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REVIEW

# Theory and method in studies of vigilance and aggregation

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Predation is considered one of the most important selective pressures on free-ranging animals. Our understanding of it derives mainly from studies of individual vigilance (visual scanning of the surroundings beyond the immediate vicinity) and aggregation in prey. Vigilance bears a direct relationship to aggregation, because animals in groups may rely on associates for early warning of danger. This review addresses the relationship between vigilance and aggregation with particular attention to the prediction that individual vigilance declines with increasing group size. Contrary to most other animals studied, primates do not support the prediction. Exploring this, I examined the assumptions underlying vigilance theory in the light of primate behaviour. First I tested whether manual harvesting and upright processing of food as seen among primates might permit them to feed and scan simultaneously. I found no support for this idea. Next I examined the targets of primate vigilance and found that one component (within-group vigilance) might explain the differences between primates and other animals. Finally, I evaluated whether individual primates in large groups face a lower risk of predation than those in small groups. A conclusion was impossible, but by separating group-level from individual-level risk, I was able to identify several common circumstances in which group size would not predict individual risk or vigilance. These circumstances arose for primates and nonprimates alike. I concluded that the relationship of vigilance to aggregation is not straightforward. The absence of a group-size effect on vigilance among primates is probably due to functional differences in vigilance behaviour or safety in groups, not to methodological differences. Furthermore, future work on animal vigilance and aggregation must fully consider both the targets of glances, and the assumption that larger groups are safer from predators. I predict that animals will not relax vigilance in larger groups if conspecific threat increases with group size. Group size will not predict individual risk of predation nor individual vigilance rates when predators do not rely on surprise, or when predators select a small subset of highly vulnerable group members.

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*To live gregariously is to become . . . the possessor of faculties always awake, of eyes that see in all directions, of ears and nostrils that explore a broad belt of air . . .* (**Galton 1871, page 356**).

To survive and protect their offspring, animals must detect threats before they inflict damage. Early detection of threats can happen in two ways. An animal can monitor its surroundings beyond its immediate vicinity (individual vigilance), or it can await signals given by other wary animals when they detect threats (collective detection). Detecting threats oneself is often more rapid and reliable than depending on associates (FitzGibbon 1989; Lima 1994; Bednekoff & Lima 1998a), but individual vigilance conflicts with other important activities (Pulliam 1973; Dimond & Lazarus 1974; Lendrem 1983; Mooring & Hart 1995). A gregarious animal can rely on associates when interruptions to scan are too costly, an option unavailable to a solitary animal. In this way, individual strategies for allocation of time and effort to vigilance are expected to vary with group size and the behaviour of associates.

Many researchers have predicted that the size of aggregations will predict individual vigilance, as animals take advantage of safety in large groups to feed, rest and groom uninterrupted (Dehn 1990; McNamara & Houston 1992; Roberts 1996; Bednekoff & Lima 1998a). This prediction is well supported. In over 50 studies of birds and mammals, individuals in larger groups displayed lower rates of vigilance, a relationship that has come to be

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**Table 1.** Primate studies that tested for a group-size effect on time spent vigilant

| Species | Group-size effect | *N* of groups | Group size range | Notes on methodology | Reference |
|---|---|---|---|---|---|
| *Alouatta pigra* | None | 6 | 2–10 | | Treves et al., unpublished data |
| *Cebus capucinus* | None | 4 | 12–24 | Excluded brief glances | Rose & Fedigan 1995 |
| *C. olivaceus* | Negative | 2 | 8–25 | Excluded brief glances | de Ruiter 1986 |
| *Cercopithecus aethiops* | * | 6 | 2–19 | Excluded brief glances | Isbell & Young 1993 |
| *C. ascanius* | None | 6 | 1–29 | † | Treves 1997, 1998a |
| *C. mitis* | None | 5 | 1–30+ | Only males† | Tsingalia & Rowell 1984 |
| *C. mitis* | None | 2 | 20–36 | Only females | Cords 1990 |
| *C. mitis* | None | 3 | 1–12 | Only males† | Treves 1997 |
| *Homo sapiens* | Negative | 394 | 1–5 | Excluded WGV‡ | Wirtz & Wawra 1986 |
| *Pan troglodytes* | None | 9 | 1–13 | Only females and juveniles | Treves 1997 |
| *Papio c. ursinus* | None | 4 | 22–55 | | Cowlishaw 1998 |
| *Procolobus badius* | None | 5 | 20–76 | | Treves 1998a |

Studies of mixed-species groups are not included because group-size differences may be confounded by interspecific differences in antipredator behaviour.
*Internal contradiction: Isbell & Young (1993) reported a significant negative relationship ($r=-0.35$) across groups (their Table 4) but showed no effect of group size when sex and dominance rank were controlled for in a factorial ANOVA (their Table 3). Furthermore, only one group showed a negative correlation (again $r=-0.35$) when tests were run within groups (as they changed in size over time).
†Comparisons of the same males in versus out of groups (Tsingalia & Rowell 1984) or as group residents versus solitaries (Treves 1997).
‡Students at a refectory: group size=number of people at a table; WGV=within-group vigilance.

called the 'group-size effect on vigilance' (Elgar 1989; Quenette 1990). However, a growing number of careful studies have failed to detect a group-size effect on vigilance (e.g. Elgar 1989; Catterall et al. 1992; Colagross & Cockburn 1993; Scheel 1993; Pöysä 1994; Jones 1998; Krams 1998). Among these are nine out of 12 studies of primates (Table 1).

