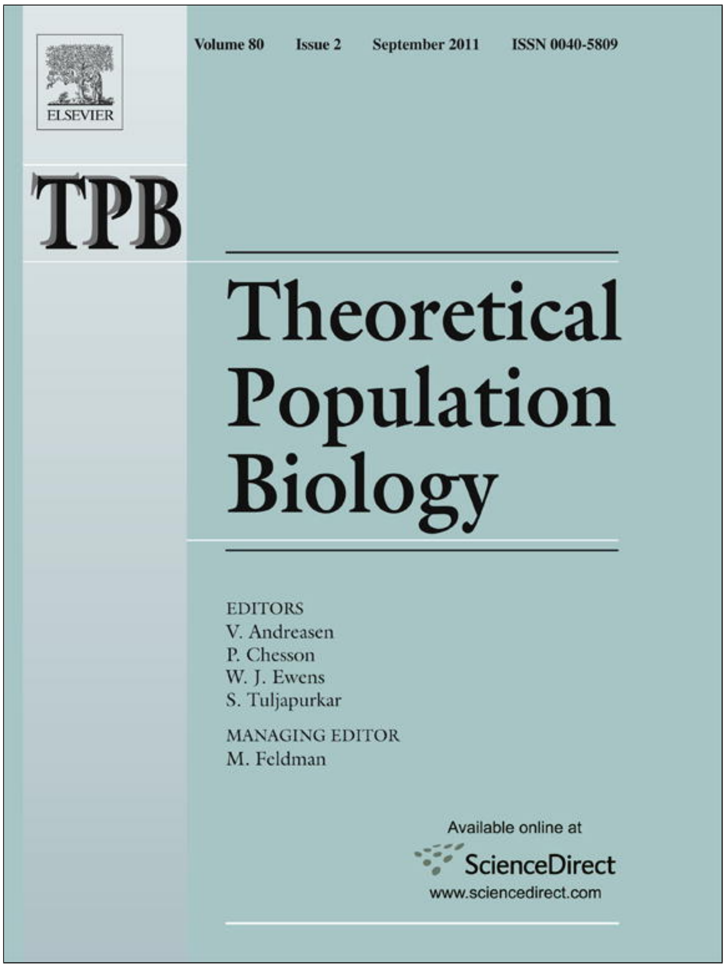
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On the evolution of group-escape strategies of selfish prey

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A B S T R A C T

The phenomenon of group escape cannot be explained by an argument of risk dilution, applied to gregarious behaviour of passive prey whose risk of predation is equally shared by all group members (Hamilton, 1971). Instead, individuals at the tail of an escaping group suffer the bulk of the group's predation risk, and thus have the highest incentive to desert it. Just because of this, desertion, in this case, may serve as a signal of vulnerability for the pursuing predator. Under wide conditions, it is therefore shown that the predator is always expected to prefer the chasing of a deserter, whenever it is observed. Consequently, an individual who finds himself at the tail of the herd must compare the risk of remaining there with that of deserting the herd and thereby becoming a likely target for predation. If the first risk is higher than the latter, the herd disperses; if the latter is higher, the herd cohesively follows the fastest individuals in its lead (we deal also with cases in which only part of the herd disperses). We see, however, that the question which risk is higher depends not only on the terrain, but also on the route of escape that is decided by the fastest members at the lead of the herd, those that are least likely to be caught. Concentrating on herds without family structure, we assume that the route of escape is selfishly chosen by these ad hoc leaders to minimize their own predation risk, regardless of the others' welfare. However, the predation risk of the leader depends very much on the willingness of other herd members to follow him, thus providing a buffer between him and the pursuing predator. Consequently, when choosing an escape route, the leader has also to consider the cohesion of the herd, i.e., the reaction of slower individuals to his choice. Under some plausible conditions, this choice may force the herd to follow, while other conditions may lead to its dispersal. In some cases the leader may choose a route that serves the needs of the entire group, and sometime only those of its more vulnerable members. In other cases the leader may choose a route that sacrifices the weakest members, thereby improving the survival probability of the others.

We employ a model of a $k + 1$ players game, a single predator, and k heterogeneous prey individuals. The predator aims to maximize the probability of a successful catch, and each individual aims to minimize his probability of being caught.

1. Introduction

In previous work (Eshel et al., 2006), we studied the gregarious behavior of evasive prey when facing the danger of a predator's attack. In the present work, we study the behavior of an already existing group of prey that is under an actual attack of the predator.[1] Both works build on the observation of Williams (1964) and Hamilton (1971) that gregarious behavior in the face of predation risk (potential or actual) is not necessarily selected to decrease the group's toll of predation (this is in contrast to the common previous view, e.g., of Lorenz, 1966, and also of later authors, e.g., King et al., 2009). Such a behavior, often inefficient from the group's point of view, results from the effort of each prey individual to decrease his own risk. Williams and Hamilton concentrated their studies on passive prey, where the risk of predation is equally shared by individuals in the same location. They succeeded in explaining the gregarious behavior on the basis of risk dilution (the formal term was introduced later by Dehn, 1990). It was further shown by Hamilton that, when the predation risk is higher on the border of the group, the prey's pressure to push into the center of the herd stabilizes the herd, while at the same time it facilitates predation. These arguments may not be sufficient to explain the establishment and maintenance of evasive herds when the struggle among individuals is less for a position

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[1] The formation of the group under attack can be caused by predation alarm, but also by other reasons, such as facilitating vigilance (Bednekoff and Lima, 1998; Bertram, 1978; Motro and Cohen, 1989), information sharing (Bednekoff and Lima, 1998; Bertram, 1978; Motro and Cohen, 1989), or, occasionally, due to concentration of food.

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far from the border but rather for a position which is furthest away from the pursuing predator. Unlike the examples given by Williams and Hamilton, this is never a struggle among equals. The slowest members of a herd (or indeed any remaining subgroup of it) are most likely to be the losers of this struggle. Crucial questions which ought to be answered are what keeps them in the herd, and what can possibly keep a herd from dispersing due to sequential desertion of its slowest and most exposed members.

