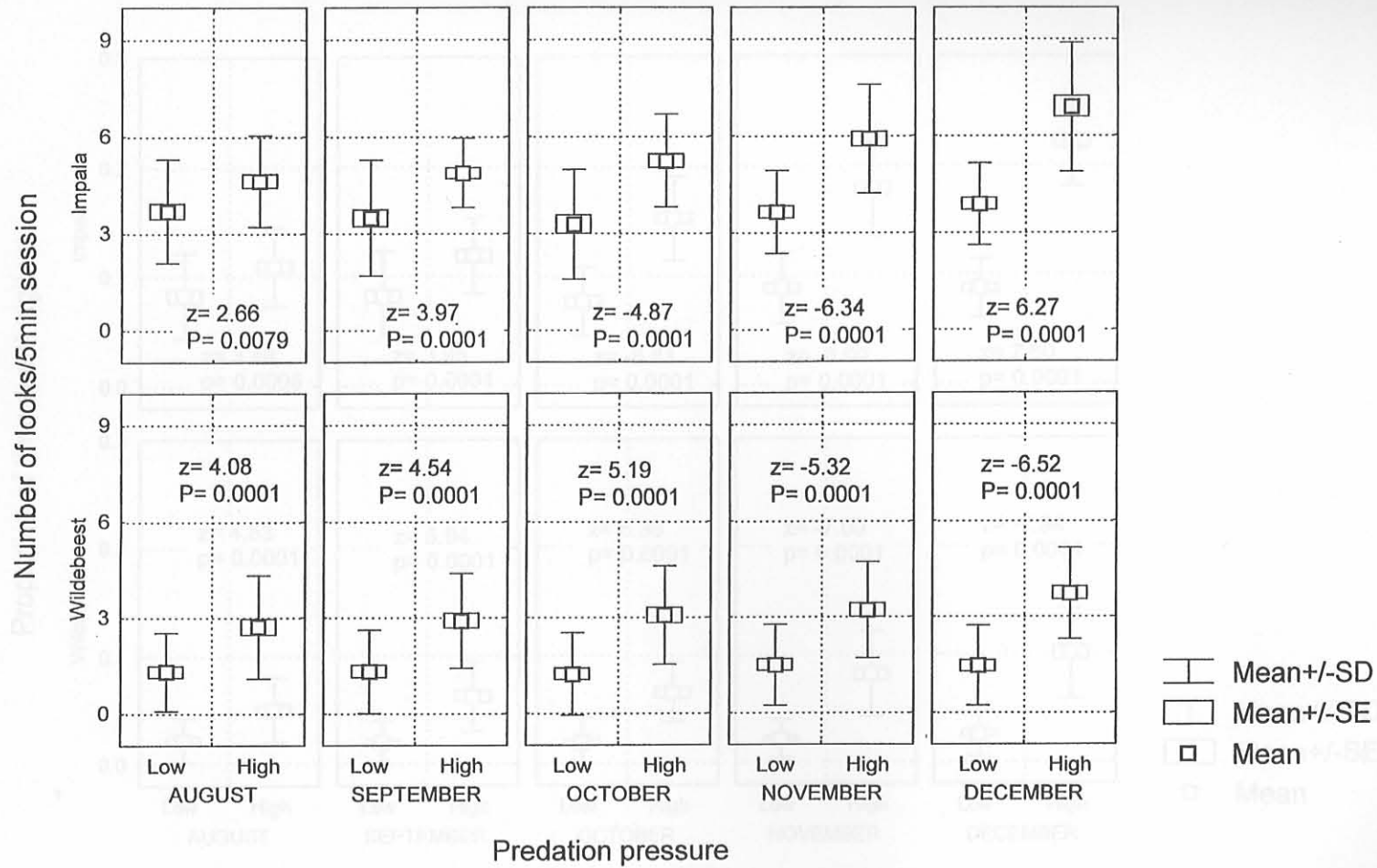
RESULTS.