The primate data present a puzzle. Because many primate studies use idiosyncratic sampling rules and definitions of vigilance, the results in Table 1 may simply be inaccurate. To evaluate this possibility, I review methodology along with theory and data. However, methods alone seem unable to account for the absence of a group-size effect on vigilance, because the primate studies are not all designed identically (Table 1). More interesting functional explanations arise when one considers why we expect a group-size effect on vigilance.

The prediction that animals will relax vigilance in large groups stems from a series of assumptions about the behaviour of predators and prey. Several authors have identified these assumptions in one form or another (Dehn 1990; Lima 1990; McNamara & Houston 1992; Bednekoff & Lima 1998a, b). I condense the various treatments into five simple assumptions.

(1) Vigilance must be costly, or animals gain nothing by relaxing their efforts.

(2) Increasing vigilance must improve predator detection, or individual vigilance will not vary with risk.

(3) The probability of being killed by a predator must decrease with increasing group size. If not, animals in large groups will behave like animals in small groups.

(4) Collective detection must lower individual risk. If unwary animals gain nothing from associating with wary animals, animals should never reduce vigilance in large groups.

(5) Animals assess the number and activity of their associates. Without somewhat reliable information about associates, individuals should not diminish their own efforts.

The last two assumptions have been reviewed recently (Bednekoff & Lima 1998a; Bahr & Bekoff 1999), and the primate data add little. However, the first three assumptions may be violated by the behaviour of primates and several other taxa. Therefore, in the next three sections, I explore assumptions 1–3 and evaluate whether primates violate them. This review is restricted to visual exploration of the environment, because little is known about auditory or olfactory vigilance.

## Assumption 1: Vigilance Must Be Costly

Vigilance requires time and visual attention. Both are limited resources (Altmann 1974; Dukas 1998). Hence, vigilance conflicts with other activities, such as sleeping, feeding, grooming and fighting (Dimond & Lazarus 1974; Caraco 1979; Lendrem 1983, 1984; Pöysä 1987; Isbell & Young 1993; Cords 1995; Mooring & Hart 1995; Brick 1998; McAdam & Kramer 1998). Most research has centred on the conflict between feeding and vigilance, because so many animals lower their heads to feed and thereby occlude their visual fields (Galton 1871; Pulliam 1973; Bertram 1980; Beauchamp & Livorell 1997; Jones 1998). Although recent experiments suggest that vigilance is not completely impaired in feeding animals (Lima & Bednekoff 1999), the conflict between feeding and vigilance is a classic behavioural trade-off (Pulliam 1973; Pulliam et al. 1982). However, there have been few studies of animals that feed in an upright position or collect and process food with their hands. For these animals, vigilance may not trigger high costs.

Some, but not all, components of feeding interrupt vigilance. If we define feeding to include finding, harvesting, processing and ingesting food, only a subset of

**Table 2.** Primate vigilance during foraging and resting

| | Measures of vigilance | | | |
|---|---|---|---|---|
| | Mean±SE frequency of scans (bouts/min) | Mean±SE time (s) spent scanning | Lapses (%)* | Feeding ecology† |
| Redtail guenons, *Cercopithecus ascanius* | | | | 2–3 kg, FI, AB |
| Foraging (*N*=217 samples) | 4.5±0.2 | 31.8±1.0 | 47.0% | |
| Resting (*N*=126) | 2.9±0.1 | 49.3±1.0 | 17.8% | |
| Blue guenons, *C. mitis* | | | | 4–6 kg, FLI, AB |
| Foraging (*N*=101) | 4.3±0.2 | 25.1±1.2 | 58.2% | |
| Resting (*N*=46) | 2.4±0.2 | 37.6±2.8 | 37.3% | |
| Red colobus, *Procolobus badius* | | | | 5–8 kg, FL, AB |
| Foraging (*N*=335) | 4.3±0.1 | 23.3±0.7 | 61.2% | |
| Resting (*N*=321) | 2.2±0.1 | 32.1±1.1 | 46.5% | |
| Chimpanzees, *Pan troglodytes* | | | | 40–60 kg, F, SU |
| Foraging (*N*=31) | 4.2±0.4 | 18.6±2.6 | 69.0% | |
| Resting (*N*=40) | 3.0±0.3 | 35.5±3.3 | 40.8% | |
| Between-species comparison: Mann–Whitney *U* test | | | | |
| Foraging | NS | $P \leq 0.001$ | | |
| Resting | $P \leq 0.001$ | $P \leq 0.001$ | | |

