Why individual vigilance declines as group size increases

GILBERT ROBERTS

Department of Zoology, University of Melbourne, Australia

Abstract. A reduction in individual vigilance with an increase in group size is one of the most frequently reported relationships in the study of animal behaviour. It has been argued that this phenomenon may not be a direct consequence of an increase in group size but may be due to other factors relating to increased group size, such as increased foraging competition. However, there is evidence for a direct relationship between group size and vigilance where other variables have been controlled. The aim of this review is to highlight the fact that the functional explanation of the group size effect remains unclear. Some authors have considered just one hypothesis, the group vigilance or 'many eyes' hypothesis. This states that, by taking advantage of the vigilance of other group members, individuals can reduce their own vigilance. However, there is an alternative, or additional, possibility that if individual vigilance declines with a reduction in individual predation risk, the group size effect could be accounted for by a reduction in individual risk at higher group sizes, as is widely thought to occur through encounter, dilution and confusion effects. In this review, it is shown that evidence previously interpreted in terms of one hypothesis may also be interpreted in terms of the other. Future research should be directed towards explicit consideration of the two effects and empirical tests to distinguish their relative importance. It is proposed that the individual risk hypothesis, with group vigilance as one element, provides a more general framework for understanding variation in vigilance behaviour with group size and with other factors.

© 1996 The Association for the Study of Animal Behaviour

A reduction in individual vigilance with increasing group size is one of the most frequently reported relationships in the field of animal behaviour (see reviews in Barnard & Thompson 1985; Elgar 1989; Lima 1990; Lima & Dill 1990; Quenette 1990). However, in spite of a large number of published studies on the subject, the functional interpretation of this decline remains poorly understood.

There are two main hypotheses to explain the widespread existence of an inverse relationship between group size and vigilance ('the group size effect' e.g. Lima 1995). In a highly influential paper, Pulliam (1973) advanced the hypothesis that animals benefit by flocking because the vigilance of flock-mates leads to an increase in the probability of detecting a predator within the time it takes to attack. I refer to this as the 'group

vigilance hypothesis'. It has also been referred to as a 'many eyes effect' (e.g. Powell 1974), as a 'collective detection effect' (Lima 1995) and as a 'detection effect' (e.g. Dehn 1990, but not as in Lima 1995). It states that individuals in larger groups can enjoy the same or improved predator detection rate while scanning less frequently and having more time to feed (e.g. Pulliam 1973).

I also examine another hypothesis. If vigilance depends on predation risk and if that risk declines with increasing group size, vigilance should also decline with increasing group size. The possibility of such an effect has been considered by Bertram (1978), Pulliam et al. (1982), Packer & Abrams (1990), Lima (1990), Dehn (1990) and McNamara & Houston (1992).

There is a third possibility in the form of the familiar caution that correlation does not imply causation. Elgar (1989) concluded that 'most if not all studies fail to adequately demonstrate an unambiguous relationship between vigilance behaviour and group size'. A reduction in vigilance with increasing group size might arise

Correspondence and present address: G. Roberts, Department of Psychology, University of Newcastle, Newcastle upon Tyne NE1 7RU, U.K. (email: GILBERT.ROBERTS@DURHAM.AC.UK)

if group size relates to some other factor which in turn affects vigilance. For example, larger groups may tend to feed on better food supplies and animals feeding on better food supplies may spend less time on other activities such as vigilance. Other potentially confounding effects include distance from cover, age, sex and observer proximity (Elgar 1989). Recent studies have addressed these concerns by measuring or controlling some or all of these factors (Burger & Gochfeld 1992; Catterall et al. 1992; Lazarus & Symonds 1992; Cresswell 1994; Pöysä 1994; Roberts 1995). All except Catterall et al. (1992) found a reduction in individual vigilance with increasing group size, although Pöysä (1994) found that this was due to an effect of neighbour distance. Most recent studies are therefore consistent with the earlier work of, for example, Caraco (1979), Lazarus (1979), Barnard (1980) and Bertram (1980).

An additional potentially confounding factor not considered by Elgar (1989) is that the perceived level of risk of attack may decline with the passing of time at a site without the appearance of a predator, while groups may build up through that time. This possibility may be eliminated by recording the vigilance of individuals in both increasing and decreasing groups. One study which does this is Roberts (1995) where individual preening crested terns, *Sterna bergii*, responded to flock arrivals by increasing their inter-scan intervals and to flock departures by decreasing their inter-scan intervals.

