Watching for lions in the grass: the usefulness of scanning and its effects during hunts

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Abstract. Scan rates of eight species of common ungulate prey of the African lion, *Panthera leo*, were measured in Serengeti National Park, Tanzania, to examine the effect of predation risk on vigilance. Vigilance was measured both during lion hunts and when lions were not present. Risk of predation was expected to vary with herd size, prey species and density, available light and cover, predator presence and predator activity. Risk was expected to decline in large herds due to dilution. Over all prey species, vigilance declined with increasing group size for three measures of herd size: (1) total herd size, (2) numbers of conspecifics and (3) number of heterospecifics in a herd. Species that were at high predation risk (measured as hunts recorded per herd seen) had low vigilance. Risk was expected to be high near dense cover and when predators were most active. Wildebeests, *Connochaetes taurinus*, and zebras, *Equus burchelli*, scanned more when lions were most active. However, wart hogs, *Phacocheroerus aithiopicus*, and wildebeests scanned less where more cover was available for lions. These results suggest that scan rates vary not only with predation risk, but also with the utility of scanning. Lions did not appear to adjust their stalking behaviour according to the vigilance of the prey group.

Scanning is generally considered to have an anti-predatory function (Pulliam et al. 1982; da Silva & Terhune 1988; Elgar 1989; FitzGibbon 1990a) and to decline with increasing group size (see Elgar 1989 for review) either because of a decline in individual risk arising through dilution, i.e. predators are limited in the number of prey they can kill from a single group (Hamilton 1971; Inman & Krebs 1987), or through group members sharing vigilance (Pulliam et al. 1982; Packer & Abrams 1990). However, risk may also be influenced by group size through several other factors. (1) Individual predation risk can be directly related to group size if it is difficult for predators stalking larger groups to remain focused on a selected individual throughout the hunt (confusion: Landeau & Terborgh 1986). (2) In groups containing more than one prey type, confusion could be counteracted if predators select odd individuals from a group (Kruuk 1972; Landeau & Terborgh 1986). The oddity of each prey type will depend on the number of all prey types in the group (Landeau & Terborgh 1986). (3) Individual position within a group can influence risk if predators preferentially attack peripheral individuals (Hamilton 1971; FitzGibbon 1990b). Depending on group configuration, the proportion of individuals in a peripheral position should decline with increasing group size. (4) Groups may communally defend themselves against predators (Kruuk 1972; Rood 1986; Krebs & Davies 1987). The success of group defence may depend on group size (Rood 1986).

However, some factors that may influence individual predation risk are not clearly linked to group size. (1) Individual risk within a group will decrease if predator detection does not increase proportionally with group size (the encounter effect, Inman & Krebs 1987). (2) Risk can increase with proximity to cover that conceals predators (Prins & Iason 1989; FitzGibbon 1990b). Risk may also increase with (3) local or seasonal shifts in predation pressure (see Results) and (4) predator preferences for particular prey types within a group (i.e. a certain species or age-sex class: FitzGibbon 1990a; Caro & FitzGibbon 1992; Scheel 1993).

The influence of the above factors on scan rates has not been thoroughly explored. Although scanning appears to be a convenient 'common currency' for comparison across prey species, each species may have different anti-predator adaptations

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that alter the utility of scanning. If so, equivalent time spent scanning may not reduce predation risk by equivalent amounts for different species. I thus expected scan rates to be influenced not only by the immediate risk of predation but also by the effectiveness of scanning in reducing that risk. Table I lists 10 variables previously known or likely to influence scan rates, nine of which may be related to expected individual predation risk and to the ability of scanning to reduce that risk (the 10th is related to foraging effort). In this paper, I examine the effect of the variables in Table I on the scan rates of several common prey of the African lion, *Panthera leo*, both in the absence of lions and when prey were being hunted by lions.