Vigilance was defined as visual scanning beyond arm's reach of the focal animal. Half of the animal's face had to be visible.
Time spent scanning was measured continuously over a 1-min focal sample.
*Time spent not scanning=60−time spent scanning, converted into a percentage.
†Body mass range for both sexes, main diet (F: fruits; L: leaves; I: insects), posture (AB: above-branch; SU: suspensory).

components will be necessarily incompatible with vigilance. For example, granivorous birds can survey their surroundings while hulling, but not collecting, seeds (Glück 1987). Similarly, ungulates can chew cud with their heads up (Lipetz & Bekoff 1982; Frid 1997). Easier tasks conflict less with vigilance (Metcalfe 1984; Lawrence 1985; Moreno & Carrascal 1991). An animal faced with easy feeding tasks that permit scanning might never experience lapses in vigilance. Does this apply to primates or specifically to those with relatively easy feeding tasks?

Primates and many other animals can feed upright or use their hands to collect food (e.g. Clarke 1987), apparently permitting them to feed while scanning. This would lower the costs of vigilance and thereby reduce the benefits of relaxing scanning in large groups (Illius & Fitzgibbon 1994). However, an early study of vigilance in *Cebus* monkeys found that feeding was associated with lower vigilance than other activities (van Schaik & van Noordwijk 1989). This hints that primates face the same trade-offs as other animals. Experiments that test whether primates can detect predators during each component of feeding are needed. A preliminary step is to compare primates that vary substantially in feeding behaviour. For example, the four species in Table 2 differ in diet, feeding posture and body size (Struhsaker 1975, 1978; Wrangham et al. 1991, 1998), yet they interrupt feeding equally often to scan their surroundings. Thus, the frequency of lapses in vigilance is largely independent of feeding behaviour. Both feeding and resting are important activities, yet both are interrupted periodically by vigilance (Table 2). This suggests that vigilance is costly for primates, and they should benefit from relaxing vigilance. In short, upright posture and use of the hands during feeding does not seem to explain the absence of a group-size effect on primate vigilance. We must look elsewhere to understand why primates do not relax vigilance in large groups.

## Assumption 2: Increasing Vigilance Must Improve Predator Detection

Most vigilance research emphasizes predator avoidance over other functions of scanning (Lima 1994, 1995; Arenz & Leger 1997; Bednekoff & Lima 1998b), such as social learning, food search and travel planning. This emphasis on predator avoidance can be justified because there is overwhelming evidence that predators affect the vigilance of prey (Elgar 1989). For example, predator stimuli can elevate vigilance in captive fish, mammals and birds (Lendrem 1984; Magurran et al. 1985; Caine 1986; Glück 1987; Caine & Weldon 1989; Price 1992; Hardie & Buchanan-Smith 1997; Koenig 1998). Seeing or hearing predators may increase vigilance in wild birds and mammals also (Lendrem 1983; van Schaik & van Noordwijk 1989; Cheney & Seyfarth 1990; Forslund 1993; Cresswell 1994; Arenz & Leger 1997; Bshary & Noë 1997; Hunter & Skinner 1998; Treves 1999a). Furthermore, vigilant animals are often safer from predators than unwary ones (FitzGibbon 1989, 1990a; Scheel 1993; Cresswell 1994). By all accounts then, predation risk shapes animal vigilance.

Although predation risk shapes animal vigilance, complete removal of predators does not eliminate vigilance (e.g. Keverne et al. 1978; Caine 1987; Gerstner & Fazio 1995; Hunter & Skinner 1998). In part, this reflects that a proportion of scanning is used to gather information unrelated to predator detection (Dimond & Lazarus 1974). Indeed some targets of vigilance may provide no

warning of predators (e.g. glances between opponents during competition: Brick 1998; Jones 1998). Therefore, the allocation of scanning time to different targets and their compatibility with predator detection are important facets of vigilance (Lima 1990).

### *Targets of vigilance*

Even if we assume for the sake of argument that predation avoidance is the sole factor governing vigilance, animals may still scan at least three different types of targets. They may try to spot predators, monitor wary associates, or survey escape routes. Spotting predators oneself provides the earliest warning of danger (Bednekoff & Lima 1998a), but it is often difficult when predators are concealed or distant. Associates are usually closer, more obvious, and can reveal that they have detected predators via escape or alert postures (e.g. FitzGibbon 1989, 1990a; Lima 1994). Finally, refuges tend to be fixed in space, hence easy to survey for escape routes. However, information on escape routes and refuges is of little use without early warning of predator approach. Thus, animals are expected to expend some effort in spotting predators or monitoring associates. Yet these two tasks differ in difficulty, and therefore in time allocation (e.g. Lawrence 1985; R. Dukas & A. C. Kamil, unpublished data). In short, the targets of vigilance can generate differences in time spent vigilant. Animals in groups can spot predators or monitor associates, but solitary animals are restricted to the former. Thus, solitary animals may have more difficult targets for vigilance. This could mimic a group-size effect, even if predation risk for solitaries and group members were equal. For this reason, information on the targets of glances is essential to understand allocation of time to vigilance.