In the present work, as in our previous one, we assume that prey individuals differ in speed: a slow one is more likely to be caught when targeted, and is more likely to be targeted when in a herd. Each member of the pursued herd should thus reconsider his decision to stay in the herd taking these probabilities into account. This decision, as we shall see, depends both on the herd's escape route, and on the strategy of the pursuing predator. Together these determine the predation risk of any individual both inside the herd and outside it, as a solitary deserter. The predator's strategy depends on the group's escape route. We assume that the choice of the escape route is made by the fastest individual or by a number of the fastest individuals in the herd, but their decision is affected by the expected reaction to it by the predator and by the slower members of the herd.

Most studies of animal group decisions concern situations in which decisions are slowly evolved within the group on the basis of individual preferences, social structure, and, possibly, distribution of information within the herd; see, e.g., Conradt and Roper (2005), Conradt and Roper (2007), Couzin et al. (2005), Couzin and Krause (2003), King et al. (2009) and Krause and Ruxton (2002). For a general overview and further references, see King and Cowlishaw (2009). However, when the herd is under a direct attack, any member that is not in the lead is faced with only two possibilities: leave the herd or follow those ahead of him. If he stays in the herd, his escape route is inevitably determined by those that are at the head of it. However, it is those ad hoc leaders that are least likely to be preyed on. For as long as they are followed by others, they are at least partly protected by the easier targets behind them. Moreover, except for the very last ones in the herd, each member is protected by those behind him. It is, therefore, only the slowest members of the herd who may have a direct incentive to leave it. This makes it best for the predator to home in on a solitary deserter, if he observed any. Thus, any individual who finds himself at the tail of the herd faces the choice between either deserting it, thus revealing his vulnerability to the predator, or sticking with the herd, thus becoming the most likely victim within it. We shall see how this decision of the slowest in herd depends on the escape strategy chosen by the leading fastest members of the herd, and how, in turn, it affects the predation risk of the latter (small as it may be): choosing an escape strategy that endangers the slowest in herd too much may sometimes be disadvantageous for the leader because it may lead to the eventual dispersal of the herd.

In order to analyze this situation, we employ a $k + 1$ players game with a single predator and k unequal prey individuals. We assume that, while evading in a group, each prey individual can assess his own speed, as well as that of any other member of the herd. The predator can assess only the speed of a prey he is chasing, whether it is a solitary prey or part of a herd. The game begins with the leading prey individual choosing a route of escape. The other members of the herd then decide (individually) whether to follow the leader or whether to desert the herd, and if so, when to leave. The predator decides whether to home in on a deserter, if he detects one, or whether to continue chasing the herd. We assume that the predator seeks to increase the probability of a successful catch, and that each prey individual seeks to decrease his own probability of being caught. This last assumption limits our analysis to herds without family structure, namely, in the terminology of Hamilton (1971), selfish herds.

Not surprisingly, we find that it is the slow prey individuals, who are exposed to predation at the tail of the herd, who have a high incentive to leave the herd, certainly higher than the fast individuals who are protected by the mere presence of the slow ones. Consequently, we show that, under quite plausible (though not the most general) assumptions, the predator will be better off pursuing a deserter, if he detects one, rather than continuing the pursuit of the remaining herd. The stability of the herd, which is crucially important to its leaders, depends, therefore, on the availability of hiding places for the potential deserter. When concealment is poor, the leader, who is certain to be followed by the whole herd, can behave as a dictator: he will choose an escape route to minimize his own risk of predation. This chosen route may or may not minimize the predation toll of the entire herd. If it happens to be optimal for the whole herd, then, following the terminology of Hamilton (1971), we call it a *seemingly cooperative leadership* (here, we have added '*seemingly*', to emphasize the selfish nature of the choice, and to distinguish it from a democratic decision). If the leader's chosen route does not minimize the herd's total predation risk, we call it an *openly selfish leadership* (as above, '*openly*' was added to emphasize the selfish nature of the leader's decision).

The situation is different when the terrain provides the potential deserter with a better chance of hiding. The leader is forced then to consider the impact of his choice on the other members of the herd, especially the slow ones. A route of escape that is too dangerous for the slowest in the herd may then start a snowball effect in which one by one individuals desert the herd, leaving the leader stripped of his defense. Taking this possibility into account forces the leader to consider the welfare of the weakest in the herd, a consideration that is often interpreted as altruistic (see, e.g., King et al., 2009 and Lorenz, 1966) or democratic (see (Kerth, 2010)). For example, leading to the open when cover is close by helps the predator to home in on slower prey individuals, thereby increasing the herd's total predation toll, but decreasing the risk of the leader. Choosing the cover-rich route is thus often interpreted as altruistic. It decreases the herd's predation toll while increasing the predation risk of the leader, relative to the case in which the leader can force the rest of the herd to follow him. But if he cannot, in some cases, as we shall see, he is better off leading to cover, thus avoiding the dispersal of the herd. We call this behavior a *seemingly altruistic leadership*.[2]

More surprisingly, our analysis demonstrates two further possible types of leadership, in which the leader is better off choosing an escape strategy that maximizes both his own risk of predation and the predation toll on the herd instead of the alternative one which, if enforced, would be better for both. Following Hamilton's terminology, we term this leadership *seemingly spiteful*. This may entail two possible extreme cases. The first case corresponds to a situation in which, in order to maintain the stability of the herd, the leader chooses an escape strategy that is excessively favorable to the slowest members of the herd, at the expense of all the others, including himself. The second case corresponds to an opposite situation in which, in order to focus the attention of the predator on the weakest in the herd, the leader chooses a route of escape that is difficult to all, but impossible for the slowest to follow, thus practically sacrificing the weakest to the predator. In the first case we call it a *seemingly populist leadership* and in the second case we speak of an *apparently spiteful leadership*.

We shall demonstrate plausible conditions under which each of the five sorts of leadership is expected to be observed.

2 Note that this term can well fit concepts such as reciprocal altruism (Trivers, 1971) and partnership (Eshel and Shaked, 2000). These, all the same, were developed to explain, on the basis of one's own long-term advantage, behavioral patterns that are commonly referred to as altruistic. Indeed, such explanation does not preclude the possibility that this sort of behavior reflects genuinely noble feelings, selected for their advantage to the individual.

