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Evolution of anti-predator traits in response to a flexible targeting strategy by predators

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Anti-predator benefits increase with vigilance rate and group size in many species of animal, while simultaneously resource intake rates usually decrease. This implies that there is an optimal group size and vigilance rate that will maximize individual fitness. While this basic theory of vigilance has been modelled and tested extensively, it has often been assumed that the predator represents a ‘fixed-risk’ such that groups of prey are essentially independent entities that exert little or no effect on one another either directly or indirectly. We argue that this is an over-simplification, and propose that the behaviour of one group of prey will likely affect the fitness of another local group of prey if the predator preferentially attacks the most vulnerable group—rather than attack both with constant rates. Using a numerical simulation model, we make the first examination of this game and allow the prey to dynamically evolve both optimal group size distributions between two habitats and vigilance rates in response to a predator with a preference for whichever group is the more vulnerable. We show that the density of prey in the population and the sensitivity of a predator to differences in prey vulnerability are likely to drive the dynamics of such a game. This novel approach to vigilance theory opens the door to several challenging lines of future research, both experimental and theoretical.

Keywords: simulation model; vigilance; game dynamics; group size

1. INTRODUCTION

Visually scanning one’s surroundings for predators (vigilance), or indeed to gather information in general, and searching for food are—to a greater or lesser extent—mutually exclusive behaviours (Pulliam 1973; Shettleworth 1998, pp. 49–94). As both options have costs and benefits, an optimal trade-off between time spent being vigilant and time spent feeding exists for a particular situation. By forming groups, animals can theoretically benefit from the many-eyes effect of having neighbours that might alert one another to a potential threat, even if a particular individual has not detected the threat for itself (Pulliam 1973; Roberts 1996; Beauchamp 2003). Forming groups also introduces a dilution effect whereby having more neighbours simply means that the chance of oneself being predated is lessened (Dehn 1990; Bednekoff & Lima 1998). There are also well-established costs of grouping: most notably these take the form of competition for resources (e.g. food or mates). Put simply, the benefits are expected to increase as a function of group size and vigilance rate while simultaneously the costs also accrue (see Krause & Ruxton 2002 for a review). It follows that there must be an optimal distribution of individuals between groups with an associated rate of vigilance that best exploits this trade-off for a particular set of functional forms describing the costs and benefits of alternative behaviours.

Underlying this theory is the assumption that the predator represents a ‘fixed-risk’ with a constant rate of attack over time. This has the effect of making groups of prey entirely independent of one another—i.e. the behaviour of one group has no bearing on the fitness of individuals in another group. As Lima (2002) pointed out, predators are not simple fixed-risks—predators will far more likely adjust their behaviour as the prey alter theirs. Indeed, Packer & Abrams (1990) presented a series of models involving in one case a predator selecting the least vigilant prey within a single group. Their models were concerned with determining the differences and similarities between selfish vigilance (where individuals attempt to optimize their own personal vigilance rate) and cooperative vigilance (all individuals collectively and simultaneously alter their vigilance rates) for individuals within a single group. They showed that differential detection rates by vigilant and non-vigilant individuals as well as predator choice of target prey will affect the optimal vigilance rates of the prey. They also found an interesting set of dynamic solutions whereby there was no single optimum vigilance rate but rather a continually fluctuating set of rates in a dynamic game between only two individuals.

We consider a similar, but novel game involving two groups of prey. While groups of prey may not affect each other directly, they may still share a common predator, which can influence their fitnesses depending on how the predator selects between groups (i.e. similar in concept to

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apparent competition between species, Holt 1977). Consider the simple case where two groups of prey are entirely separate and divided by a fence. Assume further that there is no competition for resources outside of each group. A predator sitting on the fence can see both groups and is surely most likely to attack the most vulnerable group, with vulnerability being a function of current vigilance rates and group size. Now the optimal solution for the prey in terms of group size and vigilance rates is entirely linked to what the other group is doing—if one group is not vigilant at all then there is no point in the other group being overly vigilant as the predator will presumably always attack the other, more vulnerable group. The goal for prey in this scenario is to be collectively less vulnerable than the other group, thus triggering a dynamic game between groups in terms of anti-predator traits.

We model just such a system and use an evolutionary algorithm to locate the optimal strategies for the prey, which we present as the resultant end-points of the system (these are indicators of attractor-points of a dynamic system) in terms of prey distribution and vigilance rates for a range of prey population sizes. We show that when total prey populations are small, there is only a single strategy observed whereby all the prey move into the same habitat and minimize their vigilance rates. Beyond a threshold population size, a second strategy emerges whereby the prey split into two groups of equal size and attempt to equalize their vigilance rates such that the predation risk is shared between the two groups. Furthermore, the ability of the predator to accurately detect any difference in vulnerability between the two groups is also a key factor. We show that highly sensitive predators can push the prey into a third strategy, which fails to settle down to a single point, and where near-zero vigilance rates are adopted by both groups. In this situation, migration between groups dominates as individuals attempt to escape the predator's attention; this situation is bad for the prey and good for the predator. Highly sensitive predators can also prevent the system from settling down to a single arrested point, i.e. end-points that fluctuate perpetually through time—these situations are again generally better for the predator than the prey.