If it is accepted that there is evidence for a direct relationship between group size and vigilance, then there remains the question of its functional explanation. In a recent investigation of the group vigilance advantages of flocking, Lima (1995) concluded that his results may not have fit the predictions of the group vigilance hypothesis because a dilution of risk may also be an important factor in the group size effect. This echoed Lazarus' (1979) comment that part of the group size effect may be due to a reduced risk of capture in larger groups. Given this lack of progress, it is timely and pertinent to ask whether the group vigilance hypothesis is an adequate explanation for a reduction in vigilance with increasing group size and whether the individual risk hypothesis provides an alternative or additional explanation.

It is particularly pertinent to ask this question given that the review by Elgar (1989), although widely cited as a general review of relationships between group size and vigilance, interpreted the evidence solely in terms of the group vigilance hypothesis. No consideration was given to other hypotheses such as the individual risk hypothesis. Thus, even if all workers direct their research so as to control for the confounding effects listed by Elgar (1989) and others such as time at a site and flock density, the hypothesis that increased group size provides better detection will remain untested. It will remain a possibility that increased group size does not provide better detection but reduces the pressure to be vigilant. The object of this review is to focus attention on the fact that, in spite of the large literature on vigilance behaviour, there remains a lack of understanding of the selective factors involved in the group size effect. It may be that this lack of progress is due to the apparent lack of awareness among authors such as Elgar (1989) that there are alternative functional explanations.

My aims in this paper are to highlight the fact that there are alternative explanations of the group size effect, to evaluate critically the evidence to show where it is open to alternative interpretations, to encourage explicit consideration of the two hypotheses in vigilance research, and to present some ideas as to how group vigilance and predation risk effects may be distinguished.

TESTS OF THE PULLIAM (1973) MODEL

Pulliam's (1973) model of how group detection of a predator may be expected to vary in relation to group size remains influential and most later models of vigilance behaviour can be understood as developments of this model (Pulliam et al. 1982; Hart & Lendrem 1984; Parker & Hammerstein 1985; Kaitala et al. 1989; Lima 1989; Packer & Abrams 1990; McNamara & Houston 1992). As originally formulated it described the probability of at least one member of a group detecting a predator in terms of individual vigilance rates, group size and predator approach time.

Several studies have tested the Pulliam (1973) model (see Elgar 1989 for a review). As initially presented, the model gave expected probabilities of group detection given individual vigilance levels but the model may be rearranged to predict scanning frequency in terms of group size (e.g.

Elgar & Catterall 1981). If both the time for a predator to make its final approach and the probability that at least one member of the group will detect a predator are assumed to remain constant across group size, then the scan rate should equal the reciprocal of group size multiplied by a factor depending on group detection and approach time (Elgar & Catterall 1981). Thus, the model has been widely interpreted as predicting an inverse relationship between group size and vigilance. That is to say, given a constant level of group (or 'corporate') vigilance, individual vigilance may be decreased with increasing group size. Elgar & Catterall (1981) found an approximate fit to a curve representing the reciprocal of group size; however, scan rates were lower than predicted for small group sizes. Returning to the original form of the model, Elgar & Catterall (1981) used observed scan rates to calculate that the probability of group detection increased with group size. Thus, a fit could be found to the model by relaxing the initial assumption that group detection remained constant. But allowing both sides of the equation (detection and individual vigilance) to vary with group size makes the model difficult to falsify.

The problem of falsification is also highlighted by the study of Catterall et al. (1992) which reported no relationship between group size and individual vigilance of silvereyes, *Zosterops lateralis*. The authors considered a series of reasons why the Pulliam model might fail to hold in the case of their study. In fact, their result cannot be interpreted as falsifying the Pulliam (1973) model because the model does not state that vigilance should decline with group size. There is a range of ways in which individuals might trade off detection and investment in vigilance. At one extreme they might maintain their levels of vigilance regardless of group size, benefiting from the increase in the probability of group detection. At the other extreme they might reduce their levels of vigilance such that the probability of group detection is a constant, with advantages arising through increased foraging time. Or, they may reduce their vigilance levels rather less, such that they benefit in part from an increase in group detection and in part from a decrease in time invested in vigilance. Thus, any of a range of relationships between group size and vigilance may be consistent with the model, including the lack of a relationship, as found by Catterall et al. (1992). In fact, Catterall

et al. (1992) concluded that their results may have provided support for Pulliam's (1973) model for another reason: the lack of predators on the island study site. However, as no relationship between group size and vigilance is the null hypothesis, it cannot be concluded that the lack of a relationship is due to the absence of predation.