2. The model

Consider a herd H without family structure, pursued by a single predator. The $k \geq 2$ members of the herd differ in their speed. Any member of the herd, except for the fastest individual, can choose between following those ahead of him, or leaving the herd and escaping as a solitary deserter. The escape route α of the herd (or the remaining herd) is determined by its fastest member, who, thus, becomes its *ad hoc leader*. When a prey individual $i \in H$ ($i = 1, 2, \ldots, k$) is chased by the predator as a solitary deserter, his probability of being caught is $p_i > 0$. The fastest individual has the lowest probability and the slowest has the highest, and we order the individuals by their speed $p_1 \leq p_2 \leq \cdots \leq p_k$, with the fastest one being the first. Assume further that the same individual, when homed in on by the predator while staying in group $G \subseteq H$ with an escape strategy a, has a probability $p^{\alpha}_{i,H}$ of being caught. The prey individuals are assumed to be informed about their speeds. We assume that the predator seeks to increase his probability of catching a prey, and each of the prey individuals seeks to decrease his own probability of being caught.[3]

We assume that the predator can always see a group of prey, when it exists (the entire herd, or any remaining part of it), but he observes a solitary deserter only with probability $1-q_\alpha > 0$, which may depend on the route of escape. When the predator observes some deserters, he must choose between pursuing the herd or pursuing one of the deserters. Choosing to home in on a deserter, he needs a small time $\delta > 0$ (maybe a split second) to observe, to make his decision, and to change his course. Once this decision is made, the predator cannot resume his chase of the herd, regardless of whether he caught the deserter or not. A predator's strategy is therefore determined by the probability x_α that he decides to pursue a deserter, when observed. This probability may depend on the escape route α chosen by the herd's leader. We assume, for simplicity, that the predator's strategy x_α is independent of the group he still follows, and on his previous decisions.

We assume that the predator can learn about the speed of a prey only by chasing it. When he observes more than one solitary individuals at the same time, and decides to chase one of them, he can only choose his victim at random, with equal probabilities. Instead, chasing a group of prey, he is more likely to home in on a slower prey, at the tail of the group, than on a faster one, closer to the lead. Denote by $\theta^{\alpha}_{i,G}$ the probability that a predator with a strategy x_α, while choosing a group of prey G, would home in on the individual $i \in G$. We assume the following.

Assumption 1. Pursuing a group of prey G, the predator is sure to home in on one of its members, i.e.,

$$\sum_{i \in G} \theta^{\alpha}_{i,G} = 1. \tag{1}$$

Assumption 2. The predator is more likely to home in on a slow rather than on a fast member of the group; i.e., for any $i, j \in G$ with $p_i > p_j$,

$$\theta^{\alpha}_{i,G} > \theta^{\alpha}_{j,G}. \tag{2}$$

Assumption 3. The ratio between the predator's probabilities of success when homing in on a slow and a fast prey is larger when the two are in a herd, rather than escaping as solitaries; i.e., if $i > j$, then

$$\frac{p^{\alpha}_{i,H}}{p^{\alpha}_{j,H}} \geq \frac{p_i}{p_j}. \tag{3}$$

This is due to a hindering effect exerted by the herd on individuals in its tail (see, e.g., Semeniuk and Dill (2004)), and a confusing effect exerted on the predator when homing in on individuals shielded by others (see, e.g., Smith and Warburton (1992)).

Assumption 4. If a solitary individual $j \notin G$ is slower than any member in the group G, then the predator is better off pursuing him, rather than pursuing the group G; i.e.,

$$p_j > \sum_{i \in G} \theta^{\alpha}_{i,G} p^{\alpha}_{i,G}. \tag{4}$$

This assumption is more restrictive than the previous three, as it precludes extreme situations, in which overcrowding makes the prey almost passive, and renders $p^{\alpha}_{i,G}$ much larger than p_i. The evolution of prey's gregarious behavior in such a case has already been well explained by Williams (1964) and Hamilton (1971).

Assumption 5. It is always better for a predator to pursue a group of prey G (in which case he has larger probability to home in on slower prey), rather than to pursue the same individuals as solitaries (in which case he has to pick up one of them at random).

This assumption, like the previous one, is somewhat restrictive, as it precludes cases in which the herd provides its members with some sort of passive group defense. The emergence of gregarious behavior, in this case, is easy to explain, and our analysis of ad hoc leadership is indeed irrelevant to such a case.

Finally, suppose that, at a given moment, it becomes preferable for more than one member of a pursued group G to desert it. Postponing one's desertion, in this case, is indeed costly, with higher costs for slower individuals. However, apart from the trivial case $x_\alpha = 0$, if it is in the best interest for two herd members to desert at the same time, the one who postpones his desertion for the short time interval δ after the other enjoys the advantage of a lower chance to be targeted by the predator (he may be targeted only if the predator overlooks the other). From an argument of continuity, it thus follows that, if δ (and therefore the risk of postponing one's desertion by δ) is small enough (and it is assumed to be very small), then it is advantageous to postpone one's desertion if and only if the other does not postpone it. This determines an asymmetric subgame of desertion time within the group of potential deserters (actually, a discrete asymmetric war of attrition; see, e.g., Bishop and Cannings, 1978). It is easy to see that one stable equilibrium of this subgame is the one in which any potential deserter would desert in a time lapse of exactly δ after finding himself last in group, provided that the predator then still follows the remaining group. Indeed, once such a behavioral rule is established in the population, it is advantageous for the last in the herd to desert immediately, since nobody else is expected to do it; and since he is expected to do it, it is advantageous for anybody else to wait till he will become last in the group. Moreover, while this equilibrium requires very simple reactions of the players to very simple information, other equilibria (e.g., desert only if you are second from last and when it is still in your interest to desert) require strategies that are hard to execute, unlikely to be established in the situation, and even less so to be selected. We therefore naturally assume the following.

Assumption 6. If there is a positive probability that the predator would prefer pursuing a deserter rather than following the group, then those who choose to desert the herd do it one after the other, the slowest first, with a lapse of time $\delta > 0$ between them.

In the special case when, for all $i \in H$, $p^{\alpha}_{i,H} = p_i$, we say that α is a *simple escape strategy*. Simple or close to simple escape strategies are typical for non-overcrowded groups of prey, in which

[3] "Seek", in this connotation, may conveniently stand for a behavioral pattern, favored by natural selection, that determines the choice of such a strategy. No evolutionary dynamics, however, is suggested in this work. For the evolutionary dynamics of such a pattern in the case where all prey individuals are equal, see Cressman and Garay (2009).

individuals keep close but without interfering with each other. It is easy to see that the last six assumptions are always satisfied by simple or close to simple escape strategies.