To determine whether higher scan rates have the expected effect of discouraging predators that have already located suitable prey, I also asked whether lions spent less time per hunt or travelled shorter distances per hunt when stalking more vigilant prey groups. The analyses of lion behaviour in this paper were restricted to the influence of scan rates on hunts that had already begun, and do not examine the effect of prey vigilance on the lions' choice of prey group. A separate analysis (Scheel 1993) indicates that lions prefer those species that are identified here as less vigilant.

METHODS

Lions were observed in a 2000 km² area of Serengeti National Park, Tanzania (1°–3°30′S, 34°–36°E), where they have been studied continuously since 1966. This study population currently comprises about 200 individuals (Packer et al. 1988).

Sampling Methods

Lion behaviour

Co-workers and I recorded hunting activities of radio-collared female lions and their companions during focal animal watches (Altmann 1974) just before or after full moons in September–December 1984, September–December 1985, and July 1986–December 1987. Pairs of observers located lions at the start of each watch using aerial radio-telemetry and followed them continuously for 96 h. Night observations were made using light intensifying goggles and 8 × 35 binoculars. Observations were

not made during the night of the full moon because lions are known to be less active at this time (Van Orsdol 1984).

I defined hunts as movement by at least one lion towards potential prey while using a typical stalking stance (Schaller 1972; Scheel & Packer 1991). A hunt began when any lion in a group began to stalk the prey, and ended when all lions had stopped stalking. During the 96-h watches, 198 hunts were observed in 3500 h of observation. An additional 20 hunts were observed opportunistically over the same time periods.

Co-workers and I measured distances travelled by lions during hunts using either a Leitz range finder or the vehicle's odometer, or we estimated distances visually. Visual estimates subsequently measured with the range finder and odometer were accurate to within 10% (see Scheel & Packer 1991). Lions were followed at the maximum distance permitted by light conditions to minimize disturbances to the lions and their potential prey. This was generally greater than 300 m during the day, and about 100 m at night.

Individual ungulates were considered part of a herd if they were located within 10 adult body lengths of another herd member. Some herds stalked by lions contained more than a single species (23 of 215 herds), and it was not possible during most hunts to tell which, if any, individual or species in a group had been singled out as the intended prey. Therefore, each hunt of a mixed-species herd was recorded as a hunt of each of the species present in the herd.

Prey behaviour

Prey scanning behaviour was recorded both during lion hunts and in the absence of lions. Lions were observed hunting 17 different species during the study. This analysis includes data from only those eight species that were most frequently present in herds stalked by lions (10 or more hunts, Table II). We recorded hourly censuses of all prey groups within 1000 m of the lions during 96-h watches to estimate prey availability. We did not sample scan rates of herds in the presence of lions unless the herd was stalked by lions during the 96-h watch.

We sampled scan rates of prey groups both during lion hunts and in the absence of lions (no lions known to be within 1000 m) during September–December 1985, and July 1986–December 1987.

I recorded scan rates of all groups as scan samples (Altmann 1974) of the proportion of individuals with their heads up. An animal's position for scanning (head up) was easily distinguished from that for foraging (head down). The average proportion of individuals in the head-up position is regarded as a measure of the average scan rate of individuals in a herd. For convenience, 'the average per cent of individuals scanning' and 'the average scan rate' are used interchangeably.

The size and composition of all herds were recorded as the number of individuals of each species present. For all herds, the average nearest-neighbour distance of individuals in a herd was estimated on a scale from 0 (individuals tightly clumped, often touching) to 4 (most individuals greater than six body lengths from their nearest neighbour). We recorded the availability of cover near the herd in two ways: the dominant vegetation structure of the area was recorded as the habitat type (short-, medium- or long-grass plains, open or dense woodland, riverine), and the largest cover available to lions within 50 m of the herd was recorded as cover type (short, medium, or tall grass, bushes, stream beds, rocks, etc.). When cover near a herd was tall, it was sometimes difficult to observe the herd adequately. No data were recorded when the view of the herd was obstructed. For some herds, this resulted in sampling at irregular intervals as the herd moved in and out of view.

