The collective vigilance as an example of self-organisation: a precise study on the wild boar (*Sus scrofa*).

P.Y. Quenette[1,2] and J.F. Gerard[1]

[1] Institut de Recherche sur les Grands Mammifères, I.N.R.A., B.P. 27, 31326 Castanet Tolosan Cedex, France, e-mail: joachim@toulouse.inra.fr. and [2] Centre de Recherche en Biologie du Comportement Université Paul Sabatier, 31062 Toulouse Cedex, France

Abstract

Individual and collective vigilance behaviour of captive wild boars was examined from films of individuals foraging on experimental feeding places. Individual vigilance (number of acts per unit time, proportion of time spent sacnning) decreased as group size increased, especially between solitary individuals and groups of 2. On the other hand, the collective vigilance (proportion of time during which at least one individual is vigilant) did not vary significantly with group size and was always below the individual vigilance in solitary animals.

A detailed description of vigilance behaviour, based on motor characteristics allowed three types of movement to be distinguished: the more complex, the longer the movement was. Although the mean durations of each type varied largely, they are practically independent of group size. Moreover, the relative proportions of the different vigilance acts change according to group size. Solitary individuals display more often complex behaviours than the individuals in groups.

Although the majority of studies have analysed the vigilance behaviour at the level of ultimate causation by the study of its function, the results are interpreted in terms of proximate causation. A simple mechanism based on allelomimesis allows the results to be explained. So, the collective vigilance emerges from the interactions between individuals.

Introduction

There is an abundant literature on the vigilance behaviour which concerns especially birds and mammals (Elgar 1989, Lima 1990, Quenette 1990). In all these species, vigilance behaviour is characterized by a head lift or scan in which the animal swiftly raises its head, interrupting the ongoing activity, and visually scans its surroundings. Historically, the studies of vigilance behaviour take place in the debate about the selective advantages of group living (Alexander 1974, Treisman 1975, Bertram 1978, Rubenstein 1978, Pulliam and Caraco 1984, Clark and Mangel 1986). So, most of the works are based on the study of the function of vigilance behaviour,

i.e. its adaptative or survival value, with the underlying assumption that the behaviours observed in the population have been shaped through natural selection (Houston & Mc Namara 1988). According to this framework, the animal is considered as an "animal engineer" which must optimaly resolve a problem from its environment in order to maximize its fitness: watching the environment to detect the potential predator attacks or eating so as not to die of starvation. It is now well-know that individuals of various species exhibit less vigilance (either the mean time devoted to scanning and/or scanning rate) when in groups than when solitary (except for some species in large groups, see Quenette 1990). Many authors have attributed this relationship between individual vigilance and group size to a "detection effect". That is, group living allows individual vigilance to be decreased without affecting the probability of detecting a predator (Pulliam 1973, Elgar and Catterall 1981). Individuals could also benefit from group living because each individual in a group has a smaller chance of being the one attacked and avoiding predation involves confusing the predator as the individuals take flight ("dilution effect" and "confusion effect", Hamilton 1971, Vine 1971, Bertram 1978).

Despite the numerous studies, vigilance behaviour is scarcely analysed from the point of view of proximate causation. The study of proximate causation involves understanding the mechanisms of living systems at morphological, physiological and behavioural levels, as well as the processes underlying the functioning of sets of organisms (Alberch 1980; Gray 1986; Ho and Saunders 1982; Gould 1989; Deneubourg and Goss 1989, Varela et al. 1991). This paper examines the influence of group size on individual and collective vigilance of wild boar (*Sus scrofa*) and tests the assumption that individuals scan independently of one another, as the survivorship models assume in the most cases (Bertram 1980; Pulliam *et al.* 1982; Ward 1985). We then analyse the results in the light of proximate causation. We do so in particular by taking into account the variability of motor display of vigilance behaviour which was sometimes mentioned (Lipetz and Bekoff 1982; Alados 1985; Owings *et al.* 1986; Jarman 1987; Loughry and McDonough 1988, Cezilly and Brun 1989) but never considered by the optimization models of vigilance behaviour (Lima 1990). In our mind, vigilance designates a motor act which corresponds to a head lift interrupting the ongoing activity and followed by a multisensory exploration of the surroundings. Such definition does not necessarily involve that these pauses are assimilated to surveillance for potential predator, though it is likely.

