Vigilant behaviou

among animals

by Jean-Pierre Desportes, Neil B Metcalfe and Pat Monaghan

The gazelle, hare, duck and similar creatures on the one hand; the cheetah, vulture, fox on the other are the potential prey of other animals. How does one escape from a predator? First of all, animals anticipate the predators arrival by keeping a close watch on the environment. But if a creature is forced to be on the lookout for its enemies all the time, it will find it difficult to search for food. Many strategies are employed to strike a balance between these two equally important activities. For example, some species resort to collective surveillance, others take turns at keeping watch. The study of the vigilance behaviour of animals shows that they display great ingenuity when faced with this cruel dilemma — to eat or to be eaten, or to die of hunger to avoid being eaten.

Figure 1. To eat or be eaten is the dilemma that faces animals at every moment of their lives. How do they keep on the lookout for possible predators and search for food at the same time? For the prairie dog, an American rodent, the preferred strategy is group surveillance. Several pairs of eyes are better than one pair and when collective vigilance increases there is less individual vigilance. (Photograph : Jacana).

Group surveillancle means that the members of the group trust each other

In the animal kingdom, almost all animals are a potential source of food for other species. But prey is not always captured and every predator is not successful in every attempt to hunt its prey. In this constant combat between predators and their prey, predators who have developed better hunting strategies manage to survive, and better-armed prey have greater chances of escaping from the clutches of these enemies.

The prey have several strategies to avoid being captured (and then eaten!) at their disposal. For some species, the best form of defence is morphological adaptation, like possessing sharp quills, a hard shell, a repulsive odour, an unpleasant taste or some other camouflage. Other species are not provided with these means for defending themselves and they develop special behavioural patterns to avoid their predators, like the warning calls emitted by many birds, harassment of predators by swallows, or jumping in the same place by some species of gazelles in order to locate the cheetah. Like the gazelle, many other animals rely on their ability of locating the predator, in order to be able to subsequently escape. Locating the predator by visual exploration is of crucial importance for survival. The sooner a prey locates its predator, the more effective its behavioural strategy for evasion (fig. 1). Keeping a close watch on the surroundings is undoubtedly an activity of the greatest importance for animals but it can also be very dangerous. The detection of predators and the search for food on the ground (by pecking or grazing) are often quite incompatible (fig. 2). A creature cannot simultaneously look for food with its head bent down and scan its surroundings with its head raised, so as to detect the presence of predators. Added to this is the fact that the capacity of birds and animals to simultaneously process information from competitive sources (in this case, information about predators and food) is limited. Faced with these constraints, they have to establish a delicate balance between the time devoted to the detection of predators and that spent on feeding themselves. The choice between dying of hunger (due to excessive watchfulness) and dying a violent death (for lack of watchfulness) is a cruel one.

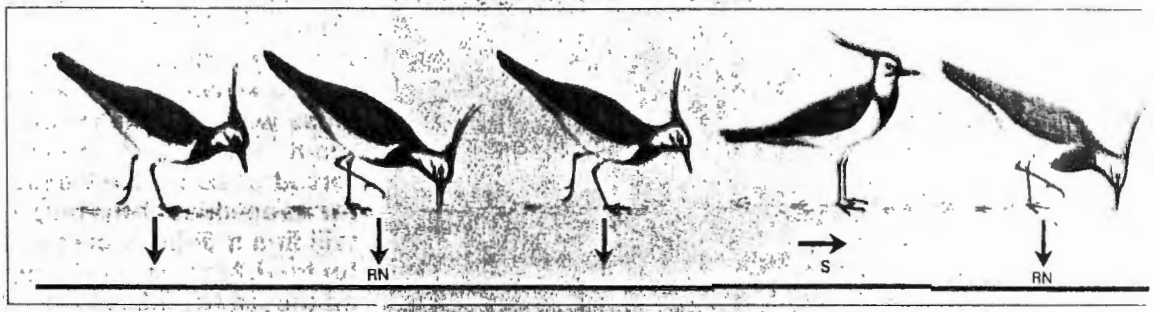
Group surveillance

From a theoretical point of view, this dilemma can be solved quite easily by preparing mathematical models of vigilance behaviour. According to studies carried out by two English research workers of the University of Nottingham, D. Thompson and D. Lendrem, since predators attack when the prey is not vigilant, the interval between the two periods of watchfulness should be less than the time taken by a predator to attack[1]. The data collected through the observation of ostriches, sparrows and tits by several different teams have made it possible to develop a model[2,3,4,5]. According to this model, the best strategy for detecting a predator is for the prey to exlore their surroundings at irregular intervals. Unfortunately, this "simple" model has a major disadvantage in that it is not really impossible for a predator to predict the sequence of intervals separating periods of watchfulness. In fact it is quite easy to predict these intervals if they are repetitive and the predator merely has to wait for the right moment (a long interval) to attack its prey (fig. 3).