We show that, for any escape strategy α, our assumptions ensure the existence of a unique subgame perfect equilibrium of the multiple conflict among the predator and the $k-1$ non-leading prey individuals. This equilibrium determines, in turn, the predation risk $R^{\alpha}_{1,H}$ of the leader who chooses the escape strategy α to minimize it. The escape strategy $\alpha = \alpha^*$ that minimizes $R^{\alpha}_{1,H}$ determines the unique subgame perfect equilibrium of the prey–predator game Γ, and will be referred to as the *equilibrium escape strategy*. Moreover, we show that, except for negligible degenerate cases, the equilibrium of the game is strict, and hence stable, and that it is the only stable equilibrium of the game.

For a different model of democratic group decisions, in which individuals can avoid decisions by leaving the group, see Kerth (2010).

3. The stable prey–predator equilibrium

3.1. Predator and non-leading prey equilibria

Once the leading fastest prey has chosen an escape strategy α, both the predator and the $k-1$ non-leading prey individuals have to choose their strategies, each seeking to maximize his own payoff, probability of a successful catch for the predator, and survival probability for the prey. We show that in the subgame Γ_α thereby determined between these players, there are always two and only two equilibria. One of the two is characterized by the predator's strategy $x_\alpha = 1$ of always preferring the pursuit of a deserter, and the other is characterized by the predator's strategy $x_\alpha = 0$ of ignoring deserters and following the herd. We shall see that the first one is subgame perfect and usually stable. The other is neither stable nor subgame perfect.

We start by distinguishing between the cases $x_\alpha > 0$ and $x_\alpha = 0$. If $x_\alpha > 0$, then any individual i within an evading group G who is first to leave it suffers a risk $1-q_\alpha$ of being observed, a risk x_α of being targeted if observed, and a risk p_i of being caught if targeted. Altogether, he suffers a risk of predation $x_\alpha(1-q_\alpha)p_i$. Staying, instead, in group, his risk would be $\theta^{\alpha}_{i,G}p^{\alpha}_{i,G}$. He would therefore be better off deserting if

$$\theta^{\alpha}_{i,G}p^{\alpha}_{i,G} > x_\alpha(1-q_\alpha)p_i, \tag{5}$$

and better off remaining in the group if the reverse of (5) holds. From this, together with (2) and (3), it follows that, if it is advantageous for some member of the group to leave it, it is so also for any slower group member. It then follows from Assumption 6 that *any deserter observed by the predator must be, at that moment, the slowest in the group*. From Assumption 4, it then follows that it is always better off for the predator to home in on a deserter, whenever observed. The only possible equilibrium strategy $x_\alpha > 0$ of the predator must, therefore, be $x_\alpha = 1$, in which case condition (5) for deserting the herd thus becomes

$$\theta^{\alpha}_{i,G}p^{\alpha}_{i,G} > (1-q_\alpha)p_i. \tag{6}$$

For a simple escape strategy, this becomes $\theta^{\alpha}_{i,G} > 1-q_\alpha$.

Denote by $H_l = \{1, 2, \ldots, l\}$ the group of the l fastest members of H ($l = 2, 3, \ldots, k$). From (6), it follows that such a group is stable under the pursuit of the predator if

$$\theta^{\alpha}_{l,H_l}p^{\alpha}_{l,H_l} < (1-q_\alpha)p_l, \tag{7}$$

and unstable if the reverse of (7) holds. Consequently, if $\theta^{\alpha}_{l,H_l}p^{\alpha}_{l,H_l} > (1-q_\alpha)p_l$ for all $l = 2, 3, \ldots, k$, then all members of the herd H are expected to desert it one by one, the slowest first. If, on the other hand, $\theta^{\alpha}_{l,H_l}p^{\alpha}_{l,H_l} < (1-q_\alpha)p_l$ for some $l = 2, 3, \ldots, k$, we denote by l_α the last index for which this inequality holds. We know that the $k-l_\alpha$ slowest members of the herd H are expected to desert it one by one, the slowest first, while the remaining group H_{l_α} of faster prey individuals would remain stable.

What remains to be considered is the case $x_\alpha = 0$, in which the predator always pursues the group of prey, if it exists. In such a case, a deserter that leaves behind him a group of at least two individuals suffers no risk. If, on the other hand, all non-leading individuals desert at the same time, the predator then observes k solitary deserters, and chases one of them at random, with equal probability $1/k$. Consequently, we expect either all non-leading group members, or all but one, to desert immediately. However from Assumption 5 it follows that, remaining in a group of two, it is better off for the slower of the two to desert as well, but in this case the delayed deserter would have half the risk of being targeted by the predator instead of the $1/k$ risk he would have if he were deserting without delay. Consequently, an immediate dispersal is the best response of the prey to the predator's strategy $x_\alpha = 0$. On the other hand, any predator's strategy ($x_\alpha = 0$ included) is a best response (in the weak sense) to the immediate dispersal of the prey. Indeed, the strategy of the predator then becomes irrelevant to the outcome of the game: in any case he would choose a random victim with equal probability $1/k$. We thus get the following.

Corollary 1. *The predator's strategy $x_\alpha = 0$ determines a unique equilibrium of the subgame Γ_a, in which the non-leading prey's strategy is to desert immediately.*

As we have seen, this equilibrium is unstable, because the predator does not lose by unilaterally shifting to another strategy. We show now that, by shifting to the strategy $x_\alpha = 1$, the predator can induce the prey to respond in a way that is better for him; hence the equilibrium determined by $x_\alpha = 0$ is also not subgame perfect (the predator should rather choose $x_\alpha = 1$ to start with).