2. MODEL DESCRIPTION

We model a prey population of fixed size (F_{tot}) that can distribute themselves between two habitats in their environment (A and B) such that $F_{\text{A}}+F_{\text{B}}=F_{\text{tot}}$. The fraction of time spent being vigilant is the same for all individuals in a group and if it changes it does so for all individuals (referred to as cooperative vigilance) in a given habitat (denoted V_{A} or V_{B}: these equate to the proportion of time spent being vigilant and take a value between 0 and 1). For this first attempt to quantify the effect of a predator choosing between more than one group of prey, we limit our model to the far simpler cooperative solutions as is common in the literature for initial investigations of such systems (Pulliam 1973). We consider the effect selfish individuals might have on our model in the discussion. The fitness of prey individuals in habitats A and B is calculated by simultaneously considering their risk of starvation and risk of predation as follows.

The feeding rate of an individual in the ith habitat is a declining function of group size and personal time spent being vigilant (i.e. space is limited in the foraging group, and declines by $1/F$ with no interference competition and faster than $1/F$ with interference: an exponential function approximates this relationship), given by:

$$f_i(F_i, V_i) = (1-V_i)f_{\max}\exp(-\mu F_i),$$

with constants $f_{\max}=10$ (the maximum feeding rate) and $\mu=0.1$. The probability of an individual starving in the ith habitat is then given by:

$$s_i(f_i) = s_{\max}\exp(-\beta f_i),$$

with constants $s_{\max}=1$ (the maximum risk of starving) and $\beta=0.05$. We now consider the effect of prey behaviour on the predator, and will return to how this function feeds-back on the prey later. There is good evidence from several empirical studies that predator detection by prey increases asymptotically with group size, most likely due to the many-eyes mechanism (Krause & Ruxton 2002, pp. 8–11). We use an exponential function to capture this relationship and calculate the probability that a predator's attack on the ith habitat will be successful by

$$a_i = A_{\text{o}}\exp(-\gamma F_i V_i),$$

with constants $A_{\text{o}}=1$ (the maximum probability of successful attack) and $\gamma=0.2$. The predator, therefore, has perfect knowledge about group size and vigilance rate at all times in both habitats. This is similar to the predator sitting on a fence observing two groups of prey on either side; it is also comparable to the case of a learning predator that can move sufficiently quickly between patches of prey before groups depart for alternative habitats.

This last equation also allows us to determine which of the two groups is the most vulnerable at any one time: this will define the predator's behaviour. A predator makes κ attacks during an arbitrary time period. On each occasion, it must make a choice as to which of the two groups of prey to attack. The predator's preferred strategy is to always attack the *most* vulnerable group (i.e. the group where its probability of success is highest) with probability 1. Whether or not a predator is able to determine accurately which prey group is the more vulnerable at a given time will undoubtedly affect the optimal behaviour of the prey. We use a function that emulates predator detection ability (or predator sensitivity). The bigger the difference between a_{A} and a_{B}, the more likely the predator attacks the more vulnerable group. When there is a small difference between a_{A} and a_{B} the predator attacks both with nearly equal probability. The function we use is:

If $a_{\text{A}}>a_{\text{B}}$, attack A with probability

$$C_{\text{A}} = 0.5+0.5(1-\exp(-v|a_{\text{A}}-a_{\text{B}}|)), \quad C_{\text{B}} = 1-C_{\text{A}}.$$

Else, attack B with probability

$$C_{\text{B}} = 0.5+0.5(1-\exp(-v|a_{\text{A}}-a_{\text{B}}|)), \quad C_{\text{A}} = 1-C_{\text{B}},$$

where v is a positive constant. This function essentially smoothes the large step in prey fitness that occurs either side of the case when $a_{\text{A}}=a_{\text{B}}$ should the predator punish the more vulnerable group completely. When $v=0$, the predator is insensitive, and is unable to detect any difference between the two groups and both are attacked with equal probability$=0.5$. As $v\rightarrow\infty$ the predator becomes hyper-sensitive and is able to detect the smallest difference in vulnerability; the most vulnerable prey are then attacked with probability$=1$.

