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### Sentinel Behaviour in Vervet Monkeys: Who Sees Whom First?

Sentinel behaviour here refers to an alert non-foraging individual stationed in a prominent place while members of its group forage nearby. The behaviour has been reported in the baboons *Papio ursinus* (Hall 1960) and *Papio cynocephalus* (Maples et al. 1976), in pigtail macaques *Macaca nemestrina* (Crockett & Wilson 1980), and in St. Kitts vervets, *Cercopithecus aethiops sabaues* (Poirier 1972). In each case, the behaviour occurred while the animals were foraging for crops in open fields; i.e. when the foragers were conspicuous and the potential predator was human. While it is assumed that sentinel behaviour is a form of vigilance, what information is being conveyed by the sentinel, how, and to whom, remain unclear. Moreover, why the behaviour should occur during crop raids, and who the sentinel should be, have not been discussed. In the present paper, we report sentinel behaviour in the vervet monkey *Cercopithecus aethiops sabaues* in Barbados, and comment on its mechanism and function.

Sentinel behaviour was observed on 28 occasions in nine feral troops during our 6-year study of vervets in Barbados. The vervets eat primarily cultivated foods, and are consequently hunted by farmers (Horrocks 1986). Apart from occasional attacks by dogs, humans are their only predators. To observe sentinel behaviour it was best for the observer to be at the site of an anticipated raid by dawn, prior to the beginning of the raid. Since it was difficult to anticipate reliably raid sites, numerous pre-dawn expeditions were necessary to obtain the 28 sentinel observations. When the vervets

forage in cultivated fields one individual, always an adult male, is typically positioned in a conspicuous place near the top of a nearby tree. He is seated, but his posture is such that the white pelage of his ventral surface is maximally exposed. The sentinel neither feeds nor changes his location while the troop is foraging, and typically does not vocalize.

There is one definite cost and one potential cost to sentinel behaviour. The first is that the sentinel does not forage while other troop members do. The second is that the sentinel risks detection by a predator. No direct benefits for the sentinel are apparent. By contrast, the foraging members of the troop should benefit from sentinel behaviour. Their risk of predation may be lower and their foraging efficiency higher, since they may have to spend less time scanning for predators. Sentinel behaviour is clearly altruistic. This is seldom true for alarm calls and signals, which may have evolved either through kin selection to warn relatives or through individual selection to reduce the signaller's vulnerability (Hamilton 1964; Smythe 1970; Woodland et al. 1980). For example, vervet alarm vocalizations may not be altruistic, since individuals do not incur greater risks by giving them, and members of each age/sex class give them most often to predator species to which they themselves are most vulnerable (Cheney & Seyfarth 1981). In Barbados, sentinels are always adult males, and are typically breeding males, since troops usually have only one male. Note that sentinels are also adult males in baboons and St. Kitts vervets (Hall 1960; Poirier 1972; Maples et al. 1976). Since females in most Old World monkeys remain in their natal troops while males emigrate at maturity, adult females will have more collateral kin in a troop than adult males (Cheney & Seyfarth 1981; Horrocks & Hunte 1983a, b), but in one-male troops, adult males often have the greatest number of offspring. In short, for an adult female, only some immature troop members are offspring, and most adults, even if kin, are female competitors. For an adult male, most troop members are either offspring or potential mates. Sentinel behaviour is therefore best perceived as paternal care or mate protection.

Sentinels may reduce the predation risk for foragers by either watching for predators and warning foragers when a predator is detected, or acting as diversions. However, if the former, why is it necessary for the sentinel to be so highly visible? A vocal warning from a hidden location should suffice. The second alternative is compatible with the sentinel's conspicuous position, but not with his silence. Moreover, a predator could quickly learn that a sentinel is a reliable cue for the presence of nearby foragers. We therefore suggest that the primary function of the sentinel is to detect

approaching predators and warn troop members, but that, at least initially, the warning is best communicated by visual signals. In short, the sentinel is conspicuously positioned, not to increase the chance of being detected by a predator, but to increase the ease with which foragers maintain visual contact with the sentinel. By observing the sentinel's behaviour, foragers may be warned of a predator's approach without the need for vocalizations that might alert the predator to the presence of both the sentinel and foragers. Note that a quiet alarm call would be ineffective given the distance between the sentinel and foragers that is required for the sentinel to have a panoramic view.