Other problems with the Pulliam (1973) model have been discussed elsewhere (e.g. Lima 1990). These include the perception of group size, awareness of the vigilance of others, the object of vigilance, and competition for food. However, even if the Pulliam (1973) model were to be rejected it would not necessarily entail rejection of the concept of group vigilance (Lima 1990).

VIGILANCE IN RELATION TO PREDATION RISK

Vigilance may have a number of functions in obtaining information about the environment (e.g. Lima 1990). Nevertheless, it is clear that predator detection is a major function in many species. As such, one would expect vigilance to increase with the risk of predation. In accordance with this, there are numerous observations of increases in vigilance on or after exposure to a predator (e.g. Powell 1974; Caraco et al. 1980; Lendrem 1983; Sullivan 1984; Gluck 1987; Pöysä 1987).

An individual's risk of predation depends on the predator attack rate, the probability of detecting a predator given that the group is attacked, and the probability of escaping given the attack and detection probabilities. Each of these may vary with group size. I discussed the relationship between group size and predator detection above. But vigilance may depend not only on group detection probability but also on other aspects of predation risk (e.g. Dehn 1990). It is generally accepted that a reduction in predation risk is an important benefit of grouping (e.g. Krebs & Davies 1993). Predator attack rate depends on an 'encounter effect' (e.g. Turner & Pitcher 1986; Inman & Krebs 1987), that is, larger groups may be more likely to be detected by a predator but this increase is unlikely to keep pace with an increase in group size. The probability of an individual escaping, given that a group is attacked

by a predator, depends on the 'dilution effect'. That is, in a larger group an individual has a lower chance of being taken (e.g. Turner & Pitcher 1986; Inman & Krebs 1987). The combined effects have been referred to as an encounter-dilution effect (Mooring & Hart 1992). Evidence for such effects has been found in monarch butterflies, *Danaus plexippus* (Calvert et al. 1979), ocean skaters, *Halobates robustus* (Foster & Treherne 1981) and redshanks, *Tringa totanus* (Cresswell 1994). If encounter and dilution effects lead to a reduction in predation risk in larger groups, then the group size effect could be explained by postulating that vigilance increases with predation risk. That is, individual vigilance may be lower in larger groups because individual predation risk is lower. Reduced predation risk as a factor affecting vigilance has been considered by Bertram (1978), Pulliam et al. (1982), Packer & Abrams (1990), Lima (1990), Dehn (1990) and McNamara & Houston (1992). A complicating factor in relating vigilance to predation risk is that vigilance might actually be reduced in order to lessen the feeding time when the animals are most exposed to predators (Lima 1987a).

A dilution effect predicts that vigilance should be dependent upon the reciprocal of group size. As this prediction is similar to that of the Pulliam (1973) model with constant group detection, the two hypotheses are difficult to distinguish. However, Dehn (1990) suggested that group vigilance (or 'detection') should have a $1/N$ effect while dilution should have a $\ln(N)/N$ effect, where N represents group size. The difference arises from the assumption that dilution is relevant only if detection fails, an assumption whose validity will depend on the particular predator–prey situation. A model incorporating both detection and dilution effects explains more of the variance in the group size–vigilance relationship of foraging elk, *Cervus elaphus*, than does a solely detection based model and therefore provides some evidence of the importance of both effects (Dehn 1990).

McNamara & Houston (1992) took the model further by incorporating separate terms for the probability of death (1) when no animal detects a predator, (2) when another animal detects a predator and (3) when the animal itself detects a predator. Further empirical work is required to test such models. However, as McNamara & Houston (1992) pointed out, there are multiple

dependencies on group size in such models, making them difficult to test.

GROUP SIZE AND PREDATOR DETECTION

Although Pulliam (1973) was largely concerned with showing how increased group size could lead to improved predator detection, or 'early warning' (Lazarus 1979), the number of studies providing evidence of an increase in predator detection with increased group size (Powell 1974; Siegfried & Underhill 1975; Kenward 1978; Lazarus 1979; van Schaik et al. 1983; Cresswell 1994) is much smaller than the number demonstrating a reduction in individual vigilance with increasing group size. This may reflect the relative difficulty of demonstrating improved detection. Evidence in these studies comes from earlier detection or an increase in the probability of detection. Perhaps the most compelling evidence comes from Cresswell (1994) who found that redshanks in small groups suffered high mortality, apparently as a result of late detection of aerial predators.

