

The effects of opportunistic and intentional predators on the herding behavior of prey

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Abstract. In this article, we study how predator behavior influences the aggregation of prey into herds. Game-theoretic models of herd formation are developed based on different survival probabilities of solitary prey and prey that join the herd and on the predator's preference of what type of prey to search for. For an intentional predator that will only pursue its preferred type of prey, a single herd with no solitaries cannot emerge unless the herd acts as a prey refuge. If neither prey choice provides a refuge, it is shown that an equilibrium always exists where there are both types of prey and the predator does not always search for the same type of prey (i.e., a mixed equilibrium exists). On the other hand, if the predator is opportunistic in that it sometimes shifts to pursue the type of prey that is observed first, there may be a single herd equilibrium that does not act as a prey refuge when there is a high level of opportunistic behavior. For low opportunistic levels, a mixed equilibrium is again the only outcome. The evolutionary stability of each equilibrium is tested to see if it predicts the eventual herding behavior of prey in its corresponding model. Our analysis confirms that both predator and prey preferences (for herd or solitary) have strong effects on why prey aggregate. In particular, in our models, only the opportunistic predator can maintain all prey in a single herd that is under predation risk.

Key words: *dynamic stability; ESS; game theory; intentional predator; opportunistic predator; predation strategy; selfish herd; solitary prey.*

INTRODUCTION

The main purpose of this paper is to demonstrate that predator preferences influence the gregarious behavior of a prey species (i.e., whether prey should aggregate by joining a herd or be solitary by staying on their own). In particular, we will see that the expected distribution of these two types of prey behavior depends on whether the predator is “intentional” (i.e., at a given time, the predator will only attack the type of prey that is its current intention) or exhibits some level of “opportunistic” behavior (i.e., the predator will also attack observed non-preferred prey with a given probability).

There are many reasons individuals choose between being solitary or part of a group (Krause and Ruxton 2002). One widely accepted explanation why prey form herds is as a defense against predation. For example, in a study by Hass and Valenzuela (2002) of white-nosed coatis populations, predation by large felids accounted for more than 50% of mortality of adult coatis. Predation rates were higher on solitary coatis than on coatis in a group, where the predation rate was inversely related to group size. Herd formation can decrease

individual predation risk for several reasons such as the following: the “dilution” effect (Dehn 1990); the “many eyes” hypothesis (Treves 2000); by confusing predators (Smith and Warburton 1992); and by mounting a cooperative defense to fight off the predator (Garay 2009). That is, there is a trade-off between safety and danger in numbers (Brown and Kotler 2004). In summary, we can claim that the individual prey's survival probability is dependent on whether the individual in question is solitary or in the herd.

All of the above effects assume individual prey are homogeneous in the sense that all solitary prey have the same quantitative advantages and disadvantages as do all prey in a herd. This is not always true. For instance, there is evidence that an individual's survival probability in the herd also depends on its position in a herd such as through the “selfish-herd” hypothesis (Hamilton 1971). In the selfish herd, if there is no refuge nearby, the best possible shelter is to be behind another prey. Individuals try to reduce their predation risk at others' expense. (Hamilton's treatment already includes a dilution effect studied later by Dehn [1990] and considers the case where danger from predation is shared equally among prey in the herd.) We will not take into account such position effects in the herd. Instead, we assume that, on average, each individual spends the same amount of time in the danger zone, thus the average survival rate of each member of the herd is the same.

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On the other hand, the above literature mostly ignores the effect of different predator behaviors. In the next section, where the predator is intentional, our model predicts that either all prey should be of one type and the predator searches only for the other type of prey (i.e., one type of prey acts as a refuge) or else there is a completely mixed equilibrium strategy. At this latter equilibrium, there are some solitary prey as well as some in the herd and the predator does not pursue only one type of prey (these equilibria were the focus of the general predator-prey two-habitat selection game introduced by Hugie and Dill [1994]). In particular, when the predator is intentional, there is no equilibrium, as in Hamilton (1971) where all prey are in the herd and the predator searches only for the herd. On the other hand, when the predator is opportunistic (see *Opportunistic predators*), an equilibrium such as Hamilton's is possible (a completely mixed equilibrium is also possible for low levels of opportunism). Our results and their applications are discussed further in *Conclusion*.

In addition to finding the equilibria of these games, we are also interested in the effect of the predator's prey preference on the evolutionary outcome. To this end, the stability properties of all equilibria in *Intentional predators* and *Opportunistic predators* are characterized. Our main conclusions are that the herding behavior of prey cannot be understood without considering predator preferences and whether it behaves intentionally or opportunistically.

INTENTIONAL PREDATORS

In this section, we study the effects of intentional predators on the herding behavior of prey. For instance, it may be the case that the successful capture of a solitary prey requires different predation skills than those needed for prey in the herd. In such circumstances, the predator is typically "intentional" (Huggard 1993a) in that it does not alter its current aim if it encounters a prey it is not searching for. The analysis of this section also applies to predator-prey systems with partial separation of regions where prey congregate into the herd and where they are solitary. When there are several regions where the prey form herds (e.g., tree stands on adjacent mountains separated by grasslands), an intentional predator ignores solitary prey encountered when moving between these regions.

Alternatively, when prey exist in two separate habitats and their herding behavior depends solely on which habitat they are in, a predator is intentional by choosing the habitat in which to search for prey. In fact, herding behavior based on habitat choice is quite common among prey species. As examples, prey species for lions in the African savanna live in bigger herds in the open habitat (Hayward and Kerley 2005) and lions prefer to hunt prey in small herds (Scheel 1993). Similarly, elk group size is typically greater in a grassland habitat than in conifer or pine stands and the wolves' predation success for elk depends on the landscape attributes of

the different habitats (Huggard 1993a, b, Hebblewhite and Pletscher 2002, Kunkel et al. 2004, Hebblewhite et al. 2005). Furthermore, avoidance of wolf predators is the most important factor in determining bison habitat selection and their herd size (Fortin and Fortin 2009, Fortin et al. 2009).

In all these circumstances, predator success depends on the behavior of its prey. Since the fitness of both predator and prey depends on all of these choices, we have a two-species game based on conflicting interest (cf. Eshel et al. 2006). The goal of this section is to predict the outcome of this conflict by determining the equilibrium strategies of the game and studying their stability. Each such equilibrium describes the expected proportion of prey in the herd as well as the proportion of time the predator devotes to each type of prey.

Although the model developed below assumes there is a single predator, it can also be based on a population of predators (of fixed number), each of whom searches for only one type of prey. The proportion of predators that search for the herd then corresponds to the predator strategy. That is, although we construct our model as if there were a single predator, our approach can be rephrased in terms of a population of such predators without changing the results.

In our model, those prey that choose a smaller herd size (including when these prey are on their own) are labeled as solitary prey. All solitary prey have one level of predation risk and all prey in the herd have another. Their only relevant individual distinguishing characteristic is whether they are part of the herd or solitary (e.g., their choice of habitat). These are the pure strategies of an individual prey. We assume that the fitness difference between these two types of prey depends solely on their predation risk (i.e., on their survival probability with respect to predation). In particular, since these assumptions mean that habitat determines herd size, we avoid the important question in ecology of what is the optimal herd size (Gerard et al. 2002). This also avoids competition between prey of different types masking the effect of the predator's prey preference on the expected outcome.

Clearly, there is a trade-off between safety in numbers and the added food competition this entails. When predation pressure is high, prey density is far from their carrying capacity, which obviously weakens the effect of food competition. For instance, Hebblewhite et al. (2002) found that wolves have a big effect on the elk population (specifically, there was a 50–70% decline in elk population after wolf recolonization in Banff National Park, Alberta). Ungulate species often live primarily in areas rich in food and with high predation risk (Grignolio et al. 2007). Predation risk is also the main factor determining prey behavior in general models of habitat selection (Hugie and Dill 1994).

Furthermore, we assume that each prey who reaches reproductive age has the same number of offspring, independent of how many times this individual encoun-

tered and survived an attack by the predator. The predator also has two pure strategies; namely, to search for and attack a prey in the herd or a solitary prey. Its fitness is then the average number of prey caught (per unit time) less its cost of hunting.

Let $x > 0$ be the total number of prey (i.e., the density of the prey population, which we assume is fixed) and p be the proportion of prey in the herd (corresponding to the average strategy of the prey population). That is, there are px prey in the herd and $(1 - p)x$ solitary prey. Similarly, the predator's (mixed) strategy is given by the proportion s of its time spent searching for the herd and $1 - s$ searching for solitary prey.

