Beyond replicator dynamics: From frequency to density dependent models of evolutionary games

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A B S T R A C T

Game theoretic models of evolution such as the Hawk–Dove game assume that individuals gain fitness (which is a proxy of the per capita population growth rate) in pair-wise contests only. These models assume that the equilibrium distribution of phenotypes involved (e.g., Hawks and Doves) in the population is given by the Hardy–Weinberg law, which is based on instantaneous, random pair formation. On the other hand, models of population dynamics do not consider pairs, newborns are produced by singles, and interactions between phenotypes or species are described by the mass action principle. This article links game theoretic and population approaches. It shows that combining distribution dynamics with population dynamics can lead to stable coexistence of Hawk and Dove population numbers in models that do not assume *a priori* that fitness is negative density dependent. Our analysis shows clearly that the interior Nash equilibrium of the Hawk and Dove model depends both on population size and on interaction times between different phenotypes in the population. This raises the question of the applicability of classic evolutionary game theory that requires all interactions take the same amount of time and that all single individuals have the same payoff per unit of time, to real populations. Furthermore, by separating individual fitness into birth and death effects on singles and pairs, it is shown that stable coexistence in these models depends on the time-scale of the distribution dynamics relative to the population dynamics. When explicit density-dependent fitness is included through competition over a limited resource, the combined dynamics of the Hawk–Dove model often lead to Dove extinction no matter how costly fighting is for Hawk pairs.

1. Introduction

Game theoretic models (e.g., the Hawk–Dove game; Maynard Smith and Price, 1973) assume that all individuals instantaneously and randomly pair, and each interaction has the same duration. These assumptions lead to the distribution of pairs that is given by the Hardy–Weinberg (HW) principle (see, for example, Eq. (2) below). Křivan and Cressman (2017) (see also Zhang et al., 2016) considered a more general situation where interaction times between different strategies can take different amounts of time. They assumed that all individuals pair immediately so there were no singles.

In this article, we do not assume instantaneous pairing, but consider random pair formation among singles based on the mass action principle instead. Thus, the population consists both of single individuals and paired individuals and we study distributional dynamics of pairs and singles assuming that the overall population numbers of each strategy are fixed. Together with distributional dynamics we also consider population dynamics that model how the numbers of each strategy evolve in two-strategy games.

In Section 2, we start with the replicator equation (Taylor and Jonker, 1978) that has often been used in the context of evolutionary modeling. Replicator dynamics assume that a strategy's growth rate is given by its average payoff (fitness). The standard approach also assumes that individuals meet at random (which implicitly means that all interaction times must be the same) and that payoff is density independent since it is given by this pairwise interaction. The replicator equation for two-strategy games then predicts that the frequencies of strategies in the population will converge to an evolutionarily stable strategy (ESS) of the game and that the

overall population will grow (or decay) exponentially thereafter (Cressman, 2003; Hofbauer and Sigmund, 1998). These two properties are captured by saying that replicator dynamics are frequency dependent but density independent. Section 2 generalizes the standard replicator equation to the case where interaction times depend on strategies and singles get some (density independent) fitnesses too. We show that the replicator equation can now lead to stable equilibria at finite, positive population size. We document evolutionary outcomes where both strategies coexist at the equilibrium using generalizations of the Hawk–Dove model and distributional dynamics that evolve on a faster time scale compared to the replicator equation. In other words, it is no longer necessary to assume *a priori* density dependent fitnesses to obtain coexistence.

Section 3 considers the effect on the stable evolutionary outcome when distributional and population dynamics operate on a commensurable time scale. To do so, the combined dynamics must model how payoffs translate into changing numbers of singles and pairs. Specifically, we assume that payoffs to singles only influence the number of singles whereas payoffs to pairwise interactions are interpreted in terms of birth and death rates of the individuals in the pair and any newborns increase the number of singles. It is shown that non-zero death rates when in pairs alter the stable evolutionary outcome in the combined dynamics. In fact, for our generalized Hawk–Dove game, we find that the stable coexistence equilibrium when distributional dynamics are fast can disappear altogether when time scales are similar and, in such cases the Doves go extinct.