Other studies have used the Pulliam (1973) model to calculate the probability of a group member detecting a predator while it makes its final uncovered approach, on the basis of observed individual vigilance levels. In a number of studies the probability of detection increases with group size, even where individual vigilance declines (e.g. Pulliam et al. 1982; Lima 1987b). Elgar & Catterall (1981) found the calculated increased probability of detecting a predator to be small and concluded that the major benefit from joining a group came through a reduction in time spent in predator vigilance. However, this presupposes how an animal scales the value of increased feeding time against the value of increased predator detection. Even in those studies where detection does increase, the effect declines as group size increases. An extreme example is Pöysä's (1987) finding that groups of more than two teal *Anas crecca*, would gain no advantage in detection. However, if the probability of detecting a predator decreases only a little, say from 0.95 to 0.90, then the probability of detecting each of 10 predators decreases considerably, from 0.60 to 0.31. Furthermore, these studies consider detection not as how soon the predator is detected but as the probability of detection within a certain time

period (corresponding to the time during which the predator makes its final uncovered approach). If it is advantageous not just to detect a predator within a certain time, but also to detect the predator as soon as possible, then it is more likely that larger groups will continue to be beneficial.

While the concept of group vigilance can explain a reduction in individual vigilance, it cannot explain a reduction in corporate vigilance. Quenette & Gerard (1992) were unusual in finding such a reduction in wild boar, *Sus scrofa*. Cresswell (1994) also found a reduction at very high group sizes. Although these authors did not interpret these results in such terms, it is possible that at high group sizes vigilance is responding not to the probability of detection but to predation risk: if risk is low, there is less need to look out for a predator. However, it is difficult to provide a demonstration of lower detection at higher group sizes independent of the detection rate calculated from observed individual vigilance. What appears to be lower detection may be due to lower perceived risk and hence delayed response.

CONSEQUENCES OF REDUCED INDIVIDUAL VIGILANCE

The Pulliam (1973) model depends on what Lima (1995) refers to as 'collective detection', the 'social transmission' of the detection (Lazarus 1979). A common observation is that if one member of a group detects a predator, an alarm call is given and the whole group is alerted (e.g. Pulliam 1973). Therefore, only one individual need detect a predator for all to benefit. The idea of social transmission has received support from a number of studies (e.g. Godin et al. 1988). However, its generality has recently been questioned. In a series of experiments involving 'ball attacks' which only one individual could detect, Lima (1995) found limited evidence for social transmission of the detection. It appears that, at least in species without alarm calls, multiple detections may be required in order to elicit a flight response from non-detectors (Lima 1994a).

Related to the idea of collective detection is the assumption that an individual values the vigilance of other group members as equivalent to its own vigilance. However, there is evidence of advantages associated with individual vigilance in that sparrows which were vigilant at the time of an alarm stimulus responded more quickly than birds with their heads down (Elgar et al. 1986). Lima (1994b) has shown that vigilant birds which could not have detected an approaching ball nevertheless flushed more quickly than non-vigilant birds in response to the alarm flight of a detecting bird. Thus, individual vigilance, even without detecting the source of danger, was advantageous. An advantage of being vigilant has also been demonstrated by FitzGibbon (1989): cheetahs, *Acinonyx jubatus*, chased those Thomson's gazelles, *Gazella thomsoni*, that were less vigilant. Such studies demonstrate that the vigilance of other group members cannot be valued as highly as an individual's own vigilance, as is assumed by the Pulliam (1973) model. However, although such findings are inconsistent with the model, it remains possible that there is a more limited group vigilance effect. The value of an individual's own vigilance relative to the vigilance of another group member will be an important factor determining the shape of any group size and vigilance relationship (McNamara & Houston 1992).

