

Vigilance, group size and social status in capybaras

M. CAROLINA YÁBER* & EMILIO A. HERRERA†

Departamento de Estudios Ambientales, Universidad Simón Bolívar, Apartado 89.000, Caracas 1080-A, Venezuela

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Abstract. Capybaras, *Hydrochaeris hydrochaeris*, live in groups of varying size averaging 10 adults of both sexes. Vigilant behaviour was studied in capybaras under natural conditions, using focal-animal sampling on individual females, dominant males and subordinate males from groups of different sizes. There was a significant negative correlation between group size and individual alert rate, and a positive correlation with total group alert rate. Although the reduction in individual rates of vigilance levelled off at group sizes of 9–10, total alert rate continued to increase. The behaviour of the females accounted for most of the variation in individual alert rate and the behaviour of subordinate males accounted for most of the variation in total alert rate. These results suggest that females benefit the most from being in larger groups due to reduced vigilance required, while subordinate males 'pay' for their group membership by the vigilance they perform.

In animals living in exposed habitats, the formation of groups confers protection against predators by means of a number of proposed mechanisms (Hamilton 1971; Alexander 1974; Bertram 1978; Turner & Pritchard 1986). One of these relates to vigilance (Kenward 1978; Hoogland 1979; Bertram 1980; Elgar & Caterall 1981; Underwood 1982; Magurran et al. 1985; Rood 1986; Brown & Brown 1987; Da Silva & Terhune 1988): animals in larger groups may (1) have a greater probability that at least one group member will detect a predator and will alert the others or (2) have a greater proportion of their time available for feeding and other activities as they reduce the amount of individual time spent in vigilance. These two factors may exist separately or simultaneously (Hoogland 1979; Cassini 1991). Not all individuals in a group, however, benefit equally from these advantages. Dominance relations and other social factors differentially impose costs and benefits to group members (Caraco & Pulliam 1984), particularly those relating to vigilance (Elgar 1989). For instance, in dwarf mongooses, *Helogale parvula*, where vigilance is vital for survival, individuals in larger groups have a greater chance of survival but only one pair in

each pack breeds successfully (Rood 1990). Other factors also may influence the frequency with which animals display alert behaviour, such as sex (Bertram 1980), or position in the group (Underwood 1982).

In this paper, we describe the variation under natural conditions of rates of vigilance in capybaras, *Hydrochaeris hydrochaeris*, in relation to group size, sex and social roles, and discuss their relevance to patterns of group living (described below). Alert behaviour (herein used interchangeably with vigilant behaviour) may be related to social factors ('social alert') rather than to predators (Bertram 1980; Loughry & McDonough 1989). The former behaviour pattern is typical of group-living species and has a different ecological significance from predator-related vigilance (Elgar 1989), but its costs are similar (in terms of time unavailable for other activities) and its social implications may be analogous: a subordinate animal may be more apprehensive in its group and therefore more socially alert, and also more vigilant for predators because it is more exposed. For these reasons, we have included social vigilance in this study and analysed it within its social context.

Capybaras are large (ca 50 kg), grazing rodents common in the seasonally flooded savannas of tropical South America, particularly Venezuela (Ojasti 1973, 1991). They live in stable social groups composed of a dominant male, several

*Present address: Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, U.S.A.
†To whom correspondence should be addressed.

females and young, and one or more subordinate males (Azcárate 1980; Macdonald 1981; Herrera & Macdonald 1987). Among the males, there is a rigid dominance hierarchy, where dominant males tend to be bigger and obtain a greater number of matings (Herrera & Macdonald 1993). Subordinate males are often at the periphery of the group while dominant males, females and young spend more time nearer the centre (Macdonald 1981; Herrera & Macdonald 1993). There seem to be few other advantages of higher rank in relation to, for instance, access to resources (Herrera & Macdonald 1993).