Unfortunately, it is very difficult to identify the targets of vigilance for most animals. The eyes of passerine birds, on which most studies of vigilance have been done (Elgar 1989), are laterally positioned, can orient independently towards near and far targets, and can survey a wide visual field (Lima & Bednekoff 1999). By contrast, primates' eyes are highly convergent with coordinated retinae containing a single fovea (Ross 1996). Thus, the direction of a glance is identifiable by the orientation of the head and pupils, while medial approximation of the pupils and other postural cues reveal range to the target (Rogers & Stafford 1993; Treves 1998a; Tomasello et al. 1999). Therefore, primates provide us with more information about targets of vigilance than most birds and mammals in the vigilance literature.

Data on the targets of primate vigilance indicate that primates spend a substantial amount of time watching associates within their own groups (Chance 1976; Keverne et al. 1978; Caine & Marra 1988; Cowlishaw 1998; Watts 1998; Treves 1999b). However, within-group vigilance has only recently received attention, in part because of the theoretical pre-eminence of predation. For example, primatologists have often excluded all glances at associates from their measurements of vigilance, because they were explicitly or implicitly studying anti-predator vigilance (Caine 1984, 1986; Wirtz & Wawra 1986; Baldellou & Henzi 1992; Gould 1996; Hardie & Buchanan-Smith 1997; Koenig 1998). This practice poses problems for several reasons.

First and most simply, exclusion of within-group vigilance in studies of primates precludes direct comparisons between primates and many nonprimates (A. Koenig, personal communication). As noted above, for most nonprimates we cannot distinguish within-group vigilance from outwardly directed vigilance. Hence, cross-taxonomic comparisons require the inclusion of within-group vigilance. Even when cross-taxonomic comparisons are not intended, within-group vigilance merits inclusion because it is frequent. Within-group vigilance is incompatible with feeding and other maintenance activities, hence excluding it will generate inaccurate estimates of scanning effort and may produce artefacts when comparing groups of different sizes. For example, individuals that differ in sex or reproductive status, or mothers whose infants differ in age often vary significantly in vigilance towards associates (Chance 1976; Keverne et al. 1978; Cowlishaw 1998; Treves 1999b). For nonprimates, similar relationships hold (Alados 1986; Waite 1987; Roberts 1988). Therefore, groups differing in size may differ in within-group vigilance because of variation in age–sex composition (Treves 1999b). Without accurate estimates of scanning effort, one cannot conclude that small groups scan more than large groups, because there is the possibility of compensation between the unmeasured component (within-group) and the measured component (outward) of vigilance. Therefore, excluding within-group vigilance will weaken conclusions about the group-size effect specifically (e.g. Hardie & Buchanan-Smith 1997).

Within-group vigilance should also be included on functional grounds, because it can affect predator detection. It may act positively or negatively, depending on the context. Within a selfish herd, escape or alert postures of associates may provide an individual with early warning. In cooperative groups, individuals may take specialized roles as sentinels and their associates then monitor the sentinels, rather than surveying the surroundings themselves (Wickler 1985; Horrocks & Hunte 1986; Rasa 1986, 1989; Ferguson 1987; Koenig 1994). Within-group vigilance may therefore contribute to predator detection. On the other hand, individuals may monitor their associates for social learning or the avoidance of conspecific threat. These functions can reduce the time available for predator detection, and thereby shape the relationship between aggregation and vigilance (Slotow & Rothstein 1995; Jones 1998; Treves 1999b).

Within-group vigilance can act in two ways to hinder detection of predators. Close associates may obstruct the visual field and block the detection of distant threats. For an animal with a narrow visual field, like a primate, monitoring associates may reduce the likelihood of detecting predators. The response might be to reduce vigilance with increasing spatial cohesion, regardless of group size. This has been observed in gulls (Burger & Gochfeld 1991). For animals with broad visual fields, the utility of a glance to associates is more difficult to assess. (Experimental techniques have been developed to measure predator detection probability under various

constraints (Lima & Bednekoff 1999), but these are elaborate and impractical for many studies.) The second way that within-group vigilance can undermine a group-size effect on vigilance is if animals monitor associates more often in larger groups (Slotow & Rothstein 1995; Jones 1998). If so, outward (antipredator) vigilance would be balanced against a countervailing within-group component (Treves 1999b). There is some evidence that within-group vigilance increases with the size of the group. For example, Knight & Knight (1986) reported that bald eagles, *Haliaeetus leucocephalus*, commonly avoid theft of food by monitoring associates. Theft increased in larger groups, so the eagles did not decrease vigilance with increasing group size (Knight & Knight 1986). A similar study of carrion-feeding marsupial carnivores found the same effect (Jones 1998). More data are needed, specifically to determine (1) whether within-group vigilance reduces predator detection probabilities; and (2) whether it increases with the severity or frequency of competition within groups. Evidence for both of these would raise the possibility that within-group vigilance can undermine the group-size effect.