Material and methods

This study was conducted during August 1989, in a 1.8-hectare enclosure situated near Arles, south-east France. The captive wild boars present in the enclosure included 17 adults (more than 1.5 years old), 26 subadults (aged between 5 and 18 months), and 31 piglets (less than 5 months). Each day, between 17.45 and 18.15 hours, the same quantity of food was distributed at feeding points in great abundance such that there was no food depletion during each observation session and in order to minimise aggressive interactions. The feeding points were spaced at between 6 and 8 m.

The animals were filmed by video camera from a hiding place positioned 21 m from the nearest feeding point. Each session of filming took place just after the distribution of food and lasted one hour. From the films, we recorded, to the nearest second, the durations of vigilance events (a scan) and feeding intervals between successive scans for each individual of a "stable group". A group is defined as an assemblage of individuals feeding at the same plot. In this context of observation time not spent scanning was almost exclusively time spent feeding. Only the groups where no individuals had left or entered the feeding point for at least one minute, were analysed in this analysis. We partitioned the data by group size (N) for N = 1, 2, 3, 4 and 5-6 individuals. Larger groups were observed but it was often impossible to observe all the animals simultaneously. Although few animals were recognizable, the limited quantity of records for each session and the focal observations spaced in time allowed the data to be considered as independent.

In order to investigate the assumption of independence, we chose, from each focal group filmed, a random number of frames. From each frame, we recorded the number of individuals scanning and the number feeding. If the individuals scan independently of one another, then the probability that n of N individuals (n = 0, 1, ..., N) are scanning at any given instant follows a binomial distribution with parameters N and p (Elcavage and Caraco 1983). The probability p is estimated by the mean proportion of time allocated to vigilance by individuals in groups of size N. Frequencies were compared using the X^2 test. Non-parametric tests (Kruskall-Wallis H test, Mann-Whitney U test and Spearman's correlation coefficient Rs) were used for the quantitative variables.

Results

We recorded at feeding points a total of 222 focal groups (85 focal observations for N=1, 52 for N=2, 38 for N=3, 25 for N=4 and 22 for N=5-6). The foraging bouts ranged from 60 s to 973 s, with an average of 137.7 s and a standard deviation of 112.8 s.
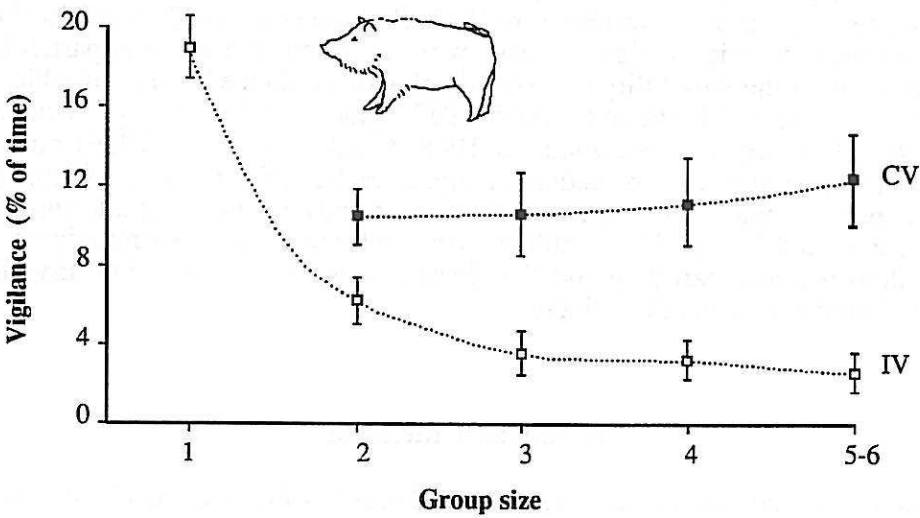

FIG. 1. Mean percentage, ± standard error, of individual (IV) and collective vigilance (CV) for different group sizes at feeding points. CV = the proportion of time that at least one individual of the group is vigilant.