As individual vigilance declines, more time becomes available for other activities. Most studies of vigilance have found an increase in feeding time as vigilance declines. This is because in most studies feeding and vigilance are mutually exclusive activities and account for a large proportion of the time budget. However, few studies have measured whether there is an increase in intake resulting directly from a reduction in vigilance. Cresswell (1994) found that, while redshanks increased their pecking rates as vigilance declined, their intake did not increase: they simply increased the number of unsuccessful pecks. Such results suggest that an increase in time for other activities may not be an important advantage of reduced vigilance and that this increased time is simply a by-product of a reduced need to be vigilant. That is, many studies concluded that reduced vigilance, whether through group vigilance or predation risk effects, brings foraging advantages, yet the main advantage of grouping may in fact be increased predator detection or reduced predation risk. The lower vigilance of animals in large groups may simply reflect a lower need to be vigilant because of reduced predation risk and thus the animals do not perform a behaviour of little or no value. Or, if vigilance is costly in terms other than time lost from feeding, there may be other advantages in reduced

vigilance. The way in which benefits associated with reduced vigilance are manifested is important in understanding the selection pressures involved. Furthermore, it is fundamental to the models of McNamara & Houston (1992), which are based on time spent feeding as a currency in which costs of vigilance are measured. It appears logical that there should be a trade-off between activities but in practice it is not clear that this trade-off provides a useful basis for predicting behaviour. This may be because animals are not always time-limited.

GROUP DENSITY AND POSITIONAL EFFECTS

Groups of animals are often irregularly spaced and difficult to define. From an observer's point of view this can lead to measurement of the number of birds within a certain radius of the focal bird rather than absolute group size (e.g. Metcalfe 1984a, b) Similarly, from the animal's own perspective, behavioural decisions may be made on the basis of the number of birds within a certain proximity. If animals do respond to group density, then this might be either because they are using group density as a convenient indicator of group size, or because group density is actually of more functional significance than group size.

Few studies have investigated the effects of group density on vigilance (Lazarus 1978; Elgar et al. 1984; Holmes 1984; Roberts 1988; Pöysä 1994). All found that vigilance increased as neighbour distance increased. In a recent study in which the effects of both group size and density were considered, Pöysä (1994) found that group size did not relate to vigilance when neighbour distance was controlled for, whereas neighbour distance did have an effect after controlling for group size.

Such a density effect is understandable in terms of the group vigilance hypothesis: information about whether other group members have detected a predator is easier to obtain from nearer individuals (Pöysä 1994). Thus, nearer individuals make better 'vigilance mates'. But a density effect on vigilance is also consistent with a 'selfish herd' (Hamilton 1971) explanation whereby animals are less at risk when density around them is greater. Edge effects, whereby animals on the edge of a group are more vigilant (e.g. Lazarus 1978; Jennings & Evans 1980; Inglis & Lazarus 1981) are also consistent with both a selfish herd explanation and an explanation based on the availability of vigilance mates.

DISTINGUISHING GROUP VIGILANCE AND PREDATION RISK EFFECTS

The group vigilance hypothesis is difficult to distinguish from the predation risk hypothesis because the two make similar predictions. In fact, the two hypotheses are not mutually exclusive alternatives. Detecting a predator is just one element of avoiding predation and so the group vigilance effect can be seen as one aspect of predation risk. This leads to difficulties of interpretation. For example, Cresswell (1994) found that although larger groups of redshanks were preferentially attacked, individual risk of attack decreased with increasing group size. Furthermore, the probability of being captured declined with increasing group size. He concluded that redshanks benefit from grouping primarily through the dilution effect (or, more precisely, through a combination of encounter and dilution effects). However, the finding that predators were more successful in attacking small groups and that late or no detection was the cause of many of these captures, suggests that the reduction in capture probability may have been due to a group vigilance effect. That is, if predators are more successful in attacking birds in smaller groups, they may attack birds in small groups preferentially. Thus, the reduction in predation risk associated with grouping may not come through dilution per se but through the vigilance benefits of large groups putting predators off attacking them at a rate proportional to group size.

In perhaps the only empirical study to attempt to distinguish group vigilance and individual risk effects, Dehn (1990) found a good fit to a model in which non-vigilant individuals were considered to contribute to lowering individual risk through dilution but not to group vigilance. He concluded that both group vigilance and dilution effects were important, group vigilance being particularly important at small group sizes and a dilution effect continuing to be important at higher group sizes. Packer & Abrams (1990) and Lima (1990)

also showed theoretically that dilution of risk with increasing group size can account for much of the group size effect. However, tests relying on quantitative fits to models may be impossible to achieve if vigilance serves functions additional to that of detecting predators, while qualitative fits may provide only a weak test. Lima (1990) considered problems in testing vigilance models.