Let f_H be the probability per unit time that the predator, searching for the herd, observes the herd and catches an individual prey in it. Similarly, f_S is the probability per unit time that the predator, searching for a solitary prey, observes one and catches it. These probabilities, f_H and f_S , are functions of the size of the herd (px) and the number of solitary prey ($(1 - p)x$) respectively. We assume that these probabilities are positive if there are prey of the targeted type (e.g., f_S is positive if there are solitary prey) and zero if not (since, for example, there is no probability that the predator will catch a solitary prey if there are none). At times, we also assume these are increasing functions. For example, the probability of observing some solitary prey increases as their number increases, since there is a higher chance the predator will meet such a prey. This, combined with a constant probability that the predator will successfully catch an observed solitary prey implies that f_S is an increasing function of $(1 - p)x$.

From the above assumptions, the fitness of a prey in the herd can be measured by its survival probability per unit time (a commonly used approach in predation risk models (e.g., Hebblewhite and Pletscher 2002)). This is the function

$$W_H(p, s, x) = 1 - s \frac{f_H(px)}{px} \tag{1}$$

since the probability this individual will be caught is the probability the predator catches a prey in the herd, $sf_H(px)$, divided by the herd size (i.e., each prey in the herd is equally likely to be caught). The factor $1/(px)$ in Eq. 1 can be interpreted as the dilution effect of Dehn (1990) whereby more prey in the herd is to their individual advantage since each is then less likely to be caught. Similarly, the individual fitness of a solitary prey is

$$W_S(p, s, x) = 1 - (1 - s) \frac{f_S([1 - p]x)}{(1 - p)x}. \tag{2}$$

We will denote

$$F_H(px) \equiv \frac{f_H(px)}{px} \tag{3a}$$

and

$$F_S([1 - p]x) \equiv \frac{f_S([1 - p]x)}{(1 - p)x} \tag{3b}$$

and assume that the values $F_H(0)$ and $F_S(0)$ exist and are positive (see Appendix: Section 1).

The predator's fitness depends on the probability per unit time of catching a prey (i.e., on $f_H(px)$ or $f_S([1 - p]x)$ as well as on the cost of hunting. Let C_H and C_S be the constant fitness costs of hunting for the herd and for solitary prey, respectively, per unit time (for instance, Kunkel et al. [2004] use the distance traveled per day as the cost of predation in the case of wolves in Montana). We denote the predator fitness when it searches only for prey in the herd (respectively, only for solitary prey) by V_H (respectively, V_S). If we define the energy unit as the expected predator income from an average prey, then predator fitness from predation is the same as the catching probability. Thus,

$$V_H = f_H(px) - C_H \tag{4a}$$

and

$$V_S = f_S([1 - p]x) - C_S. \tag{4b}$$

The above strategy spaces and fitness functions define a two-species evolutionary game (Brown and Vincent 1992, Hofbauer and Sigmund 1998) where fitness depends on the average strategies p and s of the prey population and of the predator. This predator-prey game can be viewed as a special case of two-species habitat selection models (Hugie and Dill 1994, Cressman et al. 2004) that focuses on the effect of adaptive predators on the herding behavior of prey. Its simplifying assumptions avoid several important issues for these general models such as the fitness effect of prey competition and the existence of prey refuges (Brown 1992, Brown et al. 2001, Cressman and Garay 2009). On the other hand, it clearly demonstrates that predator behavior must be taken into account in any evolutionary model that attempts to predict the formation of herds.

We are particularly interested in strategy pairs (p^*, s^*) that correspond to stable equilibria (see Appendix: Section 2, for the notion of asymptotic stability used in this article) of this evolutionary game at fixed density x . To determine stability, a mechanism is needed to model how the proportions of p and of s evolve due to the fitnesses of the pure strategies. If $W_H > W_S$, we expect that prey will move to the herd (i.e., p will increase). Similarly, if $V_H > V_S$, the predator should increase the amount of time spent looking for the herd. As a behavioral dynamics, we use the following to describe how prey and predator change their behavior in response to fitness differences:

$$\dot{p} = k[W_H(p, s, x) - W_S(p, s, x)] \tag{5a}$$

$$\dot{s} = \ell[V_H(p, s, x) - V_S(p, s, x)]. \tag{5b}$$

Here k and ℓ are positive and may depend on the state (p, s, x) (see Appendix: Section 1). In the dynamic

simulations (Figs. 1 and 2), Eq. 5 is the replicator equation from evolutionary game theory (Hofbauer and Sigmund 1998). Then $k = p(1 - p)$ and $\ell = \alpha s(1 - s)$ where $\alpha > 0$ is a parameter related to the time-scale between behavioral evolution of the predator and the prey population. In these figures, strategy pairs are represented as points in the unit square $\{(p, s) | 0 \leq p \leq 1 \text{ and } 0 \leq s \leq 1\}$.

Equilibria can either occur on the boundary of the unit square or in its interior. These are summarized in the following two cases (whose detailed analyses are given in Appendix: Section 2) when f_S and f_H are increasing functions.

Case A1: boundary equilibrium

There is a stable boundary equilibrium if and only if either $f_S(x) < C_S - C_H$ or $f_H(x) < C_H - C_S$. This is an evolutionarily stable strategy (ESS) and globally asymptotically stable under the behavioral dynamics (Eq. 5; Fig. 1A). For instance, if $f_S(x) < C_S - C_H$, then the probability the predator catches a solitary prey when all prey are solitary and the predator is searching for them is less than the cost of hunting for them. That is, hunting for solitary prey is more costly for predator fitness than the possible energy gain. Then $(p^*, s^*) = (0, 1)$ is the only stable equilibrium.

In both cases, the predator hunts for one type of prey and all the prey choose the other behavior. Thus, the prey effectively have a behavioral refuge where they are all safe from predation when their density is fixed at x . In particular, when different prey behavior occurs in separate habitats (or the predator is intentional), there is no ESS (or stable equilibrium) as described by Hamilton (1971) whereby all prey are in the herd and the predator searches only for the herd.

Case A2: interior equilibrium

When there is no stable boundary equilibrium, the model generates exactly one interior equilibrium (i.e., a (p^*, s^*) with $0 < p^* < 1$ and $0 < s^* < 1$). At this equilibrium, both prey strategies have the same fitness as do both predator strategies. That is, at (p^*, s^*)

$$W_H = W_S \tag{6a}$$

and

$$V_H = V_S. \tag{6b}$$

In terms of general predator-prey habitat selection models, this (p^*, s^*) is often called an ideal free distribution (IFD; van Baalen and Sabelis 1999), generalizing the single-species concept developed by Fretwell and Lucas (1969). As argued in Cressman et al. (2004; see also Krivan et al. 2008), it is more appropriate to consider the conditions in Eq. 6 as necessary but not sufficient for an IFD since they do not guarantee evolutionary stability of this equilibrium.

If hunting costs are the same (i.e., $C_H = C_S$), then at each interior equilibrium (p^*, s^*) , the predator spends

exactly the same proportion of its time searching for the herd as the proportion of prey that are in the herd (i.e., $s^* = p^*$). Intuitively, since the probability the predator is successful per unit time is the same at p^* whether searching for the herd or solitary prey, the prey should distribute themselves in the same proportions as the searching time of the predator to equalize their probability of survival under these two strategies. To state this in an alternative way, the best strategy of the predator is to follow the prey's (mixed) strategy when hunting costs are the same.

On the other hand, if hunting costs are not equal (i.e., $C_H \neq C_S$), then at (p^*, s^*) , the predator spends a higher proportion of its time searching for the prey with the smallest hunting cost than the proportion of this type of prey. For example, if $C_H < C_S$, then $s^* > p^*$ as in Fig. 1B. These results, that the predator follows the prey behavior adjusted by its foraging efficiencies, is a general property of many predator-prey foraging games (e.g., Huggie and Dill 1994, Brown and Kotler 2004).

The remaining question is whether the predator-prey system will evolve to this interior equilibrium (i.e., whether (p^*, s^*) is stable under the behavioral dynamics [Eq. 5]). The Appendix, Section 2, proves the game-theoretical result that (p^*, s^*) is stable if and only if p^* is an ESS for the prey population. From the perspective of the prey population with predator strategy fixed at s^* , p^* is an ESS if, when one solitary prey changes to become a member of the herd, the individual probability of dying in the herd is then greater than a solitary's probability of dying (and so there is an incentive for this particular solitary individual to stay on its own).

If f_H and f_S are convex (i.e., concave up) for prey densities in each habitat smaller than at the equilibrium, then (p^*, s^*) is stable (Fig. 1C). In biological terms, convexity results when predator success increases faster with higher prey density. For example, this occurs when a larger herd increases the danger to each individual prey (e.g., when more prey increases the rate that the predator's searching time is shortened).