In order to arrive at some kind to compromise between the time devoted to looking out for predators and the time spent in searching for food, these creatures can resort to a group strategy rather than individual strategies. Creatures in larger groups keeping a watch on their surroundings separately are more effective, since at least one member of the group is bound to be vigilant at a given moment. All things considered, several pairs of eyes are better than one. The time spent by each individual to keep a watch on the surroundings is thus reduced and the creatures are no longer forced to interrupt their search for food very frequently when there are many members in the group. Such a group strategy assumes that each individual will play his own role in keeping a watch on the surroundings. It is only then that there can be greater collective vigilance and less individual vigilance.

Although this seems very attractive, these mathematical models cannot in reality resolve the dilemma facing birds and animals - to go without food or to become somebody else's food. These creatures work out their own solutions though they are not expert calculators. Since vigilance behaviour in the form of visual scanning of the surroundings is easy to observe in many species, it is not difficult to observe how they conduct themselves. However, rigorously controlled observation of these creatures over long periods of time and in all types of weather is not always rewarding for ethologists. But such methodical observation provides a wealth of information on the significance of vigilance behaviour and the various parameters to which preyed creatures have to adjust itself.

As for lookout strategies, research workers generally confirm the group surveillance model we have briefly outlined in the preceding paragraphs. During a study of the vigilance behaviour of wild brown hares, two of us - P. Monaghan and N. Metcalfe - recorded the proportion of time spent by animals on keeping a watch on their surroundings while feeding alone or in groups of about a dozen members at the most[6]. When the number of hares increases, the time devoted by each member to keeping a watch on the surroundings decreases and collective vigilance (or the proportion of time in minutes when at least one hare is on the lookout) increases (fig. 4). This is due to the fact that in a group these creatures scan their surroundings at a greater frequency than creatures who are searching for food on their own. Searching for food



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in a group is therefore more advantageous because collective surveillance improves and individual surveillance decreases. The strategy of group surveillance is widely used in the animal world when searching for food. This is so in the case of the red-beaked weaver bird that is preyed upon by the goshawk and prairie dogs in the wildlife parks of Wyoming and Colorado studied by J. Lazarus of the University of Newcastle and J.L. Hoogland of the University of Michigan respectively[7, 8].

As we have already stressed, this strategy is really effective when every member of the group does his or her share of the job of watching out for predators. In anthropomorphic terms we may say that the creatures must have full confidence in each other. But why does cheating (like being part of a group but not doing one's proper share of sentry duties) not pay? Intuitively, a creature behaving in this fashion benefits in that it is able to devote more time to the search for food. This problem was analysed by T. Caraco's American team, which calculated the risk of predation faced by birds pecking in a group, with respect to various surveillance strategies[9]. The results show that the best strategy is to see what the other members of the group are doing and adjut one's vigilance behaviour to theirs.

Thus if a bird observes that its neighbour's vigilance frequency is comparable to that of a solitary bird (which does not therefore increase the collective vigilance), it should slow down its own frequency of scanning the environment. Finally, all the members of the group will gradually and contagiously follow the same pattern of vigiliance. As a result, all the members including the "cheater" will lose the advantage of being in a group. To increase their collective vigilance, each one of the members will benefit by increasing the frequency of his or her own vigilance. The ones that cheat, as well as the others add to the risk of falling prey to a predator. the member who is the first to detect the approach of a mortal enemy has the best chance of escaping while the cheater has a smaller chance of being the first to detect the enemy, and thus escape its clutches. We may therefore conclude that cheating does not pay and cheaters don't prosper!

This collective strategy calls for a certain amount of confidence between the various members of the group. This problem of "mutual confidence" is more acute in the case of creatures searching for food in groups consisting of individuals belonging to different species. Can they trust the members of another species to warn them of the approach of a predator? This is a delicate problem indeed, because the predators for all the different species in the group are not the same. Thus a falcon would more willingly attack smaller birds than larger ones. While studying groups consisting of turnstones and violet sandpipers, two species of waders which hibernate on the Scottish coast, N. Metcalfe realized that the smaller birds adjusted their vigilance behaviour to that of other birds of the same size in the group[10]. When they found themselves in the neighbourhood of birds larger than themselves, the smaller birds who are the preferred target of predators, behaved as if they were alone and were more vigilant.