As we already know, the prey's best response to the predator's strategy $x_\alpha = 1$ implies desertion of the slowest $k-l$ herd members one by one, the slowest first, with the establishment of a remaining herd H_l if $l > 1$. This provides the predator with a payoff that is higher than or equal to what it would be if the $k-l$ slowest members of the herd were dispersing at once, with equality if and only if $k-l = 0, 1$ (indeed, deserting one by one, the slowest first, would increase the predator's probability to home in on a slower prey). Moreover, as follows from Assumption 5, this predator's payoff could only diminish if, after the $k-l$ slowest members of the herd, the fastest l members were also spreading out, with equality if and only if $l = 0$. Finally, the predator's payoff would be even smaller in the case of immediate dispersal of all herd members, slower and faster ones together (indeed, if slower individuals spread out first, there is a higher probability that the predator with strategy $x_\alpha = 1$ would home in on one of them). But we already know that, in the case of immediate dispersal of the prey, the predator's payoff would be equal to what he would get if he were choosing the strategy $x_\alpha = 0$. This, as we see now, is less than what he could obtain by choosing $x_\alpha = 1$. We thus get the following.

Corollary 2. *Any leader's choice of a strategy α determines a unique subgame perfect equilibrium of the conditioned game Γ_α among the other players. This equilibrium is characterized by the predator's strategy $x_\alpha = 1$ of always preferring the pursuit of a deserter, and by either the dispersal of the entire herd or the establishment of a stable subherd H_{l_α}, consisting of its l_α fastest members ($l_\alpha = 2, 3, \ldots, k$), after the desertion of all the others. In both cases, those who desert do it one by one, the slowest first.*

It is easy to see that, whenever this equilibrium allows for at least one deserter (i.e., when $l_\alpha < k$), and apart from the degenerate case $\theta^{\alpha}_{l_\alpha,H_{l_\alpha}} p^{\alpha}_{l_\alpha,H_{l_\alpha}} = (1-q_\alpha)p_{l_\alpha}$, this equilibrium of the subgame is also strict, and hence stable.[4]

3.2. Leader's versus ad hoc leader's choice

We start this section by making a testable distinction between a real leader who can force his will on the others because he is leader, and an ad hoc leader, who is followed by them because he happens to be at the lead of the herd. In both cases, we assume that the individual at the lead of the herd is expected to choose the escape strategy α that minimizes his own risk of predation.[5] For a real leader, this should be his predation risk $\theta^{\alpha}_{1,H}p^{\alpha}_{1,H}$, say D^{α}_{H}, given that he is followed by all other herd members, *regardless of the route he chooses*. This is by no means guaranteed to an ad hoc leader. He is expected to choose the escape strategy $\alpha = \alpha^*$ that minimizes his predation risk $R^{\alpha}_{1,H}$, as determined by the equilibrium of the resulting subgame Γ_α among the other players. If this equilibrium allows for a non-empty herd $H_{l_\alpha} \subseteq H$, then the leader's predation risk will be equal to the probability $(q_\alpha)^{k-l_\alpha}$ that the predator would overlook the $k-l_\alpha$ deserters, multiplied by the probability $\theta^{\alpha}_{l,H_{l_\alpha}}$ that, pursuing the herd H_{l_α}, he would home in on its leader, and the probability $p^{\alpha}_{l,H_{l_\alpha}}$ that he would then catch him. Consequently, in this case,

$$R^{\alpha}_{1,H} = (q_\alpha)^{k-l_\alpha}\theta^{\alpha}_{l,H_{l_\alpha}} p^{\alpha}_{l,H_{l_\alpha}}. \tag{8a}$$

If, instead, this equilibrium involves the desertion of all followers, then, with the desertion of the last one, the predator (unlike in the previous $k-2$ desertions) no longer sees a herd, but rather two solitary deserters to target with equal probability. Taking into consideration the probability $(q_\alpha)^2$ that he would overlook both, the probability that he would then home in on the ex-leading individual is $\frac{1}{2}(1-(q_\alpha)^2)$; hence, in this case,

$$R^{\alpha}_{1,H} = \frac{1}{2}(q_\alpha)^{k-2}(1-(q_\alpha)^2)p_1. \tag{8b}$$

Once the (ad hoc) leader chooses the escape strategy $\alpha = \alpha^*$ that minimizes his predation risk $R^{\alpha}_{1,H}$, a unique stable, subgame perfect equilibrium of the entire prey–predator game is obtained. We thus call α^* the *equilibrium escape strategy*.

The equilibrium escape strategy α^* may, but may not, minimize the toll of predation $\sum_{i\in H}\theta^{\alpha}_{i,H}p^{\alpha}_{i,H}$ on the herd, and it does not necessarily minimize the predation risk $\theta^{\alpha}_{1,H}p^{\alpha}_{1,H}$ of the leader *if he were sure to be followed by the others*. Denote, for convenience,

$$\theta^{\alpha}_{1,H}p^{\alpha}_{1,H} = D^{\alpha}_{H}, \tag{9a}$$

and

$$\sum_{i\in H}\theta^{\alpha}_{i,H}p^{\alpha}_{i,H} = T^{\alpha}_{H}. \tag{9b}$$

Following Hamilton (1971), we say that the equilibrium escape strategy α represents a *seemingly cooperative leadership* if it happens to minimize both D^{α}_{H} and T^{α}_{H}. It represents an *openly selfish leadership* if it minimizes D^{α}_{H} but not T^{α}_{H}. It represents a *seemingly altruistic leadership* if it minimizes T^{α}_{H} but not D^{α}_{H}. However, we shall see that the equilibrium escape strategy cannot be interpreted merely as a one-dimensional compromise between the welfare of the herd and that of the leader. Quite surprisingly, we shall see situations in which this escape strategy represents what we have referred to as *seemingly spiteful leadership*, maximizing both D^{α}_{H} and T^{α}_{H}. These four types of leadership cover all theoretical possibilities. *Seemingly spiteful* leadership can occur when, in order to maintain the stability of the herd, it is necessary to make some sacrifice in favor of its most vulnerable members. It can also occur, in contrast, when a desertion of a slow herd member relieves the predation risk on the others, the leader included. In this case, we shall see that under certain conditions it is advantageous for the latter to choose an escape strategy which, slightly more riskily for the bulk of the herd, is unbearable for its slowest member, thus forcing him to desert and thereby become a more likely target for the predator. In the first case we speak of a *seemingly populist leadership*. In the latter one we speak of an *apparently spiteful leadership*. In the following examples, we concentrate on the case in which the leader has only two alternative routes of escape.

