Consistent waves of collective vigilance in groups using public information about predation risk

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Consistent waves of collective vigilance in prey groups using public information about predation risk. Antipredator vigilance models have long assumed that individuals in groups monitor threats independently from one another. This assumption has been challenged recently, both theoretically and empirically. In particular, recent models predict that individuals should pay attention to the vigilance state of their neighbors and become increasingly vigilant when the proportion of vigilant neighbors is higher. Such copying can lead to temporal waves of collective vigilance in groups rather than random fluctuations. Here, we investigated the robustness of these predicted waves under varying ecological situations. Using an individual-based modeling approach, we show that such waves are predicted to occur in small and large groups, when copying only involves the nearest neighbor or the radius of copying is small or large or when the shape of the group is square or rectangular. However, when the influence of neighbors was restricted (e.g., by reducing the radius of influence, by only considering the nearest neighbor, or in more elongated groups), waves involved a smaller proportion of the group. In general, collective patterns were more organized when the copying tendency was strong and the frequency at which individuals could switch state was not too high. Our results show that collective waves of vigilance are a robust phenomenon emerging from the individual social behavior of group members, thus encouraging empirical scrutiny of the connection between individual and group vigilance. 

INTRODUCTION

Animals living in groups have long been assumed to monitor threats of predation independently from other group members (Pulliam 1973; Bednekoff and Lima 1998). This hypothesis predicts that individuals can lower their investment in vigilance while still benefiting from efficient group vigilance (McNamara and Houston 1992), explaining the common observation in birds and mammals that individual vigilance is lower in larger groups (Caro 2005; Beauchamp 2008). Another consequence of the independence hypothesis is that the proportion of vigilant individuals in a group should fluctuate randomly through time. This particular prediction and underlying assumptions of the independence hypothesis have been challenged recently both theoretically and empirically.

Theoretically, animals are increasingly recognized to use public information, rather than behaving independently, to make individual choices in a wide range of activities (Danchin et al. 2004; Goodale et al. 2010). Two adaptive hypotheses suggest a role for public information on individual vigilance levels. First, individuals could use public information (e.g., alert postures or vocalizations of other group members) as a proxy for predation risk (Lima 1995; Roth et al. 2008). Pooling information from different sources could reduce uncertainty about predation risk (King and Cowlishaw 2007), thus potentially providing a better estimate of the actual predation risk (Sirot 2006). In this context, an individual may become vigilant when detecting more vigilant companions because their high level of alertness indicates that predation risk is suddenly higher (Eilam et al. 2011).

The second adaptive scenario is based on the idea that individual predation risk in a group is dependent on the level of vigilance maintained by companions: relatively less vigilant individuals may be attacked more often by predators because of their lower vigilance per se or because such individuals are slower to escape than their more vigilant companions (FitzGibbon 1989; Lima 1994; Sirot and Touzalin 2009). In this case, foragers should pay attention to the behavior of their neighbors and become more vigilant when they are vigilant to avoid attracting predators disproportionately. The converse is also true: a forager should be less vigilant if neighbors are less vigilant because risk can be diluted among a greater number of nonvigilant individuals.

Empirically, in many species of birds and mammals, sequences where many group members are vigilant at the same time have been found to be more common than expected by chance (Fernández-Juricic, Siller, et al. 2004; Ebensperger et al. 2006; Pays, Jarman, et al. 2007; Pays, Renaud, et al. 2007; Beauchamp 2009; Pays, Dubot, et al. 2009; Pays, Goulard, et al. 2009; Ge et al. 2011; Michelena and Deneubourg 2011; Öst and Tierala 2011), suggesting that individuals pay attention to the level of vigilance maintained by other group members and tend to copy the behavior of neighbors.

