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Vigilance in a selfish herd

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I explore antipredator vigilance in a spatially explicit group. In a spatially explicit group, foragers with high vigilance can shift the burden of predation to their less vigilant companions if they escape first and the predator selects laggards preferentially. I refer to this as the pass-along effect on vigilance. In a series of models, I examine changes in ESS (evolutionarily stable strategy) levels of vigilance as a function of initial distance between foragers. In a group with peripheral foragers, vigilance first decreases and then increases with decreases in the initial distance between foragers. The decrease in vigilance arises because the foragers occur further away from the predator and have a greater head start when escaping. However, as foragers occur closer to each other, the risk of being overtaken by companions increases and favours higher vigilance. This increase in vigilance with group density also occurs for centrally located foragers that are not exposed directly to attack but which can be overtaken by peripheral companions. When all foragers in a group are alerted instantaneously by the escape of companions, the relative position of prey in the group cannot change, impeding the pass-along effect. The pass-along effect on vigilance is thus expected to be more prevalent in groups with less efficient collective detection of predation threats.

Keywords: antipredator defence; collective detection; ESS; evolutionarily stable strategies; game theory; group vigilance; modelling vigilance; nearest-neighbour distance; pass-along effect

Two of the most frequently discussed factors influencing antipredator vigilance in groups are collective detection and dilution (Krause & Ruxton 2002). With collective detection, the escape response of one individual can trigger the escape response of other companions that have failed to locate the predator directly. When collective detection is perfect, detectors and nondetectors will be alerted to the presence of the predator at the same time and all may be able to escape unharmed (Pulliam 1973). The presence of companions may also reduce individual risk by a simple dilution effect if predators can only capture one group member during a successful attack (Foster & Treherne 1981). Collective detection and dilution may act together or alone to influence vigilance in animal groups (Bednekoff & Lima 1998).

Models of vigilance in groups including collective detection and dilution effects have neglected the spatial arrangement of animals in groups and in fact implicitly assume that all individuals occur at the same spot (Pulliam 1973; Lima 1987; McNamara & Houston 1992). In a spatially explicit group, however, individuals can occur at the edge or in the centre of the group and may be exposed to different foraging contingencies and experience different predation risk (Krause 1994). Therefore, variation in vigilance according to spatial position cannot be addressed with these models and is usually related to ad hoc factors such as less effective collective detection or differential predation risk, resource availability and/or intrinsic quality of individuals.

Spatially explicit models, on the other hand, have usually ignored vigilance altogether. The most explicit spatial model of predation risk in a group is the selfish-herd hypothesis (Hamilton 1971). When applied to a situation where the predator attacks from outside the group, the selfish-herd hypothesis implies that individuals at the centre of a group are buffered from predation by the presence of companions at the edge, which are closer to the predator. Individuals are thus expected to seek safer positions in the group when under attack, leading to a reduction in nearest-neighbour distances. In more recent models that seek movement rules for foragers in a selfish herd, all individuals are assumed to change position at the same time once an attack is under way (Viscido et al.

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2002). In this respect, these movement rules assume perfect collective detection and equal vigilance among foragers in the group. Therefore, selfish-herd models have not addressed the consequences of varying levels of vigilance in the group and imperfect collective detection, which may influence onset of movement by group members at different positions.

Some vigilance models have incorporated spatial features but have ignored the selfish-herd hypothesis (Proctor et al. 2003) or assumed that prey occur side by side (Packer & Abrams 1990; Bednekoff & Lima 1998). This is unfortunate because it is often thought that one benefit of maintaining a higher level of vigilance in a group is the ability to escape sooner during an attack, thus unloading the risk of predation to companions that respond later because of their lower vigilance (Lima 1994), which I refer to as the pass-along effect. In addition, studies indicate that vigilance varies as a function of the spatial arrangement of foragers, suggesting a role for a pass-along effect (Bekoff 1995; Sadedin & Elgar 1998). Here, I explore in a series of models the expected pattern of variation in vigilance as a function of nearest-neighbour distance, assuming first that the pass-along effect acts alone and then in combination with collective detection. In particular, I expected that as foragers in a group occur closer to one another, the pass-along effect would select for an increase in vigilance levels.

