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Gregarious Behaviour of Evasive Prey

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Abstract

We model the formation of a herd as a game between a predator and a prey population. The predator receives some information about the composition of the herd when he chases it, but receives no information when he chases a solitary individual. We describe situations in which the herd and its leader are in conflict and in which the leader bows to the herd's wish but where this is not to the benefit of the herd.

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Gregarious Behaviour of Evasive Prey

by I. Eshel, E. Sansone & A. Shaked

0.1 Introduction

The paper addresses two questions concerning herds in prey populations. The first problem is the reason for forming a herd and conditions for its stability. The second problem is about the possible conflict between the leader of a herd and its members.

The classical model of herd formation in biology is a model of a sedentary passive prey population by W.D. Hamilton [1]. It resembles a Hotelling location model. A finite prey population is located on a circle. The prey appears at random on the circle and catches the prey nearest to him, if there is more than one prey individual closest to him, he chooses one of them with equal probabilities. It is easy to see that each prey individual will want to move to a position in which there are many prey individuals.

In contrast, our model is of evasive prey, the prey individuals run for their life when chased by the predator. How does the predator choose an individual to home in on when the prey individuals differ in their ability to escape (their speed of running)?

The prey individuals join a herd or hide individually. The prey notices the herd or a solitary individual with probabilities that depend on the size of the herd and the group of solitaries. If he noticed both groups he decides which group to chase. The main idea of this paper is that the prey receives different information about the strength of the individuals when he chases the herd and when he pursues the solitaries. When he chases the solitaries he receives no information about them, he has to pick up one of them at random and chases this individual. He will catch the prey with higher probability if the prey is a slow individual. When the predator chases the herd he receives some information during the chase about their individual strength. He is therefore more likely to home in on a slow individual.

The formation of the herd is thus an outcome of the interaction of the prey individuals and the predator. We find conditions for forming a herd consisting of the strongest individuals in the population and its stability.

It is likely that the strongest individual in the herd will become its leader and may lead the herd to cover or he may choose to stay in the open. We describe situations in which the leader may wish to stay in the open and the herd refuses to go along with him. The leader may bow to the herd's will and lead it to cover, but this outcome will not the best for the herd's welfare: It would have been better for them to stay in the open. This models a situation in which a populist leader surrenders to the populus and acts accordingly but it would have been better for the public to have followed the leader's original wishes.

1 Herd Formation

1.1 The Model

A prey population Ω consists of n individuals distinguished by their probability of being caught by a predator when it chases them, $p_1 < p_2 < ..... < p_n$. Individual 1 is the fastest one, he has the lowest probability of being caught. Each of the individuals decides whether to join the (single) herd or to hide as a solitary individual. Let $H \subseteq \Omega$ be the set of individuals who form the herd, and let S 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. A herd of size h escapes his attention with probability q_h. We assume that it is more difficult for a larger herd not to be detected by the predator, i.e. $q_{h+1} < q_h$. A solitary individual (a herd of size 1) is unnoticed by the predator with probability $q = q_1$. Thus, the predator notices a solitary individual with probability $1 - q^s$, and he notices a particular individual in S with probability $(1 - q^s)/s$.

The predator's strategy specifies what he will do if he noticed both the herd and a solitary individual. He may use a pure strategy or a mixed one: If both the herd and solitary individuals were noticed then follow a solitary individual with probability x.

When the predator chases the herd he receives some information about the strength or weakness of the individuals in the herd and he will home in on a weak individual with a higher probability. We assume that $\theta_{i,H}$ satisfies the following three assumptions:

1. When chasing a herd, the predator will eventually home in on one of its individuals: $\sum\limits_{\eta \in H} \theta_{\eta,H} = 1$.

2. The probability that a stronger individual is pursued is lower than that of a weaker individual: If $i, j \in H$, $i < j$ then $\theta_{i,H} < \theta_{j,H}$.

3. If a stronger individual joins the herd his probability of being pursued is lower than that of a weaker individual who joins the herd. If $i, j \notin H$, $i < j$ then $\theta_{i,H\{i\}} < \theta_{j,H\{j\}}$.