Combining distributional and evolutionary dynamics suggests a natural way to extend the Hawk–Dove game to a model of competition over a limited resource. Section 4 develops such a model where the resource is a fixed number of breeding sites that are available to be occupied either by singles or by interacting pairs and any other singles are searching for sites. Fitnesses are now automatically density dependent. Although the state space of the resulting dynamical system becomes quite large in this complex model, we show that the underlying density dependence drives Doves to extinction when reasonable assumptions on the system parameters are made.

Through the models of Sections 2–4, we show how implicit and explicit density dependence arises naturally when population and evolutionary models are integrated. The Discussion (Section 5) expands further on this theme by emphasizing how the Hawk–Dove game, originally developed to model the frequency evolution of aggressive behavior in a biological species, can serve to understand the effects of competition on the combined evolutionary and population outcome.

2. Evolutionary games when distribution dynamics are independent of fitness

In this section, we generalize the replicator dynamics to the case where interaction times between strategies are not the same and there is time needed for pair formation.

2.1. Distributional dynamics, fitness, and Nash equilibrium

In what follows we consider symmetric, two-strategy games with strategies denoted as H and D (motivated by, but not limited to, the Hawk–Dove model that we use throughout this article) and payoff matrix

$$
\begin{array}{c}
\begin{array}{cc} H & D \end{array} \\
\begin{array}{c} H \\ D \end{array}\begin{pmatrix} \pi_{HH} & \pi_{HD} \\ \pi_{DH} & \pi_{DD} \end{pmatrix}.
\end{array} \tag{1}
$$

These payoffs to the row player result from pairwise interactions between players. Classic evolutionary game theory interprets the

payoffs as changes in individual fitnesses due to an interaction. To calculate fitness, one then needs to describe the distribution of interacting pairs in the population.

The classic approach assumes that individuals immediately and randomly pair. The equilibrium of the pair formation process is then given by Hardy–Weinberg distribution

$$
n_{HH} = \frac{H^2}{2N}, \quad n_{HD} = \frac{HD}{N}, \quad n_{DD} = \frac{D^2}{2N} \tag{2}
$$

where n_{ij} is the number of ij pairs $(i, j = H, D)$, $H = 2n_{HH} + n_{HD}$, and $D = 2n_{DD} + n_{HD}$, where H is the number of Hawks, D is the number of Doves, and $N = H + D$ is the population size.[1] In mixed pairs, we do not distinguish between HD and DH pairs, i.e., n_{HD} consists of all mixed pairs. Assuming that the distribution of pairs is at its Hardy–Weinberg equilibrium, the expected payoffs per interaction to a Hawk and to a Dove are

$$
\begin{aligned}
\Pi_H &= \frac{2n_{HH}}{H}\pi_{HH} + \frac{n_{HD}}{H}\pi_{HD} = \frac{H}{N}\pi_{HH} + \frac{D}{N}\pi_{HD}, \\
\Pi_D &= \frac{n_{HD}}{D}\pi_{DH} + \frac{2n_{DD}}{D}\pi_{DD} = \frac{H}{N}\pi_{DH} + \frac{D}{N}\pi_{DD}.
\end{aligned} \tag{3}
$$

Underlying the Hardy–Weinberg distribution and the resulting expected payoffs given in (3) is an assumption that interactions take the same amount of time in order that all individuals are available to randomly pair (see the pair formation dynamics (7) below when individuals instantaneously pair). Although the effect of interaction time is not generally included in classic evolutionary game theory models, it is important for us here since we will relax the assumption that all interactions take the same amount of time for the remainder of this article.

