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Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*

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Vigilance in ungulates is considered to have a predominantly antipredator function, with the frequency and duration of scans per individual decreasing with increasing group size. Social influences on vigilance scans have been overlooked in studies on ungulates, although studies in primates and birds show that conspecific scans are important determinants of vigilance behaviour. We investigated group size effects in giraffes and examined social influences on their scanning behaviour, as well as the influence of feeding posture. We found that group size has little effect on scanning behaviour in either bulls or cows, which may be attributable to our inability to measure a group as perceived by a giraffe. Time spent scanning by lone cows did not differ from that of cows in any other group type, but time spent scanning by bulls when alone was less than that in groups. The presence of calves in a group did not influence scanning behaviour. Predation risk does not appear to be a significant modifier of vigilance behaviour, although a constant level of antipredator vigilance is probably maintained. Social factors were a significant modifier of vigilance scanning. Bulls scanned the most when they were in groups with larger bulls, and least when they were with smaller bulls. A similar pattern was seen with nearest-neighbour identity, and the identity of individuals within 10 m of a focal animal. Cows were significantly more vigilant when an adult bull was close, or was the nearest neighbour. Finally, vigilance advantages have been postulated as a determinant of sexual segregation in giraffe foraging heights but we found that the posture associated with high foraging heights imposes a vigilance cost, not an advantage. We therefore conclude that differential vigilance requirements are not a determinant of feeding height segregation between giraffe bulls and cows.

Vigilance behaviour has traditionally been considered as functioning primarily for antipredator protection (Pulliam 1973). Changes in vigilance behaviour have usually been attributed to variation in predation risk. In particular, a relationship between group size and vigilance behaviour, whereby vigilance decreases with increased group size, has been considered an adaptive advantage of group living (Alexander 1974). Specifically, with increased group size, individuals benefit because there are more individuals to be vigilant, and therefore an individual's own time spent vigilant can be reduced (Pulliam 1973). Additionally, the risk of predation to each individual may be reduced in a large group as a result of dilution. Studies on ungulates, in particular, focus on the antipredator function of vigilance (e.g. Hunter & Skinner 1998; Childress & Lung 2003; Manor & Saltz 2003). Alternatively, a decrease in scanning with increasing group size may be a consequence of an increase in scramble competition for limited resources (Beauchamp 1998; Lima et al. 1999; Blumstein et al. 2001). Vigilance decreases as group size increases in a wide variety of taxa (reviewed in Elgar 1989), although many studies have also failed to show such a relationship and have been regarded as exceptions to the general rule (e.g. Catterall et al. 1992; Rose & Fedigan 1995; Cowlishaw 1998; Treves 1998, 2001).

The definition of a group can be problematic when testing for a group size effect on vigilance behaviour. Group size as perceived by the human observer may have little relevance for the species being studied. For example, individuals may respond to the presence or proximity of neighbours, but not to group size, and consequently may perceive their immediate group size in terms of neighbours, whereas the observer sees the whole group (Treves 1998; Rolando et al. 2001). For example, vigilance behaviour in

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the macropodid marsupial, the quokka, *Setonix brachyrus*, is significantly affected by the number of individuals within 10 m, but is affected to a much lesser extent by the number within 50 m (Blumstein et al. 2001). Species that communicate over large distances may perceive their group size as larger than that seen by the observer. Conversely, some studies have found a negative influence of nearest neighbours on the amount of time spent scanning, suggesting social factors may be important in determining scanning rates (e.g. Treves et al. 2001; Hirsch 2002). Vigilance scans may, therefore, be performed in response to a range of factors, among which predation risk is just one.