The significance of within-group vigilance for primates is difficult to prove beyond its raw frequency. One captive study has shown that within-group vigilance was maintained even as it reduced an animal's ability to detect predators. Biben et al. (1989) separated squirrel monkey mothers from their juveniles and provided mothers with two vantage points for vigilance. One vantage permitted the detection of 'predators' (humans passing near the juveniles' cage), while the other one only permitted the mothers to watch the juveniles. (During noisy play, the juveniles were not alert to danger, so the mothers were not gaining early warning by watching the juveniles.) In short, mothers could not simultaneously see their juveniles and detect potential threats from outside the group (Biben et al. 1989). The authors found that the onset of play among the juveniles led mothers to increase vigilance and switch repeatedly between the two vantage points. Although within-group vigilance reduced the time available for detection of outside threats, the mothers maintained their watchfulness over the juveniles. The artificial conditions of this experiment limit our ability to generalize, but these results do testify to the importance of within-group vigilance and the willingness of some primates to balance outward and within-group scanning.

We also have evidence that within-group vigilance responds to the risk of competition and aggression within the group. For example, Watts (1998) showed that female mountain gorillas, *Gorilla gorilla*, monitor enemies longer than allies. During mating periods, male redtail guenons, *Cerrophithecus ascanius*, and red colobus monkeys, *Procolobus badius*, increase the frequency with which they glance at associates (Treves 1999b). In several species, within-group vigilance increases following births and when infants stray from their mothers (Leighton-Shapiro 1986; Maestripieri 1993; Treves 1999b; A. Treves, A. Drescher & N. Ingrisanc, unpublished data). The role of competition is also revealed when animals that differ in rank are compared. Subordinate monkeys monitor associates more than dominants (Keverne et al. 1978; Alberts 1994). Interspecific comparisons are consistent with the role of conspecific competition in shaping within-group vigilance (Caine & Marra 1988; Treves 1999b). Despite all this evidence for the role of competition, we have no data showing that within-group vigilance increases in larger groups. The only study of this question in primates found no effect of group size on within-group vigilance (Treves 1999b). However, my measure of within-group vigilance was imperfect.

We do have hints that primates face more severe conspecific threat than most of the other taxa in the vigilance literature. Conspecific attacks within many primate social groups are frequent and sometimes lethal (Dittus 1980; Collins et al. 1984; Goodall 1986; Crockett & Pope 1988; Wasser & Starling 1988). Infanticide is the most common lethal form of conspecific threat in primates, reported in at least 20 genera (Treves 1998b). When initiated by males that have taken over a group, infanticide is a within-group threat, because males stalk the mothers and infants for days or weeks while living in the same group (Struhsaker & Leland 1985; Sommer 1987). Not surprisingly, the vigilance of mothers in at least one species tracks the risk of infanticide (Steenbeck et al. 1999; see also Treves 1999b; A. Drescher, unpublished data). All of the nonhuman primates in Table 1 face infanticide, and in most cases, infanticide was observed in the same populations providing vigilance data (Leland et al. 1984; Tarara 1987; Valderrama et al. 1990; Hiraiwa-Hasegawa & Hasegawa 1991; Brockett & Horwich 1995; Rose & Fedigan 1995). Conspecific threat with severe fitness consequences occurs in nonprimates as well (e.g. Packer & Pusey 1984; Le Boeuf & Mesnick 1990), but the birds and mammals that dominate the vigilance literature do not seem to face within-group threats comparable to those faced by primates.

With the information now available it appears that primates are concerned with the actions of associates because these have serious fitness consequences. Concern with associates may detract from predator detection at times. This is particularly true for animals with narrow visual fields, like primates. In this way, within-group vigilance holds promise to explain the absence of a group-size effect on vigilance among primates.

## Assumption 3: Risk Must Decrease with Increasing Group Size

Large groups are often assumed to be safer than small groups (Lima 1990; Roberts 1996). Without a group-size effect on predation mortality, individuals should not perceive safety as a function of group size and we should not expect a group-size effect on vigilance. Below I consider factors that relate group size to risk of predation. My discussion owes much to pioneering studies (Hamilton 1971; Edmunds 1974; Curio 1976; Klump & Shalter 1984; Pulliam & Caraco 1984; Lima 1993; Bednekoff & Lima 1998a). I treat the risk of being eaten by a predator as having two distinct components. The first component reflects group-level risk, or the likelihood of a predator encounter followed by the rate of successful attacks. The

second component reflects individual probability of being killed in such a successful attack. I address these two components separately in sequence.