There is a clear need for studies that distinguish group vigilance and predation risk effects. If birds benefit from the vigilance of others, as embodied in the group vigilance hypothesis, then speed or probability of predator detection should increase with flock size. As discussed above, this has been tested before. However, more studies are needed in order to determine how widespread an effect this is. One problem is the possibly confounding effect that at larger group sizes individuals may respond more slowly because their risk of predation is diluted. Thus, an alternative test of the advantages of group vigilance would be to carry out an experiment to measure the speed with which flocks of different sizes detect a stimulus indicating the availability of food. Such evidence is important because it indicates a group vigilance advantage more unambiguously than does the opposite side of the coin, the reduction in individual vigilance with increasing group size.

Higher vigilance in the presence of, or after exposure to, a predator is a common observation referred to above. It could be hypothesized that vigilance in the presence of a predator should not only be greater than in the absence of a predator but may not show the same relationship with group size. As the risk that a member of the group will be taken increases with the appearance of a predator, detection may become less important relative to dilution of risk. Thus, a distinction might be made between vigilance at some background level and vigilance that is a response to something that has been observed. Only the former may be expected to respond to group size by the group vigilance effect: once all members of the group have become aware of the danger and are more vigilant, it is less clear that a group vigilance effect should reduce individual vigilance with increasing group size. However, it would be predicted that individual vigilance in the presence of a predator should decline with group size according to a dilution effect. If the two types of vigilance can be distinguished observationally, for example by distinguishing head movements

angled towards a predator, then the relationships of the two types of vigilance with group size could be investigated in the presence and absence of a predator.

Some species show signs of apparently having detected a predator. For example, several species of rails (Rallidae) flick their tails (e.g. Alvarez 1993), Thomson's gazelles stot (Caro 1986). Tail flicking may be an indicator of perceived predation risk. If so, it would provide an interesting model system for investigating the relationship between how vigilant an animal is and how great is the risk it perceives. This relationship between risk and vigilance is fundamental to the hypothesis that a decline in vigilance may result from a decline in risk with increasing group size.

One method for distinguishing the two hypotheses depends on the inference from the group vigilance hypothesis that advantages arise from the vigilance of other group members as opposed to their mere presence, as is the case in the individual risk hypothesis. Thus, on the basis of the group vigilance hypothesis, it may be predicted that a focal individual should not reduce its vigilance in line with the number of other group members if those individuals are not vigilant. A recent study involving birds that were food-deprived and therefore less vigilant than others is relevant here. Although he was actually testing a contrasting prediction, that animals should respond in a Tat-for-Tat manner to the behaviour of others (Pulliam et al. 1982), Lima (1995) found no evidence for 'behavioural monitoring', that is, for modifying vigilance according to the vigilance of other group members. This study is therefore consistent with the individual risk hypothesis and not the group vigilance hypothesis.

A related test would be to study birds that had different levels of vigilance because they were performing different activities (feeding, preening, roosting, standing vigilant). Birds standing vigilant may be expected to contribute more to any group vigilance effect than roosting birds so, according to the group vigilance hypothesis, the reduction in vigilance with increasing flock size should be less where more of the flock are roosting. According to the individual risk hypothesis, all flock members contribute to a reduction in risk, whether they are vigilant or not. In fact, the less vigilant members may contribute more to a reduction in risk of the other birds because they

may be slower to respond and so be more likely to be taken by the predator. Thus, the two hypotheses make opposing, testable predictions. A similar test could be carried out in situations where certain classes of individuals (e.g. males) were known to have consistently higher vigilance than others: according to the group vigilance hypothesis, the presence of the more vigilant class should have a greater impact in reducing individual vigilance than the presence of the less vigilant class.

Another way in which individuals may differ in their value as vigilance mates is if some animals cannot contribute to group vigilance because their vision is obscured, for example by having a partially roofed feeding station. According to the detection hypothesis, animals in an exposed position should reduce their vigilance according to the number of other animals in exposed positions, and not according to the number that have no value in group vigilance because they are in positions from which they would be unable to detect a predator. According to the individual risk hypothesis, vigilance should be reduced according to the total number of animals present.

Conversely, it is possible to imagine situations where individuals vary in their contribution to diluting other individuals' risk of attack. If the predominant risk to a group comes from one side, then provided all individuals are in a position to detect the predator, they should be of equal value in reducing the vigilance of some focal individual. However, individuals between the focal individual and the predator should be of greater value in diluting a focal individual's risk, a prediction that could be tested by determining whether a focal individual's vigilance was more responsive to the number of birds between it and the predator than to the total group size.