As inhabitants of open savannas, capybaras are subject to predation. Man is the capybara's most important predator at present (Ojasti 1991), but sometimes feline predators (e.g. Schaller & Vasconcelos 1978; T. Pope, personal communication) and feral dogs (Macdonald 1981; Herrera 1986) can take substantial numbers of capybaras. Newborn are very vulnerable to avian predators, mainly black vultures, *Coragyps atratus*, especially in the dry season (Ojasti 1973; personal observations). The anti-predator behaviour of capybaras includes (1) vigilant or alert behaviour, where an animal regularly stops any activity and raises its head and (2) alarm calling which consists of a loud bark, often given repeatedly, and is used when an individual detects a potential predator (Ojasti 1973; Azcárate 1980; Herrera 1986). Frightened capybaras run 'en masse' to the nearest water body where they congregate in a tight huddle, sometimes with the young in the centre (Macdonald 1981).

STUDY AREA AND METHODS

This study was carried out on El Frío cattle ranch (80 000 ha; 7°46'N, 68°57'W) located in the seasonally flooded savannas of the Venezuelan Llanos. The main climatic feature of this region is the alternation of wet and dry seasons, lasting approximately 6 months each. Capybara behaviour closely follows this pattern with mating and increased social activity occurring in the early wet season (Ojasti 1973; Azcárate 1980; Herrera 1986).

The general methodology for this study was direct observation of individuals in social groups under natural conditions. Three classes of adult individuals were sampled: dominant males,

females and subordinate males. The dominant male could be distinguished from subordinates by his larger size, bigger snout scent gland or 'morrillo' (Macdonald et al. 1984) and his general behaviour (Herrera 1986).

We only recorded as 'alert behaviour' (or vigilant behaviour) instances in which the animal was (apparently) intently looking around and not simply when it raised its head to, for instance, chew a mouthful. Careful observation of context allowed us to record separately 'social alert' and 'predator alert'. Context could be any social interaction such as another animal approaching, a nearby aggressive encounter between two animals, an approach by an animal from a neighbouring group, etc. Other patterns of 'event'-type behaviour (Altmann 1974) recorded were alarm calls, aggressive chases, courtship and matings (Azcárate 1980). We recorded group size and composition of the group in which the focal animal was found every 15 min. We also noted the position of the focal animal relative to four concentric imaginary zones within the group every 15 min: zone 1 was the innermost position, while zone 2 was intermediate, zone 3 peripheral and zone 4 was outside the group. Simultaneously, we recorded the 'state' behaviour of the observed animal (Altmann 1974; Martin & Bateson 1986): grazing, walking, sitting, resting or wallowing.

We used focal-animal sampling (Altmann 1974; Martin & Bateson 1986) in sessions lasting up to 3 h (mostly continuous) during the afternoon and evening activity peaks (Macdonald 1981; Schaller & Crawshaw 1981) in May–August 1989 and October 1989–January 1990. In most cases, we observed the same individual for the entire session. However, if the focal animal went out of sight, another animal was selected, on the basis of immediate observability only. Herrera & Macdonald (1987) reported that some animals (especially subordinate males) were present in the group more often than others, and so a certain bias in favour of individuals more often seen is unavoidable. Because this is a characteristic inherent to the social structure of this species, we do not believe that this factor has affected our results. Otherwise, because the animals moved freely over mostly open habitat and the observer was not located in the same place every time, our sampling method is unlikely to be biased in favour of any one animal. We attempted to obtain at least 15 h of systematic observations for each class of

individual in each group. Although we cannot be certain that each individual in each group was sampled, we did sample all classes (dominant male, subordinate males, females) in all groups.

We define individual alert rate (or rate of vigilance, either predator-related or social) as the number of times an animal raised its head per hour of observation. Total alert rates are the number of alert events per hour for all individuals in a class or group. We obtained total alert rates for each class of individual by multiplying the mean individual rates by the average number of individuals in the class for each group size. Thus, for example, if a group had three females and the mean 'individual' rate for females was 1.3 alerts per hour, the 'total' rate for females in that group was 3.9. Adding the total rates for all classes for each group we obtained the total rate for the group. Mean individual rate in a group was calculated as the weighted average of the mean individual rates of each class of individual for each group size.