If an attack is successful, a given individual has a $1/F_i$ probability of being the victim (i.e. simple dilution of risk), so the probability of surviving a time period (Q) in which κ attacks occur is then

$$Q_i=\left(1-\left(\frac{a_i}{F_i}\right)\right)^{\kappa C_i}.$$

Note that this formula approximates predation risk to individual prey. We do not explicitly remove individuals that would be killed in the process so as to maintain population size constant during the simulation.

The fitness of a prey individual in the ith habitat (W_i) is then approximated by the product of the probability of not starving in a time period, and the probability of not being predated in a time period, $W_i=(1-s_i)Q_i$. The fitness of the predator (Z) is approximated by its combined success rates in both habitats ($Z=C_Aa_A+C_Ba_B$). Both predator and prey fitnesses are the instantaneous values as calculated at the end-point of each of the simulations determined from the system's current state $\{V_A, V_B, F_A, F_B\}$.

(a) *The simulation*

A computer algorithm is used to find regions of long-term persistent behaviour on the fitness surfaces for the prey (these regions approximate the location of attractor points). This process is not as simple as finding the peak of each of the fitness surfaces for the two groups of prey. As one group of prey moves around its fitness surface it alters the shape of the fitness surface for the other group as the predator's preference for attacking each group changes. For a given total population size in the system (F_{tot}), the following parameters are assigned randomly at the start of each simulation: V_A, V_B and F_A… ($F_B=F_{tot}-F_A$). One of the groups is then picked at random and an individual in that group is presented with the following options to choose from in order to increase its fitness.

(i) Stay in the same habitat, keep current cooperative vigilance rate (in current patch).
(ii) Stay in the same habitat, increase cooperative vigilance rate by ΔV ($=0.01$).
(iii) Stay in the same habitat, decrease cooperative vigilance rate by ΔV.
(iv) Go to the other habitat, keep current cooperative vigilance rate (in new patch).
(v) Go to the other habitat, increase cooperative vigilance rate by ΔV.
(vi) Go to the other habitat, decrease cooperative vigilance rate by ΔV.

The individual under consideration is capable of determining its fitness for each of the possible moves. During consideration the prey are essentially omniscient and they determine how the predator would change its preference in response to its actions and that intake rates would also be altered: the chosen individual selects the option that will maximize its fitness. Note that we have modelled cooperative rather than selfish vigilance, and if vigilance rates are deemed to have changed they do so for all individuals in the group to which the focus individual belongs. After this decision is made, we then pick an individual from the other group and present it with the same options. All changes to the system take immediate effect such that the predation is an instantaneous risk and food acquisition is an instantaneous intake rate. After one individual from each group has been interrogated we then select a group at random again and continue the process for 400 iterations (200 interrogations for each habitat), during which it is known that the system settles down to regular behaviour—this was achieved through observation and analysis of much longer term individual simulations (data not shown). Note also that migration in our model is motivated by either increasing intake rates or decreasing predation risk. Other behavioural rules such as simple random movements (Jackson *et al.* 2004) clearly exist but to avoid unnecessary complexity at this stage we omit them.

We used our algorithm to record the long-term dynamics of our system (after a transient period), for three values of predator sensitivity ($v=\{1, 10, 100\}$) and for the range of even-number total prey populations $F_{tot}=\{2, 4, 6, \dots, 50, 60, 70, 80, 90, 100\}$. Odd numbers of total prey generally result in fluctuating end-points as it is impossible to perfectly equalize numbers—for clarity of the figures we have left these simulations out, although the results take end-point values lying between the adjacent even-number simulations. For a given combination of v and F_{tot}, we performed 100 repetitions of the 400 iterations mentioned earlier, starting at randomly determined initial conditions (i.e. random values of V_A, V_B, F_A, F_B). We recorded the end-point values of V_A, V_B, F_A, F_B and calculated the associated predator fitness. We also recorded whether or not the resultant position of the system was an arrested-end-point, i.e. did not continue to move between iterations, or a fluctuating-end-point, i.e. continued to move without ever arresting (individual simulations ran for 10^5 iterations showed that if a system had not arrested within 400 iterations it never would). In our definition of arrested and fluctuating end-points, we do not distinguish between a system that had arrested in terms of prey distribution but fluctuated in terms of vigilance rates—if one characteristic is fluctuating then we have recorded this as a fluctuating-end-point. Furthermore, we do not classify fluctuating-end-points into limit-cycles, non-deterministic fluctuations or any other dynamic behaviour—this will require detailed analytical treatment in future work. Note that we have plotted the end-points of the system as if they were three independent data points. In reality, the end-point of a simulation for a given total prey population (F_{tot}) consists of a single point in three-dimensional space defined by $\{V_A^*, V_B^*, F_A^*\}$ (the asterisk denotes an end-point value). It is impossible to represent the end-points as a function of F_{tot} which would require a four-dimensional plot. It is, however, possible to use the patterns of fluctuating and arrested end-points to visually align values between relevant graphs. We have shown the end-point vigilance values for habitat A only (figure 1) because the results for habitat B are quantitatively similar. We present predator fitness as calculated at each end-point achieved for each simulation.