I examined two aspects of vigilance behaviour: the rate of looking and the proportion of time spent looking. Most previous studies of mammal vigilance have used only one measurement, usually the latter as this is the most meaningful when examining the trade-off between time devoted to watching and foraging (Elgar, 1989). However, this eliminates the possibility that ungulates employ different search strategies under different predation conditions: for example, animals exposed to greater predation may look more often but may "compensate" by reducing the duration of each look. This combination may be not be apparent if only the proportion of time spent vigilant is examined.

Predation Pressure.

The rate of looking where predation was high was significantly greater than under low predation for all months of the study period in both impalas and wildebeest (Fig. 59). For impalas, a significant increase in rate of looking occurred over time under high predation pressure (H = 38.45, p=0.0000, df =4) and not under low predation pressure (H = 3.65, p=0.3.65, df =4). Although this pattern was evident in wildebeest (Fig. 59), it was not significant at p ≤ 0.05 (high predation: H = 8.82, p=0.0657, df =4. Low predation: H = 1.92, p=0.7501, df =4.)

The proportion of time spent vigilant by both species was also significantly greater under high predation for all months (Figure 60). For impalas, as in their rate of looking, the time spent vigilant increased over time under high predation (H = 115.75, p=0.0000, df =4) and not under low predation (H = 3.68, p=0.4507, df =4). Impalas under high predation spent a mean of 10.9% of their time vigilant in August which had increased to 22.1% by December, a growth of 203%. In low predation, impalas spent 8.3% of their time vigilant in August which differed little from the figure for December (8.8%). Wildebeest displayed a similar pattern, which, in contrast to the result for their rate of looking, was highly significant (high predation, H = 46.15, p=0.0000, df =4; low predation, H = 3.76, p=0.4389, df =4). August low predation vigilance was 2.1% of their time compared to 5% for high predation. Proportion of time spent vigilant in December in low predation was 2.5% compared to 10.1% in high predation.