Let us first return to the example of a choice between escaping to the open, α_{op}, and the alternative, α_c, of escaping to cover: α_c provides a deserter with a better chance to hide, which means that

$$q_{\alpha_{op}} < q_{\alpha_c}, \tag{10}$$

and α_{op} provides the predator with a better chance to home in on a slower prey, which means that, for any $i, j \in G \subseteq H,\ i < j \le k$,

$$\frac{\theta^{\alpha_{op}}_{i,G}}{\theta^{\alpha_{op}}_{j,G}} > \frac{\theta^{\alpha_c}_{i,G}}{\theta^{\alpha_c}_{j,G}}. \tag{11}$$

From (1) and (11), it then follows that, for all $l = 2, 3, \ldots, k$,

$$\theta^{\alpha_{op}}_{1,H_l} < \theta^{\alpha_c}_{1,H_l}; \tag{12}$$

i.e., the probability that the predator would home in on the leader is higher under cover than in the open. Employing this, one can easily demonstrate cases of seemingly cooperative, openly selfish, and seemingly altruistic leadership.

Seemingly cooperative leadership

If the probabilities $p^{\alpha_c}_{i,H_l}$ of catching the prey under cover are sufficiently small, then it is easy to see that α_c is indeed the equilibrium escape strategy. It also minimizes both $D^{\alpha}_{H} = \theta^{\alpha}_{1,H}p^{\alpha}_{1,H}$ and $T^{\alpha}_{H} = \sum_{i\in H}\theta^{\alpha}_{i,H}p^{\alpha}_{i,H}$; hence it represents a seemingly cooperative leadership. ∇

For the next two examples, assume that both α_{op} and α_c are simple escape strategies; i.e., $p^{\alpha_{op}}_{i,H} = p^{\alpha_c}_{i,H} = p_i$. Again from (1) and (11), we get

$$T^{\alpha_{op}}_{H} = \sum_{i\in H_l}\theta^{\alpha_{op}}_{i,H}p_i > \sum_{i\in H_l}\theta^{\alpha_c}_{i,H}p_i = T^{\alpha_c}_{H}. \tag{13}$$

This, together with (12), means that α_{op} represents an openly selfish leadership, and α_c represents a seemingly altruistic leadership.

Openly selfish leadership

Assume that both α_c and α_{op} guarantee the stability of the herd; (i.e., $1-q_{\alpha_{op}} > \theta^{\alpha_{op}}_{k,H}$ and $1-q_{\alpha_c} > \theta^{\alpha_c}_{k,H}$). From (12), (8a) and (8b), it then follows that $R^{\alpha_{op}}_{1,H} = \theta^{\alpha_{op}}_{1,H}p_1 < \theta^{\alpha_c}_{1,H}p_1 = R^{\alpha_c}_{1,H}$; hence the openly selfish strategy α_{op} is the equilibrium escape strategy chosen by the leader. ∇

Seemingly altruistic leadership

Let $1-q_{\alpha_c} > \theta^{\alpha_c}_{k,H}$, but $1-q_{\alpha_{op}} < \theta^{\alpha_{op}}_{l,H_l}$ for all $l = 2, 3, \ldots, k$. Escaping to cover then guarantees the stability of the herd H, while escaping to the open results with its total dispersal; hence $R^{\alpha_{op}}_{1,H} = \frac{1}{2}(q_{\alpha_{op}})^{k-2}(1-(q_{\alpha_{op}})^2)p_1$ and $R^{\alpha_c}_{1,H} = \theta^{\alpha_c}_{1,H}p_1$. But the only assumption made until now on $\theta^{\alpha_c}_{1,H}$ (the probability of homing in on the leader when leading to cover) is that it should be small (though larger than the probability $\theta^{\alpha_{op}}_{1,H}$). Thus, if $\theta^{\alpha_c}_{1,H}$ is sufficiently small,

[4] In the degenerate case $\theta^{\alpha}_{l_\alpha,H_{l_\alpha}} p^{\alpha}_{l_\alpha,H_{l_\alpha}} = (1-q_\alpha)p_{l_\alpha}$, there is, instead, a stable set of equilibria, in which the fastest $l_\alpha - 1$ members of the original herd remain in group, the slowest $k-l_\alpha$ desert, and the individual l_α deserts with any probability between zero and one.

[5] This, as we recall, limits our analysis to herds without family structure.

then $R_{1,H}^{\alpha_c} < R_{1,H}^{\alpha_{op}}$, and α_c is then the equilibrium escape strategy, representing a seemingly altruistic leadership. ∇

In order to characterize cases of *seemingly populist* and *apparently spiteful* leadership, we assume now a group of prey G that follows an escape strategy α, and ask how the behavior of an individual $i \in G$ affects the predation toll on the rest of the group. As long as i remains in the group (given that all others do so), the probability that the predator would home in on another member of it is indeed $1 - \theta_{i,G}^{\alpha}$. If, instead, i deserts the group, then the probability that the predator would home in on those who remain is equal to the probability q_α that he will overlook the deserter. Consequently, the desertion of the individual i would increase (decrease) the predation toll on the rest of the group if $\theta_{i,G}^{\alpha} > 1 - q_\alpha$ ($\theta_{i,G}^{\alpha} < 1 - q_\alpha$). But, given that α is a simple escape strategy, it follows from (6) that the individual $i \in G$ would be better off leaving the group if $\theta_{i,G}^{\alpha} > 1 - q_\alpha$, and staying in it if $\theta_{i,G}^{\alpha} < 1 - q_\alpha$.

Corollary 3. *For any individual in a herd who follows a simple escape strategy, it is advantageous to desert the herd if by doing so he increases the risk of the predator homing in on the others, and it is disadvantageous for him if by doing so he decreases the risk of the predator homing in on the others.*

Using this corollary, we see that seemingly populist leadership can emerge when it is in the best interest of the slowest in group to leave it, and it is in the best interest of the leader to invest in order to prevent his desertion. Apparently spiteful leadership can emerge when it is in the best interest of the slowest in herd to remain in it, and it is in the best interest of the leader to invest in order to cause him to leave the herd. In both the following examples we assume, for simplicity, that the leader can choose between a simple escape strategy α, and a single, non-simple alternative β, with $q_\alpha = q_\beta = q$ (a plausible assumption if both take place in the same terrain).