Considering the group as a whole, a large aggregation faces less risk than a small one, when they enjoy collective detection (fewer encounters lead to attack), and when they cooperate to deter or confuse predators (fewer successful attacks). Large aggregations face more risk than small ones when they are more conspicuous (more encounters with predators), and when members interfere with each other's vigilance and movement (more attacks and more successful attacks). The balance of advantages and disadvantages experienced by a group will vary with ecological conditions and predators. In fact, predation risk can favour small groups over large ones, under some conditions. For instance, Oro (1996) reported that Audouin's gulls, *Larus audouinii*, breeding in small subcolonies were less likely to be attacked than those in more conspicuous, larger subcolonies. This is not uncommon in birds (Caldwell 1986; Cresswell 1994). In particular, large and small groups will face equivalent risk when predators succeed despite early detection by prey (no benefits of collective detection). Consider gazelles attacked by cheetahs versus those attacked by wild dogs. Cheetahs rely on ambush and are foiled by early detection, so larger groups of gazelles have an advantage over smaller ones (FitzGibbon 1989, 1990b). By contrast, wild dogs do not rely on surprise and are therefore detected by all prey before a chase begins. Wild dogs do not preferentially hunt small or large groups of gazelles and they are equally successful against either (Fanshawe & FitzGibbon 1993). When faced by predators of this sort, large and small groups may face equal risk of encounter and successful attack.

Red colobus monkeys are commonly preyed upon by chimpanzees, a predator whose hunting tactics are similar to those of wild dogs. Hunting chimpanzees do not rely on surprise or ambush, but instead initiate hunts when their own party size is large (Boesch & Boesch 1989; Boesch 1994; Stanford et al. 1994; Stanford 1995, 1996, 1998). Red colobus usually do not attempt to flee and there is no evidence that larger groups suffer fewer successful attacks (see references above and Bshary & Noë 1997; Treves 1999a). Stanford (1998) suggests that chimpanzees preferentially attack larger groups of red colobus monkeys because these contain more immatures, their main quarry. Under these conditions one might predict that red colobus in large groups are not safer and should not lower vigilance. The effect of this on vigilance is unclear; on the one hand, he writes 'There was no correlation between group size and levels of individual vigilance' (Stanford 1998, page 524), but on the other he 'rejected . . . visual scanning as a measure of vigilance because of the number of confounding variables' (Stanford 1995, page 581). Vigilance data from another population of red colobus subject to chimpanzee predation revealed no group-size effect on vigilance, but observations of actual predation attempts were not available for the groups studied (Treves 1998a, 1999a). More research is needed to determine whether red colobus in large groups face greater risk than those in small groups.

The best data on mortality of primates due to predation reveal no group-size effects (Cheney et al. 1981; Stanford 1995). One smaller data set suggests that larger groups are more vulnerable than small ones (Wright 1998; see also Watanabe 1981). I know of no counter-example showing larger groups suffering fewer successful attacks. Yet, the rarity of observed predation on primates frustrates resolution of this question. It has led many researchers to use correlational approaches (van Schaik 1983; Anderson 1986; Treves & Chapman 1996; Hill & Dunbar 1998; Hill & Lee 1998). These generally support the hypothesis that higher predation pressure leads to larger groups. Yet, a major problem with all published correlational studies is that they rely on subjective impressions of predation risk, rather than detailed information about predator behaviour or rates of encounter (reviewed in Isbell 1994; Boinski & Chapman 1995; Boinski et al. 2000). In the absence of precise data about predator encounter rates, observed positive associations between inferred risk and group size may be shaped by open-country, terrestrial species in Asia and Africa. These associations are not conclusive because greater visibility in open habitats may increase the frequency with which neighbouring groups interact or the ability of solitary animals to gain ingress into groups. Until additional sophisticated studies of predation and primate group size are completed, it seems prudent to measure whether larger groups face lower rates of encounter and successful attack.

For individual risk of mortality during a predator attack, large groups usually present an advantage. A member of a pair is half as likely as a solitary to be killed in a successful predator attack, all else being equal (Hamilton 1971). This is referred to as dilution of risk, when individual risk declines in inverse proportion to group size.

$$\text{Individual risk} = 1/\text{Group size} \qquad (1)$$

Many empirical studies document safety through dilution (Kenward 1978; Foster & Treherne 1981; Morgan & Godin 1985; Cresswell 1994). However, before we assume that dilution of risk is a simple function of group size for all animals (equation 1), at least one condition must be met. All group members must face an equal risk of being killed.