We attempted to record scanning data for all herds stalked by lions. During hunts, observers recorded the per cent of the stalked herd in the head-up position every minute. I calculated average scan rates of herds being stalked by lions as the average per cent of individuals in the group in the head-up position over the duration of the hunt. No data were recorded when insufficient moonlight was available at night to see the stalked prey group.

Herds were sampled in the absence of lions only for the three species hunted most frequently: wart hogs, *Phacocheroerus aithiopicus*, wildebeests, *Connochaetes taurinus*, and zebras, *Equus burchelli*. In all analyses that included these three species, I included data recorded both during lion hunts and in the absence of lions. I located and observed herds sampled in the absence of lions within 2 h after first morning light or 2 h before last evening light. The first suitable herd encountered was always chosen for sampling; herds were considered suitable if they contained no species other than wart hogs,

wildebeests and zebras, visibility was adequate, no radio-collared lions were within 1000 m, and individuals were grazing not travelling. I calculated average scan rates of these herds as the average of no more than three scan samples for each herd, separated by at least 10 min, and recorded within a 40-min period.

Variables Modifying Scanning

Of the 10 variables considered in this analysis (Table I), five are among those previously known to affect scan rates of large herbivores (Berger & Cunningham 1988). I also considered the effect of alternative measures of group size (number of heterospecifics and total group size), and that of five additional variables: (1) the species of herbivore, (2) the forage quality, (3) available light, (4) available cover near the herd large enough to conceal hunting lions, and (5) the estimated average nearest-neighbour distance between individuals in a herd, measured in body lengths. As food dispersion and food stage are known to influence scan rates (Berger & Cunningham 1988), I examined the effects of forage quality, as indicated by an index of grass greenness. Grass greenness increases after rain (McNaughton 1979), is greater in the wet season than in the dry season (McNaughton 1979) and is correlated with forage quality, particularly following a dry spell (Jarman & Sinclair 1979). I examined effects of season in this analysis using two indicators of seasonal change. First, I recorded grass greenness on a scale from 0, no green at all, to 5, lush green in greater than 75% of leaves. A seasonal effect may be evident if grass greenness is a predictor of scan rates. Second, on the Serengeti plains migratory ungulate species (wildebeests, zebras and Thomson's gazelles, *Gazella thomsoni*; Maddock 1979) are absent or rare during the dry season, and abundant during the wet season (Schaller 1972; Maddock 1979; Packer et al. 1990). This results in a seasonal fluctuation in predation pressure on resident ungulates species: predation pressure is low when migrant species are abundant in an area, and high when migrant species are absent or rare (see Results). A seasonal effect may be evident if scan rates of resident ungulates fluctuate with the presence or absence of migrant species. This variable was included only in the analysis of the wart hog scan rates, as wart hogs are the only resident prey sampled both during lion hunts and in the absence of lions.

Table I. Factors known to influence scanning rates of large ungulates

Variable	Process possibly influencing risk	1988*	Serengeti†
Predator presence	Predation pressure	Yes	NS
Herd size			
Total	Dilution effect, scanning utility		$P<0.001$
Conspecifics	Dilution effect, scanning utility	Yes	$P=0.035‡$
Heterospecifics	Dilution effect, predator preference		$P=0.003‡$
Species	Predator preference		$P=0.023$
Adult female size	Smaller individuals more vulnerable, scanning utility	Yes	NS
Habitat	Predation pressure, scanning utility	Yes	NS
Season	Predation pressure	Yes	See text
Forage quality	None		NS
Light	Predators more active under favoured conditions, scanning utility		NS (See text)
Cover	Alters scanning utility		NS
Nearest-neighbour distance	Confusion effect		NS

*From Berger & Cunningham (1988).