Seemingly populist leadership

Let $\theta_{l,H_l}^{\alpha} > 1 - q$ for all $l = 2, 3, \ldots, k$. This, as follows from (6), leads to the desertion of all herd members. From Corollary 3, we know that each such desertion increases the homing in probability on the remaining group, and hence the homing in probability on the leader must then be larger than it would be if the herd remained intact. Since α is a simple escape strategy (in which the homing in risk is proportional to the risk of predation), this means that $R_{1,H}^{\alpha} > D_H^{\alpha}$. Suppose that the alternative strategy β slightly increases the predation toll on the herd, when intact (i.e., $T_H^{\beta} > T_H^{\alpha}$), but divides the predation risk more equally among its members, so that $\theta_{k,H}^{\beta} p_{k,H}^{\beta} < \theta_{k,H}^{\alpha} p_k$. If $\theta_{k,H}^{\alpha}$ is sufficiently close to (though still larger than) $1 - q$, then even if the choice of β leads to a small decrease in the predation risk of the slowest in herd, it may be sufficient to ensure the condition $\theta_{k,H}^{\beta} p_{k,H}^{\beta} < (1 - q) p_k$ for the stability of the herd. The predation risk of the leader, if choosing β, would then be $R_{1,H}^{\beta} = D_H^{\beta}$. This value, even though necessarily larger than D_H^{α}, can still be smaller than the larger value $R_{1,H}^{\alpha}$. In this case, β must be the leader's equilibrium strategy. However, $T_H^{\beta} > T_H^{\alpha}$ and $D_H^{\beta} > D_H^{\alpha}$, and hence β represents a seemingly spiteful leadership, in this case of helping the weak, a seemingly populist one.[6] ∇

Apparently spiteful leadership

In contrast to the previous case, assume now that the (simple) escape strategy guarantees the stability of the herd H and all subherds H_l of it. From Corollary 3, we know that in this case any desertion from H, inevitably unfavorable for the deserter, would decrease the homing in probability on the rest of the herd. It is reasonable to assume that, at least in some cases, it would decrease the probability of homing in on the leader. Assume that a shift from α to β would only affect the predation risks p_i, so that, for all $i \in H$,

$$p_{i,H}^{\beta} \geq p_i, \tag{14}$$

with a sharp inequality for $i = k$ (i.e., β is more risky for the slowest in the herd). A large enough value of $p_{k,H}^{\beta}$ would indeed guarantee the desertion of the slowest in herd. In such a case, if (14) is satisfied as an equality for all $i < k$, then this desertion would decrease the predation toll on the rest of the herd and, as assumed, the risk of the leader. From a continuity argument, it follows that this remains true even if, for all $i = 1, 2, \ldots, k$, (14) would become a sharp inequality, provided that the $p_{i,H}^{\beta}$–s are sufficiently close to the p_i-s (i.e., the escape strategy β *endangers mainly the slowest in herd, but it slightly endangers other herd members, including the leader*). *In such a case, β would still be the leader's best strategy. However, employing* (9a) and (9b), and the sharp version of (14), *we get $D_H^{\beta} > D_H^{\alpha}$ and $T_H^{\beta} > T_H^{\alpha}$*, and hence the escape strategy β *represents, again, a seemingly spiteful leadership, in this case of harming the weak, an apparently spiteful one.* ∇

Such an escape strategy can be demonstrated by risky maneuvers (e.g., by flocks of starlings) that are slightly dangerous for fast members of the herd, and substantially more so for the slower ones, who find it difficult to follow them. Forced to abandoned the herd, these weaklings are likely to attract the predator and thereby relieve the predation toll on the others (see, for comparison, Zahavi, 1977).

4. Summary and discussion

Escaping in a group is advantageous for those individuals that are not in the rear of the group. They are partly shielded from behind by others who follow them. A crucial question is why the last members in a group still follow those that are ahead of them. As suggested in this work (see also Eshel, 1978 and Eshel et al., 2006), the answer to it is built in the very question: since the slowest in the group are the only ones with an immediate incentive to desert, their very act of desertion may signal weakness to the predator. In fact, under a wide range of plausible conditions, it was shown that, by picking up a deserter, when one is detected, the predator can guarantee his homing in on a relatively slow victim. This finding agrees with well-established observations of predators who concentrate their attack on a single, isolated prey, a phenomenon that has been traditionally explained on the basis of the relative ease in which the predator can takeover a single prey (see, e.g., Bertram, 1978, Lorenz, 1966 and Van Lawick-Goodal and Van Lawick-Goodal, 1973). While this may be true for a predator pursuing a herd of buffaloes who may turn to defend their companion, this is an unlikely case when the prey is a herd of gnus or antelopes. Alternatively, we suggest that being isolated from the group is not a passive mistake of a group member. It represents, more likely, the optimal choice of a given individual, at a given moment, between staying at the rear of the group and revealing one's weakness by deserting it.[7] The analysis made in this work indicates that the question of which of the two choices is more risky depends, among other things, on the accuracy of the predator in choosing a victim within the group, and on his ability to detect a deserter outside it. We have further seen that if a group member

[6] More apparent are cases in which the entire herd has been occasionally observed returning to harass the predator; see, e.g., Van Lawick-Goodal and Van Lawick-Goodal (1973). However, since harassment quite generally entails at least potential risk to the predator, a thorough analysis of this phenomenon may require some further extension of the present model.

[7] Note that members of the non-evading selfish herd, as described by Hamilton (Hamilton, 1971 and references therein), always react to the risk of predation by pushing in, to the convenience of the predator.

prefers to desert the group, then any slower member would do so, and if an individual prefers to remain in group then any faster member of the group will also prefer to stay. We have shown, under quite plausible conditions, that, at any moment of the pursuit, the only prey individual that may be better off leaving the group is the one who, at that moment, finds himself last in the group. Consequently, if not all members of the group desert it, then those remaining in the group are its fastest members.