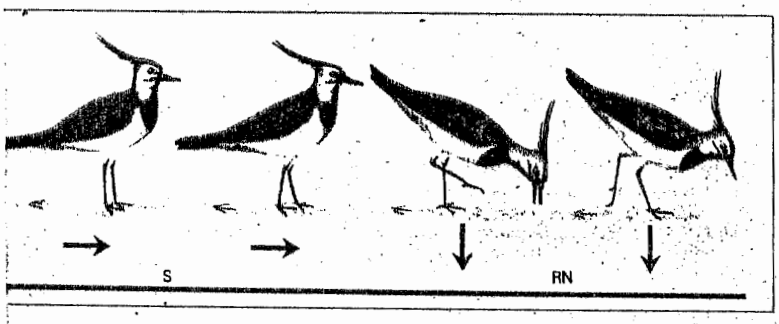

Figure 2. The lapwing cannot peck at the ground with its head bent down and keep a watch on its suroundings at the same time. These two activities are incompatible and it has to choose betwen them. The sequence illustrated on the left shows the alternation between the search for food (RN) and keeping a watch (S). Such a sequence enables us to obtain the main indications used in the analysis of vigilance behaviour, viz. the proportion of time in minutes devoted to vigilance, the frequency of vigilance, the duration of each period and the average duration of the interval between two periods of vigilance. On the basis of these calculations research workers are trying to understand how a creature can establish a delicate balance in order to find enough time to feed while protecting itself from predators.

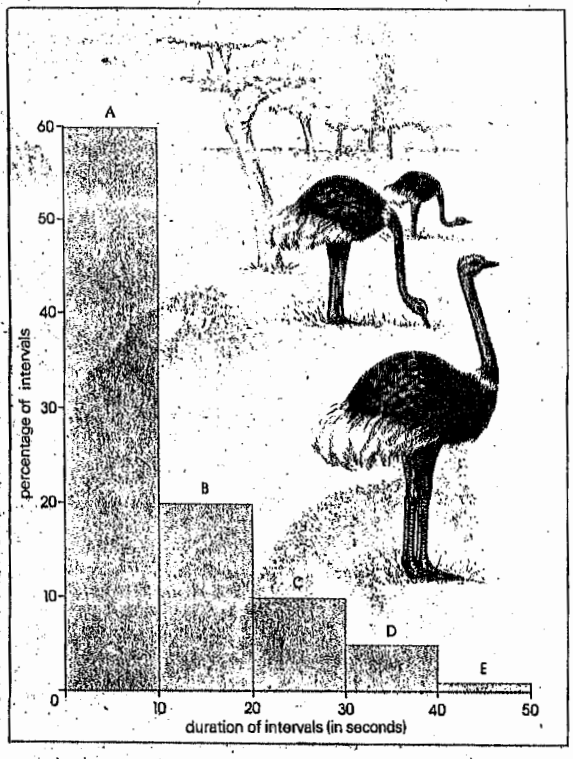

Figure 3. The observation of ostriches shows that the interval between two periods of vigilance during which the ostrich has to riase its head to see if there are any predators around, are irregular (distributed according to a negative exponential law). Contrary to what many authors claim, this irregularity does not prove that the creatures explore their surroundings in a random or unpredictable manner. Actually, the sequence of intervals is quite predictable, the proportion between the time devoted to searching for food and watching the surroundings is perfectly adjusted to the negative exponential law. For example, the sequence A-A-A-A-A-A-B-B-C-D may be repeated systematically[2].

(1) D.B.A. Thompson, D.W. Lendrem, *Anim. Behav., 33,* 1318, 1985.
(2) B.C.R. bertam, *Anim. Behav., 28,* 278, 1980.
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(5) D.W. Lendrem, *Behav. Ecol. Sociobiol., 14,* 9, 1983.
(6) P. Monaghan, N. Metcalfe, *Anim. Behav., 33,* 993, 1985.
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(8) J.L. Hoogland, *Anim. Behav., 27,* 394, 1979.
(9) R. Pulliam *et al., J. Theor. Biol., 95,* 89, 1982.
(10) N.B. Metcalfe, *Anim. Behav., 32,* 986, 1984.

Different members of some species take turns at guard duty

One solution worked out by some creatures is to take turns at guard duty so that while one member keeps on the lookout, the others can search for food. The latter can thus feed themselves at ease, since they don't have to interrupt their feeding to look out for predators. The existence of such sentries means that the group is relatively stable. A sentry cannot feed itself while on guard and it can only feed if each of the other members takes its turn at guard duty. This is the case with the jungle babbler, a species of bird living throughout the year in small stable groups of about twenty birds. All members of the groups take turns at guard duty. The sentry stands guard on one of the lower branches of a tree for several minutes while the rest of the group peck at the ground. A. Gaston of Oxford University (U.K.) has shown that the proportion of time spent on guard duty increases with the rise of the individual in the hierarchy within the group[11]. It is believed that the older dominating birds more experieneed in the search for food devote more time to vigilance than the other members of the group. The studies conducted in 1985 by R. Hegner of Oxford University on blue tits support this hypothesis. The dominant birds give more time to sentry duty than those who are dominated by them. The dominant birds are in a position to use their food resources better and therefore require less time to search for food (because their motivation in this direction decreases); they can thus spend more time on keeping a watch on their surroundings[12].