If f_H and f_S are always concave (i.e., there is safety in higher numbers of prey), then (p^*, s^*) is unstable and the biological system spirals counterclockwise outward from (p^*, s^*) towards the boundary of the strategy space. Depending on the form of the functions k and ℓ , trajectories may approach a stable limit cycle or a heteroclinic orbit around the boundary of the unit square (as they do for the replicator equation of Fig. 1D). Only in the exceptional circumstance when f_H and f_S are linear functions do we find the neutrally stable periodic cycling (Fig. 1B) of predator and prey strategies as in Lett et al. (2004).

Now, consider the case where f_H and f_S are not always increasing functions. For instance, the predator's ability to observe the herd and catch an individual prey in it may decrease after the herd increases beyond a critical size due to an improved prey cooperative defense against

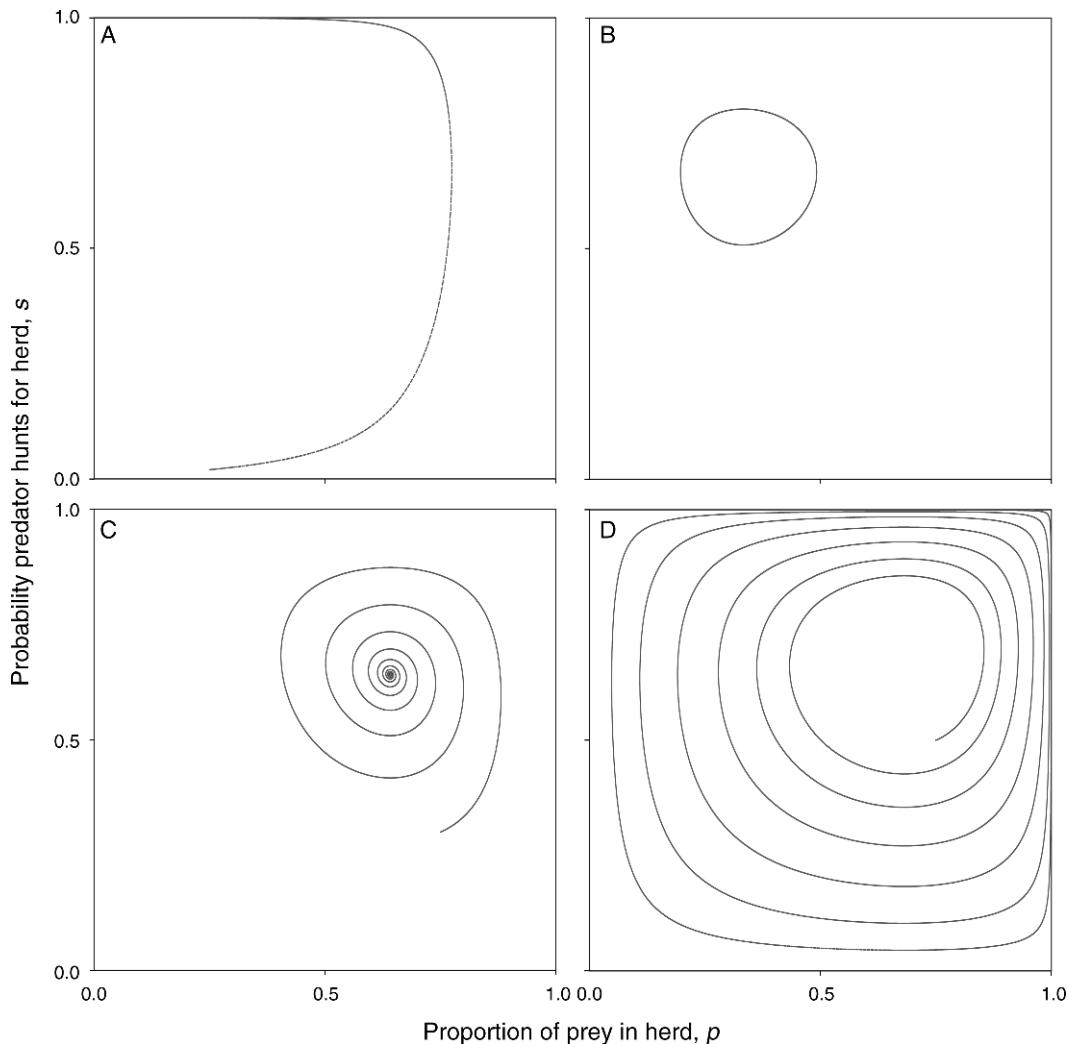


FIG. 1. Counterclockwise trajectories for the replicator equation (Eq. 5) with intentional predators (with $\alpha = 1$ and $x = 1$, where $\alpha > 0$ is a parameter related to the time-scale between behavioral evolution of the predator and the prey population and $x > 0$ is the total number of prey, i.e., the density of the prey population) and survival functions $f_H(u) = (u + 1)^a - 1$ and $f_S(u) = 2[(u + 1)^a - 1]$ where f_H is the probability per unit time that the predator, searching for the herd, observes the herd and catches an individual prey in it, f_S is the probability per unit time that the predator, searching for a solitary prey, observes one and catches it, u is the density of the prey in the herd or of solitary prey [i.e., $u = p$ (proportion of prey in the herd) in $f_H(u)$ and $u = 1 - p$ in $f_S(u)$] and a is a fixed parameter that determines the concavity of these two functions. These survival probabilities are both concave for $0 < a < 1$ and both convex for $a > 1$. With $a = 1$, $(p^*, s^*) = (0, 1)$ [where p is the proportion of prey in the herd, s is the proportion of the predator's time spent searching for the herd, and (p^*, s^*) is the strategy pair corresponding to equilibria] is globally asymptotically stable when (A) $C_H = 1$ and $C_S = 4$ and (B) there are periodic cycles around the equilibrium $(p^*, s^*) = (1/3, 2/3)$ when the constant fitness costs of hunting for the herd $C_H = 1$ and the constant fitness costs of hunting for solitary prey $C_S = 2$. With $C_H = C_S$, there is an interior equilibrium (p^*, s^*) with $p^* = s^*$ in panels C and D. It is globally (C) asymptotically stable with $p^* = 5 - \sqrt{19} \cong 0.64$ when $a = 2$ and (D) unstable with $p_1^* \cong 0.68$ when $a = 0.5$.

the predator. Then (p^*, s^*) is unstable if $V_H - V_S$ is a decreasing function of p at this point. On the other hand, there must be at least one interior equilibrium (p^*, s^*) where this fitness difference is increasing and this point is stable if and only if p^* is an ESS of the prey population.

OPPORTUNISTIC PREDATORS

In this section, we analyze individual behavior from a game-theoretic perspective when the predator's diet choice is flexible. For instance, although lions prefer

heavier prey weighing from 190 to 550 kg (Hayward and Kerley 2005) and also prefer prey in small herds (van Orsdol 1984, Funston et al. 2001), lions are opportunistic hunters and, without active searching, may capture prey that inadvertently wander close to them (Schaller 1972). In addition, Huggard (1993a) distinguished "random" kills from "intentional" kills by wolves. While hunting, wolves move relatively quickly and directly toward one of a small number of grassland locations where elk herds (the "intentional" prey of wolves) are