A brief note on the choice of parameter values used in simulations is required. Different species undoubtedly

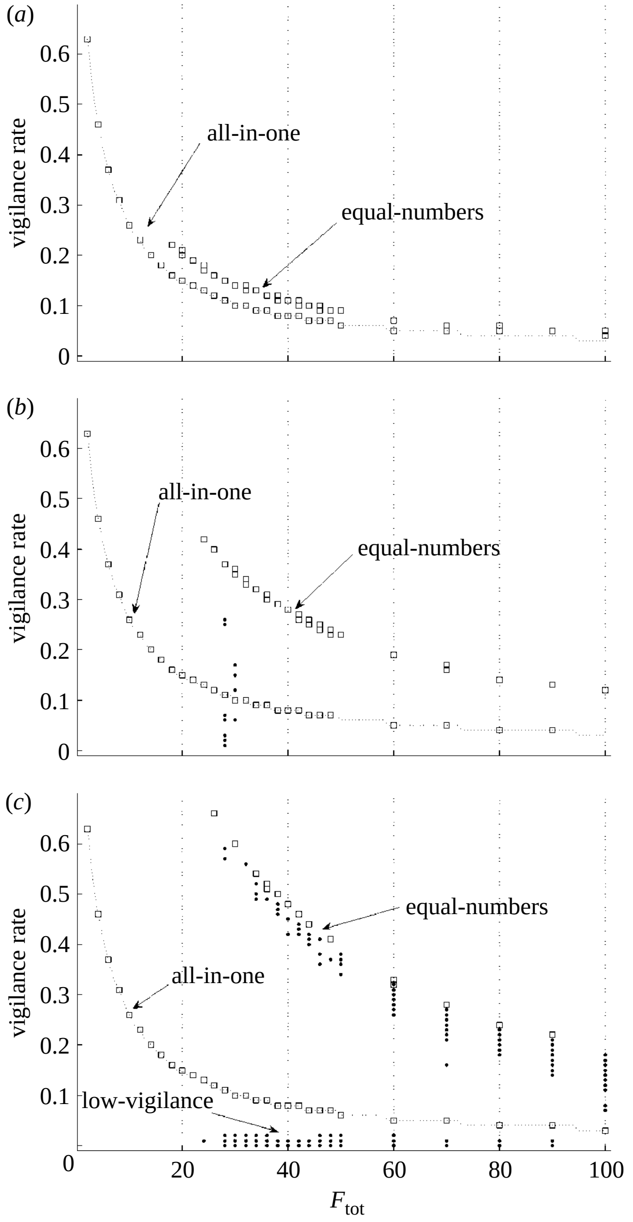

Figure 1. End-point vigilance rates for individuals in habitat A (V_A) for a variety of total prey populations (F_{tot}). Each panel represents a different predator in terms of sensitivity: (*a–c*) represent a low, medium and high sensitivity predator ($v=\{1, 10, 100\}$, respectively). Arrested end-points are depicted as filled circles and fluctuating end-points as open squares. The vertical dotted lines aid alignment of results. Labels indicate the different strategies referred to in the text.

have different functional relationships describing risk of starvation and ability to detect a predator as functions of group size and vigilance rate. We have chosen values that when combined, give an optimal group size of 10 and an optimal vigilance rate of approximately 0.26 for a fixed-risk predator. Our results remained qualitatively similar for a range of parameter values defining the functional relationships we have used (results not shown)—making us confident of the broad predictions of our model. In order to retain generality, we present our results for one set of possible values and refer to our results in a qualitative manner. Specific systems will of course have more specific values and results.