Following Křivan and Cressman (2017), we introduce the (symmetric) interaction time matrix

$$
\begin{array}{c}
\begin{array}{cc} H & D \end{array} \\
\begin{array}{c} H \\ D \end{array}\begin{pmatrix} \tau_{HH} & \tau_{HD} \\ \tau_{HD} & \tau_{DD} \end{pmatrix}
\end{array} \tag{4}
$$

where τ_{ij} is the average interaction time an ij pair takes (with all τ's positive). Furthermore, contrary to classic evolutionary game theory, we will not assume that all individuals instantaneously pair, i.e., we consider singles in the population. The problem of finding the distributional equilibrium of pairs and singles is then much more complex when compared to the Hardy–Weinberg distribution (2).

Let n_H and n_D denote the numbers of singles in the population. Consider the distributional dynamics of pairs and singles

$$
\frac{dn_H}{dt} = -\lambda n_H^2 - \lambda n_H n_D + 2\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}
$$

$$
\frac{dn_D}{dt} = -\lambda n_D^2 - \lambda n_H n_D + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}
$$

$$
\frac{dn_{HH}}{dt} = -\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2}n_H^2 \tag{5}
$$

$$
\frac{dn_{HD}}{dt} = -\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D
$$

$$
\frac{dn_{DD}}{dt} = -\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2}n_D^2
$$

that leaves the number of Hawks and Doves unchanged. These dynamics model a pair formation process (see also Mylius, 1999) that

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[1] Note that H (respectively D) is used to denote the Hawk (respectively, Dove) strategy as well as the number of Hawks (respectively, Doves). The meaning will be clear from the context in which it appears.

is based on the mass action law whereby single individuals meet at random with encounter (or pairing) rate λ. The 2's and 1/2's in these equations relate to the fact that two single individuals appear when a pair disbands and that two singles produce one pair when they meet, respectively. Appendix A shows that, given H and D, there exists a unique distributional equilibrium of (5). This distributional equilibrium can be obtained using computer algebra software (Appendix F), but it is too complicated for analysis. We observe that at the distributional equilibrium we have a generalized Hardy–Weinberg distribution

$$n_{HH} = \frac{1}{2}\lambda\tau_{HH}n_H^2, \quad n_{HD} = \lambda\tau_{HD}n_Hn_D, \quad n_{DD} = \frac{1}{2}\lambda\tau_{DD}n_D^2. \quad (6)$$

If individuals instantaneously pair (i.e., λ converges to infinity in distributional dynamics (5)), the pair dynamics are described by Křivan and Cressman (2017)

$$\frac{dn_{HH}}{dt} = -\frac{n_{HH}}{\tau_{HH}} + \frac{\left(\frac{2n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}\right)^2}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)}$$

$$\frac{dn_{HD}}{dt} = -\frac{n_{HD}}{\tau_{HD}} + \frac{2\left(\frac{2n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}\right)\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)} \quad (7)$$

$$\frac{dn_{DD}}{dt} = -\frac{n_{DD}}{\tau_{DD}} + \frac{\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)^2}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)}.$$

Provided all τ's are the same, the above pair dynamics converge to the Hardy–Weinberg distributional equilibrium (2).

We define individual fitness as average payoff per unit of time. Assuming that singles gain payoff π_H and π_D (these payoffs can be positive, negative, or zero) per unit of time, while individual i in pair ij gains payoff π_{ij} per interaction when the pair disbands (and so payoff π_{ij}/τ_{ij} per unit of time), the fitnesses for the two phenotypes are now

$$\Pi_H = \frac{2n_{HH}}{H}\frac{\pi_{HH}}{\tau_{HH}} + \frac{n_{HD}}{H}\frac{\pi_{HD}}{\tau_{HD}} + \frac{n_H}{H}\pi_H,$$

$$\Pi_D = \frac{2n_{DD}}{D}\frac{\pi_{DD}}{\tau_{DD}} + \frac{n_{HD}}{D}\frac{\pi_{DH}}{\tau_{HD}} + \frac{n_D}{D}\pi_D. \quad (8)$$