An extreme case of benefiting from the vigilance of others is where some individuals act as sentinels (e.g. McGowan & Woolfenden 1989). The significance of sentinel behaviour in this discussion is that here it is clear that advantages arise from associating with sentinels specifically because of their vigilance rather than simply through diluting individual risk. If non-sentinels retain some vigilance, one would predict by the group vigilance hypothesis that this vigilance should decline with an increase in the number of sentinels rather than total group size, as would be predicted on the basis of a simple dilution of risk.

Despite the considerable research effort into vigilance behaviour, it remains to be seen how important are advantages obtained through shared vigilance as a factor influencing individual vigilance and as a factor affecting gregariousness. Future work should develop a general framework in which group vigilance is considered as one of a number of factors affecting individual vigilance behaviour through an individual's risk of predation.

REFERENCES

Alvarez, F. 1993. Alertness signalling in two rail species. *Anim. Behav.*, **46**, 1229–1231.

Barnard, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.*, **28**, 295–309.

Barnard, C. J. & Thompson, D. B. A. 1985. *Gulls and Plovers: The Ecology of Mixed Species Feeding Groups.* London: Croom Helm.

Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Oxford: Blackwell Scientific Publications.

Bertram, B. C. R. 1980. Vigilance and group size in ostriches. *Anim. Behav.*, **28**, 278–286.

Burger, J. & Gochfeld, M. 1992. Effect of group-size on vigilance while drinking in the coati, *Nasua narica*, in Costa Rica. *Anim. Behav.*, **44**, 1053–1057.

Calvert, W. H., Hendrick, L. E. & Brower, L. P. 1979. Mortality of the monarch butterfuly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. *Science*, **204**, 847–851.

Caraco, T. 1979. Time budgeting and group size: a test of a theory. *Ecology*, **60**, 618–627.

Caraco, T., Martindale, S. & Pulliam, H. R. 1980. Avian time budgets and distance to cover. *Auk*, **97**, 872–875.

Caro, T. M. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Anim. Behav.*, **34**, 663–684.

Catterall, C. P., Elgar, M. A. & Kikkawa, J. 1992. Vigilance does not covary with group size in an island population of silvereyes (*Zosterops lateralis*). *Behav. Ecol.*, **3**, 207–210.

Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Anim. Behav.*, **47**, 433–442.

Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.*, **26,** 337–342.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.*, **64,** 13–33.

Elgar, M. A. & Catterall, C. P. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. *Anim. Behav.*, **29,** 868–872.

Elgar, M. A., Burren, P. J. & Posen, M. 1984. Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). *Behaviour*, **90,** 215–223.

Elgar, M. A., McKay, H. & Woon, P. 1986. Scanning, pecking and alarm flights in house sparrows (*Passer domesticus* L.). *Anim. Behav.*, **34,** 1892–1894.

FitzGibbon, C. D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.*, **37,** 508–510.

Foster, W. A. & Treherne, J. E. 1981. Evidence for the dilution effect and the selfish herd from fish predation on a marine insect. *Nature, Lond.*, **293,** 466–467.

Gluck, E. 1987. An experimental study of feeding, vigilance and predator avoidance in a single bird. *Oecologia* (*Berl.*), **71,** 268–272.

Godin, J.-G., Classon, L. J. & Abrahams, M. V. 1988. Group vigilance and shoal size in a small characin fish. *Behaviour*, **104,** 29–40.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31,** 295–311.

Hart, A. & Lendrem, D. W. 1984. Vigilance and scanning patterns in birds. *Anim. Behav.*, **32,** 1216–1224.

Holmes, W. G. 1984. Predation risk and foraging behaviour of the hoary marmot in Alaska. *Behav. Ecol. Sociobiol.*, **15,** 293–301.

Inglis, I. R. & Lazarus, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.*, **57,** 193–200.

Inman, A. J. & Krebs, J. R. 1987. Predation and group living. *Trends Ecol. Evol.*, **2,** 31–32.

Jennings, T. & Evans, S. M. 1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris. Anim. Behav.*, **28,** 634–635.

Kaitala, V., Lindstrom, L. & Ranta, E. 1989. Foraging, vigilance and risk predation in birds: a dynamic game study of ESS. *J. theor. Biol.*, **138,** 329–345.