Herrera & Macdonald (1987) have shown that capybara groups have a distinct and stable membership, but, at any one time, not all animals may be present and non-members may be close enough for the observer to include them in group composition. For this reason, although we did determine the size and composition of the social units, we used the actual numbers of each class of individual at the moment of data collection as a measure of group size because this is what the animals would perceive at any one time. Thus, from seven social units we have 19 group sizes. The correlation between social group size and the average instantaneous size was highly significant (Kendall's rank correlation coefficient, $r_K=0.951$, $N=7$, $P=0.003$).

RESULTS

Although vigilant behaviour is described as a preventive measure (to detect a predator or some other potential danger before any damage has been made) capybaras' vigilant behaviour appeared to occur as a reaction to something as well as 'looking around' for it, because they often seemed to look intently in one direction. In most of these cases, we were able to detect the source (e.g. a horseman, dogs, the observer when wind changed, alarm calls by nearby groups of

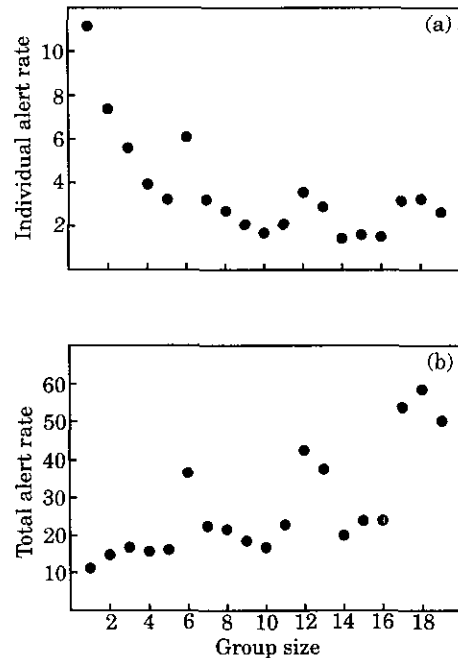


Figure 1. (a) Individual and (b) group predator alert rates (as opposed to 'social alert rates'; see text) in capybaras versus group size. Values are numbers of events per hour of observation. Data from several groups of capybaras observed at Hato El Frio, Venezuela.

capybaras, etc.). Capybaras did not react to horses without riders or to cattle except to get out of their way. During nursing, females were on continuous alert.

There was a significant negative correlation between individual alert rates (all classes of individuals averaged) and group size (Spearman rank correlation coefficient, $r_s = -0.649$, $N=19$, $P<0.006$; Fig. 1a), while total alert rate of groups (individual rates summed according to the mean number of animals in each class present) increased with group size ($r_s=0.842$, $N=19$, $P<0.001$; Fig. 1b). In other words, although each individual spent less time on vigilance in larger groups, the number of heads up per hour was greater in larger groups.

When classes of individuals were considered separately, only females significantly decreased their individual alert rates with group size ($r_s = -0.593$, $N=18$, $P<0.015$; Fig. 2a). Conversely, the mean individual alert rates of dominant and subordinate males did not vary

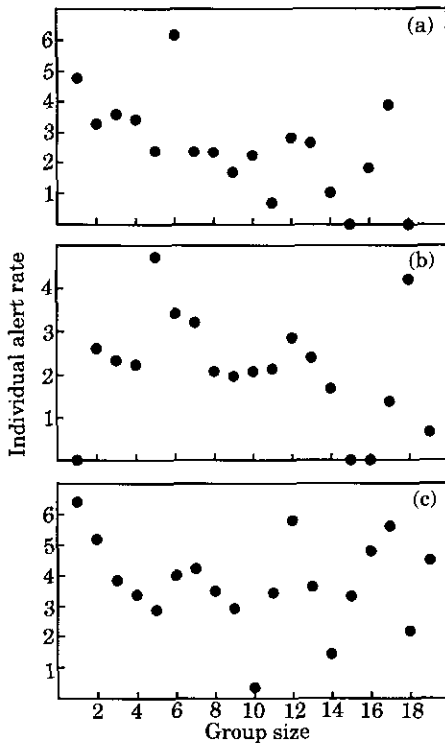


Figure 2. Individual predator alert rates for (a) female, (b) dominant male and (c) subordinate male capybaras versus group size. Values are numbers of events per hour of observation. Data from several groups of capybaras observed at Hato El Frio, Venezuela.