We now analyze the game that consists of the Hawk and Dove strategies together with their fitnesses (8) evaluated at the unique equilibrium distribution of (5). Substituting equilibrium distribution of pairs (6) in the equation for an interior Nash equilibrium (NE) $\Pi_H = \Pi_D$ and into the total population size $N = n_H + n_D + 2n_{HH} + 2n_{HD} + 2n_{DD}$ leads to the following system of equations

$$\frac{n_H\lambda\pi_{HH} + n_D\lambda\pi_{HD} + \pi_H}{n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD} + 1} = \frac{n_D\lambda\pi_{DD} + n_H\lambda\pi_{DH} + \pi_D}{n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD} + 1} \quad (9)$$

and

$$n_H(n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD} + 1) + n_D(n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD} + 1) = N. \quad (10)$$

Eqs. (9) and (10) are difficult to solve analytically as these are two quadratic equations in n_H and n_D.

However, when all τ's are the same and equal to τ, there is at most one interior NE and it is given by

$$n_H = \frac{(\pi_{DD} - \pi_{HD})(\sqrt{4\lambda N\tau + 1} - 1) + 2\tau(\pi_D - \pi_H)}{2\lambda\tau(\pi_{DD} - \pi_{DH} - \pi_{HD} + \pi_{HH})}$$

and

$$n_D = \frac{(\pi_{HH} - \pi_{DH})(\sqrt{4\lambda N\tau + 1} - 1) + 2\tau(\pi_H - \pi_D)}{2\lambda\tau(\pi_{DD} - \pi_{DH} - \pi_{HD} + \pi_{HH})}.$$

when both these expressions are positive. In this case, the proportion of Hawks in the population at NE is given by

$$p_H = \frac{H}{N} = \frac{\pi_{DD} - \pi_{HD}}{\pi_{DD} - \pi_{DH} - \pi_{HD} + \pi_{HH}} + \frac{(\pi_D - \pi_H)(\sqrt{4\lambda N\tau + 1} + 1)}{2\lambda N(\pi_{DD} - \pi_{DH} - \pi_{HD} + \pi_{HH})}. \quad (11)$$

In particular, the NE depends on population size when there are payoffs to singles. This contrasts with the classic result of evolutionary game theory whereby the strategy proportion at NE depends only on the payoff matrix and not on N. On the other hand, in the special case where the payoff to singles for both strategies are the same (i.e., $\pi_H = \pi_D$),[2] we recover the classic result (Hofbauer and Sigmund, 1998) of matrix game theory with two strategies and equal interaction times where the NE proportion of Hawks is

$$p_H = \frac{\pi_{DD} - \pi_{HD}}{\pi_{DD} - \pi_{DH} - \pi_{HD} + \pi_{HH}}.$$

In the following example, our analysis of the Hawk–Dove model with standard payoff matrix shows clearly that, in general, interior NE depend both on population size and on interaction times. This raises the question of the applicability of classic evolutionary game theory to real populations. In particular, the classic results require that all interactions take the same amount of time and that all single individuals have the same payoff per unit of time.

Example 1. The Hawk–Dove model (e.g., Křivan and Cressman, 2017; Maynard Smith and Price, 1973) has payoff matrix

$$\begin{array}{c} \\ H \\ D \end{array} \begin{array}{cc} H & D \\ \begin{pmatrix} V - C & 2V \\ 0 & V \end{pmatrix} \end{array} \quad (12)$$

where $2V > 0$ is the benefit of winning the contest (this can be interpreted as, e.g., the value of the contested resource) and $C > 0$ is the individual cost of the fight that each contestant bears (i.e., the total cost for both individuals is $2C$). When two Hawks interact, the average payoff is thus $(2V - 2C)/2$. If singles payoffs are the same ($\pi_H = \pi_D$) so that differences in payoffs are through pairwise interactions only and all interactions take the same time, then for $C > V$ from formula (11) we get the NE $p_H = V/C$, which is independent of N. This is the unique evolutionarily stable strategy (ESS) of the classic matrix game (12) (Fig. 1A). When $C < V$, all Hawks is the only NE (it is also an ESS).