Figure 59. Rate of looking by impala and wildebeest in low and high predation conditions. Z-statistic is result of Wilcoxon 2-sample comparison between predation conditions within months.
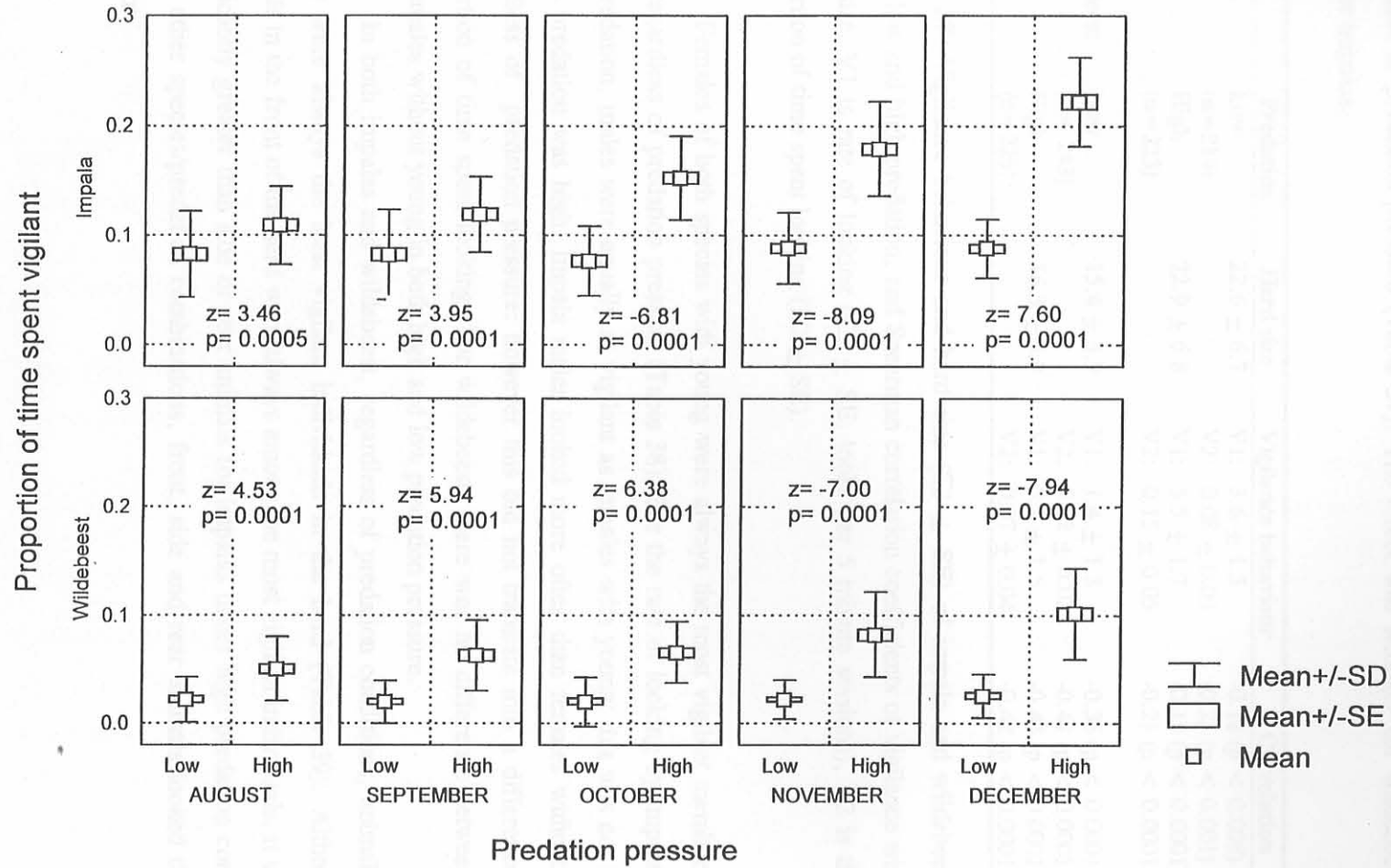
Figure 60. Proportion of time spent looking by impala and wildebeest in low and high predation conditions. Z-statistic is result of Wilcoxon 2-sample comparison between predation conditions within months.

Herd size, location in herd, and the presence of juveniles:

Mean herd size did not differ between high and low predation for impalas (see Table 37, $\chi^2 = 0.04356$, p=0.8347, df =1) however it was consistently higher in wildebeest under high predation (Table 37, $\chi^2 = 5.9885$, p=0.0144, df =1). Both species showed a negative correlation between vigilance behaviour and group size, regardless of predation pressure (Table 37). The effect was stronger for wildebeest than for impalas.

	Predation	Herd size	Vigilance behaviour		Correlation
Impala	Low	22.6 ± 6.7	V1:	3.6 ± 1.5	-0.18 (p < 0.008)
	(n=214)		V2:	0.08 ± 0.03	-0.23 (p < 0.001)
	High	22.9 ± 6.8	V1:	5.5 ± 1.7	-0.18 (p < 0.0001)
	(n=223)		V2:	0.15 ± 0.05	-0.21 (p < 0.0001)
Wildebeest	Low	15.4 ± 3.9	V1:	1.4 ± 1.3	-0.35 (p < 0.0001)
	(n= 243)		V2:	0.02 ± 0.02	-0.41 (p < 0.0001)
	High	16.3 ± 3.9	V1:	3.2 ± 1.5	-0.43 (p < 0.0001)
	(n=226)		V2:	0.07 ± 0.04	-0.42 (p < 0.0001)

Table 37: Vigilance behaviour and herd size ($\square$ ± SE) of impala and wildebeest under low and high predation, and Spearman correlation coefficients of vigilance with herd size. V1 is rate of looking ($\square$ ± SE, looks per 5 minute sessions), V2 is the proportion of time spent looking ($\square$ ± SE).