In most vertebrate groups, individual prey are not equally attractive or vulnerable to all attacking predators. For example, 90% of cheetah attacks on mixed-species groups of Grant's, *Gazella granti*, and Thompson's, *Gazella thompsonii*, gazelles were directed at the latter (FitzGibbon 1990a). In this case, individual risk is shaped by species composition more than group size (see also Wolf 1985; Landeau & Terborgh 1986; Rasa 1989; Chapman & Chapman 1996; Bshary & Noë 1997). Similarly, sexual dimorphism and the coexistence of several age cohorts make some group members more or less vulnerable. For example, male gazelles in groups suffer disproportionate predation, because males are less vigilant, more peripheral and have fewer neighbours than females, or because they lag at the rear of fleeing groups (FitzGibbon 1990b; Fanshawe & FitzGibbon 1993). Typically, immature prey

are at greater risk of predation (Schaller 1972; FitzGibbon & Fanshawe 1989; Rasa 1989; Forslund 1993). For example, immature red colobus comprise 75% of the victims of chimpanzee attacks (Stanford et al. 1994). In such a case, the vigilance of older animals may not reflect their own personal risk but that of the young (Rasa 1989; Forslund 1993). Even if all individuals are equally attractive to a predator, not all of them will be equally accessible (Hamilton 1971). For instance, arboreal primates positioned at terminal branch tips are more vulnerable than those within the canopy (Peres 1990). In short, dilution of risk often reflects predator behaviour and its interaction with prey group composition and individual exposure, rather than group size.

Group size will be an imperfect index of individual risk when predators preferentially kill a subset of group members, and when large groups encounter more predators or face more successful attacks. Currently, we have little more than anecdotes warning us about the use of group size as an index of individual risk. However, vigilance studies themselves provide further reason to be cautious about the use of group size. Although numerous studies find that group size predicts per capita vigilance, typically only 10–30% of the variation is explained (Elgar 1989; Blumstein 1996). If we wish to explain more variation between individuals and groups, we may need to consider other parameters of aggregation.

### Other Parameters of Aggregation

Many studies of vigilance do not examine internal features of groups (individual vulnerability, or group dispersion, composition and geometry) rendering conclusions about group size less convincing (Elgar 1989; Catterall et al. 1992; Pöysä 1994; Treves 1998a; Bahr & Bekoff 1999). In a variety of taxa, individual vigilance is strongly influenced by individual position within the group, spatial geometry of the group, interindividual proximity and distance to refuge (Lazarus 1978; Inglis & Lazarus 1981; Elgar et al. 1984, 1986; Burger & Gochfeld 1991; Lazarus & Symonds 1992; Pöysä 1994; Bekoff 1995; Cowlishaw 1997; Sadedin & Elgar 1998; Steenbeck et al. 1999). In several cases, group-size effects persist when these other variables are controlled (e.g. Caraco et al. 1980; Lima 1987; Bednekoff & Ritter 1994; Frid 1997). In other cases, group-size effects disappear when group composition, interindividual proximity and spatial geometry are taken into account (Colagross & Cockburn 1993; Isbell & Young 1993; Pöysä 1994; Rose & Fedigan 1995; Bahr & Bekoff 1999). Because of the multiple factors shaping vigilance, studies that examine group size alone are inadequate to describe the relationship between vigilance and aggregation.

Interindividual proximity is particularly important to primates. All the studies that report the effect of isolation or interindividual proximity have found lower vigilance when animals are close to associates (e.g. Robinson 1981; van Schaik & van Noordwijk 1989; Steenbeck et al. 1999). In the studies that measured both, interindividual proximity exerted effects independently of group size (Rose & Fedigan 1995; Cowlishaw 1998; Treves 1998a, 1999c; Treves et al., unpublished data). To date, we have no experimental evidence that proximity to associates increases individual safety, but there are strong theoretical grounds for expecting such a relationship (Hamilton 1971). If denser groups are safer, regardless of their size, we should expect a weak group-size effect on vigilance or none at all.

Group size may not be the best index of individual risk of predation and therefore individual vigilance. Larger groups are not always safer. Even the benefits of dilution of risk in large groups are reduced and complicated when predators preferentially select a subset of group members. Several primate populations face conditions that reduce the safety provided by membership in a large group. This may help to explain the absence of a group-size effect on vigilance among primates. Unfortunately, too few studies measure individual risk of predation, or compare group size to other parameters of aggregation when measuring vigilance.

## DISCUSSION

This review addresses the relationship between vigilance and aggregation with particular attention to the prediction that individual vigilance declines with increasing group size. Contrary to most other animals studied, primate behaviour is not consistent with the prediction (Table 1). Indeed, primates behave as if large groups were as safe as small ones. Thus, I used primate vigilance behaviour as a means to test three assumptions about vigilance and aggregation. The first assumption was that vigilance was costly. I tested whether manual harvesting and upright processing of food as seen among primates might permit them to feed and scan simultaneously. This idea was contradicted by a simple comparison of four species of primates that differ in feeding behaviour. Next I evaluated whether information on the targets of scanning might shed light on primate vigilance behaviour. I found that one component of vigilance, within-group vigilance, might explain the differences between primates and other animals in the vigilance literature. Finally, I evaluated the assumption that larger groups face a lower risk of predation than smaller groups. By separating group-level from individual-level risk, I was able to identify several circumstances in which group size would not predict individual risk or vigilance. In summary, I found two major functional explanations that can account for the absence of a group-size effect on vigilance among primates. These functional explanations are summarized below and testable predictions are made for nonprimates. In the last section, I review explanations based purely on the methodology used by primatologists.