Modeling approaches have repeatedly found that simple and local individual rules, such as copying neighbors, can lead to
collective patterns such as group synchronization (Camazine et al. 2001; Sumpter 2006; Jovani and Grimm 2008). For group vigilance dynamics, copying the vigilance levels of neighbors has been shown in models to produce temporal waves of vigilance in groups, with the proportion of vigilant foragers substantially rising and decreasing in nonrandom fashion through time (Sirot and Touzalin 2009) in stark contrast to the prediction derived from the independence hypothesis. However, the most obvious explanation for synchronization of vigilance is an independent response by each group member to the same external predation stimuli. Therefore, it is important to rule out such external influences to assess the relevance of internal social dynamics on collective patterns (Ruxton and Roberts 1999; Camazine et al. 2001). In perhaps the most convincing empirical evidences of nonindependent vigilance thus far, kangaroos (Macropus giganteus) and gulls (Larus spp.), without any obvious external sources of disturbance, were more likely to become vigilant when their nearest neighbors were more alert (Beauchamp 2009; Pays, Goulard, et al. 2009). In gulls, waves in the proportion of sleeping gulls as a function of time were identified using spectral analysis (Beauchamp 2011).

To summarize, modeling has determined that waves of vigilance can occur in groups when individuals use public information about predation risk. Empirical studies have determined that copying does occur in some animal groups and that collective waves of vigilance may ensue. However, little is known about the robustness of the link between individual behavior and collective patterns of vigilance. Investigating the strength of this link is important because in nature groups can occur in different sizes and shapes, and different species are likely to use public information in different ways. All these factors may influence the expression of vigilance at the group level.

To this end, we explored collective patterns of vigilance in a broader range of conditions than used in previous models. In particular, we focused on the effect of group density and group spatial configuration because these 2 factors will increase the distance between foragers and influence information transfer. We also considered changes in the strength of the copying response to determine when vigilance waves should become more likely. Finally, we considered different rules to pool information from neighbors. We predicted that waves would not occur to the same extent or be less organized when spatial density is lower or groups are more elongated, when the copying response is weaker, and when information is only pooled from immediate neighbors.

MATERIALS AND METHODS

Basic model description

We follow the ODD (Overview, Design concepts, and Details) protocol for describing individual- and agent-based models (Grimm and Railsback 2005; Grimm et al. 2006). The model was implemented in Repast Simphony for Java; see North et al. (2006) for one application.

Purpose

To explore how collective patterns of vigilance can arise when individuals use public information about predation risk and how such patterns vary in different ecological settings.

State variables and scales

The unit of the model was an individual within a group, and a single group was analyzed in each simulation. Individuals occupied a unique and fixed spatial position within the group and experienced 1 of 2 mutually exclusive states: vigilant or foraging (nonvigilant). The group occupied a 2-dimensional square habitat where each individual was randomly located in continuous space. We modeled a lattice with an edge, which means that edge individuals have fewer neighbors within a given radius than central individuals. We did so because we aimed to simulate what would happen in a real group, with unavoidable edges, rather than in a portion of a large infinite group.

Process overview and scaling

At each time step, and independently of their current state, all individuals in random order checked the vigilance state of their neighbors with probability $P_c$ (see below). Concretely, at each time step and for each individual, if $P_c$ was equal or larger than a random number drawn from a uniform probability distribution $(U(0,1))$ the individual checked the vigilance state of its neighbors; in the opposite case, the individual simply performed the same activity as before (vigilant or foraging). When an individual checked the vigilance state of its neighbors, the probability of being vigilant ($P_v$) in the next period was updated according to the information acquired during checking. Details of the calculation are shown in the next section. Again concretely, after checking the vigilance state of neighbors, an individual became/remained vigilant if a random number drawn from $U(0,1)$ was equal or smaller than $P_v$.

Asynchronous updating of state was chosen in the present model: Rather than all individuals waiting at the end of the time step to update their state simultaneously, individuals were allowed one at a time (in random order at each time step) the possibility of checking their neighbors and updating their state accordingly before the others (Ruxton and Saravia 1998; Caron-Lormier et al. 2008). This assumes that individuals do not synchronize their decision making. Vigilance choices are made continually within a group, we believe, and asynchronous updating provides a better approximation of continuous time (Caron-Lormier et al. 2008).

