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Gregarious Behaviour of Evasive Prey

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Gregarious Behaviour of Evasive Prey*†

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Abstract

Gregarious behavior of potential prey was explained by Hamilton (1971) on the basis of risk-sharing: The probability of being picked up by a predator is small when one makes part of a large aggregate of prey. This argument holds only if the predator chooses its victims at random. It is not the case for herds of evasive prey in the open, where prey's gregarious behavior, favorable for the fast group members, makes it easier for the predator to home in on the slowest ones. We show conditions under which, gregarious behavior of the relatively fast prey individuals leaves slowest prey with no other choice but to join the group.Failing to do so would signal their vulnerability, making them a preferred target for the predator. Analysis of an $n+1$ player game of a predator and n unequal prey individuals clarifies conditions for fully gregarious, partially gregarious, or solitary behavior of the prey.

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1 Introduction

Animals' gregarious behavior may result from various reasons as self defence, mating behavior, or concentration of food. As has already been noticed by Lorenz (1966), none of these causes seem applicable to evasive herds of ungulates in open plains, to shoals of fish in the open sea, or to flocks of birds. Later explanations as of vigilance (Bertram 1978, Motro and Cohen 1989, Elgar 1989, Lima1994, Bednekoff and Lima 1998) or of other sorts of information sharing (Ward and Zahavi 1973, Clark and Mangel 1984, Turner and Pitcher 1986, Templeton and Giraldeau 1995, Valone and Templeton 2002) may not be applicable to the commonly observed tendency of potential prey to aggregate in face of danger, and to escape as a group. As has already been noticed by Hamilton (1971 and references there), there is a body of evidence indicating that prey's gregarious behavior often facilitates predation (for more recent references see Hebblewhite and Pletscher 2002, Whitfield 2003).

An already widely accepted explanation, suggested by Hamilton to this phenomenon, was based on risk-sharing (see also Williams 1964): Even if a large aggregate of prey facilitates the predation of one or few individuals out of it, the chance of any of its member to be the chosen victim may still be small. Moreover, once such an aggregate is established, it becomes advantageous to any of its members to push its way to the center, thereby decreasing its own predation probability (Hamilton 1971, and later empirical evidences in Foster and Treherne 1981, Bumann et al 1997, James et al 2004).

Hamilton's model has shifted the focus of the problem from the two-player game, played by a predator and a group of prey, to that of the n-player game, played among individuals within the prey population. A tacite assumption of the risk-sharing argument, however, concerns the role of the predator as a passive nature-force, picking its prey at random, rather than an active, decision-making player, attempting to choose the most vulnerable prey in group. This is a plausible assumption for a gatherer type of a predator, and it was convincingly established for various predators of fish (Bumann et al 1997, Nonacs et al 1998, James et al 2004), tadpoles (Spieler 2003), crabs (Viscido and Wethey 2002), beetles (Romey 2004) or limpets (Coleman et al 2004). It appears to be less applicable for predators of evasive prey as flocking birds (Nishimura 2002, Cresswell and Quinn 2004) or ungulates in the open (Fanshawe 1993, Hebblewhite and Pletscher 2002). In these cases, it has been well established that the choice of a vulnerable prey is a most crucial stage of the hunt. But when this is the case, the risk-sharing effect becomes irrelevant to the most vulnerable, slowest individuals in the evasive herd. On the contrary, being part of a large group, makes this prey more easy to home in on. The question, in this case, is what prevents the dissolving of the herd due to successive desertions by those of its members that find themselves, each at a time, in its rear.

As has been suggested elsewhere (Eshel 1978), a key factor in the establishment of gregarious behavior of evasive prey lies, quite paradoxically at first sight, in the extra information this behavior reveals to the predator about the

identity of the slowest prey in herd. While this is obviously disadvantageous to the slowest prey, it is advantageous to faster members of the herd, as it decreases the probability that the predator will mistakenly home in on them. But then, not joining the herd may as well mark the vulnerability of the slower prey, rendering it preferable target for the predator. To analyze this situation, a model of an asymmetric $n+1$-player game, n unequal prey individuals and a decision-making predator, the Savannah Model, was suggested (Eshel 1978). Contrary to Hamilton's model, the Savannah Model assumes that the predator has full information both about the location of the prey, and about the identity of the slowest prey in any group it pursues. Under these extreme conditions, fully gregarious behavior of the prey resulted as the only outcome of the game. Note that, although deviating from the specific assumptions of Hamilton's risk-sharing model, the Savannah Model still follows Hamilton's most fundamental idea of a selfish prey, seeking to increase its own survival probability.

In the present work we further develop this idea under a rather general assumption about the predator's set of information. In section 2 we introduce a prey-predator game, of which Hamilton's Selfish Herd and Eshel's Savannah Model are special cases. While in environments close to these two, prey's totally gregarious behavior is shown to always be the outcome of the game, we also find conditions for partially gregarious and solitary behavior of the prey. In section 3 we implicitly characterize the equilibria and stable equilibria of the game. In section 4 we concentrate on an important set of equilibria, regular ones, in which a herd is formed either by all prey individuals, or by a subgroup of the fastest ones, and the predator always prefers to pursue a solitary prey, if it detects one. For a range of environments, close to that of the Savannah Model (the savannah environment, subsection 4.1), it is shown that a regular equilibrium always exists, and it is generally stable. Under further assumptions, all equilibria are shown to be regular. Non regular equilibria (in addition to regular ones) are shown to exist in environments close to that of Hamilton's Model.