The time devoted to guard duty is not the same for both sexes when parents have to take care of their young ones. J. Lazarus and L. Inglis proved in 1978 that in the case of couples of geese having young ones, the males spend 20% of their time on lookout duty while the females spend only 5% of their time on such activity[13]. Since the female looks after the incubation of the eggs entirely on her own, she is in poor physical shape after the eggs are hatched. She must therefore eat more than the male to recover. The male makes up for the time lost on lookout duty by pecking faster. None of these differences are found in couples of geese without young ones to look after and which are also less vigilant than those having little ones.

Less vigilance at the centre than on the periphery

The difficulties a creature encounters in finding food also constitutes an important parameter in determining the time devoted to keeping a watch on the surroundings. The British scientist, S. Lawrence of

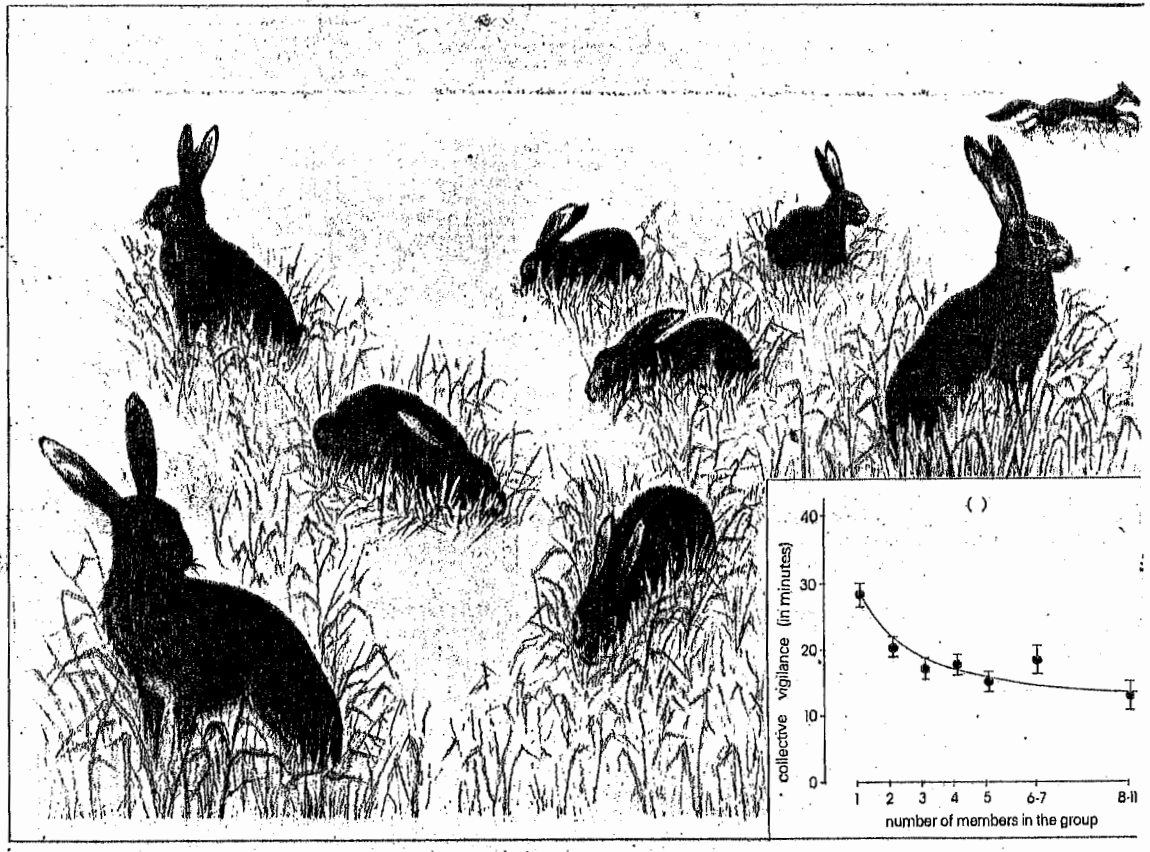

Figure 4. Like the prairie dog (fig. 1) the wild brown hare also resorts to a group strategy to look out for predators while it is feeding. A study of its vigilance behaviour reveals that it spends less time on locating predators when there are more members in the group (A). But collective vigilance (that is the proportion of time in minutes when at least one hare is vigilant) grows with the increase in the number of members of the group (B). The search for food in groups is therefore advantageous for protection from predators[6].