Design concepts

Collective patterns of vigilance will emerge from individual-level choices. Each simulation is unique in that individuals were initially randomly distributed in the habitat, each may have a unique $P_v$, and state changes were stochastic realizations of the above processes. We allowed the simulation to run for 2000 time steps before retrieving outcomes for the following 1000 time steps. This was sufficient to generate stable outcomes. We ran 100 simulations for each combination of parameter values to obtain a distribution for each outcome variable.

Initialization

A simulation started by randomly assigning 100 individuals to a position in the habitat. The habitat had a square shape with 25 arbitrary length units. The radius of interaction with neighbors was set at 8 units. Initially, each individual was assigned a state by the random realization of a binomial process with $P_v = 0.5$. The probability of checking neighbors for each individual ($P_c$) was obtained through a random draw from $U(0,1)$, $P_v$ and state changes were stochastic realizations of the above processes. We allowed the simulation to run for 2000 time steps before retrieving outcomes for the following 1000 time steps. This was sufficient to generate stable outcomes. We ran 100 simulations for each combination of parameter values to obtain a distribution for each outcome variable.

Input

No external variables (e.g., predation risk) driving group/individual behavior was defined in the model.

Submodels

The probability ($P_v$) of becoming (or remaining) vigilant irrespective of the previous state is given by:

$$P_v = \begin{cases} 
0.5 & \text{if} \quad P_v < 0.5 \\
0.5 + \text{random draw from } U(0,1) & \text{if} \quad P_v \geq 0.5 
\end{cases}$$
where \( \text{res} \) represents the residual probability of becoming vigilant, \( N_v \) the number of vigilant neighbors, and \( N_t \) the total number of neighbors. Neighbors were defined as those other individuals located within a fixed radius around the focal forager (Sirot and Touzalin 2009). The res parameter was equal for all individuals in the group. When \( \text{res} = 0.5, P_v = 0.5 \) regardless of the number of vigilant neighbors, simulating a case where copying does not occur. When \( \text{res} < 0.5, P_v \) now becomes a strictly increasing linear function of the proportion of vigilant neighbors, increasing more sharply the smaller the value (Figure 1). Therefore, copying becomes more likely when res is smaller. When no neighbors occurred within the fixed radius, \( P_v = 0.5 \), implying an equal likelihood of either state.

Robustness tests of the model

We analyzed 6 modifications of our basic model to examine potential changes in collective patterns of vigilance. We made changes that impose constraints on information transfer between individuals as would occur in real animal groups. Specifically, we made the following changes, one at a time, from our basic model: 1) smaller radius for checking neighbors (1 unit), 2) smaller number of individuals in the group (10); 3) including only the nearest neighbor in the calculation of \( P_v \) (this topological rule has been suggested recently as driving flight decisions in flocking starlings; Ballerini et al. 2008); 4) using a rectangular group shape, thus increasing the edge effect (5 \times 125, keeping area the same); 5) making \( P_v \) constant rather than variable for all group members to investigate the effect of variability among foragers in the probability of checking neighbors; and 6) changing the probability of checking neighbors for all foragers to examine how the speed of updating can influence waves characteristics (\( P_v = 0.1, P_v = 0.5, P_v = 0.9 \)).

Spectral analysis

Each simulation yielded 3000 observations of the proportion of vigilant individuals in the group from which we analyzed the last 1000 time steps. For each set of parameter values, we produced 100 such sequences. We subjected each sequence of observations to spectral analysis (Brockwell and Davis 2002). The methodology is described in full details in Beauchamp (2011) and will be summarized here.