2 The Herd Formation Model

A prey population Ω consists of n unrelated individuals within the territory of a single predator. The individuals within the prey population are distinguished by their probability of being caught by a predator, when it pursues them, $p_1 < p_2 < ..... < p_n$. Individual 1, the fastest prey, has the lowest probability of being caught. Each of the individuals chooses whether to join the (single) herd or to hide as a solitary individual. Let $H \subseteq \Omega$ be the set of individuals that form the herd, and let $S = \Omega - H$ be the set of solitary individuals. Note that either H or S may be empty if all individuals (or none) join the herd. Let h be the number of individuals in the herd, and let s be the number of solitary individuals, with $h + s = n$.

The (single) predator surveys the terrain and tries to locate a prey. The predator aims to catch a single prey. Once it catches one prey, the chase ends.

A herd of size h escapes the predator's attention with probability q_h. We

assume that it is more difficult for a larger herd to pass undetected by the predator, i.e. $q_{h+1} < q_h$ (This assumption may not be valid for cases in which sharing of information helps large herds to avoid predators, e.g. Turner and Pitcher 1986. The present model, however, suggests an alternative explanation to prey's gregarious behavior). A solitary individual will escape the attention of the predator with probability $q_1 = q < 1$, hiding solitarily does not guarantee safety. Detecting prey, whether solitary individuals or a herd, are assumed to be independent events.

If the predator detects only the herd (but fails to detect any solitary prey), it will pursue the herd. If it fails to observe the herd but detects some solitary prey, it will pursue one of the solitaries it detected. The predator's strategy specifies what it will do if it detected both the herd and some solitary individuals. The predator may use a pure strategy or a mixed one: It will pursue the herd with probability $1 - x$, and one of the solitary individuals with probability x.

The main difference between the herd and the group of solitary prey is the information the predator receives about the prey it pursues. When pursuing one of the solitary individuals, it receives no signal about their speed, and it therefore homes in on one of those it detected with equal probabilities. In contrast, when the predator pursues the herd, it is more likely to home in on a slow individual.

Let $\theta_{i,H}$ be the probability that, pursuing the herd H, the predator will home in on individual i. We assume that $\theta_{i,H}$ satisfies the following three assumptions:

1. When pursuing a herd, the predator will eventually home in on one of its members: $\sum_{\eta \in H} \theta_{\eta,H} = 1$.

2. The predator homes in on a faster prey individual with lower probability than on a slower one: If $i, j \in H$, $i < j$, then $\theta_{i,H} \leq \theta_{j,H}$.

3. If a faster individual joins the herd, its probability of being pursued by the predator is lower than that of a slower individual that joins the herd: If $i, j \notin H$, $i < j$ then $\theta_{i,H\cup\{i\}} \leq \theta_{j,H\cup\{j\}}$.

The following is an example of a function $\theta_{i,H}$ that satisfies the above 3 assumptions:

Example:

$$\theta_{i,H} = \frac{p_i^\rho}{\sum_{\eta \in H} p_\eta^\rho},$$

where $\rho \geq 0$. The parameter ρ measures the precision of the information the predator receives when pursuing the herd. For $\rho = 0$, the predator receives no information and will home in on any of the individuals with equal probabilities. For the limit case $\rho = \infty$, the predator makes no mistake and homes in on the slowest individual in the herd. These two extreme cases correspond to

Hamilton's (1971) selfish herd model ($\rho = 0$), and Eshel's (1978) savannah model ($\rho = \infty$).

The assumptions given above define a Herd Formation Game, in which each prey individual chooses whether to join the herd, and the predator chooses whom to pursue when it observes both the herd and some solitaries. The payoff of each prey individual is its probability of not being caught, and the predator's payoff is its probability of catching a prey.

An equilibrium of this game consists of a strategy of the predator plus a partition of the prey population into a herd and solitary individuals, such that no individual can gain by deviating from its strategy. The strategies of the players in this game can be described by the pair $\langle H, x \rangle$, where $0 \leq x \leq 1$ is the predator's strategy (the probability with which it will pursue a solitary individual in the case that it detected both the herd and some solitaries), and $H \subseteq \Omega$ is the herd (formed by those prey individuals that choose to join the herd). $S = \Omega - H$ is the corresponding set of solitary individuals.

Being interested in the formation and stability of herds, we restrict our analysis to equilibria with pure prey's strategies. This will sometime require the consideration of the predator's mixed strategies.

Definition:

(i) The pair $\langle H, x \rangle$ is an equilibrium if each prey individual plays a best response to the strategies of all the others (prey and predator), and the predator's strategy x is a best response to the partition of the prey population.

(ii) The pair $\langle H, x \rangle$ is a stable equilibrium if the strategy of each prey individual is the unique best response to the strategies of all others, and the predator's strategy x is the unique best response to the partition of the prey population.

3 Best Responses and Equilibria

In this section we analyze the best response of the predator to each partition formed by the prey population, and the best response of each prey individual to both the predator's strategy and the partition formed by all other prey. Consequently we characterize the equilibria and stable equilibria of the game.

3.1 The Predator's Best Response

Given the prey's choices, a herd H of size h has been formed ($s = n - h$ is the size of the group of solitaries). The predator's strategy $0 \leq x \leq 1$ determines the predator's action when detecting both the herd and some solitary prey. In this case, the predator pursues a random solitary in probability x, and pursues the herd in probability $1 - x$. In all other cases, the predator pursue the only group of prey it detected, independently of its strategy. This means that when all prey individuals took the same decision, either to form a single herd, or to

remain solitary, the predator is indifferent between its strategies, each of them leads to the same action and is, therefore, a best response to the prey's choice.