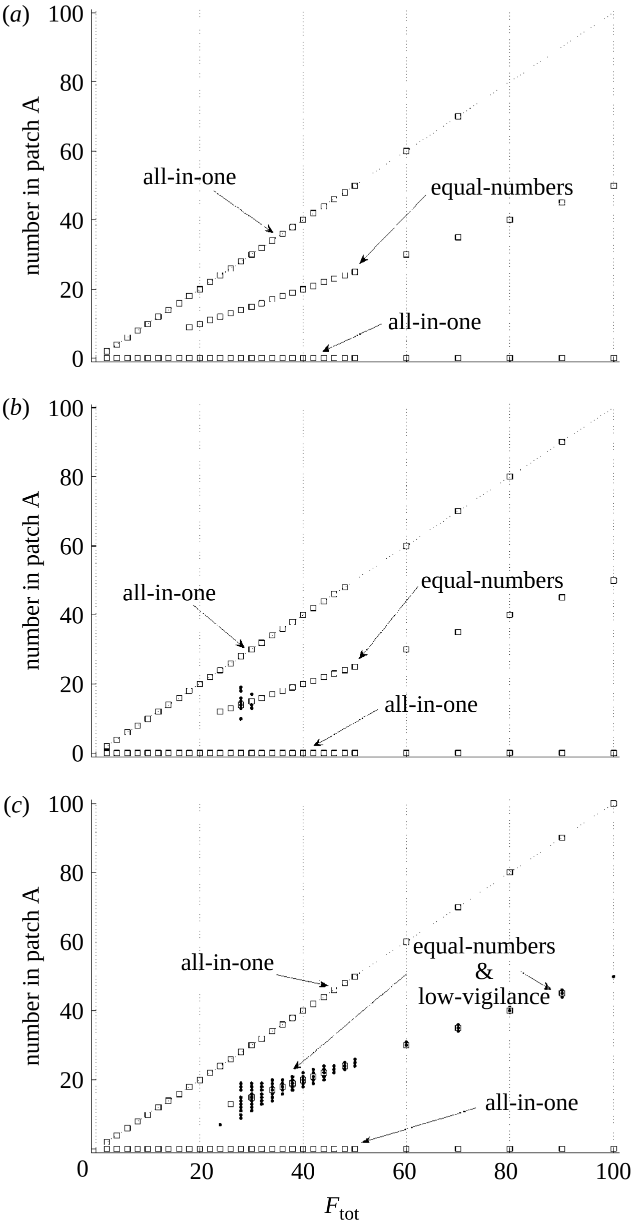

Figure 2. End-point prey distributions for a variety of total prey populations (F_{tot}). Values given are for the number of individuals in habitat A (F_A) at the termination of the simulation. Note that $F_B=F_{tot}-F_A$. (*a–c*) represent a low, medium and high sensitivity predator respectively. Arrested end-points are depicted as filled circles and fluctuating end-points as open squares. Labels indicate the different strategies referred to in the text.

3. RESULTS

The general pattern in all our results is that when the total number of prey in the system is low ($F_{tot}<20$ approx.), the prey always move such that they end up occupying the same habitat (call this the all-in-one distribution) and adopt the vigilance rate that maximizes their fitness (figures 1 and 2). Beyond a threshold number of total prey ($F_{tot}=\{17, 22, 22\}$ when $v=\{1, 10, 100\}$, respectively) the prey begin to arrive at another set of end-points with nearly equal numbers of prey in each habitat (call this the equal-numbers distribution). When the equal-numbers distribution is approached, the prey adopt vigilance rates that are slightly higher than those associated with the all-in-one distribution. The all-in-one distributions are always arrested-end-points. In contrast, the equal-numbers distributions begin to show some fluctuating-end-points when the predator becomes more sensitive ($v=\{10, 100\}$, figures 1*b*,*c* and 2*b*,*c*). The predator's ability to detect differences in vulnerability clearly affects the resultant end-points adopted by the prey. Because the predator does not have a choice about which group to attack when prey adopt the all-in-one distributions, the results remain identical across all three value of predator sensitivity (v) that we investigated. However, the equal-numbers distributions show the common pattern of increased vigilance rates as the predator becomes more sensitive (i.e. as $v \rightarrow 100$, figure 1). Fluctuating-end-points tend to occur when $v=100$ and F_{tot} is high (e.g. greater than 50). A further feature is that when a fluctuating-end-point occurs, the resultant vigilance rates tend to be lower on average than an arrested-end-point for the same value of F_{tot}, when $v=100$.

A third set of end-points emerge for more sensitive predators when $v=\{10, 100\}$: figures 1*b*,*c* and 2*b*,*c*. These occur close to the threshold value of F_{tot} when the equal-numbers distribution first appears. They are associated with fluctuating prey-distributions with large deviations around the equal-numbers solution (figure 2*b*,*c*) and are characterized further by much lower vigilance rates than occur in the other sets of end-points: call these solutions the low-vigilance end-points. For the case of a moderately sensitive predator ($v=10$; figure 1*b*) the vigilance rates range between zero, and those higher values normally associated with the equal-numbers distribution within a narrow range of F_{tot} values ($=[28,30]$). This large scale range is reduced to very low vigilance rates (approaching zero) when a highly sensitive predator is considered ($v=100$; figure 1*c*). Fluctuating end-points are generally driven by movements of individuals between groups, because migration tends to have a stronger effect on fitness than an incremental change in vigilance rate (at least for lower population sizes). These fluctuations generally have a small amplitude, tend to be random as a consequence of the randomness in the algorithm, and involve only a differential of less than 10 individuals and 0.1 vigilance rate. As the total population increases, the effect of fluctuations of individuals becomes lower and that of vigilance rates becomes higher—because their relative affect on fitness changes.