(11) A. Gaston, *Anim. Behav., 25,* 828, 1977.
(12) R.E. Hegner, *Anim. Behav., 33,* 762, 1985.
(13) J. Lazarus, I. Inglis, *Behaviour, 65,* 62, 1978.
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the University of Southampton has recently shown that blackbirds in search of visible prey spend twice as much time on vigilance than those looking out for prey whose colour merges with the soil (and are therefore less visible)[14]. As a matter of fact, blackbirds that attack camouflaged prey have to spend more time looking for food, at the cost of vigilance. Birds and animals can certainly select types of food requiring less visual attention, or change their mode of feeding to be able to devote more time to the detection of predators. This is the behaviour of stickleback fish, as shown by the research undertaken in 1979 by M. Milinski of the Ruhr University, Germany. In normal conditions, the stickleback looks for its prey (small crustaceans called dephnids) in places where they are most abundant in order to maximize their intake of food[15]. But when there is a bait resembling a predator, they change their method of feeding; they look for food in places where there are fewer dephrids but where they can detect the predators more easily[16]. Similarly, D. Lendrem of Oxford, has

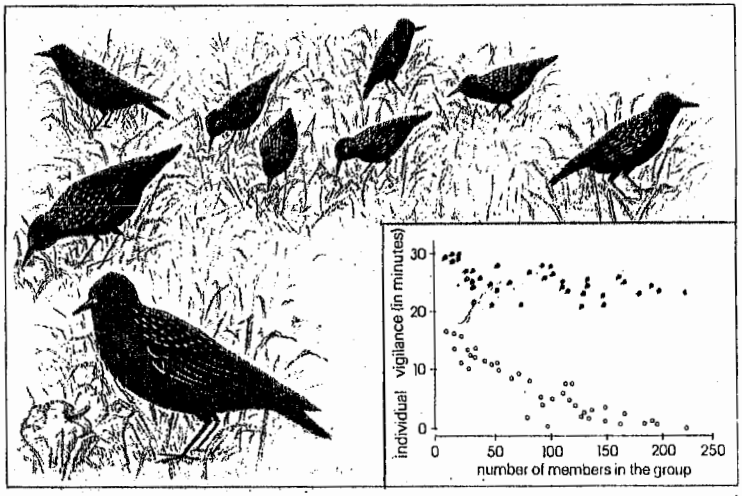
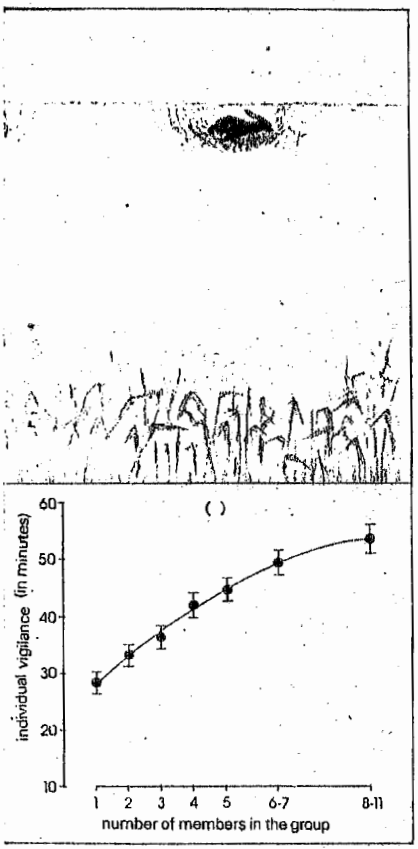


Figure 5. Predators like fish, falcons or cats prefer to attack creatures found on the periphery of a group. Thus creatures that are likely to fall prey to the enemy adjust their vigilance behaviour to suit their position in the group. In a group of starlings, the birds in the middle (white dots) have to be less vigilant than the birds on the edge of the group (red dots). When the number of members of the group increases, there is a decrease in individual vigilance (as in figure 4)[22].



shown that doves change their feeding habits when they have to keep a more careful watch on their surroundings. When there is a predator in the vicinity, doves peck less often but for longer periods each time[17].

The time spent by a creature in keeping a watch on its surroundings affects a compromise, and varies according to the importance given to rival needs, the need for food on one hand and the need to protect itself from predators on the other. The time allotted to various activities (including vigilance) is flexible because the creature has to adapt itself to changes in its surroundings. When the risk of being captured is greater, they devote more time to vigilance and less to searching for food. Among the numerous research projects devoted to the study of this adjustment of behaviour when faced with risks, one of the most illustrative is the one undertaken by T. Caraco on the yellow-eyed junco[18]. This small bird is a native of North America and normally lives on the ground in small groups, in wooded areas. If it notices a predator (like a falcon) in the vicinity, it flies away quickly towards the nearest tree or bush to hide itself. A classic more of behaviour, also observed by the American scientist K. Sullivan among woodpeckers is that birds are most vigilant just before they fly away[19]. As shown by T. Caraco, they adjust their vigilance behaviour as a function of the distance they have to cover to seek shelter. So the farther they are from a tree or a bush, the more vigilant they are before they flee. Juncos also adapt their behaviour according to the number of predators as observed by T. Caraco's group, who used trained falcons in their experiment[20].