Assume that neither the herd H, nor the group S of solitaries is empty. The predator's best response to the prey's choice, in this case, is the strategy that will provide it with the highest probability of success when detecting both the herd and some solitaries. Pursuing the herd, the predator has a probability $\theta_{\eta,H}$ to home in on its member $\eta \in H$, with a conditional probability p_η of success. Its total probability of success is then $\sum_{\eta \in H} \theta_{\eta,H} p_\eta$. On the other hand, pursuing a solitary, the predator has equal probabilities both to detect and to pursue, if it detected, each of the s solitaries, hence it has a probability $1/s$ to home in on any solitary. Homed in on the specific solitary $\sigma \in S$, it has a conditional probability p_σ of success. Its total probability of success, if pursuing a solitary, is therefore $\frac{1}{s} \sum_{\sigma \in S} p_\sigma$.

Proposition 1 *Assume that neither the herd H, nor the group S of solitaries is empty, then:*

(i) If

$$\sum_{\eta \in H} \theta_{\eta,H} p_\eta > \frac{1}{s} \sum_{\sigma \in S} p_\sigma, \tag{1}$$

then the predator's unique best response is to pursue the herd, whenever detected ($x = 0$).

(ii) If the reverse of (1) holds as a strict inequality, then the predator's unique best response is to pursue a solitary prey, whenever it detect one ($x = 1$).

(iii) A (non unique) best response of the predator can be a mixed strategy only if inequality (1) is replaced by an equality. This is possible only for a zero-measure set of parameters.

3.2 The Prey's Best Response

We now calculate one prey individual's best response to the predator's strategy $0 \leq x \leq 1$ and to all other prey individuals' choices, i.e. to their partition into herd and solitaries. We first find a condition for a prey individual i that is currently in the herd, to be better off remaining there. For this we have to compare its probability to be caught if staying in herd, with its probability to be caught if leaving it.

Staying in herd, the probability that it will be caught is $\theta_{i,H} p_i$ times the probability that the predator will pursue the herd. The predator will pursue the herd for sure if it detects the herd and no solitary prey. This occurs in probability $(1 - q_h)\, q^s$. It will pursue the herd in probability $1 - x$ if it detects both the herd and some solitaries. This occurs in probability $(1 - q_h)\,(1 - q^s)$. Summing up, the probability of i to be caught, if remaining in herd, is:

$$\left[(1 - q_h)\, q^s + (1 - x)\,(1 - q_h)\,(1 - q^s)\right] \theta_{i,H} p_i.$$

To calculate its probability to be caught if leaving the herd, we distinguish between the cases where $h \geq 3$, and the one in which $h = 2$. In the first case, if prey i deserts the herd and joins the solitaries, the herd shrinks to $H' = H - \{i\}$, and the set of solitaries expands to $S' = S \cup \{i\}$. In this case, the probability that individual i will be caught is $p_i/(s+1)$ times the probability that the predator will pursue a solitary (as there are now $s+1$ of them). The predator will pursue a solitary for sure if it only detects the solitaries. This occurs in probability $q_{h-1}\left(1-q^{s+1}\right)$. It will pursue a solitary in probability x if it detects both the herd and some solitaries. This occurs in probability $(1-q_{h-1})\left(1-q^{s+1}\right)$. Thus the probability of prey i to be caught if leaving the herd is:

$$\left[q_{h-1}\left(1-q^{s+1}\right)+x\left(1-q_{h-1}\right)\left(1-q^{s+1}\right)\right]\frac{1}{s+1}p_i.$$

Individual i is therefore better off in the herd than hiding as a solitary iff:

$$\begin{aligned} & \left[\left(1-q_h\right)q^s+(1-x)\left(1-q_h\right)\left(1-q^s\right)\right]\theta_{i,H}p_i \\ < \quad & \left[q_{h-1}\left(1-q^{s+1}\right)+x\left(1-q_{h-1}\right)\left(1-q^{s+1}\right)\right]\frac{1}{s+1}p_i. \end{aligned}$$

By a simple manipulation, denoting the right hand side of the following inequality by $\tau_h(x)$, individual i is better off staying in the herd iff:

$$\theta_{i,H} < \frac{\left(1-q^{s+1}\right)\left[(1-x)q_{h-1}+x\right]}{(s+1)\left(1-q_h\right)\left[xq^s+1-x\right]} = \tau_h(x) \qquad h \geq 3 \tag{2}$$

In the case that the herd has only 2 members ($h = 2$), if prey i abandons it, the herd dissolves and all individuals become solitaries. The condition for being better off when remaining in the herd in this case is:

$$\theta_{i,\{i,j\}} < \frac{\left(1-q^n\right)}{n\left(1-q_2\right)\left[xq^{n-2}+1-x\right]} = \tau_2(x). \tag{3}$$

The right hand sides of the last two conditions, $\tau_h(x)$, are independent of i, they depend only on the size of the herd (h) and on the predator's strategy (x).

Note that if condition (3) holds for some i, j, then the situation in which all individuals hide solitarily is not an equilibrium. The slowest of the two individuals i, j, assume it is i, will join j to form a herd, and since prey j is faster, $\theta_{j,\{i,j\}} < \theta_{i,\{i,j\}}$, and prey j will be better off staying in this herd of size two rather than dissolve it.

In an analogous way, prey i, that is currently solitary, will be better off staying as a solitary iff:

$$\theta_{i,H\cup\{i\}} > \frac{\left(1-q^s\right)\left[(1-x)q_h+x\right]}{s\left(1-q_{h+1}\right)\left[xq^{s-1}+1-x\right]} = \tau_{h+1}(x). \tag{4}$$

Note that all the above inequalities will be strict inequalities for almost all sets of parameters, equalities hold for a set of parameters of measure zero.

It follows (as is shown in Proposition 2) that if the slowest individual in H is better off staying in the herd, then all other individuals in the herd will also be better off in the herd than hiding as solitarily.

Proposition 2 *For any predator strategy* $0 \leq x \leq 1$:

(i) If an individual in the herd is better off in the herd than being solitary, then all faster individuals in the herd are also better off being in the herd.