To pin things down we assume that the probability with which the predator homes in on individual i is:

$$\theta_{i,H} = \frac{p_i}{\sum\limits_{\eta \in H} p_\eta}.$$

In contrast, when the predator notices solitary individuals he receives no signal about their speed and strength and pursues one of those he noticed with equal probability.

This situation defines a Herd Forming game in which each prey individual chooses whether to join the herd and the predator chooses whom to pursue when he observed both the herd and the solitaries. The payoff of each prey individual is his probability of survival (it is 1 minus the probability of him being caught). The predator's payoff is his probability of catching a prey.

We can now define an equilibrium. An equilibrium is a strategy of the predator plus a partition of the prey population into a herd and solitary individuals such that no individual wishes to deviate from his strategy.

Definition 1 *Let (H, S, x) be such that $\{H, S\}$ is a partition of the prey population into a herd H and a group of solitary individuals S, and let x be a strategy of the predator (the probability in which he will pursue a solitary individual in the case that he observed both the herd and some solitaries). The triple (H, S, x) is an equilibrium if no prey individual prefers to move from his group to the other and the predator's strategy x is a best response to the partition of the prey population.*

1.2 The Predator's Decision

The predator notices the herd only with probability $(1 - q_h)\, q^s$, he notices only a solitary individual with probability $q_h\,(1 - q^s)$ and he notices both with probability $(1 - q_h)\,(1 - q^s)$.

Thus, if his strategy is to pursue the herd when he notices both, his expected catch is:

$$(1 - q_h)\, q^s \sum_{\eta \in H} \theta_{\eta,H} p_\eta + (1 - q_h)\,(1 - q^s) \sum_{\eta \in H} \theta_{\eta,H} p_\eta + q_h\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma,$$

the first two terms describe what happens when the predator noticed the herd, he homes in on one of the individuals in the herd with probability $\theta_{\eta,H}$ and catches it with probability p_η. If he noticed a solitary individual but the herd escaped his attention then he homes in on one of them with probability $\frac{1}{s}$ (s - the total number of solitary individuals) and will catch it with his characteristic probability p_σ.

If the predator's strategy is to pursue a solitary individual when he noticed one, his expected catch is:

$$(1 - q_h)\, q^s \sum_{\eta \in H} \theta_{\eta,H} p_\eta + (1 - q_h)\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma + q_h\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma.$$

The first strategy (pursuing the herd) yields a higher catch if:

$$\begin{aligned} & (1 - q_h)\, q^s \sum_{\eta \in H} \theta_{\eta,H} p_\eta + (1 - q_h)\,(1 - q^s) \sum_{\eta \in H} \theta_{\eta,H} p_\eta + q_h\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma \\ > \; & (1 - q_h)\, q^s \sum_{\eta \in H} \theta_{\eta,H} p_\eta + (1 - q_h)\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma + q_h\,(1 - q^s)\, \frac{1}{s} \sum_{\sigma \in S} p_\sigma. \end{aligned}$$

or, (assuming that the predator has a positive probability of noticing a single solitary individual,and hence larger herds $1 > q$) :

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

The predator simply compares where his expected catch is larger and pursues that group when he noticed both groups.

1.3 Herd Formation and Regular Herds

Assume that the predator plays a mixed strategy x, i.e. if he notices both the herd and a solitary individual he pursues a solitary individual with probability x. Once a herd H is formed an individual $i \in H$ has the following probability of being pursued and caught:

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

The first part describes the probability that the predator will pursue the herd, either he observes only the herd or else he observes both the herd and the solitaries but he chooses to pursue the herd (with probability $1-x$). The second part describes the probability that the predator will home in on individual i and that he will be caught.