Note that the different end-points have different frequencies of occurrence that are somewhat dependent on the initial conditions (colour figures with associated frequencies available in electronic supplementary material). The general trend is for the all-in-one strategy to become less likely to occur as total prey population increases, becoming replaced by the equal-numbers strategy, with the low-vigilance strategy occurring at moderate frequencies when it occurs. The random choice of which group alters its behaviour first ensures that the end-point achieved is not deterministic. Our model probably underestimates the true stochastic processes in a real system such as disturbance and individual differences. Occasionally, the all-in-one distribution does not occur in one of the patches e.g. there were no recorded set of end-points with zero individuals in habitat A above 70 individuals in figure 1*a*: this is not to say they cannot occur, only that they were not observed within the number of repeated simulations we ran. Also, fluctuating-end-points occur more frequently than stable ones as the predator becomes more sensitive.

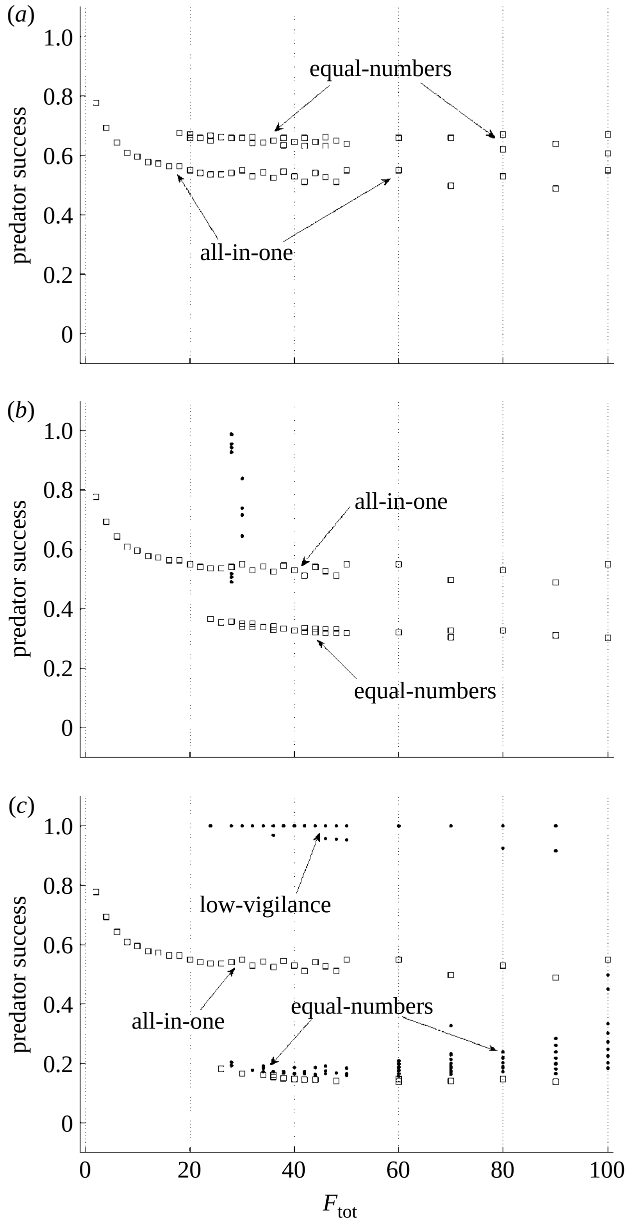

Figure 3. The predator's fitness (Z) for each of the end-points depicted in figures 1 and 2. (*a*–*c*) represent a low, medium and high sensitivity predator, respectively. Arrested end-points are depicted as filled circles and fluctuating end-points as open squares. Labels indicate the different strategies referred to in the text.

A further characteristic of the system that we have so far not considered is how the predator's fitness (in terms of its overall probability of success) is affected by the different strategies adopted by the prey. These results are depicted in figure 3*a*–*c* for $v=\{1, 10, 100\}$, respectively. The predator does much better when the prey adopt the equal-numbers distribution as opposed to the all-in-one strategy (figure 3*a*,*b*) except when the predator is very sensitive (figure 3*c*). When the prey adopt the all-in-one strategy, predator fitness initially declines quickly as F_{tot} increases but tends to level-off for all prey strategies when $F_{\text{tot}} > 20$ approximately. Intuitively, the predator achieves the highest fitness when the prey adopt the low-vigilance strategy associated with a moderate and highly sensitive predator ($v=\{10, 100\}$). All predators have the same fitness when the prey adopt the all-in-one distribution. Interestingly, although the highly sensitive predator ($v=100$) can achieve the highest fitness, when the prey adopt the low-vigilance strategy, they in fact do worse than either the low or moderately sensitive predator when the prey adopt the equal-numbers distribution.