(ii) If a solitary individual is better off as solitary than in the herd, then all slower solitary individuals are better off being solitary than joining the herd.

Proof. (i) Let individual $i \in H$ be better off staying in the herd than hiding solitarily, and let $\eta \in H$ be a faster prey than i. In this case $\theta_{\eta,H} \leq \theta_{i,H}$, and by inequality (2), $\theta_{i,H} < \tau_h(x)$, hence $\theta_{\eta,H} < \tau_h(x)$. But this is the condition for individual η to be better off staying in the herd.

(ii) Let individual i be a solitary individual. If its best response is to stay solitary, then by inequality (4): $\theta_{i,H\cup\{i\}} > \tau_{h+1}(x)$. Let η be a solitary prey slower than i. By our assumptions on the homing in probabilities: $\theta_{i,H\cup\{i\}} \leq \theta_{\eta,H\cup\{\eta\}}$ (when a slower individual joins a herd its probability of being pursued is higher than that of a faster individual that joins the herd). It follows that $\theta_{\eta,H\cup\{\eta\}} > \tau_{h+1}(x)$, which implies that individual $\eta's$ best response is to remain solitary. ■

Conclusion: Given a partition of the prey population into a herd and a group of solitaries, it suffices to test whether the slowest individual in the herd and the fastest solitary individual play their best response. If these two individuals play their best response, then all other individuals necessarily play their best response.

3.3 Equilibria and Stable Equilibria

From Proposition 2 and inequalities (1) - (4) we get:

Proposition 3 *The pair* $\langle H, x\rangle$ *is an equilibrium iff the three following conditions are satisfied:*

i) $\theta_{i,H} \leq \tau_h(x)$*, where* i *is the slowest member of* H*,* $\tau_h(x)$ *being defined in (2) and (3).*

ii) $\theta_{j,H\cup\{j\}} \geq \tau_{h+1}(x)$*, where* j *is the fastest solitary prey, if there is a solitary prey.*

iii) x *is a predator's best response to the formation of the herd* H*.*

$\langle H, x\rangle$ *is a stable equilibrium iff inequalities (i) - (ii) are strict, and* x *is the unique predator's best response to the formation of the herd* H*.*

4 Regular Herds

Proposition (2) introduces some regularity into the equilibrium partitions of the prey population. It suggests that herds, in which the slowest member is faster then all solitary individuals, are reasonable candidates for equilibrium. We show conditions under which such equilibria exist, and conditions under which only such equilibria exist.

Definition: A (non empty) herd H is a *regular herd* if its slowest member is faster than any solitary prey. We denote by R_h the regular herd of size $h, (h = 2, 3, ...n)$, consisting of the fastest h prey individuals.

Note that the grand herd $R_n = \Omega$, corresponding to the fully gregarious behavior of the prey, is regular.

Proposition 4 *The strategy $x = 1$ (pursuing a solitary prey whenever it is detected) is always a predator's best response to a regular herd. It is the unique predator's best response to any regular herd R_h, where $h \leq n - 1$.*

Proof. We already know that, once the grand herd was formed, the predator is indifferent between all its strategies, all of them amount to pursuing the herd, if it was detected. In this case any predator's strategy, $x = 1$ included, is a predator's best response to Ω.

Assume a regular herd R_h with $2 \leq h \leq n - 1$, then any solitary individual $\sigma \in \Omega - R_h$ is slower than any member $\eta \in R_h$ of the herd, hence $p_\eta < p_\sigma$. It follows that any weighted average of the values p_η over all $\eta \in R_h$ is smaller than any average (weighted or not) of the values p_σ over all $\sigma \in \Omega - R_h$, and as a special case

$$\sum_{\eta \in R_h} \theta_{\eta,R_h} p_\eta < \frac{1}{s} \sum_{\sigma \in \Omega - R_h} p_\sigma.$$

From part (ii) of Proposition 1 it follows that the predator's unique best response to R_h is to pursue a solitary prey, whenever it is detected. ■

From the propositions 4 and Proposition 3 it follows that the pair $\langle R_h, 1\rangle$ is an equilibrium iff $\theta_{h,R_h} \leq \tau_h(x)$ and, when $h < n$, if $\theta_{h+1,R_{h+1}} \geq \tau_{h+1}(x)$.

We now show that either a large size of the prey population or a low probability of escaping the attention of the predator are sufficient to ensure the existence of an equilibrium with a regular herd.

Proposition 5 *If the prey population is sufficiently large, and the prey's probability q to hide is sufficiently small, so as to satisfy*

$$nq^{n-2} < 1 - q^n, \tag{5}$$

then there exists an equilibrium $\langle R_h, 1\rangle$, with a regular herd R_h, regardless of the homing in probabilities $\{\theta_{i,H}\}$.

Proof. We already know that the strategy $x = 1$ is a predator's best response to any regular herd R_h. From and the definition of $\tau_2(1)$ (see (3)) it follows that, if (5) holds, then $\tau_2(1) = (1-q^n)/nq^{n-2}(1-q_2) > (1-q^n)/nq^{n-2} > 1$, hence $\theta_{2,R_2} \leq 1 < \tau_2(1)$. In this case it follows from (3) that, given the predator's strategy $x = 1$, the slowest member of the regular herd R_2 would be better off staying in it. If, in addition, $\theta_{3,R_3} \geq \tau_3(1)$, then it follows from inequality (2) that individual 3 is better off staying solitary. From propositions 3 it follows that $\langle R_2, 1\rangle$ is then an equilibrium. If, on the contrary, $\theta_{3,R_3} < \tau_3(1)$, then the slowest member of the regular herd R_3 would be better off staying in it. Repeating this argument, either there is a regular herd R_h, with $2 \leq h \leq n-1$, for which $\langle R_h, 1\rangle$ is an equilibrium, or else, $\theta_{n,R_n} < \tau_n(1)$, which, implies that $\langle \Omega, 1\rangle$ is an equilibrium. ■

Note that the condition (5), guaranteeing the existence of a regular herd, is satisfied under quite moderate requirement on n and on q. Thus, any probability $q \leq 0.2$ to hide as solitary is sufficient to guarantee the existence of an equilibrium with a regular herd for any prey population of a size larger than two. Even when the probability of hiding solitary increases to a level as high as $q = 0.8$, the condition (5) guarantees the existence of such an equilibrium for any prey population larger than 16.