If a prey individual deserts the herd and joins the solitaries, the herd becomes smaller, it shrinks to $H' = H - \{i\}$, and the set of solitaries has expands to $S' = S \cup \{i\}$. His probability of being pursued and caught now that he has joined the solitaries is:

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

Therefore, individual i will stay in the herd iff:

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

Or:

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

The right hand side of this condition is independent of i, it depends only on the size of the two groups, the herd and the solitaries. It follows (as is shown in lemma 2) that if the weakest (slowest) individual in H wishes to stay in the herd then all other individuals in the herd also prefer staying to being solitary.

Similarly, a solitary individual i prefers *not* to join the herd iff:

$$\theta_{i,H \cup \{i\}} > \frac{(1 - q^s)\left[(1 - x) q_h + x\right]}{s\left(1 - q_{h+1}\right)\left[x q^{s-1} + 1 - x\right]} = \tau_{h+1,s-1} \tag{3}$$

Lemma 2 *(i) If the weakest individual in the herd prefers staying in the herd to hiding solitarily then all other individuals in the herd prefer to stay in the herd.*

(ii) If the strongest solitary individual prefers to stay solitary than all other solitaries prefer to hide solitarily rather than join the herd

Proof. (i) Let individual i be the weakest in the herd H: $p_i \geq p_\eta$ for all $\eta \in H$. Let individual i prefer to stay in the herd rather than desert it. By inequality 2: $\theta_{i,H} < \tau_{h,s}$. The probability of the predator homing in on a stronger individual (η) is lower than homing in on $i : \theta_{\eta,H} \leq \theta_{i,H}$. Hence: $\theta_{\eta,H} < \tau_{h,s}$ and individual η prefers to stay in the herd.

(ii) Let individual i be the strongest solitary individual, if he prefers to remain solitary then by inequality 3: $\theta_{i,H\cup\{i\}} > \tau_{h+1,s-1}$. If any other individual (η)weaker than individual i joins the herd (instead of individual i) then his probability of being pursued is higher than the corresponding probability of individual $i : \theta_{\eta,H\cup\{\eta\}} > \theta_{i,H\cup\{i\}}$. Thus, $\theta_{\eta,H\cup\{\eta\}} > \tau_{h+1,s-1}$ and individual η prefers to remain solitary. ■

What sort of herds can be formed in equilibrium? We will be particularly interested in 'regular' herds, which consist of the strongest individuals.

Definition 3 *A herd H is a* regular herd *if there exists an integer $k, 0 \leq k \leq n$ s.t. $H = \{1, 2, 3, ...k\}$. Note that the empty herd and the grand coalition, the fully gregarious behaviour, are* regular.

Are there equilibria with irregular herds?

Lemma 2 introduces some regularity into the partitions of the prey population: If a certain individual prefers to stay in the herd then all stronger individuals in the herd prefer to stay there, and if an individual prefers not to join the herd then all weaker solitary individuals prefer to remain solitary. However, this regularity does not guarantee that an equilibrium herd will necessarily be regular. The problem lies with function q_h. We required that q_h, the probability that a herd of size h will not be noticed by the predator, be monotonic decreasing with h. We have made no further assumptions about how it varies with h. Extreme cases of the function, when a herd of size h always escapes the attention of the predator, while a herd of size $h+1$ is always noticed by it ($q_h = 1, q_{h+1} = 0$) may lead to an irregular herd. The herd may consist of some individuals and escape the attention of the predator. The herd may be irregular, i.e. there exists a solitary individual who is stronger than some individual in the herd. He may not wish to join the herd for by doing so the herd will be noticed by the predator with certainty and his personal probability of escaping will be lower than as a solitary individual (we skip the details of this example).

Are there equilibria with regular herds?

The existence of a regular herd hinges on the formation of a small herd of 2 individuals. The herd, in contrast to solitary animals runs in one direction thus sending a mixed signal to the predator about the strength of the individual member of the herd. Forming a herd requires cooperation of its individuals. Starting from a situation where all are solitary a herd of 2 cannot be formed unless both individuals prefer it. Formally, we require somewhat more than a single deviation to verify that the 'all solitary' state is not an equilibrium. We need also assume that the types are uniformly distributed in the prey population. In particular we assume that the first and second strongest individuals in the population are closer to each other (in their speed, their probability of being caught) than any other two types.