If all interactions take the same time τ and $\pi_H \neq \pi_D$, then the proportion of Hawks (11) at an interior NE is given by

$$p_H = \frac{V}{C} - \frac{(\pi_D - \pi_H)(\sqrt{4\lambda N\tau + 1} + 1)}{2C\lambda N} \quad (13)$$

and is no longer independent of population size N. The dependence of p_H on λ and N is illustrated in Fig. 1, left panels. When total population N tends to infinity, the proportion of Hawks converges to V/C as in the classical case. When $\pi_D > \pi_H$, we see from (13) that p_H decreases with smaller λ and N (Fig. 1, panels A, C, E, G) and larger τ. On the other hand, when $\pi_D < \pi_H$, we observe the opposite effect as seen in Fig. 1, Panel I.

When interaction times are not all the same, interior NE can be approximated by numerically solving Eqs. (9) and (10). The proportion of Hawks at NE are shown in the right panels of Fig. 1 as a function of τ_{HH} when all other interaction times are 1. The top

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[2] These equal payoffs to singles can be considered a type of strategy-independent background fitness (Cressman, 1992) that does not affect the evolutionary outcome since it is selectively neutral. From this perspective, $\pi_H \neq \pi_D$ is a form of heterogeneity in background fitness (see also Hauser et al., 2014) that alters the evolutionary outcome to (11).
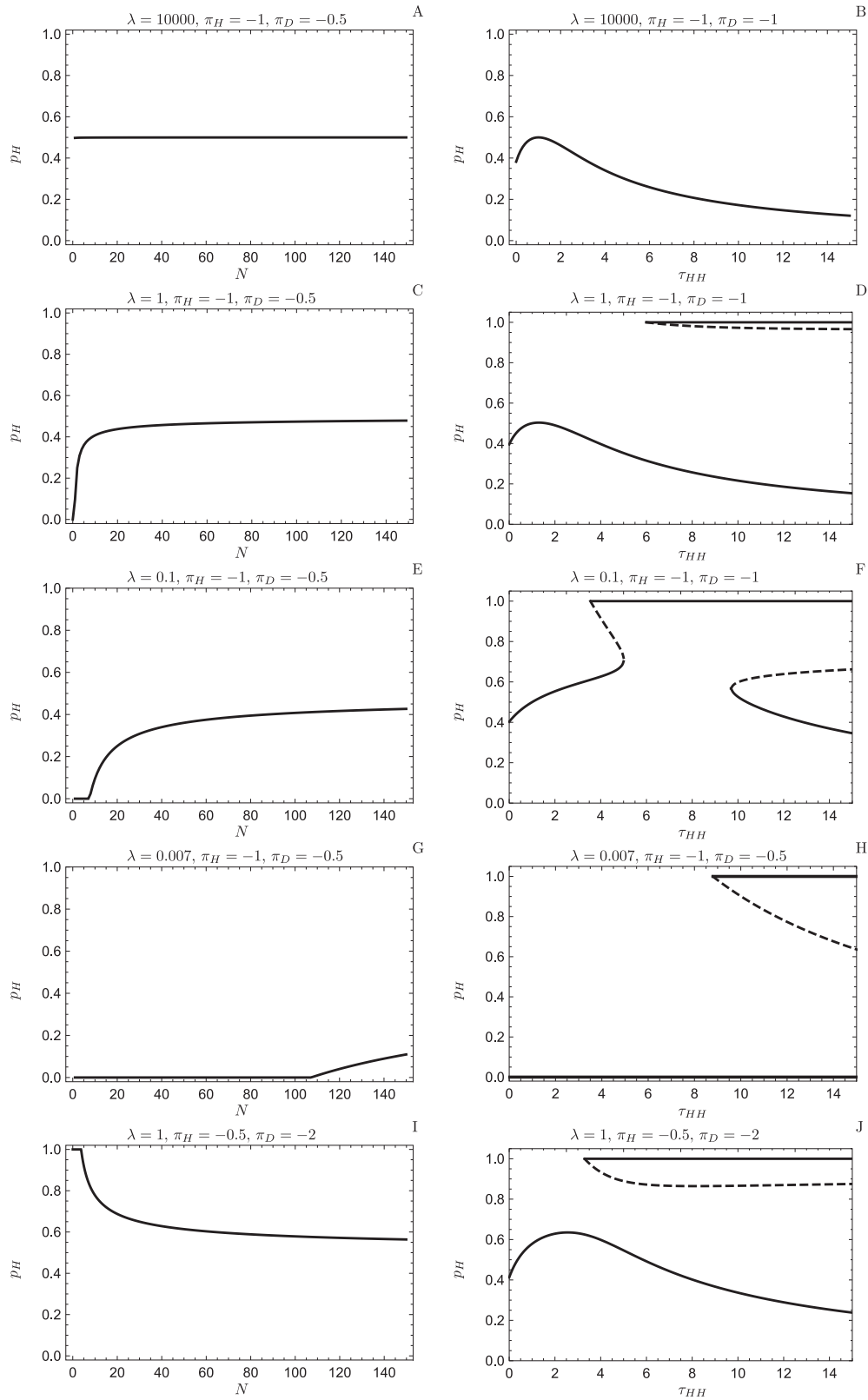
Fig. 1. The proportion of Hawks (p_H) at the NE for the Hawk–Dove game parametrized by (12) as a function of population size N (left panels) and of interaction time between Hawks τ_{HH} (right panels). Stable (unstable) NE are indicated by solid (dashed) curves. The left panels assume that all interaction times are the same (in particular, $\tau_{HH} = 1$) and in the right panels the constant total population size is $N = 100$. The top row assumes very fast pairing rate ($\lambda = 10,000$), the second and fifth rows intermediate pairing rate ($\lambda = 1$), the third and fourth row low and very low pairing rates ($\lambda = 0.1$ and $\lambda = 0.007$, respectively). Since there are effectively no singles in the top row, the left panel gives the NE of the classic Hawk–Dove game with payoff matrix (12) and the right panel reproduces Fig. 3B in Křivan and Cressman (2017). The top three panels on the left (A, C, E) assume