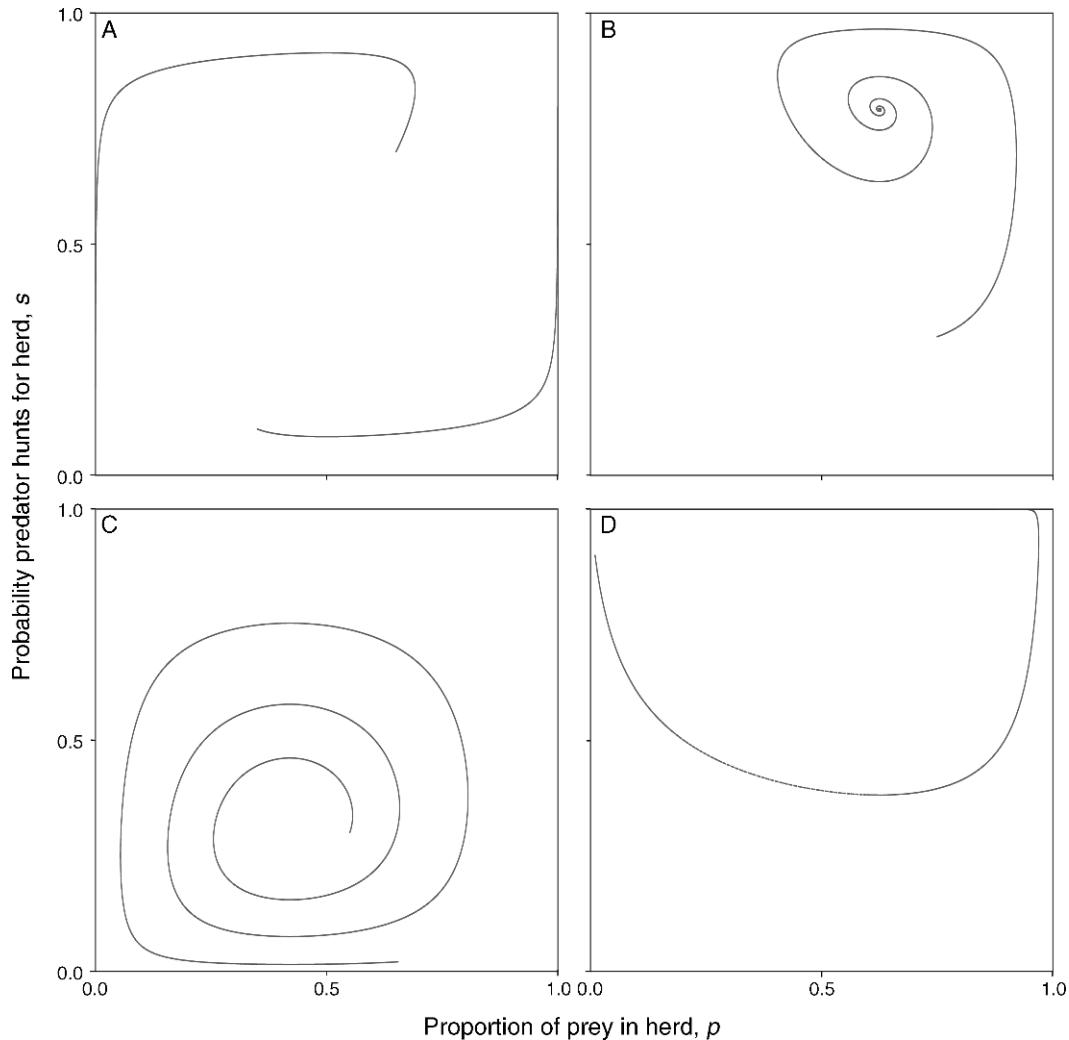


FIG. 2. Counterclockwise trajectories for the replicator equation with opportunistic predators (with $x = 1$ and $C_H = C_S$). In panel A [where $f_H(u) = (u + 1)^a - 1 = f_S(u)$, $a = 0.5$ and $r = 0.9$], two trajectories are shown, one converging to $(p^*, s^*) = (1, 1)$ and the other to $(p^*, s^*) = (0, 0)$, both of which are locally asymptotically stable. In the other three panels, $f_H(u) = (u + 1)^a - 1$ and $f_S(u) = (u + 2)^a - 2^a$. With $r = 0.4$, there is an interior equilibrium that is (B) globally asymptotically stable for $a = 2$ and (C) unstable for $a = 0.5$. (D) There is a globally asymptotically stable boundary equilibrium with $s^* = 1$ when $a = 2$ and $r = 0.7$. The parameter r measures the predator’s level of opportunism or its “partial preference” for prey.

predictably found. Deer (the “random” prey of wolves) are often captured after being flushed out by these wolves while traveling. To include the above mentioned random kills, we introduce the following mathematical model of this kind of “opportunity” when there is a single prey species.

An opportunistic predator is one that changes its strategy (i.e., its original aim) with a certain probability r if it encounters prey that it is not searching for. The parameter r measures the predator’s level of opportunism or its “partial preference” for prey (Garay and Mori 2010) that is often observed in experiments on diet composition (e.g., Rechten et al. 1983). Although our assumption that r is a fixed constant is clearly an oversimplification of this biological phenomenon, our

analysis of this case highlights differences between the effects of opportunistic and intentional predators.

When $r = 0$, the predator only makes intentional kills as in *Intentional predators*. At the other extreme, when $r = 1$, the predator pursues the first prey it sees regardless of its own strategy, and so it only makes random kills. In this latter case, predator fitness will be independent of its strategy (i.e., there is no game from the predator perspective).

In this section, we avoid these two extremes and assume that there is a balance between random and intentional kills (i.e., $0 < r < 1$). To concentrate on the changes in behavioral outcome due to the presence of opportunistic predators, we will only consider the case where there are equal costs of hunting solitary prey and

prey in the herd (i.e., $C_H = C_S = C$). In fact, we take these costs as zero since our analysis does not depend on C . When there are few prey in the herd, we assume that their probability of being killed is the same as if they were solitary (see Appendix: Section 1). (This assumption, as well as equal hunting costs, are reasonable from biological considerations when there is a single habitat and hunting costs are based on predator traveling time per day.) Finally, assume that the functions $f_H(px)$ and $f_S((1 - p)x)$ introduced in *Intentional Predators* are increasing functions of px and $(1 - p)x$, respectively, and that they are either both concave or both convex. These functions have a slightly different meaning here. For example, $f_H(px)$ is now the probability per unit time that the predator observes the herd and, if it decides to pursue the herd, catches an individual prey in it. Thus, the predator's fitness when its strategy is to search for the herd is

$$V_H = f_H(px) + rf_S([1 - p]x)$$

since it always pursues the herd when it is observed but only pursues an observed solitary prey with probability r . Similarly, the predator's fitness when searching for a solitary prey is

$$V_S = f_S([1 - p]x) + rf_H(px).$$

Furthermore, the survival probability of an individual prey who is in the herd or who is solitary is then given by

$$W_H(p, s, x) = 1 - [s + (1 - s)r] \frac{f_H(px)}{px}$$

and

$$W_S(p, s, x) = 1 - [(1 - s) + sr] \frac{f_S([1 - p]x)}{(1 - p)x}$$

respectively.

Our two-species evolutionary game is specified by these four fitness functions and the fixed opportunistic level r . The stable equilibria of this game are summarized in three cases: pure-strategy equilibrium pairs; equilibria in the interior; and non pure-strategy pairs on the boundary. The detailed analyses are in Appendix: Section 3.

Case B1: pure strategy equilibrium

Suppose that (p^*, s^*) is a stable equilibrium under the dynamics (Eq. 5) with all prey in the herd (i.e., $p^* = 1$). Then the predator searches only for the herd (i.e., $s^* = 1$). In fact, this is an ESS if and only if, when all prey are in the herd, the probability that an individual prey there is killed by a predator searching for the herd is less than this probability if it left the herd (i.e., if it became solitary). That is, if and only if

$$rF_S(0) > F_H(x) \tag{7}$$

where F_H and F_S are defined in Eq. 3. Intuitively, the predator ensures it is to the prey's disadvantage to

switch to solitary behavior by being opportunistic at a sufficiently high level r . With an opportunistic predator, this outcome matches Hamilton's (1971) result whereby the evolutionary outcome yields all prey in the herd and the predator searching only for the herd (Fig. 2A).

By the analogous argument, there is an ESS with all prey solitary and the predator searching only for solitaries if and only if

$$rF_H(0) > F_S(x). \tag{8}$$

Case B2: interior equilibrium

If an interior equilibrium (p^*, s^*) exists, it is unique and p^* is independent of the parameter r that measures the level of opportunistic behavior of the predator (i.e., p^* has the same value as in *Intentional predators*). Also

$$s^* = p^* + \frac{r}{1 - r}(2p^* - 1) \tag{9}$$

and so $s^* > p^*$ if and only if $p^* > 1/2$. Thus, at an interior equilibrium, the predator will always spend a higher proportion of its time searching for the type of prey that is most abundant than the proportion of this type of prey.

Furthermore, when an interior equilibrium (p^*, s^*) exists and f_H and f_S are both convex, then (p^*, s^*) is the only equilibrium (in particular, there are none on the boundary) and it is a locally asymptotically stable ESS (Fig. 2B). On the other hand, when f_H and f_S are both concave, then (p^*, s^*) is not an ESS and so unstable. Either the system consists of unstable outward spirals near this interior equilibrium (Fig. 2C) or (almost) all trajectories converge to one of the pure strategy equilibria found in Case B1. In particular, when an interior equilibrium exists, it is asymptotically stable if and only if the interior equilibrium for the intentional predator (with equal hunting costs) is asymptotically stable.