The time devoted to surveillance and to the search for food is not only determined by the risk of predation. It also varies as a function of the food intake of a creature. The greater its need for food, the more time it devotes to searching for food at the risk of exposing itself to its predators. This is very well illustrated by the behaviour of migratory birds during the period preceding their departure. Long migrations take up a lot of energy, that has to be stored up by accumulating large reserves of fat (upto 30% of the normal body weight) to be able to withstand the journey. Birds build up these reserves by devoting less time to vigilance. The study conducted by N. Metcalfe and F. Furness on turnstones migrating from the western coast of Scotland to Greenland and Canada covering a distance of about 3,500 kilometres, shows that these birds prepare themselves for their journey by reducing their vigilance during the three weeks preceding their departure. On the other hand, birds that do not migrate do not show any changes in their normal vigilance behaviour[21].

The hunting technique of predators also affects changes in the vigilance behaviour of their prey. Most predators attack creatures found on the periphery of the group. Either they attack an individual directly or they try to separate it from the rest of the group. These tactics

(15) M. Milinski, *Anim. Behav., 32,* 1157, 1984.
(16) M. Milinski, R. Heller, *Nature, 275,* 642, 1978.
(17) D.W. Lendrem, *Anim. behav., 32,* 298, 1984.
(18) T. Caraco *et al., Auk, 97,* 872, 1980.
(19) K.A. Sullivan, *Anim. Behav., 33,* 328, 1984.
(20) T. Caraco *et al., Nature, 285,* 400, 1980.
(21) N.B. Metcalfe, R.W. Furness, *Behav. Ecol. Sociobiol., 15,* 203, 1984.
(22) T. Jennings, S. Evans, *Anim. Behav., 28,* 634, 1980.
(23) J.G. Robinson, *Anim. Behav., 29,* 1036, 1981.

are used by fish, falcons and cats. But whatever the tactics employed, the creatures on the periphery are more exposed to predators than those in the centre of the group. They are also more vigilant. Thus starlings looking for food on the edge of the group have to be more vigilant than those in the centre[22] (fig, 5). This result also applies to other creatures in the animal kingdom which are quite different from starlings. J. Robinson of the Zoological Research Department of the Smithsonian Institute, Washington has observed that capuchin monkeys living in the forests of Venezuela are always more vigilant when they are at the edge of the group than when they are in the middle[23].

The fact that these creatures are not so difficult to locate by their predators also has an effect on their vigilance behaviour. Among ducks, the females warming eggs have dull coloured feathers which make them less conspicuous. On the other hand, during the mating season the males have brightly coloured feathers which makes it easy for the predators to find them. D. Lendrem has shown that among the mallard ducks the males modify their vigilance behaviour on account of their bright plumage and are more vigilant than the females[24]. When they sleep on the banks of a river, ducks are faced with the same problem as when they are feeding. They have to wake up from time to time, opening their eyes (or just one eye) to make sure that there is no predator around. But even during sleep, males are more vigilant than females. But once the mating season is over, the males moult and acquire a brown plumage that is less conspicuous. From then on their vigilance behaviour changes and they have more time to sleep (fig. 6). Their vigilance behaviour is therefore determined by whether they are easily noticed by their predators.

In the same manner, vigilance behaviour also depends on the ability of the prey to locate their predators. This ability

Figure 6. The creatures that are the easiest to spot are the most vigilant. The male mallard duck wears a brightly coloured plumage during the mating season and is therefore forced to keep a closer watch on its surroundings than the dull coloured female. After moulting, when the male acquires a dull coloured coat, it can reduce its vigilance. This behaviour is observed both during feeding and sleeping. (Photograph : Jacana).