The analysis of the influence of group size shows that the individual vigilance (IV) decreased as group size at the feeding point increased (Fig. 1, Rs=-0.49, P<0.001, N=544). This pattern was due to the decrease of both the scanning rate per unit time (Fig. 2) and the mean duration of the vigilance acts (Rs=-0.22, P<0.001, N=1083). However, this correlation results from the solitary individuals since we observe no difference of mean durations if solitary individuals are not taken into account (Rs=-0.053, P=0.17, N=661). Moreover, the collective vigilance (CV) did not significantly vary according to group size (Rs=0.021, P>0.8, N=137, Fig. 1), but it was clearly smaller than the vigilance of the solitary individuals (Mann-Whitney test: z=-3.4, P<0.001). In others words, although the number of individuals increased, the proportion of time that at least one individual of the group is vigilant (collective vigilance) was constant.
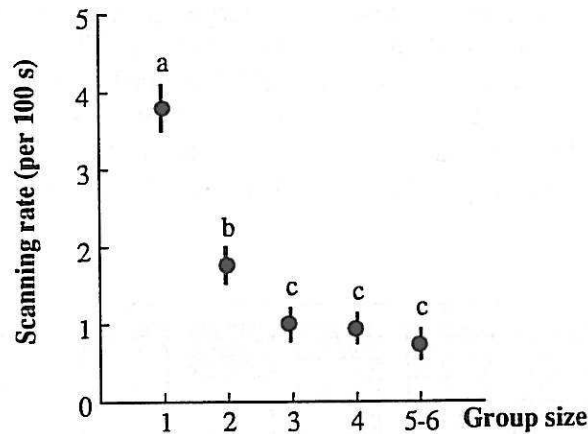
FIG. 2. Mean scanning rates, ± standard error, for different group sizes at feeding points. Different letters represent significant differences (Mann-Whitney U test, P < 0,001).

The assumption of independence was tested only for groups of size 2 through 5, insofar as the sample size was too small for N=6. For a group of size N the observed frequencies correspond to the number of times where n of N individuals scan simultaneously, the expected frequencies are determined under the binomial distribution. The comparison of the two distributions does not allow the null hypothesis of independence for each group size to be rejected (For N=2, X^2=1.63, P=0.20, for N=3, X^2=0.78, P=0.38, for N=4, X^2=0.91, P=0.34, for N=5, X^2=0.00, P=0.97).

From the analysis of the films, we have distinguished three types of vigilance behaviour according to the position and the movement of head and body (Fig.3). The first, S1, corresponds to a simple head up position at variable height, in the sagital plane. The second, S2, corresponds to head up followed by the orientation of the head in the horizontal plane in different directions. The most complex, S3, is defined as head up and the orientation of the whole body in several directions associated with small displacements, the more often followed by a short immobilization in each direction. The mean duration of each type of movement varied largely: the more complex, the longer it was. So, the mean duration (±s.e.) in seconds was 2.4 (±1.8) for S1, 5.4 (±3.1) for S2 and 9.5 (±6.4) for S3. Furthermore, the durations of movements S2 and S3 did not vary according to group size (solitary individuals included, Rs=-0.031, P>0.1, N=224 for S2, Rs=-0.096, P>0.1, N=161 for S3), while S1 decreased slightly in the same conditions (Rs=-0.19, P<0.01, N=698).
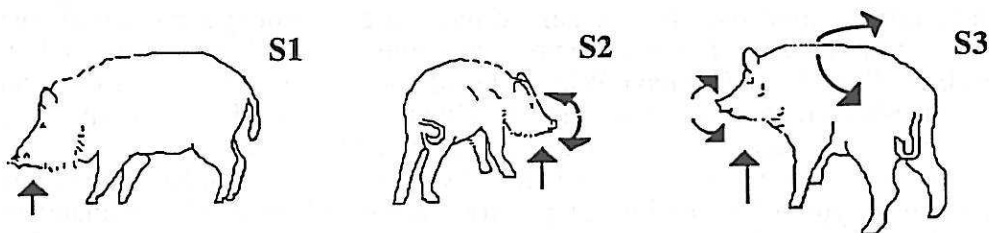
FIG. 3. Motor characteristics of the three types of vigilance act.