4. DISCUSSION

The system we have considered is interesting because the behaviour of one group of prey affects fitness in the other group. This effect does not occur directly, but rather through a common predator. Because of this indirect coupling, we find that the optimal strategy any one group should employ depends on what the other group is doing at a particular time, and also on the ability of the predator to assess relative group vulnerability. Two main patterns are evident: in one, the prey all occupy the same habitat; and in the other, two groups of nearly equal numbers form. When the prey adopt the all-in-one distribution, the adopted vigilance rate is identical to what we would expect if there were only one possible habitat that could be occupied. Alternatively, the prey distribute themselves into two groups containing nearly equal numbers of prey. A higher rate of vigilance is achieved when the prey adopt the equal-numbers distribution because the dilution effect is not as strong in the resulting smaller groups, and there is less competition for food. It is the density of prey in the overall population (F_{tot}) that drives the formation of either one or two groups. When the total number of prey in the system is low we only observe the all-in-one distribution, as dilution and collective detection effects out-weigh the costs of competition for food that result from the proximity of many individuals. However, as the number of prey increases, the cost of competition for food begins to surpass the benefits of forming such a large group and the overall tendency is for the prey to split into two groups of near-equal size. We might have expected several sets of end-points, with a smaller group adopting a higher vigilance rate compared with the other larger group's lower vigilance rate. Instead, when two groups persist, we observed that individuals in our model tended towards the equal-numbers distribution only. This occurred because the effect of dilution is generally stronger than an incremental change in vigilance rates: i.e. switching to the other group is likely to have a more profound effect on an individual's fitness than altering the cooperative vigilance rate (Bednekoff & Lima 1998; Dehn 1990).

The more sensitive the predator is to small differences in prey susceptibility, the greater the adopted vigilance rate tends to be for the prey—of course this only occurs when the prey split into two groups; else the optimal vigilance rate is the same. Increasing the predator's sensitivity also has the effect of destabilizing the prey's distribution (causing fluctuating end-points). Furthermore, the emergence of the low-vigilance strategy is mediated by increasing predator sensitivity. This counter-intuitive strategy is achieved primarily because the highly sensitive predator attacks the most vulnerable group nearly exclusively—the other group is then essentially living in a predator free world. The attacked group essentially admits defeat and reduces its vigilance to zero (it cannot overcome the predator's preference through incremental increase in vigilance rates), while the risk-free group maintains a marginally non-zero vigilance rate. Individuals in the attacked group respond by moving to the risk-free group—an near infinitely better situation. As the numbers in the risk-free group increases, they lower their vigilance rate such that it becomes possible for the attacked-group to reduce their vulnerability by increasing theirs. Eventually, the vulnerability of the groups is reversed such that the predator switches its preference to the larger of the two groups. Migration then occurs sequentially from the attacked group until vulnerability again switches to the other group: the system cycles in this manner *ad infinitum*. It is the fact that the risk-free group incurs no predation that drives the system towards zero-vigilance rates. The race to be the least vulnerable is contested mainly by migration and also by subtle changes in vigilance rates. In our model, the risk-free group maintains a non-zero vigilance as to adopt a zero-vigilance would make it as vulnerable as the other group. It is possible that allowing larger (or even unrestricted) changes in vigilance rates between iterations would prevent this strategy from occurring and push the system towards either the equal-numbers or all-in-one situation—although Packer & Abrams (1990) find a similar situation which they term the 'war of vigilance' between two prey individuals in the same group. What about more than two groups? In our model, we chose to limit the number of groups of prey that can form to two for ease of model formulation and description as well as having only a single predator. As in our model, where we observed a tendency for the prey to split equally between two groups above a threshold number of total prey in the system, we suppose that above another threshold there will be a tendency for the prey to split between three groups of equal numbers, and so on.

The predator generally achieves a higher success rate the more sensitive it is to differences in prey vulnerability between the groups. However, when the predator is highly sensitive, we observed that the predator actually began to do worse when the prey adopted the equal-numbers strategy. This occurs because the prey are driven towards a very high rate of vigilance, which in turn reduces the predator's success rate. The predator also tends to do slightly better when the prey fail to settle down to an arrested end-point—so what might be slightly sub-optimal behaviour for the prey turns out to be better for the predator. Whether or not predators can actively take advantage of this is another question, but perhaps other extrinsic factors that prevent prey from perfectly equalizing their vulnerability will favour the predator rather than the prey. These results suggest that it may not always pay predators to develop highly efficient discrimination. A full model including adaptive changes in behaviour by the predators as well as the prey is needed to examine this intriguing possibility. Abrams (1986) has already shown that such a co-evolutionary game will likely be affected by the relative rates at which different traits can change for both prey and predators.