Case B3: boundary equilibrium

There is a stable boundary equilibrium that is not a pure strategy pair if and only if f_H and f_S are both convex and the level of predator opportunism r is sufficiently high so that s^* given in Eq. 9 does not satisfy $0 < s^* < 1$ (Fig. 2D). This equilibrium (\hat{p}, \hat{s}) is unique and globally asymptotically stable. Here, the predator searches exclusively for the type of prey that would be most abundant if the predator were intentional and the prey adopt a mixed strategy \hat{p} that makes this type of prey even more abundant.

CONCLUSION

Our models of prey herd formation, based on their survival probability under predation, clearly demonstrate that the evolutionary outcome depends to a large extent on the success of different predator behaviors. The classical theories on herd formation usually start with prey under attack by a predator. However, before

this situation occurs, the predator must spend time and energy to find its prey after choosing the type of prey to search for (i.e., either the herd or solitary prey). Whenever predation success depends on the gregarious behavior of prey, we have an evolutionary game in which the counteracting interests of the “players” (prey and predator) affect each other’s fitness. We analyze this game for intentional and for opportunistic predators, obtaining the following results.

First, the intentional predator will search exclusively for the type of prey with the smaller hunting cost when these costs are substantially different. Furthermore, if the predator searches for the herd in this case, all prey will choose to be solitary (or vice versa). In effect, being solitary corresponds to a prey refuge based on the cost of predation rather than on a location where predators cannot come.

On the other hand, there are only mixed equilibria (p^* , s^*) when hunting costs for both types of prey are more similar. In fact, if hunting costs are the same, the intentional predator spends exactly the same proportion s^* of its time searching for the herd as the proportion p^* of prey that are in the herd (i.e., $s^* = p^*$). That is, the predator follows the prey’s mixed strategy when hunting costs are the same. For small differences in hunting costs, the predator spends a higher proportion of its time at (p^* , s^*) searching for the prey with the smaller hunting cost than the proportion of this type of prey.

If the two types of prey are in separate habitats, our intentional prey model is an example of a predator–prey habitat selection game with prey fitness measured by survival. In contrast to the two-habitat model developed by Hugie and Dill (1994) where all equilibria are interior and evolutionarily stable, our interior equilibrium is stable (when predator success increases with higher prey density) if and only if p^* is a single-species ESS of the prey population with predator behavior given by s^* . These ESS conditions are related to the convexity of the predator fitness functions (in biological terms, convexity results when predator success increases faster with higher prey density).

Second, when the predator exhibits a high level r of opportunism, there are two possible stable equilibria corresponding to all prey of one type and the predator searching exclusively for this type. This occurs when the prey behavior is an ESS at the equilibrium and requires concave predator fitness functions. Thus, a stable outcome whereby all prey are in the herd and the predator searches only for the herd requires an opportunistic predator. Such equilibria (with all prey in a single herd or with no prey in a herd) are also found in the models of Hamilton (1971) and Eshel et al. (2006), although they did not fully analyze the equilibrium’s evolutionary stability.

On the other hand, for low levels of opportunistic behavior, there is no boundary equilibrium but an interior one does exist and it is stable if and only if there is a stable interior equilibrium of the model based on an

intentional predator. The example studied by Hebblewhite and Pletscher (2002; see also Hebblewhite et al. 2005) agrees with our theoretical results. The wolves are clearly opportunistic in their wolf–elk predator–prey system. Moreover, in the pine stands habitat, elk use mixed herding behavior and the wolf hunts for both types of prey (i.e., the equilibrium is interior). For intermediate levels of opportunism when predator fitness functions are convex, there is a globally stable equilibrium on the boundary where prey adopt a mixed strategy but the predator only searches for the type of prey that is most abundant.

Our theoretical analysis has several important practical implications. First, in order for all prey to form a herd under predation risk, there needs to be an opportunistic predator. An intentional predator that spends any time searching for the herd in this situation will only look for this herd (and so a mutant prey, adopting the solitary strategy by leaving the herd, will be free from predation risk and have higher fitness). This implication is testable and agrees with the observed herding behavior of prey for wolves (Huggard 1993a) and lions (Schaller 1972), which are both opportunistic. Second, the evolutionary stability of an equilibrium for our herd formation models does not require an ESS analysis of mutant predator behavior. Thus, predator behavior can be assumed fixed at its equilibrium value while the single-species ESS conditions for the prey are investigated, a result which is consistent with predator equilibrium behavior following the lead of the prey.

The results we obtain for the herding behavior of prey all rely on game-theoretic arguments based on individual fitness functions of prey and of the predator. In particular, existence of equilibria is then guaranteed for our models and their stability can be determined through an appropriate evolutionary analysis.

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LITERATURE CITED

- Brown, J. S. 1992. Patch use under predation risk: I. models and predictions. *Annales Zoologici Fennici* 29:301–309.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Brown, J. S., B. P. Kotler, and A. Bouskila. 2001. Ecology of fear: foraging games between predator and prey with pulsed resources. *Annales Zoologici Fennici* 38:71–87.
- Brown, J. S., and T. L. Vincent. 1992. Organization of predator–prey communities as an evolutionary game. *Evolution* 46:1269–1283.
- Cressman, R., and J. Garay. 2009. A predator–prey refuge system: evolutionary stability in ecological systems. *Theoretical Population Biology* 76:248–257.

- Cressman, R., V. Krivan, and J. Garay. 2004. Ideal free distributions, evolutionary games and population dynamics in multiple-species environments. *American Naturalist* 164:473–489.
- Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* 26:337–342.
- Eshel, I., E. Sansone, and A. Shaked. 2006. Gregarious behavior of evasive prey. *Journal of Mathematical Biology* 52:595–612.
- Fortin, D., and M.-E. Fortin. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. *Animal Behavior* 78:887–892.
- Fortin, D., M.-E. Fortin, H. L. Beyer, T. Duchesne, S. Courant, and K. Dancose. 2009. Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* 90:2480–2490.
- Fretwell, S. D., and J. H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Funston, P. J., M. G. L. Mills, and H. C. Biggs. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology* 253:419–431.
- Garay, J. 2009. Cooperation in defence against a predator. *Journal of Theoretical Biology* 257:45–51.
- Garay, J., and T. F. Mori. 2010. When is predator's opportunism remunerative. *Community Ecology* 11:160–170.
- Gerard, J. F., E. Bideau, M. L. Maublanc, P. Loisel, and C. Marchal. 2002. Herd size in large herbivores: encoded in the individual or emergent. *Biology Bulletin* 202:275–282.
- Grignolio, S., I. Rossi, B. Bassano, and M. Apollonio. 2007. Predation risk as a factor affecting sexual segregation in Alpine ibex. *Journal of Mammalogy* 88:1488–1497.
- Hamilton, W. D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Hass, C. C., and D. Valenzuela. 2002. Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behavioral Ecology and Sociobiology* 51:570–578.
- Hayward, M. A., and G. I. H. Kerley. 2005. Prey preference of the lions (*Panthera leo*). *Journal of Zoology* 267:309–322.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111:101–111.
- Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800–809.
- Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* 80:789–799.
- Hofbauer, J., and K. Sigmund. 1998. *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge, UK.
- Huggard, D. J. 1993a. Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology* 71:130–139.
- Huggard, D. J. 1993b. Prey selectivity of wolves in Banff National Park. II: Age, sex and condition of elk. *Canadian Journal of Zoology* 71:140–147.
- Hugie, D. M., and L. M. Dill. 1994. Fish and game: a game theoretical approach to habitat selection by predators and prey. *Journal of Fisheries Biology* 45:151–169.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford, UK.
- Krivan, V., R. Cressman, and C. Schneider. 2008. The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theoretical Population Biology* 73:403–425.
- Kunkel, K. E., D. H. Pletscher, D. K. Boyd, R. R. Ream, and M. W. Fairchild. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management* 68:167–178.
- Lett, L., P. Auger, and J. M. Gaillard. 2004. Continuous cycling of grouped vs. solitary strategy frequencies in a predator–prey model. *Theoretical Population Biology* 65:263–270.
- Rechten, C., M. Avery, and A. Stevens. 1983. Optimal prey selection: Why do Great Tits show partial preferences? *Animal Behavior* 31:576–584.
- Schaller, G. B. 1972. *The Serengeti lion*. University of Chicago Press, Chicago, Illinois, USA.
- Scheel, D. 1993. Profitability, encounter rate, and prey choice of African lions. *Behavioral Ecology* 4:90–97.
- Smith, M. F. L., and K. Warburton. 1992. Predator shoaling moderates the confusion effect in blue-green chromis, *Chromis viridis*. *Behavioral Ecology and Sociobiology* 30:103–107.
- Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behavior* 60:711–722.
- van Baalen, M., and M. W. Sabelis. 1999. Nonequilibrium population dynamics of “ideal and free” prey and predators. *American Naturalist* 154:69–88.
- van Orsdol, K. G. 1984. Foraging behavior and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 22:79–99.