ASSUMPTION: *For each individual $k \geq 2$ in the prey population*

$$\frac{p_2}{p_1 + p_2} \leq \frac{p_k}{p_{k-1} + p_k},$$

or alternatively:

$$\frac{p_2}{p_1} \leq \frac{p_k}{p_{k-1}}.$$

Using these assumptions we can show that there exists an equilibrium with a regular herd.

Lemma 4 (i) *The predator's strict best response to any regular herd R_k, $k = 2, 3, ..., n-1$ is to follow the solitaries, $x = 1$.*

(ii) *All of the predator's strategies are best responses to $R_n = \Omega$.*

Proof. (i) Consider a regular herd R_k, $k = 2, ..., n-1$. By (1), the predator pursues the herd if:

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

But if the herd is regular then all p_η, $\eta \in H$ are smaller than any $p_\sigma, \sigma \in S$. Hence the above inequality is violated and the predator prefers to pursue the solitaries, i.e. $x = 1$.

(ii) When the grand regular herd $R_n = \Omega$ has formed, the predator will never observe a solitary individual since it does not exist. Hence *any* strategy x is a best response to the partition (Ω, Φ). ■

Lemma 5 *There exists an equilibrium with a regular herd.*

Proof. From Lemma 4 , the predator's best response to any regular herd is to choose $x = 1$. Let $R_k = \{1, 2, ..k\}$ denote the herd of the k strongest individuals.

Consider the Grand Coalition: R_n. If the weakest individual in the population n prefers to stay in the herd then $(R_n, \Phi, 1)$ is an equilibrium. If, however, individual n wishes to desert the herd, then we consider the herd R_{n-1}. If its weakest individual prefers to remain in the herd then $(R_{n-1}, \{n\}, 1)$ is an equilibrium. Else we consider R_{n-2} and so on. This process continues until we find an equilibrium with a regular herd k, or else we reach the herd R_2 of the two strongest individuals and individual 2 wishes to leave the herd. We thus reach the 'all solitary' situation and we know that the herd R_2 is not stable. But from our last assumption this implies that the weak individual in any herd of 2 individuals will wish to desert the coalition. Hence the 'all solitary' situation with the empty (regular) herd is an equilibrium. ■

1.4 Stability of the Fully Gregarious Behaviour

Under what conditions is the fully gregarious behaviour an equilibrium, and when is it stable?

Assume that the entire population joined the herd. The predator will never observe a solitary individual and so all strategies are best response to $H = \Omega$. Assume that the predator plays $x = 1$. The herd consisting of the entire prey population is an equilibrium if the weakest individual in the population (n) wishes to stay in the herd (part (i) of lemma 2). By inequality 2 this occurs when:

$$\theta_{n,\Omega} < \frac{(1-q)}{(1-q_n)} = \tau_{n,0} \tag{4}$$

This has been obtained from inequality 2 by setting $H = \Omega, h = n, s = 0, x = 1$.

Thus if condition 4 is satisfied then $(\Omega, \Phi, 1)$ is an equilibrium. Unfortunately this is not a stable equilibrium: The predator is indifferent between all his strategies and may drift away from $x = 1$. If he plays $x < 1$ with a sufficiently low x, some weak individuals may desert the herd. In the herd they are likely to be identified as the slowest individuals and be pursued by the predator, while if they hide as solitary individuals and x is sufficiently low the predator is less likely to pursue the solitaries and they may be better off deserting the herd. This may start a snowball effect, for the weakest individuals of the now shrunk herd may find it beneficial to desert the herd and thus move the situation further away from the equilibrium.

However, small deviations from the equilibrium strategy $x = 1$ may encourage only the weakest individual (n) to desert the herd, but once he deserted the predator's strict best response is to play $x = 1$ (lemma 4), it is then best for individual n to return to the herd.