As illustrated in Fig. 4, the relative proportions of the vigilance movements differed significantly according to group size (X^2=39.9, df=8, P<0.001). Vigilance behaviour S1 tended to be more frequent in the larger groups whereas the occurrence of S2 and S3 was more frequent in the smaller groups. There was no significant difference between the distributions of S2 and S3 according to group size (X^2=4.9, df=4, P=0.29). Again, a strong difference of the distributions was observed between solitary individuals and two-sized groups (X^2=15.2, df=4, P<0.001), but no difference was noted between groups of size 2 through 5-6 (X^2=7.36, df=6, P>0.2).
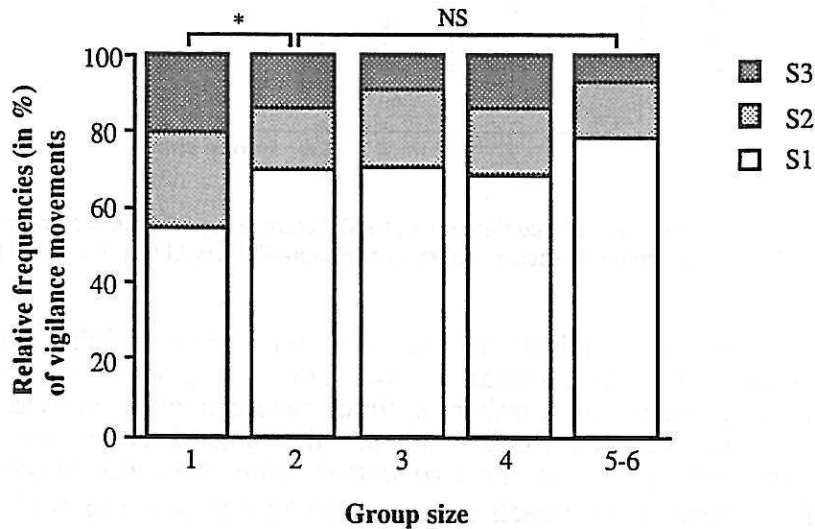

FIG. 4. Relative occurence frequencies of the vigilance movements S1, S2 and S3 for different group sizes. Comparisons of the distributions between solitary individuals and two-sized groups, and between groups of size 2 through 5-6 (X^2 test, *: P < 0,001).

Discussion

Our study lead us to accept the null hypothesis according to which individuals feeding in groups scan independently of one another, as shown in several other studies (Rubenstein 1978, Bertram 1980, Elcavage and Caraco 1983, Monaghan and Metcalfe 1985). This result means that the individuals do not seem to coordinate their vigilance acts, but it does not mean that coordination of vigilance between group members necessarily requires scanning time to monitor the other individuals as sometimes assumed (Pulliam et al. 1982, Ward 1985). In situations where the animals are close to one another and not disturbed by visual obstructions, as in our case, they can monitor through peripheral vision, without head lift, the vigilance activity of their neighbours while they are feeding. Indeed, we have observed that the animals on feeding points frequently turned upon themselves, head down, so performing a particular visual scanning. Furthermore, when flock members are invisible, Sullivan (1985) on downy woodpeckers (*Picoides pubescens*), Wickler (1985) on various species of african birds and Rasa (1986) on dwarf mongoose (*Helogale undulata*) show that these species use acoustical cues to coordinate their vigilance and foraging behaviour.