†A single multi-variable ANOVA of the effects of these variables on average scan rates included data from eight prey species sampled during lion hunts, three of which were additionally sampled in the absence of lions. Scanning rates were negatively correlated with all measures of herd size. For other effects listed here, see Tables II–IV.

‡A separate ANOVA, where the variables number of conspecifics and number of heterospecifics were substituted for total group size.

Scan rates were analysed using reverse step-wise multiple linear models with the average proportion of individuals of each species in a group scanning as the dependent variable. Model parameters were then re-estimated using only the remaining predictors from the step-wise models. Results are considered to achieve statistical significance for $P \leqslant 0.05$. When models contained a categorical (nominal) variable such as species, analysis of variance tests (ANOVAs) were used. The variable $\log(\text{number}+1)$ was used for all measures of ungulate group size because the number of heterospecific individuals (i.e. individuals not of the species being sampled) within a group varied from zero to greater than 10 000. I used log of group size ($+1$) for total group size and for number of conspecifics in order to be consistent over all measures. I performed separate analyses of the scan rates of wart hogs, wildebeests and zebras using the same variables as in the analysis of all prey species. I also tested the additional variable of the seasonal abundance of migratory herds in the analysis of wart hog scan rates only. For this analysis, migrant species were considered 'abundant' only when at least one herd of wildebeest or zebras containing more than 100 individuals was present in the area.

Table II. Eight species most frequently hunted by lions during the study

Common name	Number of hunts*	Hunts/ herd†	Hunts/ individual†
Buffalo	10	0.17	0.003
Grant's gazelle	25	0.03	0.001
Kongoni	11	0.05	0.007
Thomson's gazelle	28	0.03	0.0003
Topi	15	0.04	0.007
Wart hog	51	0.27	0.12
Wildebeest	39	0.05	0.00009
Zebra	38	0.06	0.0002

*Number of lion hunts during which each species was present in the group.

†Calculated from the number of hunts and from hourly censuses of 3705 herds recorded during 3500 h of focal-animal samples on lions.

RESULTS

Average Proportion of Individuals Scanning

Scanning of eight common prey species

The eight most frequently hunted species (Table II) were present in the group being stalked during

Table III. Average ($\pm$SE) scan rates of the eight species most frequently hunted by lions

Species	N	Average scan rate* (SE)	Adult female body weight† (kg)
Wart hog	41	35·0 (38·0)[a]	52
Zebra	45	39·4 (38·7)[b]	219
Buffalo	8	44·3 (40·0)[ab]	446
Wildebeest	41	46·6 (43·4)[b]	203
Topi	11	64·6 (32·0)[ab]	108
Grants gazelle	7	68·4 (30·5)[abc]	42
Kongoni	7	75·6 (26·3)[bc]	126
Thomson's gazelle	12	81·8 (21·6)[c]	16

*Percentage of herd in head-up position differed significantly between species (ANOVA: $F_7 = 2\cdot413$, $P = 0\cdot023$). There were no significant differences between values marked with the same superscript letter (Fisher's least significant differences test).

†Body weights are from Sachs (1967). Scan rates did not scale closely with body weight. See text for details.

89% of all hunts of single-species herds ($N = 192$) and during 100% of the hunts of mixed-species herds ($N = 23$). These eight species also occurred in 91% of all herds ($N = 3705$) recorded in hourly censuses during 96-h lion watches. I attempted to record the scan rates of all herds stalked by lions ($N = 215$) and sampled the scan rates of additional herds containing wart hogs ($N = 13$), wildebeests ($N = 15$) or zebras ($N = 21$) in the absence of lions.

As expected, scan rates declined with increasing total group size (conspecifics plus heterospecifics) within each of the eight species (sign test: $N = 8$, $P < 0\cdot01$). This trend was highly significant when considered in a multi-variable ANOVA across all species and taking other significant effects into account (ANOVA: $F_1 = 20\cdot9$, $P < 0\cdot001$. See below for other effects). In addition, scan rates declined with increasing numbers of conspecifics and increasing numbers of heterospecifics within each of the eight species (in each case, sign test: $N = 8$, $P < 0\cdot01$). These trends were significant when considered in a multi-variable ANOVA across all species and taking other significant effects into account (ANOVA, log(conspecifics + 1): $F_1 = 4\cdot5$, $P = 0\cdot035$; log(heterospecifics + 1): $F_1 = 8\cdot9$, $P = 0\cdot003$. See below for other effects).