significantly with group size (Fig. 2b, c). Individual alert rates of dominant males, subordinate males and females were compared using ANCOVA, with group size as the covariant, and were found to be significantly different ($F_{2,53}=7.898$, $P=0.001$). A Tukey test (Sokal & Rohlf 1969) revealed that the differences between subordinate males and the rest accounted for most of the variation found, because they had greater mean individual alert rates ($\bar{X} \pm SE = 3.76 \pm 0.64$) than the other two classes ($t=0.05$; $\bar{X} \pm SE$ for females = 2.51 ± 0.66 ; for dominant males = 2.11 ± 0.52).

Total alert rate for subordinates (i.e. the rate for subordinates taken as a group) increased significantly with group size ($r_s=0.767$, $N=19$, $P<0.001$), while that of females did not.

Because capybaras are not equally exposed when in the group, we obtained the individual alert rates in each of the four zones (inner,

intermediate, peripheral and outside the group) and compared these to expected values calculated from the proportion of time each animal was in each zone. Table I shows that all classes of animals were slightly more vigilant when exposed (zone 4). As expected, all animals in the more protected zone 1 were significantly less vigilant (see partial values of χ^2 , Table I) and this was particularly noticeable in subordinate males.

Mean individual rates of social alert were significantly different between the three classes of individual (ANCOVA: $F_{2,53}=5.898$, $P=0.005$) due to the greater mean individual rate of social alert by subordinates ($\bar{X} \pm SE = 3.40 \pm 1.04$) with respect to other two classes (Tukey test $t=0.05$; $\bar{X} \pm SE$ for females = 0.90 ± 1.04 ; for dominant males = 2.05 ± 0.99). There was no correlation between individual social alert rate and group size nor between total social alert rate and group size.

DISCUSSION

Alert behaviour in capybaras appeared to be both defensive and preventive in nature because there frequently appeared to be a cause for its occurrence. Perhaps the closeness of human habitation of the groups selected, producing numerous potential alert stimuli, and the relatively rare occurrence of actual danger made it somewhat unnecessary for them to be constantly alert. None the less, because the animal that reacts, even a posteriori, does inform the rest of the group with alarm calls, the functional significance of this behaviour pattern is present.

As with other mammalian species, capybaras in larger groups obtain greater benefits from alert behaviour because with a smaller individual effort (Fig. 1a) they have a greater probability of detecting a predator (Fig. 1b). Other studies have shown that by reducing time spent in vigilance, group living allows a greater foraging time while the total vigilance rate of the group or colony increases (Berger 1978: *Ovis canadensis californiana*; Hoogland 1981: *Cynomys leucurus* and *C. ludovicianus*; Lipetz & Bekoff 1982: *Antilocapra americana*; Monaghan & Metcalfe 1985: *Lepus europaeus*; Ruiter 1986: *Cebus olivaceus*; Cassini 1991: *Cavia apereda*).

The shape of the curve in Fig. 1a indicates that any advantages related to reduced individual vigilance increase rapidly up to groups of eight or

Table I. Numbers of times (scans) that each class of individual was observed in the alert posture in each of four imaginary concentric zones*

	Zone	Observed frequency	Expected frequency†	χ^2
Females	1	81	106	6.01
	2	177	152	4.14
	3	8	13	2.06
	4	54	49	0.60
		$\chi^2=12.81, df=3, P<0.01$		
Dominant males	1	50	69	5.25
	2	176	156	2.46
	3	12	14	0.42
	4	44	42	0.09
		$\chi^2=8.22, df=3, P<0.05$		
Subordinate males	1	6	24	13.15
	2	114	111	0.07
	3	23	20	0.50
	4	158	146	0.94
		$\chi^2=14.66, df=3, P<0.05$		

*Zones are: 1 innermost; 2 intermediate; 3 peripheral; 4 outside the group.