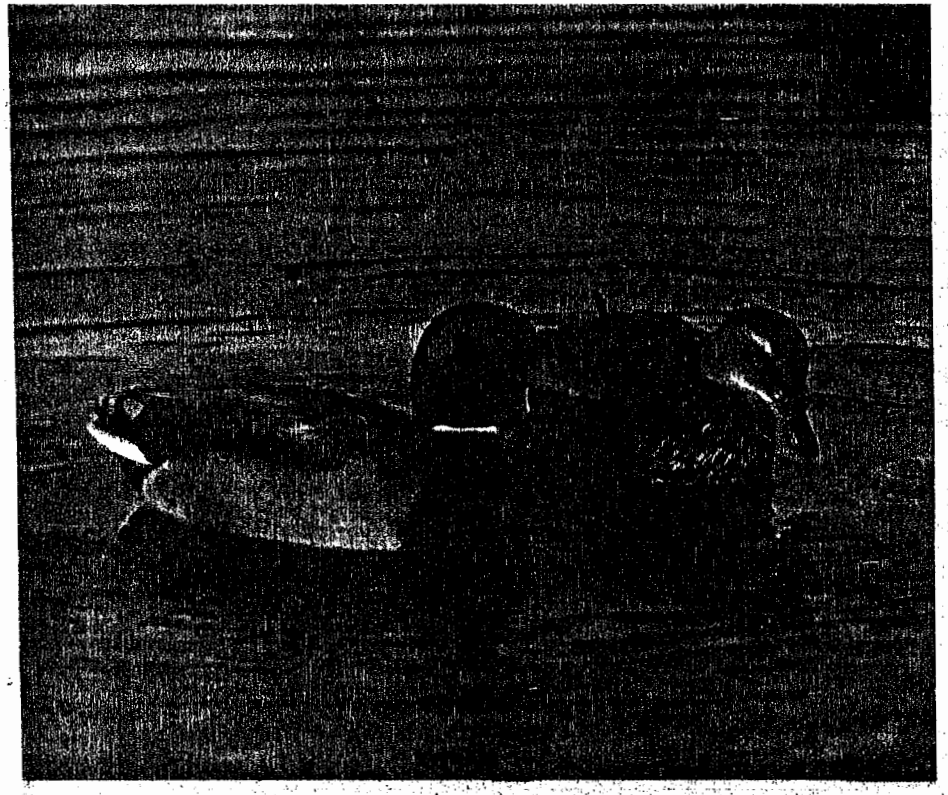
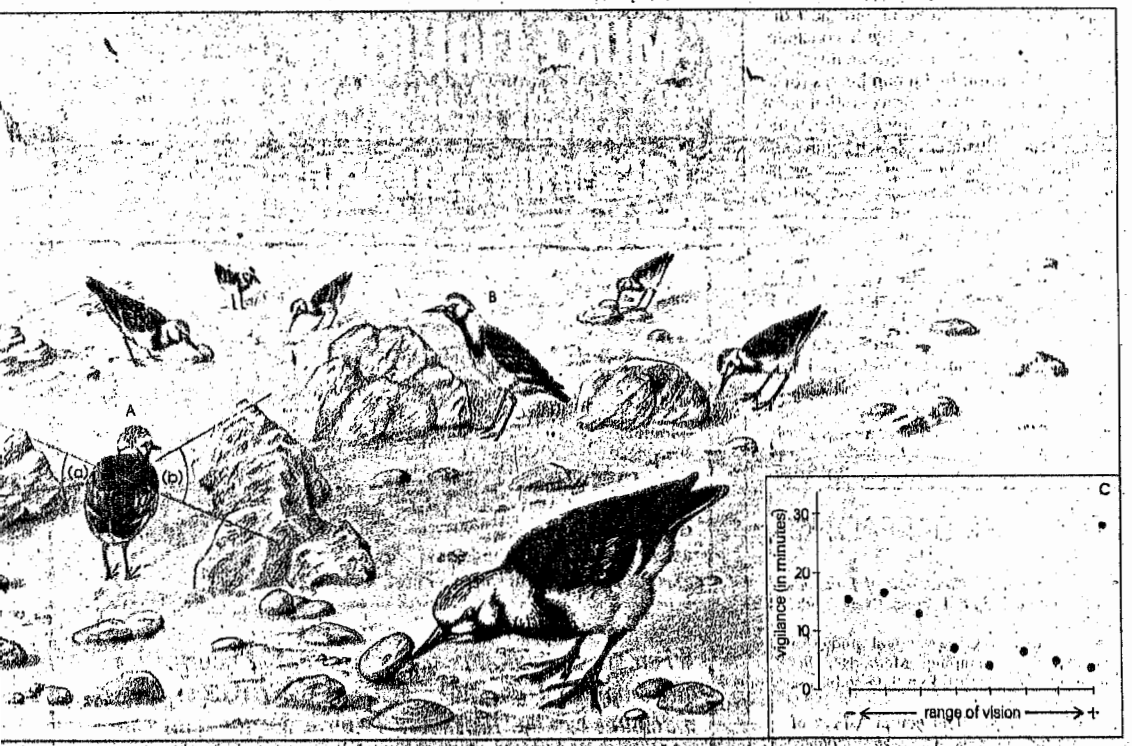


