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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 indeterminant 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 $\{(p, s) \mid 0 \leq p \leq 1$ 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

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

(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 deceasing 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,

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & 0 \end{bmatrix} \tag{A.4}$$

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

$$\begin{aligned} J_{11} &= -k^* \frac{\partial}{\partial p} \left(\frac{s^* f_H(px)}{px} - \frac{(1-s^*) f_S((1-p)x)}{(1-p)x} \right) \\ &= -k^* \left[s^* \frac{\partial}{\partial p} \left(\frac{f_H(px)}{px} \right) - (1-s^*) \frac{\partial}{\partial p_1} \left(\frac{f_S((1-p)x)}{(1-p)x} \right) \right] \end{aligned} \tag{A.5}$$

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

$$\frac{-k^*s^*}{p^*}\left(f_H'(p^*x)-\frac{f_H(p^*x)}{p^*x}\right)+\frac{k^*(1-s^*)}{(1-p^*)}\left(-f_S'((1-p^*)x)+\frac{f_S((1-p^*)x)}{(1-p^*)x}\right) \tag{A.6}$$

$$= -k^*\left(\frac{s^*}{p^*}\left(f_H'(p^*x)-\frac{f_H(p^*x)}{p^*x}\right)+\frac{(1-s^*)}{(1-p^*)}\left(f_S'((1-p^*)x)-\frac{f_S((1-p^*)x)}{(1-p^*)x}\right)\right)$$

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
$\dot{p}_1=k(p)\left(-sF_H\left(px\right)-(1-s)F_S\left((1-p)x\right)\right)$,
$\dot{s}=\ell(s)\left(f_H\left(px\right)-f_S\left((1-p)x\right)\right)$. 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

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

The divergence of this vector field is

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

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 $J_{11} < 0$. 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 $V_S = rf_H(x)$). 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

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

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.

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

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).

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

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

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

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 $(\widehat{p}^*, \widehat{s}^*)$ must have $\widehat{s}^* = 0$ or $\widehat{s}^* = 1$.

Now suppose that $p^* > \frac{1}{2}$ and that there is a boundary equilibrium $(\widehat{p}^*, \widehat{s}^*)$ 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 $(\widehat{p}^*, \widehat{s}^*)$ with $p^* < \widehat{p}^* < 1$ and $\widehat{s}^* = 1$. A similar calculation with $s = 0$ shows that there is no equilibrium on this edge since $W_H > W_S$ for $0 \leq p \leq \widehat{p}^*$. Global asymptotic stability of $(\widehat{p}^*, \widehat{s}^*)$ follows from the vector field of the two-dimensional phase diagram.

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