### Within-group Vigilance

The activities of associates can divert individual vigilance away from the surroundings to events within groups. This may reduce predator detection ability or escape probability, if associates block one's view of the surroundings, or if investment in vigilance toward one

target reduces the time available for others. Primates seem to face a unique challenge in balancing antipredator vigilance with within-group vigilance, because they have narrow visual fields and face frequent or severe threats from associates. Generalizing from these findings, we should expect deviations from the predicted group-size effect on vigilance when: (1) animals have convergent eyes or otherwise narrow visual fields (e.g. cats, owls); (2) animals display a positive relationship between group size and the frequency or severity of conspecific competition (e.g. animals feeding in dense groups: Knight & Knight 1986; Jones 1998); or (3) animals use a sentinel system in which most group members do not detect predators themselves but rely on associates (e.g. dwarf mongooses, *Helogale parvula*, Rasa 1989; sparrow-weavers, *Plocepasser mahali*, Ferguson 1987). This may vary with the number of sentinels contributing their time to group defence (Savage et al. 1996; Koenig 1998).

## Safety in Groups

The risk that a predator encounters and attacks a group successfully depends on that group's conspicuousness and ability to detect and evade attack. When faced with predators that do not rely on surprise, large groups lose most of the benefit of collective detection and face a disadvantage if they are more conspicuous than small groups. The risk that a given individual is killed during a successful attack declines with increasing group size, all else being equal. All else is not equal when a group contains a mix of species, sexes, age classes or safe and vulnerable individuals. Under these common circumstances, group size per se will not adequately measure individual risk. Primates often seem to face the conditions described above. I cited cases in which immatures or adult males were most vulnerable, and cases in which predators attacked without relying on surprise. Unfortunately, quantitative studies of predation on primates remain elusive. However, based on the logic laid out here, we should expect deviations from the predicted group-size effect on vigilance among: (1) animals that face predators that do not rely on surprise, or animals that live in groups whose conspicuousness increases significantly with group size; (2) animals that differ significantly in vulnerability to predators (e.g. buffalo faced by lions: Scheel 1993; geese with goslings: Forslund 1993; dwarf mongooses using sentinels: Rasa 1989); (3) animals that form groups so dense and obstructive that they impede vigilance of members (e.g. gulls: Burger & Gochfeld 1991); or (4) animals that face very low predation pressure (e.g. teal: Pöysä 1994; chimpanzees: Treves 1997).

Although within-group vigilance and the decoupling of group size and predation risk have the potential to explain the absence of a group-size effect on vigilance among primates, there remain concerns about the methods used in primate studies. The most common mistake I found was the exclusion of within-group vigilance. This reflects an erroneous assumption about predator detection strategies and obscures the importance of conspecific threat in shaping primate vigilance. As an assumption about vigilance, it forms part of a more general problem stemming from uncertainty about the targets of glances. Although the exclusion of within-group vigilance plagues primate studies, this cannot explain the lack of a group-size effect on vigilance. All but one of the studies in Table 1 (Wirtz & Wawra 1986) included within-group vigilance. In the same vein, exclusion of brief glances (Table 1) was only used in three studies, thus this cannot explain the pattern. Therefore we must look elsewhere to explain differences between primates and other animals.

Another explanation for the absence of a group-size effect on vigilance among primates centres on the size of the groups studied in Table 1. Many of these groups contained more than 10 animals, and therefore exceeded the size that would generate large intergroup differences in per capita vigilance (Quenette 1990). This is a serious problem. The first study in Table 1 (black howlers, *Houatta pigra*) was designed to address this problem explicitly. Groups of this species range in size from 2–10 animals, the range that should show dramatic differences in per capita vigilance. However, no group-size effect was found (Treves et al., unpublished data). This upholds the claim that primates generally do not display a group-size effect on vigilance, but more studies are needed to confirm this, including revisits to populations that showed such an effect.

In conclusion, vigilance and aggregation are related in complex ways that reflect the fundamental costs and benefits of group-living. This review has identified socio-ecological features that will lead animals to scan their surroundings without regard to group size. For those studying nonprimates, attention to parameters of aggregation other than group size is essential, as is attention to the targets of vigilance. For primatologists, the unusual features of primate vigilance behaviour provide exciting avenues for future research, but they also require rigour both in testing assumptions transferred from other taxa and in research design.

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