Species also differed in their average scan rates (statistics are given in Table III; significant pair-wise differences are indicated by different letters, other pair-wise comparisons were not significant). Differences in adult female body size did not account for differences between species. Using a linear model following a log/log transformation of average scan rates and adult female body size (equivalent to a power model of the untransformed variables), I did not find a significant correlation between body size and scan rates when group size was accounted for (ANOVA, log body size: $F_1 = 1\cdot4$, $P = 0\cdot236$). Other variables considered did not significantly influence scan rates (Table I).

Ascending rank order of average scan rates (least vigilant first) were correlated with descending rank order of predation risk (highest risk first) measured as hunts per herd (Tables II, III; Spearman's rank correlation coefficient: $N = 8$; $r_s = 0\cdot83$; $P = 0\cdot01$). Thus, species that ranked high in predation risk were ranked low in vigilance.

Scanning of zebras

Scan rates of zebras were affected significantly by two of the factors expected to influence risk. Zebra scan rates were negatively correlated with the total herd size (ANOVA, log(herd size): $F_1 = 12\cdot0$, $P = 0\cdot001$). This was primarily due to the effect of conspecifics on scan rates (ANOVA, log(conspecifics): $F_1 = 9\cdot3$, $P = 0\cdot004$); however, the negative correlation (mentioned above) between scan rates and the number of heterospecifics in the herd was not significant when other significant factors were considered.

Zebra scan rates were highest on moonlit nights, and lower during the day (a pattern similar to that of wildebeests; Table IV). This effect of light on scan rates was significant (ANOVA: $F_5 = 2\cdot7$, $P = 0\cdot036$). Other variables considered (Table I) did not significantly influence zebra scan rates.

Scanning of wildebeests

Wildebeest scan rates were influenced significantly by two factors (light and cover). Wildebeests scan rates were significantly influenced by the available light (ANOVA: $F_4 = 8\cdot0$, $P < 0\cdot001$). Wildebeests scanned less during the day, and more during twilight and on moonlit nights, a pattern similar to that of zebra (Table IV). Wildebeest scan rates were also correlated with the available cover near the herd large enough to conceal hunting lions (ANOVA: $F_4 = 3\cdot5$, $P = 0\cdot020$).

Table IV. Effects of light, habitat and cover type on average scan rates of wart hogs, wildebeests and zebras

	Wart hogs	Wildebeests	Zebras
Light			
Night			
No moon	No data	No data	47·0 (1)[ab]
Moon, cloudy	100·0 (1)	68·2 (5)[ab]	63·9 (8)[a]
Moon, clear	No data	80·0 (6)[ab]	100·0 (2)[ab]
Twilight	83·4 (4)	82·6 (4)[a]	39·2 (4)[ab]
Day			
Cloudy	28·7 (27)	23·1 (22)[b]	29·8 (28)[b]
Sunny	38·4 (9)	62·5 (4)[ab]	10·5 (2)[ab]
ANOVA	NS (see text)	P<0·001	P=0·036
Habitat type			
Short grass plains	37·1 (5)[a]		
Open woodland	39·3 (7)[a]		
Long grass plains	30·4 (6)[ab]		
Closed woodland	25·0 (2)[ab]		
Riverine	0 (1)[ab]		
Medium grass plains	19·1 (13)[b]		
ANOVA	P=0·015		
Cover type			
Stream bed, rocks		71·8 (4)[a]	
Medium grass		67·7 (8)[a]	
Short grass		38·2 (23)[ab]	
Long grass		21·0 (3)[ab]	
Bushes		20·0 (2)[b]	
ANOVA		P=0·020	

Values indicate the average scan rates of wart hogs, wildebeests and zebras under the indicated conditions. The numbers of herds sampled are given in parentheses. See Results for test statistics. Within each effect and species, there were no significant differences between values marked with the same superscript letter (Tukey honestly significant differences multiple comparisons test).