APPENDIX

The existence and stability of equilibria (*Ecological Archives* E092-038-A1).

The Effects of Opportunistic and Intentional Predators on the Herding Behavior of Prey

Appendix: Existence and Stability of Equilibria

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Section 1. Evolutionary Dynamics

It is well-known from evolutionary game theory (Hofbauer and Sigmund 1998) that, at a stable equilibrium (p^*, s^*) of a behavioral dynamics of the form (see (5) in the main text)

$$\begin{aligned}\dot{p}_1 &= k(W_H(p, s, x) - W_S(p, s, x)) \\ \dot{s}_1 &= \ell(V_H(p, s, x) - V_S(p, s, x)),\end{aligned}\tag{A.1}$$

no individual can improve its fitness on its own by adopting a different strategy. A strategy pair that satisfies this condition is called a Nash equilibrium (NE) and so (p^*, s^*) is a NE of our two-species game. Although not all NE are stable (Hofbauer and Sigmund 1998), this game-theoretic reasoning narrows considerably the strategy pairs we need to examine as stable equilibria. In Sections 1 and 2, we first find the NE for our models of intentional and opportunistic predators respectively and then determine their stability.

First, there are some technical issues connected to (A.1) that need to be addressed. As mentioned in the main text, k and ℓ may depend on the state (p, s, x) . In fact, conditions on k and ℓ are needed to guarantee that all trajectories of (A.1) stay in the unit square. For instance, if $W_H > W_S$ for some (p, s, x) with $p = 1$, then k must be zero at this point.

Furthermore, W_H and W_S as given in terms of (3) in the main text are not defined when the denominator on the right-hand side is zero. Mathematically, we can extend these functions in this case. For example, the indeterminate form $F_H(px) = \frac{f_H(px)}{px}$ when $px = 0$ can be taken as the

derivative of f_H evaluated at zero by L'Hôpital's rule since $f_H(0) = 0$. In biological terms, $F_H(0)$ approximates the probability the first prey that begins to form a herd is killed by a predator searching for the herd. Our assumption in Section 3 is that $F_S(0) = F_H(0)$ (i.e. that this prey has the same probability of being killed as a single solitary prey).

The prey dynamics in (A.1) is often interpreted as a selection dynamics whereby individuals who use the more successful strategy have more offspring (Taylor and Jonker 1978). Since it is problematic for an individual prey to alter its strategy after it is killed by the predator, expressions such as "one solitary prey changes to be a member of the herd" are somewhat misleading in the main text, even though this terminology is quite common in evolutionary game theory. These expressions can be rephrased in terms of the effect on fitness if the proportion in the herd changes. The number of solitary prey then evolves through different reproductive success of the two types of prey.

Section 2. Existence of Equilibria and Their Stability for Intentional Predators

CASE A1: Boundary Equilibrium

Suppose that $f_S(x) > C_S - C_H$ and $f_H(x) > C_H - C_S$. We claim that there is then no equilibrium (p^*, s^*) on the boundary. For instance, if all prey are solitary at (p^*, s^*) (i.e. $p^* = 0$), then

$$\begin{aligned} V_S &= f_S((1 - p^*)x) - C_S = f_S(x) - C_S \\ &> -C_H = f_H(0) - C_H = f_H(p^*x) - C_H \\ &= V_H. \end{aligned}$$

That is, at (p^*, s^*) , the predator has an incentive to hunt only for solitary prey and so $(p^*, s^*) = (0, 0)$ is the only possible NE with $p^* = 0$. However, with $s^* = 0$, all prey have an incentive to be in the herd since $W_H = 1 > W_S$ for all $0 \leq p \leq 1$. Thus, $(p^*, s^*) = (0, 0)$ is not a NE and so there is none on the edge $p = 0$. Similar arguments show that there is none on any of the other three edges of the unit square $\{(p, s) \mid 0 \leq p \leq 1 \text{ and } 0 \leq s \leq 1\}$ either.

Now suppose that the probability the predator catches a solitary prey when all prey are solitary and the predator is searching for them is less

than the extra cost of hunting for them (i.e. suppose $f_S(x) < C_S - C_H$). Then the predator is always better off searching for the herd no matter how few prey exhibit this behavior (i.e. $V_H > V_S$ for all $0 \leq p \leq 1$). Thus, any NE must satisfy $s^* = 1$. In this case, $W_S = 1 > W_H$ for all $0 \leq p \leq 1$ and so all prey will choose to be solitary (i.e. $p^* = 0$). In game-theoretic terms, $(p^*, s^*) = (0, 1)$ is then called a strict NE since each individual is strictly worse off if it unilaterally adopts a different strategy than it is currently using. It is well-known (Hofbauer and Sigmund 1998) that a strict NE is an ESS. For our model, there can be no other equilibrium besides $(p^*, s^*) = (0, 1)$ since, at any other (p, q) , either the individual prey or the predator can increase its payoff by adopting a different strategy. From Hofbauer and Sigmund (1998), a strict NE is automatically locally asymptotically stable under the evolutionary dynamics (A.1). That is, all trajectories that are initially close to (p^*, s^*) stay close and eventually evolve to this equilibrium. Moreover, $(p^*, s^*) = (0, 1)$ is globally asymptotically stable for (A.1) (i.e. in addition to local stability, all interior trajectories evolve to (p^*, s^*)) since $\dot{s} > 0$ for $0 < s < 1$ and, once s is close to 1, $\dot{p} < 0$ for all $0 < p < 1$.

In the borderline case where $f_S(x) = C_S - C_H$, $V_H > V_S$ for all $0 < p \leq 1$ and so $s^* = 1$ if p^* is positive. From the above argument, if $s^* = 1$, then $p^* = 0$. Thus, if (p^*, s^*) is a NE, $p^* = 0$. On the other hand, $\dot{s} = 0$ for $0 \leq s \leq 1$ when $p = 0$ since $V_H = V_S$. That is, every $(0, s)$ with $0 \leq s \leq 1$ is an equilibrium of (A.1) and so none is an ESS or asymptotically stable.

By an analogous argument, if $f_H(x) < C_H - C_S$, the only ESS has all prey in the herd and the predator only hunts for solitary prey (i.e. $(p^*, s^*) = (1, 0)$). In summary, there is a unique boundary ESS if and only if either $f_S(x) < C_S - C_H$ or $f_H(x) < C_H - C_S$. Furthermore, this ESS is globally asymptotically stable for (A.1)

CASE A2: Interior Equilibrium

From Case A1, interior equilibria (i.e. a (p^*, s^*) with $0 < p^* < 1$ and $0 < s^* < 1$) can only exist if $f_S(x) > C_S - C_H$ and $f_H(x) > C_H - C_S$. To be such an equilibrium, it must be the case that both pure strategies of the prey species have the same fitness there as well as both pure strategies of the predator. That is,

$$W_H = W_S \quad \text{and} \quad V_H = V_S. \tag{A.2}$$

To see this, suppose that $W_H > W_S$. Then individual prey in the herd will have higher fitness than individual solitary prey and so these solitary prey will have an incentive to switch strategy and join the herd (contradicting the NE property). That is, from general game-theoretic reasoning, an interior NE must satisfy (A.2).

From $V_H = V_S$ at the equilibrium, p^* is a solution to $g(p) = 0$ where

$$g(p) \equiv f_H(px) - C_H - (f_S((1-p)x) - C_S) \quad (\text{A.3})$$

(i.e., $g = V_H - V_S$). From our assumptions that $f_S(x) > C_S - C_H$ and $f_H(x) > C_H - C_S$, $g(0) < 0$ and $g(1) > 0$. Thus, there is at least one interior p^* with $g(p^*) = 0$. In fact, since $f_H - f_S$ are increasing functions of px and $(1-p)x$ respectively, g is an increasing function of p . Thus p^* is unique. With p fixed at p^* ,

$$\begin{aligned} W_H - W_S &= 1 - sF_H(p^*x) - (1 - (1-s)F_S((1-p^*)x)) \\ &= (1-s)F_S((1-p^*)x) - sF_H(p^*x) \end{aligned}$$

is a decreasing function of s that is positive when $s = 0$ and negative when $s = 1$. Thus, there is a unique $0 < s^* < 1$ for which (p^*, s^*) is an interior equilibrium.