This leads on to another point: how are the prey supposed to know what the other group is doing, especially if they cannot see them? The prey could use a form of continuous updating based on the number of predator attacks they incur over time as a way to determine what the other group is doing: if they are only being attacked very infrequently, then this would suggest that the other group is more vulnerable. This process of continuous updating might be similar to that proposed for determining the resource value of a good patch (Iwasa *et al.* 1981; Green 1988).

The model we have presented opens up a new dimension in anti-predator behaviour research that can be explored both experimentally and theoretically in future work. Most obviously, if would be interesting to know whether groups of prey adjust their vigilance behaviour in response to the presence of other groups. If this were the case, we might expect individuals within the same group to adjust their behaviour according to their neighbour's vulnerability. However, both experimental Beauchamp 2002) and field based work (Lima & Zollner 1996) have failed to show such monitoring within the same group, but Elgar *et al.* (1984) found evidence supporting such monitoring in house sparrows (*Passer domesticus*) and more recently Fernández-Juricic & Kacelnik (2004) have shown that flocking starlings (*Sturnus vulgaris*) appear to pay attention to the vigilance status of their close neighbours—whether this extends to separate flocks adjusting their behaviour as we predict ought happen has yet to be investigated. Further, information on how predators choose between multiple prey groups when deciding which one to attack would be highly informative.

There are also many new avenues that could be pursued theoretically. Ultimately, it would be very interesting to generate a fully individual-based model in which each individual acts entirely selfishly as in the analytical models described by Packer & Abrams (1990) and McNamara & Houston (1992). We suspect that such a model will generate similar results to ours, although we expect quantitative differences—the direction of this difference will likely be specific to several parameters such as differential probabilities of predator detection by vigilant and non-vigilant prey (Packer & Abrams 1990). If one considers the case where there are equal numbers of individuals in each group, and vigilance rates are equal across all individuals, then a single individual has the capability of making its group, and consequently itself, less vulnerable than the other by simply increasing its own vigilance rate. Indeed, the effect of having a choosy predator might be a strong proponent of so called 'honest' vigilance (where individuals do not simply parasitize their neighbours' vigilance). This will be a challenge either mathematically or computationally, as it will generate at least two simultaneous dynamic games for the prey with predators dynamically choosing both between groups of prey and between individuals within a group.

Indeed the game-dynamics we have described between groups of prey, with a substantial pay-off associated with only being slightly less vulnerable than one's flock-mates are likely to take a similar form within the groups. Theoretical evidence comes from Packer & Abrams (1990), and empirical evidence from observations of cheetah preferentially attacking the least vigilant gazelle comes from Fitzgibbon (1989). In our version of the model, there is no cost incurred by the prey when they switch groups, a fitness cost is often assumed in other models such as optimal foraging (Charnov 1976; Cézilly & Benhamou 1996). Including such a cost would most probably prevent some of the fluctuating end-points that arise from the movement of prey between patches. This would probably also result in asymmetric vigilance rates occurring as the groups attempt to compensate for the small difference between the numbers of prey residing in each patch. Analytical treatment of this system will provide detailed information about the dynamics of this interesting game—although it will be challenging to build a generic model with non-specific functions describing the costs and benefits of grouping for the full range of group sizes. Stability analysis will also provide robust descriptions of the dynamics observed in our model around the local attractor points.

Predator behaviour has often been omitted from models of vigilance or at least simplified into a single, fixed-risk entity (except see Packer & Abrams 1990; Bednekoff & Lima 1998; Scannell *et al.* 2001). We have shown that although the broad predictions of vigilance theory still hold (decreasing vigilance with increasing group size), by adding a predator that has a choice to make as to which group to attack, some new interesting dynamics are brought to light. Specifically these are that: prey will tend to split into at least two groups when competition for resources out-weighs predation risk; and predators may not always benefit from being highly sensitive to differences in prey vulnerability. The optimal behaviour of the prey is likely to be highly dependent on the density of prey in the environment and the behaviour of their predators. We also predict that the number of groups into which they form (or are able to form) will strongly affect the dynamics of the predator–prey game. Ultimately, the game we have described does not require that any individual prey (or group of individuals) has to do particularly well, they only have to do slightly better than their neighbours in order to achieve a potentially substantial pay-off (as in the War of Attrition games; Maynard Smith 1974).

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