Figure 7. The vigilance behaviour of birds depends on their ability to spot predators which is determined by their range of vision. In the case of turnstones found on the Scottish coast, their range of vision can be reduced by the presence of rocks. In this case (A) its vision is obstructed by two rocks in the horizontal plane, for a total angle (a+b) of about 102°. In the other case (B), the vertical angle is reduced to a greater extent on the vertical plane by the rock on the left than by the rock on the right. The birds adjust their vigilance behaviour according to the visibility conditions(C). For example, turnstones devote most of their time to keeping a watch with their heads raised while they are feeding when their range of vision is less[25].

is determined for example by their field of vision. In coastal areas, the range of vision of turnstones and violet sandpiper may be reduced to some extent by the presence of rocks. In these conditions, N. Metcalfe says, the birds compensate for the decrease in their range of vision by increasing their vigilance by raising their heads more frequently when searching for food[25]. These coastal birds are generally found to be living in groups; which may be attributed wholly to increased vigilance for the detection of potential predators. We know that creatures living in groups adjust their vigilance behaviour according to that of their fellow-creatures. It may therefore be assumed that the increase in



vigilance, when the range of vision is reduced, is also partly related to the presence of fellow-creatures in the group (or even to the detection of the prey).

What about primates?

We have said a great deal about vigilance against predators, that has been the subject of many research programmes. On the other hand, the vigilance necessary for the detection of prey and the vigilance of fellow-creatures has not been the subject of a detailed study. As a result, information about vigilance involved in the location of prey is very fragmentary and limited only to birds like plovers studied by M. Pienkowski of Durham University (U.K.)[26] and lapwings studied by N. Metcalfe[27]. Information concerning vigilance of fellow-creatures is equally scarce and essentially limited to primates other than humans. Among the talapoin monkeys living in groups in equatorial Africa, outsiders are subjected to strict surveillance as shown by two British research workers of Birmingham, D. Scruton and J. Herbert[28]. A surveillance hierarchy is established because the low-ranking individuals in the group are more watchful than the others and keep an eye on the "dominant" animals in the group[29]. As for the capuchin monkeys of Venezuela, J. Robinson tried to find out how much importance was given to looking out for predators, keeping a watch on fellow-creatures (particularly outsiders and dominant members of the group) and the vigilance required to find food (fruits and insects)[23]. The results of this research worker show that under the conditions in which he made his observations, the vigilance of the capuchin monkeys was directed mainly against predators.

The study being carried out at present by one of the members of our group (J.-P. Desportes) on Barbary macaques living in a ten-hectare reserve in France, suggests that it is necessary to create special conditions (by filtering out unwanted elements) to understand the other functions of vigilance behaviour. From this point of view a reserve is almost ideal. As there are no predators, the search for food does not pose any problems (sun-flower seeds are strewn on the ground) and the macaques' vigilance is directed mainly towards their fellow-creatures. The sequential development of this behaviour illustrates perfectly how these animals arrive at an effective compromise between vigilance and the search for food. With their heads bent towards the ground the macaques pick up sun-flower seeds. When they have collected a handful, they eat them with their heads raised while looking around them for a few seconds. Thus the search for food (at least its final phase involving its consumption) and keeping a watchout are not as incompatible as it would seem at first sight.

It is not only the conditions in a macaque reserve that are interesting for analysing the behaviour concerning surveilance over fellow-creatures; from this point of view the observation of a "particular" species viz. human beings, is equally interesting. About ten years ago, while analysing films of persons in the process of eating, I. Eibl-Eibesfeldt, a German research worker now the Director of the Centre for Research on Human Ethology of the Max Plank Institute, made the following observations : after a few mouthfulls individuals raised their eyes from their plates to look around[30]. According to I. Eibl-Eibesfeldt this behaviour is automatic because human beings face no danger when they are eating. But as M. Argyle of Oxford University and M. Crook of Swansea (U.K.) have shown, the duration and frequency of looks directed to other persons vary a great deal,

(24) D.W. Lendrem, Anim, Behav., 31, 535, 1983.
(25) N.B. Metcalfe, *Anim. Behav., 32,* 981, 1984.
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depending on the situation and the individuals concerned, to be able to conclude that there is a certain "automatism" in visual exploration by human beings (or a vestige of the evolution process) that does not serve any purpose any longer[31]. The study of the adjustment of such behaviour to different situations and the inter-individual variability (for example, observations being carried out by J.-P. Desportes in a university library reveal the female students tend to look around them longer than their male counterparts) should provide ample material for a more detailed analysis of vigilance behaviour under conditions where there are no so-called predators around. So-called because according to Plautus (254 to 184 B.C.), an ethologist who wrote comic verse in his spare time, every man is a wolf to his fellow-men.

FOR FURTHER READING

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- J. Altman, "Observational Studies of Behaviour : Sampling Methods", *Behaviour*, 44, 247, 1974 on data-collection procedures.
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- The *Journal of animal behaviour* edited by the Association for the Study of Animal Behaviour publishes the majority of articles on vigilance behaviour.