Females of both species with young were always the most vigilant members of the herd regardless of predation pressure (Table 38). For the rate of looking by impalas under low predation, males were equally as vigilant as females with young: this was not the case where predation was high. Impala males looked more often than females without young, regardless of predation pressure: however this did not translate into a difference in the proportion of time spent looking. For wildebeest, there was no difference between males and females without young in both high and low predation pressure.

In both impalas and wildebeest, regardless of predation conditions, animals in the centre were always the least vigilant individuals in the herd (Table 39). Although the animals in the front of the herd were always among the most vigilant individuals, it was only significantly greater than side or rear animals for impalas under high predation conditions. In all other species/predation combinations, front, side and rear animals looked the same amount.

		Male	Female	Mother	Most vigilant to least vigilant and Kruskal-Wallis test results.
Impala					
Low predation	V1	3.8 ± 1.5 (102)	3.2 ± 1.7 (82)	4.2 ± 0.96 (30)	mothers = males > females: 13.23 (p= 0.0013)
	V2	0.08 ± 0.03	0.08 ± 0.03	0.11 ± 0.03	mothers > males = females: 15.33 (p=0.0005)
High predation	V1	5.6 ± 1.7 (103)	4.9 ± 1.4 (82)	6.7 ± 1.7 (38)	mothers > males > females: 27.96 (p=0.0000)
	V2	0.15 ± 0.05	0.14 ± 0.04	0.2 ± 0.05	mothers > males = females: 37.16 (p=0.0000)
Wildebeest					
Low predation	V1	1.2 ± 1.2 (118)	1.3 ± 1.2 (94)	2.2 ± 1.3 (31)	mothers > males = females: 14.03 (p=0.0009)
	V2	0.02 ± 0.02	0.02 ± 0.02	0.03 ± 0.02	mothers > males = females: 14.16 (p=0.0008)
High predation	V1	2.9 ± 1.4 (98)	3.0 ± 1.6 (80)	4.0 ± 1.5 (48)	mothers > males = females: 14.28 (p=0.0008)
	V2	0.07 ± 0.03	0.06 ± 0.03	0.1 ± 0.04	mothers > males = females: 29.66 (p=0.0000)

Table 38: Vigilance behaviour as function of sex and parenthood for impala and wildebeest under low and high predation.

V1 is rate of looking ($\square$ ± SE, looks per 5 minute sessions), V2 is the proportion of time spent looking ($\square$ ± SE). Number of observations in parentheses. The Kruskal-Wallis result indicates that a significant difference existed when all combinations of males, females and mothers were compared. For the sake of brevity I used symbols (<, =, >) to illustrate where the significant differences existed (at P = 0.05) in subsequent analyses of sex pairs.

		Front	Centre	Side	Rear	Z-statistic (p)
Impala						
Low predation	V1	4.0 ±1.6 (49)	2.7 ± 1.4 (59)	3.8 ± 1.4 (56)	4.0 ± 1.3 (50)	25.54 (0.0000)
	V2	0.09 ± 0.03	0.07 ± 0.03	0.09 ± 0.03	0.09 ± 0.04	18.75 (0.003)
High predation	V1	6.5 ± 2.0 (50)	4.5 ± 1.5 (49)	5.4 ± 1.3 (64)	5.5 ± 1.6 (60)	29.30 (0.0000)
	V2	0.17 ± 0.06	0.14 ± 0.05	0.16 ± 0.05	0.15 ± 0.05	8.25 (0.04)
Wildebeest						
Low predation	V1	1.7 ± 1.3 (48)	0.84 ± 1.14 (57)	1.6 ± 1.2 (77)	1.4 ± 1.3 (61)	15.87 (0.001)
	V2	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.02	14.82 (0.002)
High predation	V1	3.7 ± 1.4 (57)	1.9 ± 1.2 (58)	3.6 ± 1.3 (59)	3.5 ± 1.5 (52)	54.60 (0.0000
	V2	0.08 ± 0.04	0.05 ± 0.03	0.08 ± 0.04	0.07 ± 0.03	39.98 (0.0000)

Table 39. Vigilance behaviour as a function of location in herd for impala and wildebeest under low and high predation.