We now concentrate on two important environments in which the condition of Proposition 5 is likely to be satisfied, and for which we shall be able to be more specific about the type of herd that will be formed in equilibrium.

1. The first is the Savannah Environment, in which the predator can detect any prey with high probability. For this environment we show that if the predator is not as efficient in homing in on the slowest member of a pursued herd as it is in detecting prey, then, for values of x sufficiently close to one, the pair $\langle \Omega, x\rangle$ is an equilibrium, and no other regular equilibria can possibly exist. If, on the contrary, the predator is more efficient in identifying the slowest member of any herd than in detecting a solitary prey, we shall see that no equilibrium $\langle H, x\rangle$ can exist, in which H is a not regular herd, nor can there be equilibria of the form $\langle \Omega, x\rangle$. Yet if, in this case, the population is not too small, then there exist an equilibrium $\langle R_h, 1\rangle$, with a regular herd smaller than Ω.

2. The second environment is Hamilton's regime of the Selfish Herd. Here, the predator has low probabilities of detecting any prey, whether solitary or in group, and when detecting a group of prey, the predator receives little information about its various members; it then homes in on any one of them with almost equal probabilities. Under these assumptions, our model yields the original Hamilton's condition for the formation and stability of the grand herd. We further find conditions under which stable equilibria $\langle H, x\rangle$ exist, where H is a partial herd. In this case we show that stable equilibria exist, both with regular and irregular herds.

4.1 The Savannah Environment

Under the title of the Savannah Environment, we study the Herd Formation Game when the probability q of hiding as solitary (and hence the probability $q_h < q$ that a herd of size $h > 1$ will escape the attention of the predator) is small.

Proposition 6 *i) If the predator's probability $\theta_{n,\Omega}$ to home in on the slowest member of the grand herd Ω is smaller than its probability $1-q$ to detect a solitary prey, then for a sufficiently small value of q, and for x sufficiently close to one, $\langle \Omega, x \rangle$ is an equilibrium.*

ii) If for any *herd H, the predator's probability $\theta_{i,H}$ of homing in on its slowest member is smaller than $1-q$, then, for a sufficiently small q, all the regular equilibria are of the form $\langle \Omega, x \rangle$.*

iii) If, on the other hand, $\theta_{n,\Omega} > 1-q$, then there is no equilibrium of the form $\langle \Omega, x \rangle$; but if, in addition, q is still sufficiently small and the prey population is sufficiently large, then there exists an equilibrium $\langle R_h, 1 \rangle$, with a regular herd R_h such that $h < n$.

iv) If for any *herd H, the predator's probability $\theta_{i,H}$ of homing in on its slowest member is larger than $1-q$, and q is sufficiently small, then all equilibria of the model have a regular herd. Recall that in this case, if the size of the prey population is sufficiently large, we know that such an equilibrium exists.*

Proof. i) If $\theta_{n,\Omega} < 1-q$, then indeed $\theta_{n,\Omega} < (1-q)/(1-q_n) = \tau_n(1)$, and from continuity argument it follows that for x sufficiently close to one, $\theta_{n,\Omega} < \tau_n(x)$. Since any predator's strategy is best response to Ω, it follows from propositions 3 that $\langle \Omega, x \rangle$ is an equilibrium.

ii) Assume now that for any herd H and its slowest member i, $\theta_{i,H} < 1-q$, and let $\langle R_h, 1 \rangle$ be an equilibrium with $h < n$. Since the individual $h+1$ is the slowest in R_{h+1}, we know that $\theta_{h+1,R_{h+1}} < 1-q$. But for all $q, q_h < 1$ and for all s :

$$(s+1)(1-q_h)q^s < (s+1)q^s < \sum_{i=0}^{s} q^i = \frac{1-q^{s+1}}{1-q},$$

hence for $s = n-h$

$$\theta_{h+1,R_{h+1}} < 1-q < \frac{1-q^s}{s(1-q_{h+1})q^{s-1}} = \tau_{h+1}(1), \tag{6}$$

and it follows from (2) that, given the predator strategy $x = 1$, $\langle R_h, 1 \rangle$ cannot be an equilibrium: The solitary $h+1$ will then be better off joining the herd. But since, as a special case, $\theta_{n,\Omega} < 1-q$, we already know that for x sufficiently close to one, $\langle \Omega, x \rangle$ is an equilibrium

iii) If $\theta_{n,\Omega} > 1-q$, then

$$q_n < q < 1-(1-q)/\theta_{n,\Omega}.$$

This implies that

$$\tau_n(1) = \frac{1-q}{1-q_n} < \theta_{n,\Omega},$$

and $\langle \Omega, 1 \rangle$ is not an equilibrium.