Wildebeests scanned less when near substantial cover such as thick bushes or tall grass, but scanned more when available cover was limited to short or medium grass, or when cover was discontinuous (stream beds, rocks, etc). This pattern is similar to that shown by wart hogs in different habitat types (Table IV).

The negative correlations of scan rates with all measures of herd size (conspecifics, heterospecifics and the total of both) mentioned above were not significant for wildebeests once other significant factors were considered. This was true even for herds containing fewer than 20 wildebeests, i.e. when the dilution of predation risk would be strongest. Of the other variables considered (Table I), none significantly influenced wildebeest scan rates.

Scanning of wart hogs

Predation pressure on wart hogs was 17–1000 times higher than that on other species when measured as hunts per individual (likelihood ratio test: $G=486$, $df=1$, $P<0·001$), and four to nine times higher than that of all species other than buffalo, *Syncerus cafer*, when measured as hunts per herd (likelihood ratio test: $G=85$, $df=1$, $P<0·001$; Table II). In addition, predation pressure on wart hogs fluctuated seasonally (Fig. 1). Wart hogs experienced low predation pressure from lions during the season of migrant abundance, when wildebeests and zebras were the primary prey (Fig. 1; of hunts when migrants were abundant only 8% were of wart hogs). When the migrants were scarce, however, wart hogs became the most frequently hunted prey of lions and experienced sharply
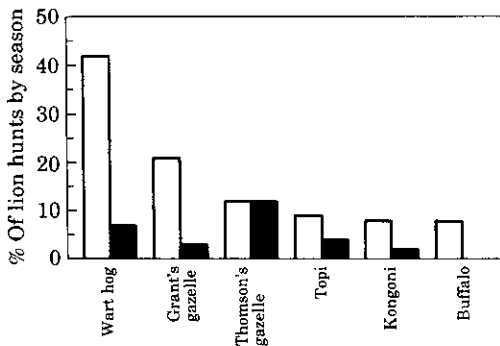
Figure 1. Percentage of observed hunts of each of five resident or semi-resident species when: migrants (wildebeests, zebras and Thomson's gazelles) were scarce, □: $N=114$, and when migrants were common, ■: $N=85$. Predation pressure from lions was highly seasonal for wart hogs, buffaloes and Grant's gazelles (likelihood ratio test, wart hogs: $G=17.5$, $df=1$, $P<0.001$; buffaloes: $G=8.6$, $df=1$, $P<0.01$; Grant's gazelles: $G=9.8$, $df=1$, $P<0.01$). Wart hogs were the primary prey of lions when wildebeests and zebras were scarce. Wildebeests (37% of hunts) and zebras (31% of hunts) were the primary prey when common.

increased predation pressure (Fig. 1; of hunts when migrants were scarce 36% were of wart hogs).

Despite this, wart hog scan rates varied with only a few of the indicators of predation risk. Wart hog scan rates were significantly higher in the absence of zebra herds than when zebra herds were within sight (ANOVA: $F_1=7.4$, $P=0.014$). However, a similar trend was not found for wart hogs in the vicinity of wildebeest herds. Although the presence or absence of zebra was correlated significantly with wart hog scan rates, the number of zebra present was not. Furthermore, the negative correlations of wart hog scan rates with all measures of herd size (conspecifics, heterospecifics or the total of both) mentioned above were not significant.