V1 is rate of looking ($\Box \pm$ SE, looks per 5 minute sessions), V2 is the proportion of time spent looking ($\Box \pm$ SE). Number of observations in parentheses.

To ensure that location effects were not the result of separation of sexes in different locations, I further examined the vigilance behaviour of males, females and mothers in the four different locations within the herd (Table 40). All adults occurred in all locations and centre animals were always the least vigilant. Mothers were always the most vigilant individuals regardless of all other factors.

			Front	Centre	Side	Rear
Impala						
Low Predation	male	V1	4.0 ± 1.7 (32)	3.1 ± 1.3(25)	3.8 ± 1.5 (22)	4.13 ± 1.4 (23)
		V2	0.09 ± 0.03	0.07 ± 0.03	0.09 ± 0.04	0.09 ± 0.04
	female	V1	4.2 ± 1.9 (12)	2.1 ± 1.4 (26)	3.5 ± 1.5 (24)	3.75 ± 1.3 (20)
		V2	0.09 ± 0.02	0.05 ± 0.03	0.08 ± 0.03	0.09 ± 0.02
	mother	V1	4.2 ± 0.83 (5)	3.8 ± 0.9 (8)	4.5 ± 1.1 (10)	4.3 ± 0.95 (7)
		V2	0.11 ± 0.02	0.10 ± 0.02	0.11 ± 0.03	0.10 ± 0.02
High Predation	male	V1	6.5 ± 2.0 (20)	4.4 ± 1.5 (17)	5.2 ± 1.2 (29)	5.7 ± 1.4 (29)
		V2	0.16 ± 0.03	0.12 ± 0.05	0.15 ± 0.05	0.16 ± 0.05
	female	V1	5.6 ± 1.4 (15)	3.9 ± 1.2 (19)	5.2 ± 1.3 (25)	4.7 ± 1.4 (23)
		V2	0.16 ± 0.04	0.12 ± 0.03	0.15 ± 0.04	0.13 ± 0.04
	mother	V1	8.4 ± 2.1 (7)	5.6 ± 1.3 (13)	6.6 ± 1.2 (10)	7.1 ± 1.2 (8)
		V2	0.23 ± 0.05	0.18 ± 0.04	0.21 ± 0.05	0.21 ± 0.3
Wildebeest						
Low Predation	male	V1	1.6 ± 1.4 (20)	0.5 ± 0.8 (25)	1.4 ± 1.0 (35)	1.3 ± 1.3 (38)
		V2	0.03 ± 0.03	0.008 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
	female	V1	1.5 ± 1.4 (23)	0.7 ± 0.9 (19)	1.5 ± 1.3 (32)	1.4 ± 1.2 (20)
		V2	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.02
	mother	V1	2.8 ± 0.4 (5)	1.7 ± 1.5 (13)	2.5 ± 0.8 (10)	2.0 ± 1.7 (3)
		V2	0.04 ± 0.008	0.02 ± 0.02	0.04 ± 0.009	0.02 ± 0.02
High Predation	male	V1	3.3 ± 1.2 (26)	1.9 ± 1.1 (21)	3.2 ± 1.3 (26)	3.0 ± 1.6 (25)
		V2	0.08 ± 0.03	0.04 ± 0.03	0.08 ± 0.03	0.07 ± 0.03
	female	V1	3.7 ± 1.3 (18)	1.4 ± 1.3 (23)	3.7 ± 1.03 (20)	3.6 ± 1.1 (19)
		V2	0.08 ± 0.03	0.03 ± 0.03	0.08 ± 0.02	0.07 ± 0.03
	mother	V1	4.5 ± 1.5 (13)	2.8 ± 1.05 (14)	4.3 ± 1.5 (13)	4.5 ± 1.4 (8)
		V2	0.12 ± 0.05	0.07 ± 0.03	0.11 ± 0.05	0.11 ± 0.04