Since $\tau_n(x)$ is an increasing function of x, it follows that $\langle \Omega, x \rangle$ cannot be an equilibrium for any $0 \leq x \leq 1$. But Proposition 5 implies that if the prey population is sufficiently large, then there exists an equilibrium $\langle R_h, 1 \rangle$ with a regular herd. Since $\langle \Omega, 1 \rangle$ is not an equilibrium, we know that $h < n$.

iv) Assume now that for any herd H, if i is its slowest member, then $\theta_{i,H} > 1-q$. If $\langle H, x \rangle$ is an equilibrium, and i is the slowest member in H, then i should then be better off staying in herd, hence from (2) and the assumption $\theta_{i,H} > 1-q$ we get:

$$1-q < \theta_{i,H} \leq \tau_h(x) = \frac{\left(1-q^{s+1}\right)\left[(1-x)\,q_{h-1}+x\right]}{(s+1)\,(1-q_h)\left[xq^s+1-x\right]}. \tag{7}$$

But for q sufficiently small (it is enough, in this case, to require $q \leq 1/2$), inequality (7) can only be satisfied if the predator's strategy x is bounded away from 0, since when $x = 0$, the right-hand side of (7) is

$$\tau_h(0) = \frac{q_{h-1}\left(1-q^{s+1}\right)}{(s+1)\,(1-q_h)} < \frac{1}{s+1} < \frac{1}{2} \leq 1-q,$$

which contradicts inequality (7).

We now show that H cannot be an irregular herd. Suppose it is, then there exists a solitary individual j which is faster than individual i. The condition for individual j to remain solitary is (inequality (4)):

$$\theta_{j,H\cup\{j\}} \geq \tau_{h+1}(x).$$

But j, if it joins the herd H, would not be the slowest member in the newly created herd $H \cup \{j\}$. Individual i would then still be the slowest in the herd. As the slowest individual, it will be chosen by the predator with probability of at least $1-q$, hence individual j will be homed in on with probability of at most q. This, together with the previous inequality, implies:

$$q \geq \theta_{j,H\cup\{j\}} \geq \tau_{h+1}(x) = \frac{\left(1-q^{s}\right)\left[(1-x)\,q_{h}+x\right]}{s\,(1-q_{h+1})\left[xq^{s-1}+1-x\right]}. \tag{8}$$

From inequalities (7) and (8) we obtain:

$$q > (1-q)\,\frac{(1-q_h)}{(1-q_{h+1})}\,\frac{(1-q^s)}{(1-q^{s+1})}\,\frac{\left[(1-x)\,q_h+x\right]}{\left[(1-x)\,q_{h-1}+x\right]}\,\frac{(s+1)}{s}\,\frac{\left[xq^s+1-x\right]}{\left[xq^{s-1}+1-x\right]} \tag{9}$$

For a sufficiently small q, the first three terms of the right-hand-side of (9) can be made arbitrarily close to 1. Since, as we observed, x is bounded away from 0, the fourth term can also be made close to 1, by making q, and therefore q_h, q_{h-1} sufficiently close to 0. The next term $(s+1)/s$ is clearly greater than

1, while the last term is greater than q. Thus, by choosing q sufficiently small, the right hand side of (9) can be made greater than q, contrary to inequality (9) , hence H cannot be a non regular herd.

Finally, from Proposition 5 we know that if the size of the prey population is sufficiently large, then an equilibrium $\langle R_h, 1\rangle$, where R_h is a regular herd, exists. ■

Indeed, if there is a sufficiently large number of solitaries around, then a predator with a strategy $x = 1$ of pursuing solitary prey, if detected, will very rarely pursue the regular herd, and even the slowest member in this herd will be better off staying in it. Proposition 5 guarantees, in this case, the existence of an equilibrium $\langle R_h, 1\rangle$ with a regular herd. Proposition 6 characterize conditions under which no other sort of an equilibrium exists.

4.2 Hamilton's Regime of the Selfish Herd

We now analyze the second environment, Hamilton's regime of the Selfish Herd. In Hamilton's original model the gatherer-predator's main difficulty is in finding the prey. Once it found one, it has no difficulty in catching it. It is also assumed that, once the predator detected a group, it does not distinguish between the prey individuals in the group, and it homes in on one of them with equal probabilities. In the terminology of our model, this means that q, q_h are close to 1, and that $\theta_{i,H} = 1/h$. We generalize Hamilton's model, and refer to it as Hamilton's Regime by assuming that the homing in probabilities $\theta_{i,H}$ are close to $1/h$, with $\theta_{i,H} \geq \theta_{j,H}$ whenever i is slower than j.

Hamilton's original results can be re-stated as following:

Proposition 7 *(Hamilton's Theorem) Assume that the homing in probability $\theta_{i,\Omega}$ on any prey individual $i \in \Omega$ is sufficiently close to $1/n$. If the probability $1 - q_n$ that the predator will detect the grand herd is less than n times the probability $1-q$ that it will detect a solitary prey, $(1-q)/(1-q_n) > 1/n$, then, for a hiding probability q sufficiently close to one, the grand herd Ω is stable for all of the predator's strategies. That is, for each of the predator's strategies $0 \leq x \leq 1$, the unique best response of each prey individual is to remain in the herd Ω.*

If, on the other hand, $(1-q)/(1-q_n) < 1/n$, then there is no equilibrium in which the grand herd Ω forms.

Proof. (i) From (2) and the requirement $(1-q)/(1-q_n) > 1/n$ it follows that for q (and therefore for $q_n, q_{n-1} \geq q$) sufficiently close to one, $\tau_n(0) = q_{n-1}(1-q)/(1-q_n) > 1/n$, hence for $\theta_{n,\Omega}$ sufficiently close to $1/n$, $\tau_n(0) > \theta_{n,\Omega}$. Recall that $\tau_n(x)$ is an increasing function of x, hence for any predator's strategy x, $\theta_{n,\Omega} < \tau_n(x)$. From (2) it thus follows that for any predator's strategy x, any prey n is strictly better off staying in herd.