Although there were insufficient data from each cover type (i.e. cover immediately adjacent to the herd) to examine the effects of cover on wart hogs, scan rates were different in different habitats (i.e. dominant vegetation type in the area. ANOVA: $F_5=3.9$, $P=0.015$). Wart hogs scanned more in short grass habitat and open woodland and less in taller grass habitat or dense woodland. This is similar to the pattern shown by wildebeests near different cover types (Table IV). Forage quality also influenced scan rates (ANOVA: $F_5=3.4$, $P=0.027$), although no trend was apparent as greenness increased. Wart hogs scanned least when available grass was very lush and scanned the most both when grass was very dry, and when it was moderately green. Scan rates did not vary significantly with available light. However, wart hogs were active almost exclusively during the day, and hence were almost never sampled during twilight or after dark (Table IV). Other factors considered (Table I) were not significant.

Scan Rates and Stalking by Lions

Prey scan rates may be expected to influence the amount of time or energy lions invest in stalking potential prey. Lions may have difficulty successfully approaching herds in which many individuals are in the head-up position. As herd size increases, the average scan rate (the percentage of the herd in the head-up position) is expected to decrease while the total number of head-up individuals at any one time may increase (da Silva & Terhune 1988; Elgar 1989). Lions did stalk larger groups and groups with greater absolute numbers of individuals in the head-up position for significantly greater durations than smaller groups (ANOVA, number 'head up': $F_1=6.6$, $P=0.012$; total group size: $F_1=14.5$, $P<0.001$). However, neither the species hunted nor the relative proportion of the herd with head-up significantly affected the duration of hunts (ANOVA, species: $F_7=0.4$, $P=0.873$; proportion head-up: $F_1=0.07$, $P=0.793$).

There was no significant effect of the average scan rate, the absolute number of individuals head-up, nor of the species present in a hunted prey group on the distance travelled by lions during that hunt (ANOVA, scan rate: $F_1=2.2$, $P=0.137$; number head-up: $F_1=0.29$, $P=0.590$; species hunted: $F_1=1.2$, $P=0.308$). The effect of total numbers of head-up individuals and of group size on hunt duration, but not on distance travelled during hunts, suggests that large or more vigilant groups may be more difficult for lions to approach.

DISCUSSION

The finding that herbivores vary their scan rates flexibly in response to changes in their environment is well supported, both by these results and by numerous studies of scanning in other organisms (see Elgar 1989 for review). Perhaps the best

known example of this flexibility is the well-documented decline in scan rates as group size increases (Elgar 1989). Across all species I also found this effect.

Predation and Scan Rates of Common Prey Species

Scan rates varied significantly across species. Berger & Cunningham (1988) found that differences in average adult female body mass could account for much of the between-species variance in scan rates within a single group size for large, North American herbivores: large species scanned less than small ones. However, although the smallest of the eight species examined closely in this study (Thomson's gazelle) was also the most vigilant, I found no similar relationship between body size and vigilance once group size effects were accounted for. Furthermore, a simple ranking of scan rates did not correspond well to that of adult female body size (Table III). Thus, although the body size may account for some of the variation in scan rates between species, a greater amount of variation must be attributed to other differences.

The effects of light on scan rates of wildebeests and zebras suggest that scanning may be influenced by individual predation risk without being linked to dilution. Thus, scan rates were low during the day, when lions were generally inactive (Schaller 1972; Van Orsdol 1984), but were higher at night, when lions were most likely to hunt (Schaller 1972; Van Orsdol 1984).

The eight prey species in this study exhibit considerable variation in their use of anti-predator behaviour other than vigilance. Buffaloes can often successfully defend themselves against attacks by lions and are the only one of these species known to kill lions (Schaller 1972; Packer 1986). Wart hogs are active only during the day (Schaller 1972; Table IV) and spend the night hidden in burrows (Schaller 1972). Wildebeests are believed to escape predation through formation of extremely large herds (Kruuk 1972; Sinclair 1977, 1985), leading to predation saturation (compare hunts/herd and hunts/individual, Table II). Like buffaloes, zebras also actively defend themselves against attacking predators (Kruuk 1972). In addition, zebras are often found in mixed-species herds with wildebeest (Maddock 1979; Sinclair 1985). Sinclair (1985) suggested that zebras associate with large numbers of wildebeests in order to reduce predation pressure from lions. This hypothesis is supported by my finding that scan rates over all species respond not merely to the number of conspecifics in the herd, but to the number of heterospecifics as well.