†Expected values were calculated on the basis of the number of times (scans) that each class was in each zone and the mean alert rate of the class, assuming equal probability of being alert in each zone.

nine individuals while remaining almost constant in larger groups. Similarly shaped graphs have been obtained by Alados (1985) in Spanish ibex, *Capra pyrenaica*, and Rasa (1989a) in dwarf mongooses. In contrast, the graph in Fig. 1b shows that total group alert rate increases slowly at first and faster after group sizes of about nine. It is interesting that the average group size reported by Herrera & Macdonald (1987: $\bar{X} \pm SE = 9.6 \pm 3.8$) is close to the point where curvature changes in both graphs. At this group size, the greater benefits arise from having more time available for feeding or other activities, as a result of the reduction in individual alert rate. Benefits arising from increased vigilance (i.e. total alert rate, Fig. 1b) are maximized in the less common group sizes of more than 12–15 animals. Several models of optimal group size indicate that benefits reach a plateau above a given number of animals (Giraldeau 1988). It is plausible that above a certain size, an increase in the group's rate of vigilance does not bring a net benefit. Also, other costs such as competition for resources may become greater in the upper range of group sizes. We found no increase, however, in individual social alert rate in larger groups, and previous studies have shown that although total aggression rate in the group does increase with group size, the

individual aggression rate does not (Herrera 1986). Hence, this type of social cost does not appear to place a ceiling on the size of groups.

It must be noted, though, that the trend described is mainly due to the females' behaviour, indicating that they benefit the most from this effect. This is perhaps not unexpected because females in a sexually monomorphic species have greater nutritional needs for gestation and lactation, and must spend as much time as possible feeding (Ojasti 1973). Gauthier & Tardiff (1991) have reported much lower rates of vigilance for female than for male snow geese, *Chen caerulescens*, while Smith & Gao (1991) found similar results for pikas, *Ochotona curzoniae*. Both of these papers relate their findings to the role of females in reproduction.

Our results indicate that capybara groups benefit most from the behaviour of subordinate males because their total alert rate was the only one that increased significantly with group size, and their individual alert rates were greatest. This partly explains the tolerance towards them displayed by the dominant males, which rarely showed overt aggression towards them. As Davies & Houston (1984) have argued, subordinates may 'pay' for their acceptance in the group by bringing some benefit to the dominant male and to the

females. Also, the fact that subordinate males were more often at the periphery of the group (Herrera & Macdonald 1993), and that they were not more vigilant when in the inner zone of the group (Table I), suggests that their increased rate of vigilance is due to the fact that they are more exposed, rather than to their status per se. By being more exposed, subordinate males are more likely both to detect a predator and to be preyed upon, hence their greater individual alert rates. Furthermore, their social alert rates were also higher, possibly in order to stay away from the dominant male and to reduce the number of times they could be chased by him. Caine & Marra (1988) have pointed out that individuals that need to be socially vigilant have less time to scan for predators. Subordinate capybara males, however, exhibit high rates of both types of behaviour. Thus, subordinate males carry most of the burden in terms of both kinds of alert behaviour: social and anti-predator. This scenario is analogous to the situation described by Rasa (1989b) for the more social dwarf mongooses. It could be argued that such a system is open to cheating: a subordinate male may obtain the benefits derived from group membership and perform little vigilance. However, by continually chasing subordinates to the periphery of the group (Herrera 1986; Herrera & Macdonald 1993), the dominant male forces them into exposed positions. There, subordinate males need to be vigilant for their own sake, and, by doing this, they benefit all other group members.

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