As we have seen, the combination of group escape with the predator's tendency to home in on a single deserter is advantageous to all but the slowest group members. Regardless of what these slow members do, they are anyhow doomed to take over the bulk of the predation toll. The behavior adopted by the predator and all prey individuals except for the slowest can therefore be interpreted as a hedonic coalition against the latter (see Eshel et al., 2006 for more details). However, we see that these slowest members may not always be limited to the role of just passive victims. Quite often they play a crucial role in influencing the herd's route of escape, to their own benefit. While, at any step of the chase, the decision to desert or to stay in the group depends on the hunting accuracy of the predator when homing in on the group, and on the chance of a single prey individual to escape his attention as a deserter, these two factors often depend, in turn, on the route of escape followed by the group. For example, escaping to the open renders it easier for the predator to detect a deserter and home in on him. It was therefore shown that, in some (though not in all) situations, adopting such a route of escape, even if increasing the toll of predation on the entire group, makes it disadvantageous for the last in the group to desert it, and hence it ensures the stability of the evading group. This means that the leading fast members of the group are then sure to be protected by slower individuals that follow them. But these leading individuals are exactly those that determine the group's route of escape. Assuming that they choose this route according to their selfish interest of maximizing their own survival probability, it is therefore a not a surprising result that, under given situations, these ad hoc leaders are expected to prefer an escape to the open, even if thereby increasing the predation toll on the herd. (The situation is indeed different in small groups with a family structure; see Hamilton, 1964 and Hamilton, 1972. For a somehow different approach, see also Eshel, 1972.) But what if it is not in the best interest of other group members to follow them (i.e., if the risk to the last in herd is then too high)? This, as we see, makes a clear demarcation between a leader who can force his will on others, and what we refer to as an ad hoc leader. The latter, as was shown, would be better off refraining from adopting a too openly selfish behavior that may cause the desertion of other group members. Taking this into consideration, we have seen that, out of pure selfish motivation, an ad hoc leader may be better off choosing an escape route that would otherwise (i.e., if sure to be followed by others) increase his own risk of predation. This route may either increase or decrease the predation toll on the entire herd.

Following the terminology of Hamilton (1971), we therefore distinguish between four possible sorts of ad hoc leader's behavior, according to the effect of this behavior on both the predation toll on the entire herd, and the predation risk of the leader himself, if followed by the others.

In the simplest case, where there is no conflict of interest between the leader and the followers, the ad hoc leader's best route of escape was easily shown to minimize both his predation risk and the predation toll on the entire herd. In such a case, we have used the term *seemingly cooperative leadership*. Here, the word "seemingly" was added because we know that, in any case, the behavior of the ad hoc leader (as well as of all other participants of the conflict) is selfish.

The possibility that an escape strategy adopted by a group of prey is not necessarily the one that minimizes the predation toll on it may be demonstrated by the observation that finches, escaping to cover, suffer a predation risk that is lower than that of the faster and more maneuverable starlings that lead to the open (Amotz Zahavi, personal communication). Indeed, escaping to the open renders it easier for the predator to detect slower members of the herd, thereby increasing the predation toll on the entire herd, but decreasing the predation risk of its faster members, leader included. We referred to the choice of such an escape strategy as *openly selfish leadership*. It was shown to be chosen when the risk of desertion is too high (i.e., when the terrain offers a too poor cover), and the leading individual is therefore sure to be followed regardless of the route of escape he may choose.

However, in other cases, a route of escape that is too risky for whoever finds himself at the tail of the group may lead to its dispersal, with an apparent disadvantage to ad hoc leaders. This is likely to account for escape strategies, often observed in nature (e.g., finches escape to cover), that are traditionally explained on the basis of group's welfare. They indeed decrease the predation toll on the group, seemingly on the expense of its leading fastest members. We referred to such escape strategies as *seemingly altruistic leadership*, but we explain them on the basis of selfish interest of the leader to maintain the stability of the group.

In some cases, it was further shown that the ad hoc leader's best route of escape is, surprisingly, the very one that maximizes both his own predation risk and the predation toll on the entire herd. In this case, still following the terminology of Hamilton, we speak of a *seemingly spiteful leadership*. We have seen that this is possible in one of two extreme cases. The first one was shown to occur when some extra help to the most vulnerable members of the herd is required in order to maintain the stability of the group, even if thereby increasing not only the predation risk of the leaders but also the predation toll on the entire group. In this case, we speak of a *seemingly populist leadership*. The other case may occur when, in contrast, a route of escape that is slightly dangerous to all, but mainly to the slowest in herd, forces the latter to desert, thereby revealing himself as a preferred target for the predator, to the relief of the others. In such a case we speak of an *apparently spiteful leadership*.

The results demonstrated in this work are based on a study of an analytical model that, as such, cannot cover all natural versions of the conflict in question. In most natural situations, it is still hard to tell seemingly altruistic leadership from a real one, based on hidden kin selection (Hamilton, 1964, 1972), or effects of group selection (Eshel, 1972; O'Gorman et al., 2008; Wilson and Wilson, 2007) (these, however, cannot explain the more extreme cases of populist leadership); nor can we prove that the complex maneuvering of starlings really represents a spiteful leadership, rather than being aimed at confusing the predator (Smith and Warburton, 1992). As mentioned by an anonymous referee, the predictions of our model might have been different if we allowed simultaneous initiations of escape in different directions. The preference of other group members to follow a more seemingly altruistic route may then introduce an apparent deviation from the predictions of our model toward more democratic way of decision making, suggested by Kerth (2010). A crucial question, in this case, is whether the initiation of a seemingly altruistic route of escape, even if followed by others, can be a preferable strategy for a relatively fast individual, whose interest may not be much different from that of the fastest in group. Following the openly selfish ad hoc leader would leave him reasonably protected by a tail of followers. Initiating, instead, an alternative, seemingly altruistic route of escape would force him to more equally share his predation risk with his slower followers, an apparent disadvantage for a relatively fast individual. But then, if an initiation of a seemingly altruistic route of escape is restricted to slow group members, then the best predator's strategy should, most likely, be to follow any seemingly altruistic branch of the group. It might be interesting to study more carefully a range of parameters for which the possibility of double initiation may introduce some bias toward a more democratic behavior of the group.

We maintain, though, that any analysis of a conflict, involving a predator and an evasive group of prey, should take into consideration the fact that the route of escape of such a group is inevitably determined by those who find themselves at its lead; that these individuals are the least likely to be preyed on; that sticking to the group is still advantageous for the "silent majority" of prey individuals that find themselves neither at the lead, nor at the rear of the group; and that the coherence of the group, and hence the safety of its ad hoc leaders, therefore depends on the incentive of those that remain last in the group to stick to it.

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