In contrast to buffaloes, wart hogs, wildebeests and zebras, the remaining four species exhibit relatively few types of anti-predatory behaviour other than vigilance. Kongonis, *Alcelaphus buselaphus*, topis, *Damaliscus korrigum*, Grant's gazelles, *Gazella granti* and Thomson's gazelles are not known to successfully attack lions or hide in burrows, and do not form herds nearly as large as those of wildebeests and zebras. These species appear to rely heavily on vigilance to mitigate predation risk (Schaller 1972).

These differences in anti-predatory behaviour may affect the utility of vigilance in reducing individual predation risk. The four species in this study with comparatively low vigilance exhibit a wider range of anti-predator behaviour than do the more vigilant species. For each species, the reduction of risk via defence, hiding or dilution may limit the utility of vigilance as a means of further reducing individual risk.

The value of vigilance must also be limited by its effectiveness at detecting predators. In this study, the least vigilant species, wart hogs, was also the shortest. This, combined with the fact that wart hogs scanned more in open habitats and where the dominant vegetation was short, suggests that scanning from such a low vantage may only be effective in locating predators under limited circumstances. Scan rates were also lower for wildebeests when visibility was restricted by bushes or tall grass.

Individuals in the interior of a group generally scan less than those on the group's periphery (Elgar 1989). This pattern is usually ascribed to the fact that peripheral individuals may be at higher risk than interior ones (Elgar 1989; FitzGibbon 1990b). However, reduced visibility may explain the general decrease in scan rate in large herds, if scanning is less successful at locating predators when an individual's view is blocked by other members of the herd. Further data concerning the effects of position, group size and visibility on both the risk of predation and the effectiveness of vigilance are needed.

In this study, scan rates were generally lower in situations where visual scanning may have been ineffective in locating approaching predators. If there is a cost to vigilance, low vigilance may be the favoured response under such conditions, even if predation risk is considerably higher than in areas where visibility is less restricted.

Effects of Scan Rates on Stalking by Lions

The effect of herd size on the duration of a hunt, but not on the distance stalked during the hunt, may be due to the tendency of stalking lions to delay moving closer to a herd until all individuals in the herd were in the head-down position. Thus, lions spent a longer time watching, but did not travel a greater distance towards, larger herds with more vigilant individuals relative to smaller herds with fewer vigilant individuals.

In addition to approaching vigilant herds more cautiously, predators might be expected to preferentially stalk herds when their chances of success would be higher. It is suggestive that of the eight major prey species, the four with the lowest scan rates are the most important prey species for Serengeti lions both in terms of investment in hunting, and of food obtained via predation (Scheel & Packer 1991), and also make up the lions' 'optimal' diet (Scheel 1993). The lions appear to take advantage of low vigilance by selectively hunting wart hogs during the dry season, and wildebeests and zebras during the wet season. Large lion groups also selectively forage for buffaloes (Scheel 1993).

If species at high predation risk were found in the same herds as low risk/low vigilance species this might have resulted in the negative correlation between predation risk (measure as hunts per herd) and vigilance. However, species preferred by lions (wart hogs, wildebeests, zebras and buffaloes; Scheel 1993) were both at higher risk (Table II) and had lower vigilance (Table III) than less preferred species. Thus, the negative correlation of risk and vigilance does not depend on the association of both high and low risk species in the same herds. The fact that the species that experience the most predation pressure from lions exhibit the lowest vigilance suggests that either vigilance is limited by high costs or that increased vigilance would not substantially reduce individual predation risk for those species.

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