(ii) Since the prey individual n, being the slowest in a herd of n members, has a probability larger than average to be chosen by the predator, we know

that $\theta_{n,\Omega} \geq 1/n$. Together with the inequality $(1-q)/(1-q_n) < 1/n$, this implies $\theta_{n,\Omega} > (1-q)/(1-q_n) = \tau_n(1) \geq \tau_n(x)$ for all $0 \leq x \leq 1$, hence no equilibrium $\langle \Omega, x \rangle$ can exist. ■

Inequality $(1-q)/(1-q_n) < 1/n$, as we see, does not preclude the existence of an equilibrium with a smaller herd than Ω.

Proposition 8 *Assume that there exists an integer h, $2 \leq h < n$, for which*

$$\frac{1-q_h}{h} < 1-q < \frac{1-q_{h+1}}{h+1}, \tag{10}$$

then for values of q (and hence q_h and q_{h-1}) sufficiently close to 1, any herd of size h is a part of an equilibrium $\langle H, x \rangle$.

Proof. Let H be any herd with h members, and let x be the predator's best response to the herd H. By (2), individual $i \in H$ is better off staying in the herd if:

$$\theta_{i,H} < \tau_h(x) = \frac{\left(1-q^{s+1}\right)}{(s+1)} \frac{\left[(1-x)\,q_{h-1}+x\right]}{\left(xq^s+1-x\right)} \frac{1}{(1-q_h)}. \tag{11}$$

By choosing q sufficiently close to 1, the first term of the right hand side of (11) can be made to be close to $1-q$ $\left(\text{since } 1-q^{s+1} = (1-q)\sum_{k=0}^{s} q^k\right)$, and the second term close to 1. The right hand side of (**??**) then becomes as close as we wish to $(1-q)/(1-q_h)$ hence, choosing, in addition, $\theta_{i,H}$ sufficiently close to $1/h$, the left hand part of condition (10), $(1-q_h)/h < 1-q$, guarantees (**??**), which implies that all individuals in the herd H are better off staying in the herd.

Similarly, the right hand part of requirement (10), $1-q < (1-q_{h+1})/(h+1)$, ensures that $\theta_{i,H\cup\{i\}} > \tau_{h+1}(x)$, hence all prey individuals that are not in H are better off staying solitaries. It follows that $\langle H, x \rangle$ is an equilibrium. ■

The last Proposition implies the possible existence of irregular herds: If for some $2 \leq h < n$, condition (10) holds, then all herds of size h are stable. There are $\binom{n}{h}$ such herds, but only one of them is regular. Note, moreover, that except for a zero-measure set of parameters, all these equilibria are stable, with a predator strategy either $x = 1$ or $x = 0$.

4.3 Stability and Weak Stability of the Prey's Fully Gregarious Behavior

We have seen that, except for a zero-measure set of parameters, an equilibrium $\langle H, x \rangle$ with $2 \leq h < n$ is stable, with either $x = 1$ or $x = 0$. This is not the case for $H = \Omega$. When the grand herd Ω forms, the predator never observes a solitary prey, and therefore all of its strategies are best responses to Ω. The

condition for $\langle \Omega, x \rangle$ to be an equilibrium is that the slowest prey individual n is better off in the herd:

$$\theta_{n,\Omega} < \tau_n(x) = \frac{1-q}{1-q_n}\left[(1-x)\, q_{n-1} + x\right]. \tag{12}$$

The right hand side of (12), $\tau_n(x)$, is an increasing function of x, hence if this condition is satisfied for some x, it must hold for all larger x, and in particular for $x = 1$,

$$\theta_{n,\Omega} < \tau_n(1) = \frac{1-q}{1-q_n}. \tag{13}$$

i.e. $\langle \Omega, 1 \rangle$ is an equilibrium. If inequality (12) holds for $x = 0$ as a strict inequality, namely if

$$\theta_{n,\Omega} < \tau_n(0) = \frac{1-q}{1-q_n} q_{n-1}, \tag{14}$$

then $\langle \Omega, x \rangle$ is an equilibrium for all $0 \leq x \leq 1$.

In that case, moreover, the set $\{\langle \Omega, x \rangle \,|0 \leq x \leq 1\}$ is stable: The predator may use any of its strategies, but it is always strictly beneficial for all prey individuals to remain in the herd.

This stability condition, (14), is satisfied in Hamilton's environment, whenever $(1-q)/(1-q_n) \geq 1/n$ and q is close to 1. It is never satisfied in the Savannah environment, where q is close to 0, even if condition (13) is satisfied, and $\langle \Omega, 1 \rangle$ is an equilibrium. The fully gregarious behavior Ω cannot then be stable.

If the fully gregarious behavior is an equilibrium, but not a stable one, i.e. if:

$$\tau_n(0) = \frac{1-q}{1-q_n} q_{n-1} \leq \theta_{n,\Omega} < \frac{1-q}{1-q_n} = \tau_n(1),$$

then there exists a unique solution x_0, $0 \leq x_0 < 1$, to the equation $\theta_{n,\Omega} = \tau_n(x)$. For all $x > x_0$, $\theta_{n,\Omega} < \tau_n(x)$, hence the grand herd Ω is stable as long as the predator's strategy is in $(x_0, 1]$. But as long as all prey individuals are in the herd, there is no reason why the predator's strategy should remain within this interval. Thus, there is no stable equilibrium $\langle \Omega, x \rangle$, nor a set of equilibria which is stable.

However, a weaker concept of stability was suggested for a similar model by Binmore and Samuelson (1999). This was based on the assumption that if a player is indifferent between strategies, he may drift between them, but the change in its strategy will then be slow, whereas when an individual does not play its best response, there is more pressure in the direction of the best response, and the adjustment in this direction will be much faster. Applying this assumption to the case $\tau_n(0) \leq \theta_{n,\Omega} < \tau_n(1)$ in our model, the grand herd Ω remains stable as long as the predator's strategy drifts within the interval $(x_0, 1]$, but as it first crosses x_0, the best response of the slowest prey individual n will be to leave the herd. This will happen faster than any additional change in the predator's strategy, which might enable also the prey individual $n-1$ to leave the herd. But we already know that, once the herd R_{n-1} is formed,

it is the predator's best response to play $x = 1$, and then it becomes the best response of the slower prey to return to the herd, this way we return to $\langle \Omega, 1 \rangle$.