The analysis of the motor characteristics of vigilance behaviour led to distinguish three movement types of increasing complexity. Each type is probably associated with differential intensity of the exploration of the environment. The mean duration of each vigilance type was globally constant for all group sizes, except for S1 which decreased slighty, and we noted that the relative rate of occurrence of the simplest acts S1 increased with group size while S2 and S3 decreased. So, the general decrease of the mean duration of the vigilance acts was due to the variation of the relative rates of S1,

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S2 and S3. Indeed, both this variation and the decrease of individual scanning rate explain the observed decrease of the individual proportion of time allocated to vigilance with increasing group size.

This decrease of individual vigilance is consistent with most results recorded in birds and mammals. On the other hand, we also observed that the collective vigilance did not increase with group size and was systematical lower than the vigilance of solitary individuals. This seems to be inconsistent with the prediction that the probability of predator detection increases with group size. It is moreover in opposition with the results of some field studies (Lazarus 1979 in the red-billed weaver bird, Bertram 1980 in the ostrich, Monaghan and Metcalfe 1985 in the brown hare), but consistent with Barnard study (1980) on house sparrow which observes any significant variation of collective vigilance with flock size.

Although the studies of vigilance behaviour are usually assessed at the level of ultimate causation, our results suggest that this behaviour can be analysed at the level of proximate causation. Indeed, we can interpret the pattern of collective vigilance as the result of an allelomimetic mechanism i.e. doing what the others do. The mere presence of congeners feeding on the same patch can lead an individual to increase, by imitation, the time allocated to feeding, and thus to decrease vigilance activity. Our results suggest that this interaction is maximal as soon as an individual is in the presence of an other. When an individual is feeding with at least one other individual, it strongly decreases its vigilance activity. In the conditions of this study, this mechanism may be underlaid by a continuous visual monitoring of the closer animals while they are feeding. So, the collective vigilance represents a phenomenon of self-organisation which emerges spontaneously from the local interactions between the individuals in the group. This allelomimetic mechanism involving a strong decrease of individual vigilance between solitary and groups of size 2 or 3 could be a general rule for superior vertebrates. Indeed, for all birds and mammals species examined from the literature, the decreasing's pattern of individual vigilance with group size is qualitatively identical (either a hyperbolic, parabolic or negative exponential curve, see Elgar 1989, Quenette 1990). Moreover, the rate of decreasing, estimated either from the mean proportion of time spent scanning or from the mean scanning rate, is always the strongest between solitary and group size 2 or 3 and ranges from 1.3 to 1.7 for mammals (Alados 1985, Risenhoover and Bailey 1985 a,b, Schall and Ropartz 1985, Monoghan and Metcalf 1986, Wawra 1988, Burnett and Hosey 1987), and from 1.3 to 1.9 for birds (Bertram, 1980, Abramson 1979, Lima 1987, Studd *et al.* 1983, Elgar and Catterall 1981, Caraco 1979, Goldman 1980, Mayhew 1987, Sullivan 1984, Pulliam *et al* 1982). The results etablished in experimental conditions by Tolman (1964, 1965) and Lazarus (1979) also show that this mechanism (named by these authors social facilitation, see also Zajonc 1964) reached a ceiling with three individuals. Actually, such autocatalytic interaction is well documented in many species and must be important for group activities such as foraging, locomotion or resting (Deneubourg and Goss 1989, Pösä 1987).

Furthermore, the results concerning the variability of vigilance movements observed according to group size reinforce this interpretation. Whereas the individuals feeding alone display a greater diversity of vigilance movements with a high frequency of long and "attentive" interruptions, they mainly exhibit simple and rapid scans as soon as they are feeding in groups. This simplification of the motor display of vigilance behaviour suggests a shift of the attention processus which is likely oriented towards the intake of food when the group size increases.

The purpose of such a study is to provide a possible mechanism to explain how a collective pattern can be generated by the behaviour of interacting individuals. This approach is not exclusive of the functional approach of vigilance behaviour, but is distinct from it through the questions it raises and, obviously, the answers it gives.

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