The aim of spectral analysis is to break down sequences of observations into cyclic components involving cosines and sines. In these cycles, the period \( T \) is the time required to complete one full cycle and the frequency \( k \) is the number of cycles per unit time. A linear combination of cosines and sines, across a range of different frequencies, forms the basis to predict the proportion of vigilant foragers at each \( t \):

\[
g(t) = \mu + \sum_{k=1}^{n} \left( A_k \cos(2\pi k t) + B_k \sin(2\pi k t) \right),
\]

where \( g(t) \) is the proportion of vigilant foragers and \( \mu \) represents the average proportion of vigilant individuals in the data. Cosines and sines are used to model the temporal rises and decreases in this proportion. Temporal data may be a combination of many different frequencies overlapping each other and each contributing to the overall pattern. In a sequence of \( n \) observations, we focused on the Fourier frequencies \( k/n, k = 1, \ldots, \lfloor (n - 1)/2 \rfloor \), where \( \lfloor x \rfloor \) represents the greatest integer \( \leq x \). The parameters in this model, namely \( A \) and \( B \), were chosen so as to minimize the residual sum of squares.

These parameters do not have a straight biological meaning. However, in the fitted model, the value \((n/2)(A_k^2 + B_k^2)\) represents the contribution of the harmonic component with frequency \( k/n \) to the total variation, similar to an \( R^2 \) value in a multiple regression model. In the above model, 100% of the variation can be explained using all Fourier frequencies. Practically, though, adding more frequencies to the model yield diminishing returns in terms of explained variation. We thus focused on the frequency that explained the most variation in the proportion of vigilant foragers through time (see an example in Figure 2). In sequences where a large proportion of variation was explained by one frequency, additional frequencies explained relatively small amount of variation (typically less than 10%) and were thus ignored. As a final technical comment, we used weighing of the harmonic component contributions. In particular, triangular weights provide a moving average of the harmonic component contributions with more weight given in the middle \((3/9)\) and less weight at the extremities \((1/9)\). This smoothing often reduces the number of peaked harmonic components (Brockwell and Davis 2002).

Periods that we uncovered with spectral analysis are limited by the time window that we selected because it is not possible to have a larger period than 1000. Selecting a different time window would yield different periods. However, our purpose was not to predict periods exactly because it is not clear what the

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\text{Figure 1}
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Relationship between the probability of being vigilant \((P_v)\) at one time step as a function of the proportion of neighbors that are vigilant within a given radius around a focal forager. When the residual probability \((\text{res})\) is equal to 0.5, \( P_v = 0.5 \) and is independent of the state of neighbors. As \( \text{res} \) becomes smaller, foragers are more likely to be vigilant the higher the proportion of vigilant neighbors.

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\text{Figure 2}
\]

Wave characteristics in a simulation of the model. The gray line represents simulated data and the black line fitted data. The \( R^2 \) value is shown along with the fitted equation. The period and the range in the proportion of vigilant foragers are shown.
time window should be in any particular case. Rather, we used the model in a comparative fashion to determine how changes in ecological variables should affect wave characteristics using a fixed time window throughout.

We characterized waves using 3 parameters (Figure 2): 1) $r^2$: the highest percentage of variation in the temporal data explained by one frequency during the last 1000 time steps, 2) period: the period associated with this largest $r^2$ value, and 3) range: range in the proportion of vigilant foragers during the last 1000 time steps. Range is a proxy for the amplitude of the waves that pass through the group.

RESULTS AND DISCUSSION

When $\text{res} = 0.5$ (see Figure 1), regardless of the behavioral state of near neighbors, the proportion of vigilant foragers fluctuated little around 0.5 (Figures 3 and 4). Such fluctuations represent the expected temporal variation in the proportion of vigilant foragers under the independent vigilance hypothesis.

We stress that in the baseline model not all foragers could switch state at each time step because the probability of checking neighbors per time step ($P_c$) varied among individuals from 0.1 to 0.9. Therefore, the proportion of vigilant foragers at any given time step is dependent on the proportions that occurred in previous time steps, thus creating a slight temporal autocorrelation in the data ($r^2 < 3\%$; Figure 4). Collective waves of vigilance can thus ensue with short periods and small ranges (Figure 4).