Table 40. Vigilance behaviour as a function of location in herd for sex/parenthood classes for impala and wildebeest under low and high predation. V1 is rate of looking (☐ ± SE, looks per 5 minute sessions), V2 is the proportion of time spent looking (☐ ± SE). Number of obervations in parentheses.

DISCUSSION

The main finding of this study is the clear increase in both the rate of looking and the proportion of time spent looking by impalas and wildebeest exposed to increased levels of predation. Many predictions about vigilance theory have been tested by measuring changes in vigilance in response to changes in factors that should affect predation risk. An increase in vigilance behaviour has been demonstrated in some bird species following exposure to a simulated predator or threat (Powell, 1974; Gluck, 1987; Lima and Zollner, 1996), alarm calls (Lazarus, 1979), and in closed habitats versus open (Repasky, 1996). Similarly, pronghorn antelope were more vigilant when exposed to human induced disturbances than undisturbed animals (Berger *et al,,* 1983). In the present research, the proportion of time spent looking by both species exposed to high predation underwent an increase of over 200% in the five month study period. This suggests that as almost universally assumed, the risk of being preyed upon is the principal reason ungulates are vigilant. The fact that vigilance remained at very low levels in ungulates exposed to low predation conditions suggests that the relationship between vigilance and other factors such as intraspecific interactions or finding food, is weak in these species. At Phinda, impalas in the low predation treatment looked for around 8% of their time: for wildebeest, the mean figure was just over 2%. This is comparable to the time animals spent vigilant in Underwood's (1982) study where most of their major predators were absent. Individuals apparently freed of high predation pressure appear to also be freed of most of the need for vigilance.

Having said this, I believe that the possibility of predation, however low, contributed to the maintenance of vigilance behaviour in animals under low predation pressure. Contrary to our expectations, I found that many of the patterns of vigilance behaviour evident amongst ungulates exposed to low predation pressure did not substantially alter when predation pressure was increased. The negative correlation between vigilance and group size for both predation conditions suggests that even when predation pressure is very low, the anti-predation benefits of grouping may still be realised. Underwood (1982) found a similar pattern amongst four species of African ungulates (including wildebeest) in low predation conditions, though interestingly, impalas displayed a positive correlation between vigilance and group size. He suggested that under low predation conditions, impalas used scanning to promote group cohesion rather than as an anti-predatory measure. My data do not indicate this and other evidence suggests that even at low levels, predation risk is a strong factor in maintaining vigilance. For example, animals in the centre of the herd were always the least vigilant, and front, side and rear animals generally looked the same amount regardless of predation pressure. Similarly, female ungulates with young were the most vigilant individuals in the herd in both predation conditions. If

animals were looking for social or feeding reasons, one would expect this to become more evident where risk of attack is low. Increased predation appears to result in a concomitant increase amongst vigilance in all individuals, hence the patterns of the behaviour remained the same in both low and high predation.