THE MODELS

Model 1: Pass-along Effect Acting Alone

I consider the simplest situation compatible with the pass-along effect, namely two peripheral foragers separated from each other and directly exposed to potential attacks by a predator. The case of a group with central and peripheral foragers is considered in model 2. I first neglect collective detection. This is not entirely unrealistic since several studies reveal that escape signals are often ignored or trigger responses in the group after a delay (Elgar 1986; Lima 1994, 1995; Hilton et al. 1999; Kaby & Lind 2003; Quinn & Cresswell 2005). This model provides a baseline to compare results from more complex models.

I assume that a predator targets each side of the group, and therefore each forager, with equal probabilities and that in response to an attack a forager moves away in the opposite direction. The predator then attempts to overtake the closest forager. A genetic algorithm approach is used to find the evolutionarily stable strategy (ESS) level of vigilance as a function of the initial distance between the two foragers. The model includes one gene, coding for individual vigilance levels, and incorporates mutation events but no recombination.

At the beginning of the first generation, vigilance level v for each forager is selected randomly from the uniform distribution. At the onset of each generation, the foragers and the predator are positioned on a one-dimensional array containing 50 units of distance. Foragers are initially located at the same distance relative to their respective end of the array. Hence, if a forager occurs at position x, the companion occurs at position $50 - x$ and the distance between the two is $50 - 2x$. The predator appears initially at position 0 or 50 with equal probabilities and moves towards the group at constant speed p (in units of distance per time step). At each time step, foragers can be either vigilant or nonvigilant. The forager is vigilant if a number drawn randomly from the uniform distribution at this particular time step is smaller or equal to the set vigilance level, and nonvigilant otherwise. When nonvigilant, foragers are impervious to the presence of the predator and remain at the same location during the time step. Empirical evidence suggests indeed that nonvigilant foragers are less likely to detect predators (Krause & Godin 1996; Lima & Bednekoff 1999; Kaby & Lind 2003; Bednekoff & Lima 2005). When vigilant, a forager detects the predator and moves away in the opposite direction at constant speed f. A forager will therefore only detect the predator when first vigilant regardless of the distance between the predator and the prey.

At each time step, the position of the predator and of the two foragers is updated according to the above rules. The position at which the predator is first detected by each forager is noted. The predator attempts to capture the first forager it can overtake. The probability of capture is given by $\exp(-k_1 i)$, where k_1 is a positive constant and i is the distance between the forager and the predator at the time of detection. This function assumes that the risk of capture decreases exponentially with distance between the forager and the predator at the time of detection, reflecting the benefit of a head start by the forager. The model assumes no collective detection, so the relative position of the two foragers can change during an attack if the forager initially closest to the predator overtakes its nonchalant companion.

Each generation consists of 1000 simulated predation events, each repeating the above steps using the same two foragers. The mean probability of capture for each forager over all these simulated predation events is calculated. Fitness for each forager at the end of one generation is given by the product of survival and feeding time $(1 - v)$, with survival given by exp(−attack rate × mean probability of capture per attack) (Houston et al. 1993). The attack rate represents the number of attacks per generation. In this equation, high vigilance decreases feeding time but increases survival, creating a trade-off between foraging success and survival. At the end of each generation, the forager with the lowest fitness adopts the vigilance level of the other forager to simulate differential reproduction. Mutation occurs with probability 0.1 each generation for each forager. After a mutation, vigilance levels change by 0.1 up or down with equal probabilities. I ran a total of 1000 generations, which is sufficient to obtain stable ESS levels of vigilance in this and the following models. I calculated mean vigilance and fitness levels over the last 500 generations. At equilibrium, mean values over the last 100 generations did not differ from those over the last 500 generations.

The ESS level of vigilance represents the selfish solution to the game. A cooperative solution can be obtained by assuming that the two foragers adopt initially the same vigilance level (Pulliam et al. 1982). The cooperative