Moreover, if $C_H < C_S$, then $f_H(p^*x) = V_H + C_H = V_S + C_H < V_S + C_S = f_S((1-p^*)x)$ and so, when $s = p^*$,

$$\begin{aligned} W_H &= 1 - p^* \frac{f_H(p^*x)}{p^*x} = 1 - \frac{f_H(p^*x)}{x} \\ &> 1 - \frac{f_S((1-p^*)x)}{x} = W_S. \end{aligned}$$

Since $W_H - W_S$ is a decreasing function of s , there is a unique $p^* < s^* < 1$ where $W_H = W_S$. Similarly, if $C_H > C_S$, then $0 < s^* < p^*$. Finally, if hunting costs are the same (i.e. $C_H = C_S$), then $p^* = s^*$.

The following method to examine stability of an interior equilibrium (p^*, s^*) applies to all our dynamical systems of the form (A.1) where k and ℓ are positive for $0 < p < 1$ and $0 < s < 1$. The asymptotic stability of (p^*, s^*) is determined by the Jacobian matrix J of (A.1). For our fitness functions,

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & 0 \end{bmatrix} \quad (\text{A.4})$$

where $J_{11} = -k^* s^* \frac{\partial(F_H(px))}{\partial p} + k^* (1 - s^*) \frac{\partial(F_S((1-p)x))}{\partial p}$,
 $J_{12} = -k^* F_H(px) - k^* F_S((1-p)x)$, and
 $J_{21} = \ell^* \left(\frac{\partial(f_H(px) - C_H)}{\partial p} - \frac{\partial(f_S((1-p)x) - C_S)}{\partial p} \right)$.

These expressions are evaluated at (p^*, s^*) . Also, k^* and ℓ^* are the positive values of k and ℓ respectively at (p^*, s^*) . J_{12} is negative since F_H and F_S are positive functions and J_{21} is positive since f_H and f_S are increasing functions of the herd size and the number of solitary prey respectively. Thus, (p^*, s^*) is stable if $J_{11} < 0$ and unstable if $J_{11} > 0$.

We give two interpretations (one biological and the other more mathematical) of this (in)stability condition. From the biological point of view, notice that

$$\begin{aligned} J_{11} &= -k^* \frac{\partial}{\partial p} \left(\frac{s^* f_H(px)}{px} - \frac{(1-s^*) f_S((1-p)x)}{(1-p)x} \right) \\ &= -k^* \left[s^* \frac{\partial}{\partial p} \left(\frac{f_H(px)}{px} \right) - (1-s^*) \frac{\partial}{\partial p} \left(\frac{f_S((1-p)x)}{(1-p)x} \right) \right] \end{aligned} \quad (\text{A.5})$$

is the derivative of the difference in probabilities of an individual prey dying in the herd or as a solitary. For stability, we need $J_{11} < 0$. This means that, when one solitary prey changes to become a member of the herd, then the individual probability of dying in the herd is now greater than a solitary's probability of dying. The incentive for this particular solitary individual to stay on its own means that p^* is an ESS for the prey population when the predator strategy is fixed at s^* . That is, (p^*, s^*) is stable for (A.1) if and only if p^* is an ESS for the prey population.

In general, one must be careful asserting this (single-species) ESS is dynamically stable in a two-species system (Cressman and Garay 2003a; 2003b). However, in this special case on our herd formation game, the single-species ESS condition is equivalent to asymptotic stability for an interior equilibrium. It is interesting to note that the analogous derivative of the difference of success of the predator when a single solitary prey moves to the herd (i.e. $J_{21} = \frac{\partial(f_H(px) - C_H)}{\partial p} - \frac{\partial(f_S((1-p)x) - C_S)}{\partial p}$) is automatically positive.

For the second interpretation, we can rewrite J_{11} as

$$\begin{aligned} & \frac{-k^*s^*}{p^*} \left(f'_H(p^*x) - \frac{f_H(p^*x)}{p^*x} \right) + \frac{k^*(1-s^*)}{(1-p^*)} \left(-f'_S((1-p^*)x) + \frac{f_S((1-p^*)x)}{(1-p^*)x} \right) \\ & = -k^* \left(\frac{s^*}{p^*} \left(f'_H(p^*x) - \frac{f_H(p^*x)}{p^*x} \right) + \frac{(1-s^*)}{(1-p^*)} \left(f'_S((1-p^*)x) - \frac{f_S((1-p^*)x)}{(1-p^*)x} \right) \right) \end{aligned} \quad (\text{A.6})$$

where f'_H is the derivative of f_H . In general, if f is a function satisfying $f(0) = 0$, then $\frac{f(z_0)}{z_0}$ is the slope of the secant from $z = 0$ to $z = z_0$ whereas $f'(z_0)$ is the approximate change in f if z is increased by 1 from z_0 (i.e. the slope of the tangent to the function at z_0). From (1), an elementary mathematical condition to ensure $J_{11} < 0$ is to require f_H and f_S to be always convex (i.e. concave up) since the slope of the secant is then less than that of the tangent. This global property of the predator's catching probabilities also has consequences of biological significance. Specifically, the convexity of f_H and f_S implies that (p^*, s^*) is globally asymptotically stable when the positive functions k and ℓ in (A.1) depend only on own species' strategy (e.g. k depends only on p) as is the case for the replicator equation used in Figure 1 of the main text.

To see this, when the functions k and ℓ in (A.1) depend only on own species' strategy, the dynamics (A.1) has the form $\dot{p}_1 = k(p) (-sF_H(px) - (1-s)F_S((1-p)x))$, $\dot{s} = \ell(s) (f_H(px) - f_S((1-p)x))$. The corresponding vector field multiplied by the function $h(p, s) \equiv \frac{1}{k(p)\ell(s)}$ ($h(p, s)$ is called a Dulac function (Hofbauer and Sigmund 1998) for the system (A.1)) is then

$$\left(\frac{1}{\ell(s)} (-sF_H(px) - (1-s)F_S((1-p)x)), \frac{1}{k(p)} (f_H(px) - f_S((1-p)x)) \right).$$

The divergence of this vector field is

$$\begin{aligned} \text{div} & \equiv \frac{\partial}{\partial p} \left(\frac{1}{\ell(s)} (-sF_H(px) - (1-s)F_S((1-p)x)) \right) \\ & \quad + \frac{\partial}{\partial s} \left(\frac{1}{k(p)} (f_H(px) - f_S((1-p)x)) \right) \\ & = \frac{-s}{\ell(s)} \frac{\partial}{\partial p} (F_H(px)) + \frac{1-s}{\ell(s)} \frac{\partial}{\partial p} (F_S((1-p)x)). \end{aligned}$$

If f_H and f_S are both convex (respectively, both concave), the divergence is positive (respectively, negative) for all (p, s) inside the unit square. In either case, the Bendixson-Dulac test (Hofbauer and Sigmund, 1998) implies no periodic orbits exist inside the unit square. Furthermore, no interior trajectory converges to a point on the boundary since the flow is always counterclockwise there. Thus, in the convex case, the unique interior equilibrium (p^*, s^*) is globally asymptotically stable and, in the concave case, trajectories approach a heteroclinic orbit around the boundary.

Remark. From the biological view point, the catch probability f is called the predator functional response $f(x)$ (e.g. f_H is the functional response of the intentional predator who searches for the herd) and may take many forms. For instance, Holling type II (e.g. the concave function $f(x) \equiv \frac{ax}{b+x}$) and type III (e.g. the sigmoidal function $f(x) \equiv \frac{ax^2}{b+x^2}$) where a, b are positive parameters are common choices (Abrams and Ginzburg, 2000). If f is a Holling III function with prey carrying capacity without predation less than the inflection point of this sigmoidal function, then f will be always convex in practical terms for any realistic prey density x . We expect predator functional response to increase fastest as prey density increases if the overall prey x density is small. In particular, if the density of both types of prey at the equilibrium is much smaller than the carrying capacity, we expect f_H and f_S will be convex.

Now, suppose that f_H and f_S are not always increasing functions. In such cases, the function $g(p)$ in (A.3) may be increasing or decreasing. There may now be several solutions to $g(p) = 0$ for $0 < p < 1$, each of which will correspond to an interior equilibrium (p^*, s^*) of (A.1). If $g(p)$ is a decreasing function of p at p^* , then $J_{21} < 0$ and so (p^*, s^*) is unstable since the determinant of the Jacobian matrix J in (A.4) is now negative. On the other hand, there is at least one interior equilibrium (p^*, s^*) where g is increasing and this point is stable if and only if $J_{11} < 0$. That is, this equilibrium is stable if and only if p^* is a stable ESS of the prey population with predator strategy fixed at s^* .