Kenward, R. E. 1978. Hawks and doves: attack success and selection in goshawk flights at wood-pigeons. *J. Anim. Ecol.*, **47,** 449–460.

Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology.* 3rd edn. Oxford: Blackwell Scientific Publications.

Lazarus, J. 1978. Vigilance, flock size and domain of danger in the white-fronted goose. *Wildfowl*, **29,** 135–145.

Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.*, **27,** 855–865.

Lazarus, J. & Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. *Anim. Behav.*, **43,** 519–521.

Lendrem, D. W. 1983. Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.*, **14,** 9–13.

Lima, S. L. 1987a. Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol.*, **124,** 303–316.

Lima, S. L. 1987b. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour*, **102,** 231–238.

Lima, S. L. 1989. Iterated prisoner's dilemma: an approach to evolutionarily stable cooperation. *Am. Nat.*, **134,** 828–838.

Lima, S. L. 1990. The influence of models on the interpretation of vigilance. In: *Interpretation and Explanation in the Study of Animal Behaviour: Vol. 2. Explanation, Evolution and Adaptation* (Ed. by M. Bekoff & D. Jamieson), pp. 246–267. Boulder, Colorado: Westview Press.

Lima, S. L. 1994a. Collective detection of predatory attack by birds in the absence of alarm signals. *J. Avian Biol.* **25,** 319–326.

Lima, S. L. 1994b. On the personal benefits of anti-predatory vigilance. *Anim. Behav.*, **48,** 734–736.

Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group size effect. *Anim. Behav.*, **49,** 11–20.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68,** 619–640.

McGowan, K. J. & Woolfenden, G. E. 1989. A sentinel system in the florida scrub jay. *Anim. Behav.*, **37,** 1000–1006.

McNamara, J. M. & Houston, A. I. 1992. Evolutionarily stable levels of vigilance as a function of group size. *Anim. Behav.*, **43,** 641–658.

Metcalfe, N. B. 1984a. The effects of visibility on the vigilance of shorebirds: is visibility important? *Anim. Behav.*, **32,** 981–985.

Metcalfe, N. B. 1984b. The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? *Anim. Behav.*, **32,** 986–993.

Mooring, M. S. & Hart, B. L. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour*, **123,** 173–191.

Packer, C. & Abrams, P. 1990. Should co-operative groups be more vigilant than selfish groups? *J. theor. Biol.*, **142,** 341–357.

Parker, G. A. & Hammerstein, P. 1985. Game theory and animal behaviour. In: *Evolution: Essays in Honour of John Maynard Smith* (Ed. by P. J. Greenwood, P. H. Harvey & M. Slatkin), pp. 73–94. New York: Cambridge University Press.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.*, **22,** 501–505.

Pöysä, H. 1987. Feeding–vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. *Behaviour*, **103,** 108–122.

Pöysä, H. 1994. Group foraging, distance to cover and vigilance in the teal, *Anas crecca. Anim. Behav.*, **48,** 921–928.

Pulliam, H. R. 1973. On the advantages of flocking. *J. theor. Biol.*, **38,** 419–422.

Pulliam, H. R., Pyke, G. H. & Caraco, T. 1982. The scanning behaviour of juncos: a game-theoretical approach. *J. theor. Biol.*, **95,** 89–103.

Quenette, P.-Y. 1990. Functions of vigilance in mammals: a review. *Acta oecol.*, **11,** 801–818.

Quenette, P.-Y. & Gerard, J.-F. 1992. From individual to collective vigilance in wild boar (*Sus scrofa*). *Can. J. Zool.*, **70,** 1632–1635.

Roberts, G. 1995. A real-time response of vigilance behaviour to changes in group size. *Anim. Behav.*, **50,** 1371–1374.

Roberts, S. C. 1988. Social influences on vigilance in rabbits. *Anim. Behav.*, **36,** 905–913.

van Schaik, C. P., van Noordwijk, M. A., Warsono, B. & Sutriono, E. 1983. Party size and early detection of predators in Sumatran forest primates. *Primates*, **24,** 211–221.

Siegfried, W. R. & Underhill, L. G. 1975. Flocking as an anti-predator strategy in doves. *Anim. Behav.*, **23,** 504–508.

Sullivan, K. A. 1984. The advantages of social foraging in downy woodpeckers. *Anim. Behav.*, **32,** 16–22.

Turner, G. F. & Pitcher, T. J. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.*, **128,** 228–240.