To investigate why weak collective waves of vigilance can be detected with the spectral analysis even when copying is not possible, we ran simulations with $\text{res} = 0.5$ as before but with $P_c = 1$ for all individuals this time. With such parameters, copying did not occur but individuals could change state at each time step. We expected that the temporal autocorrelation would be reduced now given the more frequent updating of state of all individuals. As expected, we obtained a white noise pattern, with $r^2 < 1\%$ and short time periods and ranges (Figure 4).

First, we examined what would happen generally when copying neighbors is allowed. When $\text{res} < 0.5$, thus allowing copying, the temporal pattern in the proportion of vigilant foragers became more organized. A typical example is shown in Figure 3 along with the state of foragers in the square lattice at different time periods. In stark contrast to the near white noise pattern that was documented when copying neighbors was not possible, a wave of collective vigilance was evident when copying is allowed. In the following, we investigated how changes in ecological variables affect characteristics of such waves.

In the baseline model, as copying tendency increased (i.e., res decreased), periods associated with the highest $r^2$ value increased, $r^2$ values also became larger, and waves involved a greater proportion of foragers. For instance, when copying tendency was high, the proportion of vigilant foragers could vary from all to none and show many peaks and troughs (Figure 4). We conclude that when the tendency to copy neighbors is stronger, waves of collective vigilance become more apparent and involve a greater proportion of foragers in the group.

Turning now to the robustness tests, our analyses revealed that the above patterns, in terms of $r^2$ values and periods, were robust to changes in radius length (1 vs. 8), in group size (10 vs. 100), and in group spatial configuration (rectangular vs. square) (Figure 4). Whether foragers checked the state of all neighbors with a given radius or only that of the nearest neighbor also had little influence on these patterns.

However, changes occurred with respect to the range in the proportion of vigilant foragers through time (Figure 4). In particular, the range was much lower when foragers checked neighbors within a smaller radius or when they only checked the state of their nearest neighbor. In these 2 cases, waves may have different characteristics compared to the baseline model.
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Figure 4
Box plots of wave characteristics (Range, Period, and $r^2$) as a function of model parameters. White noise: 100 foragers, lattice 25 × 25, radius of copying $= 8$, $P_c = 1$ for all individuals, $res = 0.5$. Basic model: 100 foragers, lattice 25 × 25, radius of copying $= 8$, $P_c = U(0.1,0.9)$, res varying in different simulations from 0.5 to 0.01. In each robustness test, only one specified parameter was changed from the baseline model. $P_c = 0.1$, $P_c = 0.5$, $P_c = 0.9$, and $P_c = 1$ means that $P_c$ was equal for all individuals instead of being drawn from a distribution as in the basic model. Each box ranges from the 25th to the 75th percentile, and the line in the box shows the median. Whiskers extend to 1.5 times the interquartile range, and data points beyond whiskers are shown as dots.

Our modeling approach shows that copying the vigilance behavior of neighbors has marked influences on collective patterns of vigilance in groups. As opposed to near random dynamics when copying does not occur, copying induced systematic increases and decreases in the proportion of vigilant individuals, which can be tracked with statistical waves. It is impor-

not propagate to a large part of the group because the influence of each forager did not extend very far. Waves also involved a relatively smaller proportion of the foragers when the group was distributed on a rectangular grid, which is also understandable using the above logic because, in such a spatial arrangement, any forager has fewer available neighbors from which to copy in any given radius.