Section 3. Existence of Equilibria and Their Stability for Opportunistic Predators

CASE B1: Pure Strategy Equilibrium

If (p^*, s^*) is a NE with all prey in the herd (i.e. $p^* = 1$), then the opportunistic predator does better to search for the herd than for a solitary prey (i.e. $V_H = f_H(x)$ is greater than $V_S = r f_H(x)$). Thus, the predator must search only for the herd at (p^*, s^*) (i.e. $s^* = 1$). Now, at this equilibrium, the prey will have no incentive to switch to solitary behavior if and only if $W_H > W_S$. Since $s^* = 1$, $W_H = 1 - F_H(x)$ and $W_S = 1 - rF_S(0)$. Thus, $(p^*, s^*) = (1, 1)$ is an ESS (in fact, a strict NE) if and only if

$$rF_S(0) > F_H(x). \quad (\text{A.7})$$

Here we ignore the borderline possibility that (A.7) is an equality (i.e. that $(1, 1)$ may be a Nash equilibrium that is not strict).

In summary, $(1, 1)$ is an ESS and asymptotically stable under the dynamics (A.1) if and only if inequality (A.7) holds. By the analogous argument, $(0, 0)$ is an ESS and asymptotically stable under the dynamics (A.1) if and only if the following inequality holds.

$$rF_H(0) > F_S(x) \quad (\text{A.8})$$

If neither inequality holds, then there are no pure strategy NE.

Both inequalities (A.7) and (A.8) may hold at the same time. There is then bistability as in Figure 2 (Panel A) of the main text with two locally asymptotically stable equilibria; namely, $(p^*, s^*) = (1, 1)$ and $(p^*, s^*) = (0, 0)$. That is, depending on initial conditions, the biological system either evolves to all prey being solitary or all prey in the herd (and the predator searching exclusively for this type of prey). (This situation is discussed further at the end of the following Case B2. We will see there that f_H and f_S must both be concave.) Such bistable outcomes were also found in the predator-prey model of Lett et al. (2004) that included multiple predators who could either search as solitaries or in a group.

If f_H is convex, $rF_S(0) < F_S(0) = F_H(0) < F_H(x)$ and so $(p^*, s^*) = (1, 1)$ cannot be an ESS. Similarly, $(p^*, s^*) = (0, 0)$ is not an ESS if f_S is convex. That is, if f_H and f_S are both convex, there can be no pure strategy equilibrium.

CASE B2: Interior Equilibrium

From the same argument leading to (A.2), $V_H = V_S$ at an interior equilibrium (p^*, s^*) . That is,

$$f_H(p^*x) + rf_S((1-p^*)x) = f_S((1-p^*)x) + rf_H(p^*x).$$

This condition simplifies to $(1-r)f_H(p^*x) = (1-r)f_S((1-p^*)x)$ which, since $0 < r < 1$, is the same necessary condition that must hold at an interior equilibrium for intentional predators when hunting costs are the same (i.e. $C_H = C_S$). Thus, p^* is independent of the parameter r . We also require that $W_H = W_S$. That is,

$$1 - [s^* + (1-s^*)r] \frac{f_H(p^*x)}{p^*x} = 1 - [(1-s^*) + s^*r] \frac{f_S((1-p^*)x)}{(1-p^*)x}$$

or $\frac{s^* + (1-s^*)r}{p^*x} = \frac{(1-s^*) + s^*r}{(1-p^*)x}$. Solving for s^* in terms of p^* , we have (see equation (9) in the main text).

$$s^* = p^* + \frac{r}{1-r} (2p^* - 1). \quad (\text{A.9})$$

Suppose that an interior equilibrium (p^*, s^*) exists. The 2×2 Jacobian matrix J of (A.1) now has entries

$$\begin{aligned} J_{11} &= -k^*(s^* + (1-s^*)r) \frac{\partial F_H(p^*x)}{\partial p} + k^*((1-s^*) + s^*r) \frac{\partial F_S((1-p^*)x)}{\partial p} \\ J_{12} &= -(1-r)k^*(F_H(p^*x) + F_S((1-p^*)x)) \\ J_{21} &= \ell^*(1-r) \left(\frac{\partial f_H(p^*x)}{\partial p} - \frac{\partial f_S((1-p^*)x)}{\partial p} \right) \\ J_{22} &= 0. \end{aligned}$$

Since f_H and f_S are increasing functions, $J_{21} > 0$ as in Section 2.

If f_H and f_S are both convex, then F_H and F_S are both increasing positive functions and so $J_{11} < 0$ and $J_{12} < 0$. Thus, J has negative trace and positive determinant, implying (p^*, s^*) is locally asymptotically stable. In addition, if k and ℓ in (A.1) only depend on p_1 and s_1 respectively, the Bendixson-Dulac method used in Section 2 applies here as well to assert that (p^*, s^*) is globally asymptotically stable. This result also shows that there can be no boundary equilibrium for any choice of positive functions k and ℓ in (A.1).

If f_H and f_S are both concave, then $J_{11} > 0$ and so (p^*, s^*) is unstable. Moreover, there can be no equilibrium on an edge that is not a pure strategy since concavity of f_H and f_S implies that W_H is decreasing and W_S is increasing in p_1 . Thus, if $rF_S(0) < F_H(x)$ and $rF_H(0) < F_S(x)$, then $W_H < W_S$ on the edge $s = 1$ and $W_H > W_S$ on the edge $s = 0$. That is, there is no boundary equilibrium and so, by the Bendixson-Dulac method, if k and ℓ in (A.1) only depend on p_1 and s_1 respectively, the system consists of unstable spirals around (p^*, s^*) that approach the boundary of the unit square. However, if $rF_S(0) > F_H(x)$ and $rF_H(0) > F_S(x)$, then the system is bistable with stable equilibria at $(p^*, s^*) = (1, 1)$ and $(p^*, s^*) = (0, 0)$.

CASE B3: Boundary Equilibrium

First recall that, by the argument at the beginning of Case B1, any boundary equilibrium (\hat{p}^*, \hat{s}^*) must have $\hat{s}^* = 0$ or $\hat{s}^* = 1$.

Now suppose that $p^* > \frac{1}{2}$ and that there is a boundary equilibrium (\hat{p}^*, \hat{s}^*) on an edge of the unit square that is not at a vertex. (Analogous results emerge in the symmetric case $p^* < \frac{1}{2}$.) By the arguments above, f_H and f_S are then both convex, there is no interior equilibrium, $rF_S(0) < F_H(x)$ and $rF_H(0) < F_S(x)$. From (A.9), $s^* > 1$. With $s = 1$ and $p = p^*$,

$$\begin{aligned} W_H &= 1 - F_H(p^*x) > 1 - [s^* + (1 - s^*)r] F_H(p^*x) \\ &= 1 - [1 - s^* + s^*r] F_S((1 - p^*)x) \\ &> 1 - rF_S((1 - p^*)x) = W_S. \end{aligned}$$

Also, at $p = 1$, $W_H = 1 - F_H(x) < 1 - rF_S(0) = W_S$ and so, for some $p^* < p < 1$, $W_H = W_S$. Moreover, $V_H > V_S$ for $p > p^*$, and so there is an equilibrium (\hat{p}^*, \hat{s}^*) with $p^* < \hat{p}^* < 1$ and $\hat{s}^* = 1$. A similar calculation with $s = 0$ shows that there is no equilibrium on this edge since $W_H > W_S$ for $0 \leq p \leq \hat{p}^*$. Global asymptotic stability of (\hat{p}^*, \hat{s}^*) follows from the vector field of the two-dimensional phase diagram.

References

- [1] Abrams, P.A., and L. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *TREE* 15: 337-341.
- [2] Cressman, R., and G. Garay. 2003a. Evolutionary stability in Lotka-Volterra systems. *J. Theor. Biol.* 222: 233-245.
- [3] Cressman, R., and G. Garay. 2003b. Stability in N-species coevolutionary systems. *Theor. Pop. Biol.* 64: 519-533.
- [4] Hofbauer, J., and K. Sigmund. 1998. *Evolutionary Games and Population Dynamics*. Cambridge Univ. Press, Cambridge.
- [5] Lett, L., P. Auger, and J.M. Gaillard. 2004. Continuous cycling of grouped vs. solitary strategy frequencies in a predator-prey model. *Theor. Pop. Biol.* 65: 263-270.
- [6] Taylor, P.D., and L. Jonker. 1978. Evolutionarily stable strategies and game dynamics. *Math. Biosci.* 40: 145-156.