Thus there is an $\bar{x}$, $0 < \bar{x} < 1$ such that $\{(\Omega, \Phi, 1), \{(R_{n-1}, \{n\}, x)\} | \bar{x} < x < 1\}$ is a stable equilibrium component. Starting from the equilibrium $(\Omega, \Phi, 1)$, the predator may change his strategy within $[\bar{x}, 1]$, the weakest individual may desert the herd, the predator will then switch back to $x = 1$ and the exiled individual n will return to the herd.

The strategies interval in which the predator may drift may be increased to allow more of the weaker individuals to desert the herd. once they left the herd the predator reverts to his best response $x = 1$ and forces the deserters to return to the herd.

2 The Herd and its Leader

It is natural for the fastest individual in the herd to be its leader, determining when and what path the herd takes to escape the predator. In this section we would like to propose a model of the interaction and the conflicts between the herd and its leader.

2.1 The Model

The model in this section differs from the last model in a few details. As before, the prey individuals are ranked by their speed. However, we assume that everything happens in an open savannah and that any herd standing in the open or any individual running for shelter will be noticed by the predator with probability 1. We assume that the grand herd $H = \Omega$ has been formed. The herd or any individual may run for shelter. When pursued by the predator while running for shelter individual $i's$ probability of being caught is αp_i, $0 \leq \alpha \leq 1$, the constant α represents how close the shelter is, small α corresponds to a close shelter. We distinguish between running as a herd and running individually: When running as a herd the predator will home in on one individual with probability $\theta_{i,\Omega}$ as in the previous model, while when running individually the predator will home in on one individual with equal probabilities. If all reached shelter without being caught, a sheltered individual has probability q of escaping the predator's attention. However, once a sheltered individual is noticed by the predator there is no escape and the individual is caught.

2.2 Stability of the Grand Herd

For the grand herd to be stable we need two conditions, the first is that the weakest individual (n) does not wish to desert the herd, and the second is that the predator follows a single individual when he notices it. The condition for the weakest individual to remain in the herd is:

$$\theta_{n,\Omega} p_n < \alpha p_n + (1 - \alpha p_n)(1 - q)$$

this assumes that the predator will follow the single running individual once it observed it. However, when the grand herd formed the predator never observes a solitary individual and he is therefore indifferent between all his strategies. The condition for the predator to follow the single deserting individual is:

$$\alpha p_n + (1 - \alpha p_n)(1 - q) > \sum_{i=1}^{n-1} \theta_{i,R_{n-1}} p_i.$$

Combining these two conditions:

$$\theta_{n,\Omega} p_n < 1 - q + \alpha q p_n > \sum_{i=1}^{n-1} \theta_{i,R_{n-1}} p_i.$$

This ensures that the grand herd together with the predator's strategy $x = 1$, is stable in this model. Like in the previous section, the predator may drift and play a nearby strategy, this may cause the weakest individual to abandon the herd, but then the strict best response of the predator is to play $x = 1$ (follow the solitary runner), this will force the individual back to the herd.

This double condition can hold when the individuals are sufficiently fast (the probabilities p_i are small), and q, the probability of not noticing a sheltered individual, is also small.

2.3 Conflict between the Herd and its Leader

When the herd stands in the open the predator's probability of catching a prey is

$$\sum_{i=1}^{n} \theta_{i,\Omega} p_i,$$

when the herd runs for shelter the predator's probability of catching a prey is:

$$\alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i + \left[1 - \alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i\right] (1 - q^n).$$

Thus, running for shelter is better for the population, it expects to lose fewer individuals ,if

$$\alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i + \left[1 - \alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i\right] (1 - q^n) < \sum_{i=1}^{n} \theta_{i,\Omega} p_i$$

or:

$$1 - q^n < \frac{(1-\alpha) \sum_{i=1}^{n} \theta_{i,\Omega} p_i}{1 - \alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i}. \tag{5}$$

What would the leader, the fastest individual (1), wish to do? If he stays in the open, and the herd follows him, his probability of being caught is $\theta_{1,\Omega} p_1$. If he leads the herd to shelter his probability of being caught is:

$$\alpha \theta_{1,\Omega} p_1 + \left[1 - \alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i\right] \frac{(1 - q^n)}{n}.$$