So far, we have always considered that individuals vary in their propensity of checking neighbors at each time step, with some being slower than others in updating state throughout the simulation ($P_c$ was drawn from $U(0.1,0.9)$). We ran simulations with $P_c = 0.5$ for all individuals (the average of $U(0.1,0.9)$) and obtained similar results, showing that variability in $P_c$ among foragers did not influence wave characteristics (Figure 4). How-

The range in the proportion of vigilant individuals through time was the most sensitive wave characteristic to variation in ecological variables. We found that when the influence of neighbors was restricted, for instance, by reducing the radius of influence, by only considering the nearest neighbor, or in more elongated groups where foragers are closer on average to the edges, waves involved a smaller proportion of the population. Few data are available to examine the relevance of these predictions. Beauchamp (2011) noted waves in small and large groups of gulls and a wide variation in the
amplitude of the waves from group to group. Unfortunately, neither the density nor the shape of the groups was noted. Head movements in birds feeding in a linear array, as opposed to a circular arrangement, were less coordinated in one species of bird (Bekoff 1995), which is compatible with the observation here that waves are less organized in more elongated groups. Work with starlings (Sturnus vulgaris) indicates that companions that are further away are more likely to behave independently in terms of vigilance and foraging, again suggesting that group density is a crucial factor in copying (Fernández-Juricic and Kacelnik 2004; Fernández-Juricic, Siller, et al. 2004).

Overall, our results are important in showing that vigilance waves are not only an interesting phenomenon emerging from some particular model construction and parameterization but a robust emergent property when individuals copy the behavior of neighbors. It is also interesting to note that although collective waves may not always emerge with the same strength, this does not deny (at least not in our model) the occurrence of individual copying. This should encourage the search for copying even in groups without strong collective patterns of vigilance and, more importantly, to explore its adaptive value.

We made some simplifying assumptions in the model, and we now discuss some implications. We did not allow individuals to move during a simulation to ensure a stable group configuration. This is not unrealistic as many groups are relatively static over time. Examples include resting groups, obviously, but also groups of animals foraging over abundant resources (Pay, Renaud, et al. 2007; Pays, Goulard, et al. 2009). It would be interesting to model the consequences of movements in a group on wave characteristics. We surmise that movements may both facilitate or inhibit waves depending on the resulting changes in density and the relationship between movement and copying speed.

Another assumption that deserves further investigation is the shape of the copying response. We assumed a strictly linear increase in the probability of being vigilant as a function of the proportion of vigilant neighbors (Figure 1). This copying response makes sense when predators show a strong preference for stragglers and when information transfer about threats within the group is weak (Sirot and Touzalin 2009). Models show that when information transfer is stronger, the probability of being vigilant will initially tend to decrease rather than increase as more neighbors become vigilant (Sirot and Touzalin 2009). Nevertheless, as vigilance increases in frequency in the group, copying eventually represents the optimal solution. With stronger information transfer about threats, we suspect that it will be more difficult to build up large numbers of vigilant foragers in waves because it should pay individuals at times to avoid copying neighbors.

The ability to gather information from neighbors may also vary depending on the sensory capability of each species and on the postures adopted when foraging, some of which may be less conducive to information acquisition (Fernández-Juricic, Erichsen, et al. 2004). We did not model information acquisition explicitly, but future work could incorporate sensory capacity in the model to examine consequences for vigilance wave patterns.

It is ironic that the copying response, which can evolve to reduce the likelihood of being a straggler highly prone to predation, produces regular collective patterns of vigilance. Such regularity in vigilance could easily be detected by observant predators who could mount attacks when collective vigilance is low (Scannell et al. 2001). In such a case, the only line of defense available is risk dilution because the risk of being selected by the predator is divided among all nonvigilant foragers. This speculation suggests again that waves may be less likely in systems with more efficient transfer of information about threats within the group and also in systems with observable predators. Information transfer about threats in sleeping gulls was probably low because individuals are not very alert when sleeping, and the main sources of threats for gulls, such as people, dogs, or bald eagles (Haliaeetus leucocephalus), are not observable predators (Beauchamp 2011). These features may help explain why waves of sleeping occurred in these birds. Further empirical investigations in systems with varying levels of information transfer about threats and different types of predators should shed more light on the evolution of collective patterns of vigilance in animal groups using public information about predation risk.

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