In such a case, following Binmore and Samuelson, we speak of weak stability of the fully gregarious behavior of the prey, predicting that the herd Ω will be observed most of the time, with occasional deviations of the slowest prey, while the predator's strategy will drift at the vicinity $(x_0, 1]$ of $x = 1$.

5 Discussion

5.1 The model - Motivation and Justification

The present work attempts to explain the commonly observed tendency of potential prey to aggregate in face of danger, and to escape in group. Contrary to other situations of gregarious behavior of a potential prey, this phenomenon is hard to explain on the basis of sharing information (e.g. Valone and Templeton 2002, and references there) or group vigilance (e.g. Bednekoff and Lima 1998, and references there), especially in face of recent findings (e.g. Hebblewhite and Pletscher 2002, Whitfield 2003) that gregarious behavior often facilitates rather than hinder predation. Moreover, gregarious behavior of evasive prey is hard to be explained, as we have seen, by Hamilton's argument of risk-sharing (1971), since a crucial tacit assumption in this argument is that members of the aggregate share more or less the same risk of predation. This is not the case with evasive herds, in which slowest members take big share of the risk of predation. A crucial question in this case is what keeps such herds from being repeatedly abandoned by their slowest members.

As we suggest here, a key factor in the answer to this question lies in the function of group escaping as a test of speed, exposing the slow prey as a preferred target for the predator. Not participating in such a test may, under certain conditions, be even more revealing (see, for comparison, Zahavi 1977). This does not mean that staying in herd is, under any circumstances, the best strategy for all prey individuals. To characterize the exact conditions for the maintenance of various forms of prey groups, we studied an $n + 1$ player game: A predator, seeking to increase its probability of a successful hunt, and n prey individuals, different from one another in speed, each seeking to decrease its own probability to be caught by the predator. The term "predator", in this context, may well be represented by a pack of predator's, provided one prey, at the most, is hunted at a time.

5.2 Main Results and Interpretation

In section 3 we have presented characterization of equilibria and stable equilibria of the game. Conditions for the formation of fully gregarious behavior of

the prey were demonstrated in 4.3. Given all other parameters, it was shown that the predator's inefficiency in detecting the slowest member in herd, and its efficiency in detecting solitary prey, are crucial prerequisites for the formation of fully gregarious behavior. The first of the two is typical to Hamilton's regime of the model (section 4.2), the latter is typical to the savannah environment, in which shelter is rare (section 4.1). Conditions for partially gregarious behavior of the prey were also demonstrated throughout section 4. In the case of a predator's high efficiency in detecting solitary prey, characterizing the savannah environment, it was further shown that all partial herds, maintained at equilibrium, are regular in the sense that they consist of the fastest prey individuals. The predator's behavior, in such equilibria, was characterized by its preference for solitary prey, whenever it detects one.

The establishment of a regular herd, either total or partial (in comparison to solitary behavior of the prey), was shown to always be in the advantage of the fastest prey individuals, and in the disadvantage of the slowest ones. It decreases the probability that the predator will home in on a fast prey, and increases the probability that it will home in on a slow one, either if solitary or in the herd. Consequently, the formation of a regular herd is always in the advantage of the predator. As such, it can be interpreted as a stable coalition between the predator and the fast prey individuals.

Quite interesting is the fact that the formation of a regular herd is not necessarily in the advantage of even all members of the herd. Certainly it is not in the advantage of the slowest member of the grand herd, but similar examples can be easily demonstrated also for partial herds. In such a case, the formation of a single group by some fastest prey individuals may force the next fastest ones to participate in a coalition that is harmful for them . Not doing so may then be even more harmful for them. As we have shown, this process may either end up with the establishment of a partial regular herd, or continue till the grand herd is formed, depending on environmental parameters.

The present model generalize both Hamilton's model of the selfish herd (1971), and Eshel's savannah model (1977).

5.3 Supporting Evidence and Comparison with Alternative Models

The prediction that predators in open plains prefer to attack solitary prey, and that by doing so they reach their highest rate of success, is supported by a bulk of field observations (e.g. Hebblewhite and Pletscher 2002, Whitfield 2003, and references there), yet this finding is not indicative, as it stands as well in agreement with the predictions of both the vigilance and the information-sharing models.

The predicted favorable effect of low availability of shelter on prey's gregariousness stands in agreement with the observations of Hebblewhite and Pletscher (2002) that elks, mainly dwellers of open plains, tend to escape in group, while

mule deer, whitetail deer and moose, often bush dwellers, tend to spread off when attacked. The same difference is well documented between the tendency of the open plain dwellers, gnu and zebras, to escape in group, and the tendency of bush dwelling antelopes to spread off.

The predicted negative effect of recognizable differences among individuals within a group of prey on its coherence may be supported by the apparent size-homogeny of shoals of fish or of groups of small birds, even when of different species.

The prediction that gregarious behavior of evasive prey increases the total predation probability is already well supported by a bulk of field observations (Hebblewhite and Pletscher 2002, Whitfield 2003, but see also references in Lorenz 1966, Hamilton 1971). This finding is more difficult to explain on the basis of theories as of vigilance or information-sharing, that attempt to explain gregarious behavior on its effect to decrease the predation probability.

We are well aware of the fact that supporting evidence to our model is too meagre to rule out alternative explanations, but it is by no means our intention to rule them out.

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