The leader prefers to stay in the open if:

$$\theta_{1,\Omega} p_1 < \alpha \theta_{1,\Omega} p_1 + \left[1 - \alpha \sum_{i=1}^{n} \theta_{i,\Omega} p_i\right] \frac{(1 - q^n)}{n},$$

or:

$$\frac{(1-\alpha)\, n\theta_{1,\Omega}p_1}{1-\alpha\sum\limits_{i=1}^{n}\theta_{i,\Omega}p_i} < 1-q^n. \tag{6}$$

Comparing inequalities 5,6 we can find the condition for a conflict between the leader and the herd: The leader wants to stay in the open while the welfare of the group requires that it looks for shelter

$$\frac{(1-\alpha)\, n\theta_{1,\Omega}p_1}{1-\alpha\sum\limits_{i=1}^{n}\theta_{i,\Omega}p_i} < 1-q^n < \frac{(1-\alpha)\sum\limits_{i=1}^{n}\theta_{i,\Omega}p_i}{1-\alpha\sum\limits_{i=1}^{n}\theta_{i,\Omega}p_i},$$

indeed the R.H.S. of the last inequality is greater than its L.H.S. $n\theta_{1,\Omega}p_1 < \sum\limits_{i=1}^{n}\theta_{i,\Omega}p_i$, since $p_1, \theta_{1,\Omega}$ are the smallest probabilities in the sum. This guarantees a range of $q's$ for which there is a conflict between the leader and the herd. The reverse conflict cannot happen: If it is better for the herd to stay in the open (inequality 5 is violated) then it follows that the leader would also wish to stay in the open (inequality 6).

2.4 Total Instability of the Herd.

Dissatisfaction among members of the herd may lead to desertion and the breakdown of the herd. The leader of the herd and its strongest members do not care much when some weak individuals desert the herd, but once more individuals abandon the group they will begin to notice it and suffer from the decreased size of the herd. Assume that the predator can identify the weakest member of the herd with little error, this will be the case when $\theta_{i,H} = \frac{p_i^\beta}{\sum_{\eta\in H} p_\eta^\beta}$ for a sufficiently large β. Once a weak person leaves the herd, the next type in line becomes the weakest in the herd and may wish to desert it. We describe the conditions for this snowball effect to happen. The condition is that the predator follows the herd whatever its size.

$$\sum_{i=1}^{k}\theta_{i,R_k}p_i > \frac{\alpha}{n-k}\sum_{i=k+1}^{n}p_i + \left[1-\frac{\alpha}{n-k}\sum_{i=k+1}^{n}p_i\right]\left(1-q^{n-k}\right), \qquad k=2,3,..,n-1. \tag{7}$$

These conditions may be satisfied in the following case: Assume that the prey population is nearly homogeneous, let $p_i = p$ for all i. The above condition can be written as:

$$p > \alpha p + (1-\alpha p)\left(1-q^{n-k}\right), \qquad k=2,3,..,n-1$$

or:

$$p > 1-q^{n-k} + \alpha q^{n-k}p, \qquad k=2,3,..,n-1$$

this will hold for all k in the range if:

$$p > 1 - q^{n-2} + \alpha q^{n-2} p,$$

or:

$$\frac{(1-\alpha)\,p}{1-\alpha p} > 1 - q^{n-2}. \tag{8}$$

If this last inequality holds then one can find a range of probabilities $p_1 < p_2 < \ldots < p_n$ all close to p s.t. inequalities 7 hold for all k in the range and the herd is totally unstable.

2.5 The Populist Leader

When the grand herd is totally unstable the leader has no choice but to surrender to the populus and lead them to shelter.

In this section we will assume that the predator makes little mistakes in identifying the weakest individual in a herd and that the prey population is nearly homogeneous. We will, in fact, prove our results under the assumption that the predator makes *no mistakes* and that the prey population *is homogeneous* ($p_i = p$). Since (nearly) all our results depend on inequalities, they can be shown to hold for populations close to homogeneous populations and to predators making small mistakes.