The within-group surveillance hypothesis suggests that vigilance functions not only for individuals to protect themselves against predators, but also as protection against competitors, which are usually conspecifics (Renouf & Lawson 1986; Alberts 1994; Yáber & Herrera 1994; Artiss & Martin 1995; Slotow & Coumi 2000). In particular, males may be more vigilant than females when they are in groups, because males compete for females (Reboreda & Fernandez 1997). Vigilance behaviour may also be used for opportunities to steal food items (Robinette & Ha 2001), to detect forage items or patches (Coolen et al. 2001), particularly where other group members are foraging successfully (Bertram 1980; Templeton & Giraldeau 1996; Smith et al. 1999), and to detect potential mates (Burger & Gochfield 1988; Dunbar et al. 2002). Vigilance may also be a sexually selected trait, where females prefer more vigilant males (Dahlgren 1990). The balance of vigilance has been shown to shift from predominantly antipredator to predominantly group surveillance as group size increases (Treves 1999). Although within-group vigilance has been predominantly described in primate species, nonprimate mammals are also known to monitor their conspecifics (e.g. Alados 1986; Renouf & Lawson 1986). There are, therefore, a range of factors that can influence rates of vigilance scanning, but only antipredator vigilance has been extensively investigated (Beauchamp 2001).

Most research on ungulate vigilance behaviour has focused on the influence of predation risk (e.g. Hunter & Skinner 1998), but previous studies on giraffes have suggested that there may be a social element to vigilance behaviour. Three nonmutually exclusive hypotheses for higher male vigilance in the wet season were proposed by Ginnett & Demment (1997). (1) Groups are larger in the wet season, which may lead to an increase in socially related vigilance. (2) There may be a seasonal shift in prey preference by lions, which are the major predators of giraffes. (3) Higher forage intake rates during the wet season may allow males to allocate more time to predator avoidance and social monitoring. Studies on vigilance behaviour have shown that more satiated individuals tend to contribute more to sentinel or vigilance behaviour (ungulates, Illius & Fitzgibbon 1994; meerkats, *Suricata suricatta*, Clutton-Brock et al. 1999).

Vigilance has been implicated as playing an important role in giraffe behaviour, potentially contributing to the maintenance of sexual segregation in foraging heights (Young & Isbell 1991). In all populations of giraffes where foraging behaviour has been investigated, males tend to feed at higher levels in the canopy than females (Pellew 1983, 1984; du Toit 1990; Young & Isbell 1991; Ginnett & Demment 1999). Because males are taller than females, the absolute difference in feeding height is larger than the relative difference in neck angles (Ginnett & Demment 1999). Young & Isbell (1991) argued that males forage with their necks held higher in order to be more vigilant for predators, mate competitors and to maintain dominance. On the contrary, du Toit (1990) suggested a vigilance cost to foraging higher, as the extreme neck angle inhibits visual scanning of the surrounding environment.

We investigated giraffe vigilance behaviour in terms of frequency and total time spent scanning. We tested for a group size effect, and tested whether group type influenced scanning, including individuals that were alone. Social influences were further investigated by measuring nearest-neighbour distances and identities, and the identity of individuals close to a focal animal. To our knowledge, this is the first study to investigate social influences on vigilance scans in an ungulate (except the costs of allogrooming in impala, *Aepyceros melampus*, Mooring & Hart 1995). Finally, we tested whether different foraging heights resulted in differences in vigilance scanning, and consequently foraging efficiency.

METHODS

The study was conducted in the central region of the Kruger National Park, South Africa, based at the Tshokwane ranger station (24°47′S, 31°52′E). The woody vegetation is dominated by *Acacia nigrescens* and *Sclerocarya birrea* trees on a basaltic plain, a preferred giraffe habitat type. All major predators of giraffes are present (with lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta*, posing the biggest threat to giraffes; Pellew 1984). The study was conducted between July 2001 and July 2002.

We located giraffes opportunistically while driving on predetermined routes through the study area during all daylight hours and recorded group composition as soon as a group was encountered. A giraffe was considered a member of a group if it was within 100 m of another giraffe, with the core of the group being the largest obvious aggregation. This is an arbitrary assignment of a group that follows the methodology employed by other researchers (e.g van der Jeugd & Prins 2000). It usually included all giraffes that were visible to the observer. We recorded any individuals that joined or left the group, and the time that they did so. The group size was recorded as the number of individuals in the group at the beginning of a focal sample. We classified each individual by sex and age, and recorded its identity if it was individually known. We recorded the presence of calves and yearlings, although these individuals were not sampled for their behaviour. We recorded whether a female was adult or subadult based on her size. For males, we recorded whether they were adult or subadult based on their size, and also recorded their size relative to the other group members.

We sampled scanning behaviour using focal animal samples (Altmann 1974). Individuals were sampled throughout the day, with each category of individual being sampled equally from each part of the day, and