On 26 of the 28 occasions when sentinel behaviour was observed, the sentinel did not vocalize. During 13 of the 28 occasions, a person unknowingly approached the foraging vervets and sentinel. In 11 cases, the approach was detected from a distance, the sentinel left his position without vocalizing, and the foragers then retreated into the surrounding woodland. The intruder apparently remained unaware of the presence of the vervets. On two occasions the intruder was not detected until close at hand. When thus surprised, the sentinel held his ground and vocalized loudly and repeatedly. In short, when the sentinel and perhaps the foragers may already be detected, the appropriate response is apparently vocalization. This would instantly warn the foragers, and might briefly distract the predator.

Our hypothesis that sentinel behaviour is visual communication between conspecifics is consistent with other characteristics of the behaviour. For example, since the sentinel remains in one location throughout the foraging event, visual contact with the foragers is facilitated. Frequent scanning for predators is replaced by periodic glances at the sentinel. The fact that sentinel behaviour occurs when foragers are in open areas may not be because the latter are particularly vulnerable, but because foragers can only maintain visual contact with the sentinel under such circumstances. Finally, it is of interest that sentinel behaviour is apparently restricted to crop-raiding, i.e. when humans are the potential predators. Humans differ from most predators of primates by having limited olfactory capabilities, but often have the capacity to kill from a distance.

Typical animal alarm signals either require that the predator has already detected the prey (e.g. pursuit invitation, Smythe 1977; pursuit deterrent, Woodland et al. 1980; distraction displays, Wilson 1975), or that the predator will have an increased probability of detecting the prey, if that has not already occurred (e.g. vocal alarms, Cheney & Seyfarth 1981). Faced with a predator that does not

hunt by scent but can kill from some distance, a silent alarm system is advantageous. Not only will a silent alarm decrease the mortality risk for foragers but it may permit a retreat that is only temporary, so that foraging can be resumed quickly once the danger has passed.

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### Infanticide in White-footed Mice, *Peromyscus leucopus*

Female white-footed mice (*Peromyscus leucopus*) are intrasexually territorial and maintain exclusive core areas by aggressive behaviour (Wolff et al. 1983). I hypothesized that one of the functions of female territoriality is to prevent infanticide. In the laboratory, we demonstrated that females with litters could deter intruding females effectively, and that when the dam was removed, intruding females do kill pups (Wolff 1985a). In this paper, I describe an instance of infanticide in nature and discuss its implications.

At 1400 hours on 19 October 1985 I was checking nest boxes at our field site at the Mountain Lake Biological Station in southwestern Virginia (Wolff et al. 1983; Wolff 1985b). One arboreal nest box contained five dead 8-day-old pups and an unmarked adult female. The female was not pregnant or lactating. Each pup had been bitten in the head or neck, but had not been eaten. The bite marks were those of rodent incisors and similar to those made by *P. leucopus* in the laboratory. The pups had been dead for less than 10 h. The known mother of the pups had died in a trap that morning. She had probably been away from her pups for less than 10 h. The nest box was located in the centre of the grid, so the infanticidal female was not a neighbour and came from at least 50 m away. The new female has been caught subsequently in the same area and apparently has taken over the territory.

Harland & Millar (1980) estimated that lactating *P. leucopus* average 5.7 foraging bouts per night with a mean duration of 53 min/bout. Our own data suggest that mothers forage near the nest area and return to their nests often. Dispersal and immigration of non-related animals is high during the breeding season (Wolff 1985b). Consequently, the threat of infanticide may be a strong selective force favouring short foraging bouts and territorial defence, especially around the nest area.

These results have important implications for studying small mammals in nature. Mice are frequently detained in live traps for more than 10 h, which may be sufficient time for strangers to take over a territory and commit infanticide. As *Peromyscus* and most other small mammals are nocturnal, intrusion would occur during the night, when

resident animals are foraging and are caught in traps. Infanticide occurs within seconds after a strange mouse encounters non-familiar pups (Wolff 1985a). Thus, loss of pups by infanticide occurs because the mother is not able to defend the nest site. If specific foraging and activity patterns reduce the probability of intraspecific infanticide, then trapping would have demographic consequences by affecting recruitment, dispersal and colonization, social structure and other behavioural and ecological features of the population. Infanticide may occur in natural populations more frequently than previously expected and should be taken into consideration in designing experiments and interpreting their results.

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### Influence of Spatial Patterning of Resources on Search Orientation of Adult *Drosophila melanogaster*

Search orientation, the active movement of animals in relation to environmental resources, is influenced by internal and external sensory information gained while foraging, as well as by information contained in the genome and memory (for a review see Bell 1985). One component of the information an animal can gain as it locates resources is the spatial arrangement of resources,