Lemma 6 *Let the herd $H = \Omega$ be totally Unstable, then it is better for the leader to lead its herd to shelter than try to keep it in the open if*

$$1 - q^n < \frac{p}{1-\alpha p} \tag{9}$$

.

Proof. When the herd is totally unstable, the leader will be left on his own, he may choose to run for cover himself, now each prey individual runs for cover on his own and the probability of the leader to be caught is:

$$\frac{\alpha p_1}{n} + \left[1 - \frac{\alpha}{n}\sum_{i=1}^{n} p_i\right]\frac{1-q^n}{n}. = \frac{\alpha p}{n} + [1-\alpha p]\,\frac{1-q^n}{n}$$

(the prey chooses a prey with equal probabilities and chases him, if he failed he may identify a sheltered individual and catch him)

If the leader takes the initiative and leads the herd to cover, the herd will follow him with the possible exception of individual n (he may desert the herd, but then the predator will follow him and individual $n-1$ will be better off staying with the herd). The probability of the leader to be caught when leading the herd to shelter is:

$$\alpha\theta_{1,\Omega} p_1 + \left[1 - \alpha\sum_{i=1}^{n}\theta_{i,\Omega} p_i\right]\frac{1-q^n}{n} = (1-\alpha p)\,\frac{1-q^n}{n}.$$

The latter probability is clearly less then the first one, so the leader will choose to lead his herd to shelter rather then lose the herd. The abandoned leader has another option, he may not run for cover but run away from the prey in the open, his probability of being caught is then: $\frac{p}{n}$. He will prefer to lead the herd to cover if: $\frac{p}{n} > (1-\alpha p)\frac{1-q^n}{n}$. or: $\frac{p}{1-\alpha p} > 1-q^n$. ■

The herd has three options: It can stay with the leader in the open, it can disperse and run to shelter individually, or it can be lead by the leader to shelter. In which of these situations is the probability of a loss to the herd minimized?

- If the herd stays in the open, the probability of a loss is: $\sum_{i=1}^{n} \theta_{i,\Omega} p_i = p$
- If it runs to shelter as a herd: $1 - q^n + \alpha q^n \sum_{i=1}^{n} \theta_{i,\Omega} p_i = 1 - q^n + \alpha q^n p$
- If it disperses and runs to shelter individually; $1 - q^n + \alpha q^n \frac{1}{n} \sum_{i=1}^{n} p_i = 1 - q^n + \alpha q^n p$.

Note that running to shelter individually always involves lower loss to the herd, except in the homogeneous case when $p_i \equiv p$ and the losses are equal.

The herd's welfare is highest when it stays in the open when:

$$p < 1 - q^n + \alpha q^n p,$$

or:

$$\frac{p(1-\alpha)}{1-\alpha p} < 1 - q^n. \tag{10}$$

Let us now combine the conditions for

1. Total Instability of the herd (inequality 8)
2. The leader prefers to lead the herd to shelter when staying in the open will completely disperse the herd (Lemma 6, inequality 9)
3. The total welfare of the herd is higher when it stays in the open (inequality 10)

$$\frac{p}{1-\alpha p} > 1 - q^n > \frac{(1-\alpha)p}{1-\alpha p} > 1 - q^{n-2}$$

It is straightforward to see that one can find values of p, q which will satisfy these inequalities. It is then possible to define a prey population $p_1 < p_2 < .... < p_n$ and a 'homing in function' $\theta_{i,H} = \frac{p_i^\beta}{\sum_{\eta \in H} p_\eta^\beta}$ such that the following holds: The herd will disperse if asked to stay in the open, so the populist leader leads it to cover, but then the welfare of the herd is minimized, it would have been best for the herd to stay in the open.

References

[1] W. Hamilton. Geometry for the selfish herd. *J. Theoretical Biology*, 31(2):291–311, 1971.