I intentionally avoided discriminating between different levels or types of vigilance. LaGory (1986) differentiated between vigilance apparently directed towards conspecifics and towards the observer in white-tailed deer and found that deer spent a mean of between 1.0% to 2.3% of their time alert to other deer, depending on the availability of cover. While this is revealing, animals may be gathering information about different factors not immediately apparent to the observer. Alados (1985) considered two levels of vigilance in Spanish Ibex: actively searching the surroundings and "weak" watching in which animals had raised heads but were not looking around. Active watching, but not weak watching, was negatively correlated with group size and Alados suggested the latter is not related to predator detection. However, animals engaged in weak watching are almost certainly gathering information from their conspecifics about the threat of predation. I suggest that the vigilance behaviour displayed by animals under the low predation conditions at Phinda represented a maximum in terms of time they devoted to the behaviour, regardless of its focus. Even if one disregards the evidence that predation pressure was contributory, animals in this study are clearly devoting very little time to being alert where predation is minimal. It must be noted that my observations took place during periods of relatively low social activity. Heightened social interaction such as occurs during the mating season increases vigilance behaviour (Leuthold, 1977, Alados, 1985). In the study region, the rut in impalas occurs between March and June (Vincent, 1972), and peaks in April and August in wildebeest (Attwell, 1977), periods prior to the study. Accordingly, the levels of vigilance specified here should not be assumed to apply for months outside the study period.

The maximum time animals devoted to vigilance when exposed to increased predation was comparable to other studies (cf Fitzgibbon, 1990a; Bedneokff & Ritter, 1994; Burger & Gochfield, 1994). At Phinda, under high predation, the mean time spent vigilant peaked in December at 22.1% for impalas and 10.1% for wildebeest. Presumably, ungulates reach a threshold in the amount of time they spend vigilant as predation pressure increases. While this may ultimately have increased beyond the peaks observed in the final month of the study, the current research was too short in duration to establish a maximum with any certainty. The observed increase over time in vigilance is probably due to numerous factors. Individual predation risk probably increased over time as re-introduced cats began making an impact on prey herds. While this was a minor effect at the population level during the study period for most species (Hunter, unpubl. data: but compare for wildebeest and reedbuck; Chapter 7), the

effect on each herd may have been accumulative given that group sizes were small and so removal by predation of even a few animals would increase substantially the risk to remaining herd members. Additionally, the increase may simply have been due to increased awareness of predation over time. While all my observations took place in areas known to be used by re-introduced cats, individual herds sometimes experienced long periods between "bouts" of predation as lions and cheetahs dispersed and established home-ranges following re-introduction. Qualitatively, I felt that individual ungulates did not immediately assume and maintain a certain level of vigilance following their first experience with re-introduced cats. Naïve prey populations probably require some repeated exposure to predation before individuals "realise" the risk of attack is ongoing. Nonetheless, it is interesting that vigilance behaviour seemed to increase rapidly following release of cats. At the inception of this study, individuals in the high predation treatment had been exposed to increased pressure from cheetahs for only five months and from lions for three months (cheetahs being more important predators on impala than wildebeest and vice-versa for lions, Chapter 6). Unfortunately I have no data on the period immediately following release but by August, high predation ungulates were already more vigilant (Fig.s 59 & 60).

Ungulates may reduce the chance of being preyed upon in other ways. Scheel (1993) suggests that wildebeest show a tendency to develop large aggregations as a defence against predation (the dilution effect, see Dehn, 1990). Similarly, Berger et al (1983) found a strong effect on grouping in pronghorn antelope which, when exposed to human-induced disturbance, formed increased group sizes. In the present study, wildebeest showed larger group sizes when exposed to high predation whereas impalas did not (Table 37). While a consistent pattern suggesting this emerged from our data, this should be treated with caution. Actual group size in wildebeest in the high predation site was a mean of only 0.9 animals greater than low predation herds and the increase may be a statistical artefact. Herd size in the present study was low compared to other studies (de Boer & Prins, 1990; Scheel, 1993; Table 37), a characteristic of wildebeest populations in the region (Attwell, 1977) and a constant small difference may return a significant result. Although this was consistently the case for all months, it is premature to conclude that a definite anti-predatory response in grouping behaviour was occurring. The opportunity to explore this and other details of anti-predatory behaviour under changing predation conditions exists increasingly in South Africa where re-introduction programs of predators are flourishing in response to increased eco-tourism. It will be intriguing to assess the response of prey populations to these manipulations as field experiments proliferate.