different singles payoff ($\pi_H = -1$, $\pi_D = -0.5$) whereas the top three panels on the right (B, D, F) assume equal singles payoff ($\pi_H = -1$, $\pi_D = -1$). Panels G and H assume $\pi_H = -1$ and $\pi_D = -0.5$ as in A, C, E whereas panels I and J assume $\pi_H = -0.5$, $\pi_D = -2$. Other parameters used in simulations: $\tau_{HD} = 1$, $\tau_{DD} = 1$, $V = 1$, $C = 2$.
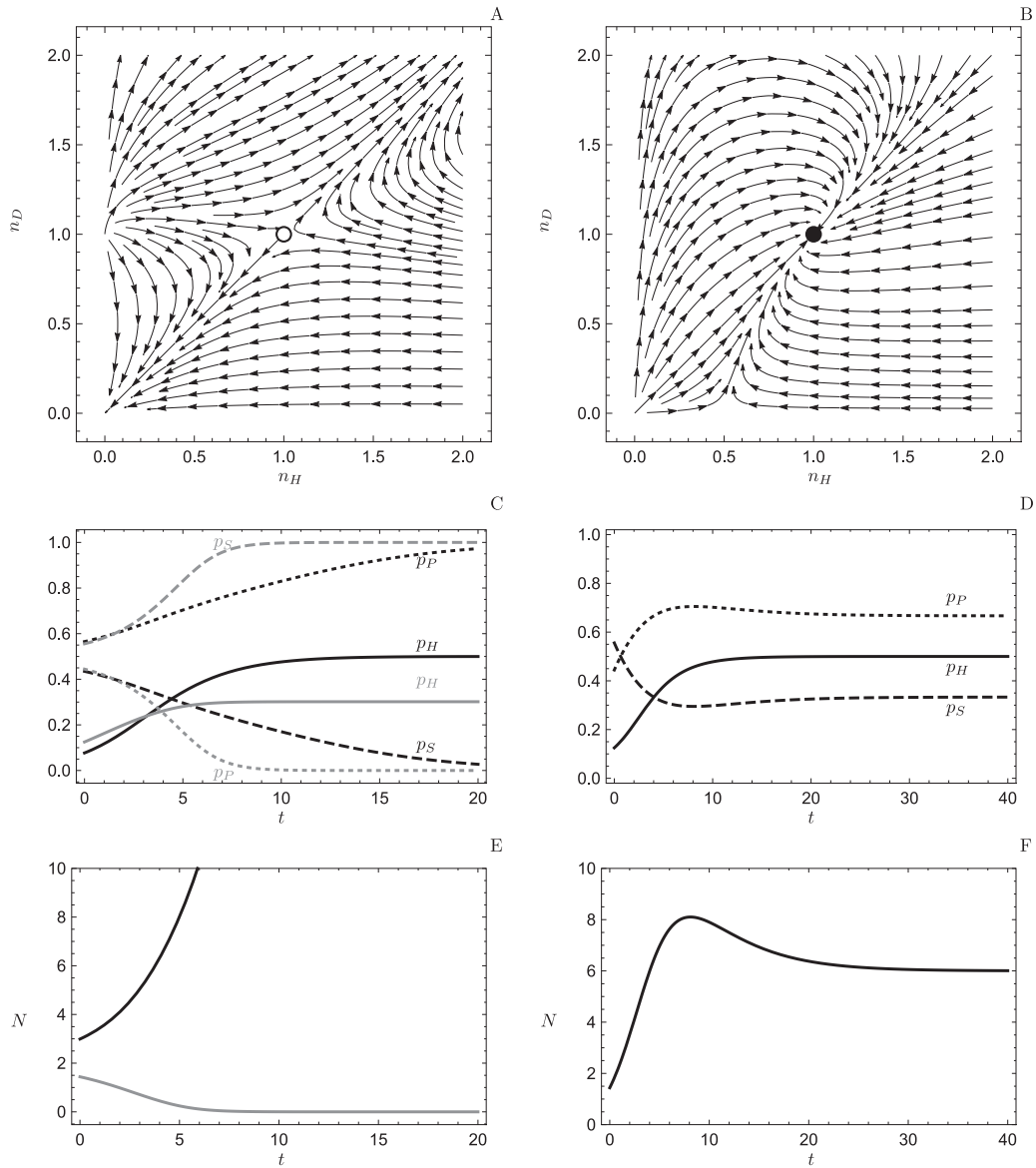
Fig. 2. Simulations of Hawk and Dove population dynamics (16). Left panels correspond to Example 1 ($\pi_H = \pi_D = -1$) and right panels to Example 2 ($\pi_H = \pi_D = 1$). Top row shows stream plot of singles population dynamics (18). The middle row shows frequency of Hawks (p_H), frequency of single individuals (p_S) and frequency of individuals that are in pairs (p_P) in the population as a function of time. The bottom row shows the total population size as a function of time. Panels C and E show two trajectories. Along one (black lines) the population grows to infinity, while along the other (gray) it declines to extinction. Other parameters: $\tau_{HH} = 1$, $\tau_{HD} = 1$, $\tau_{DD} = 1$, $\lambda = 1$, $V = 1$, $C = 2$.
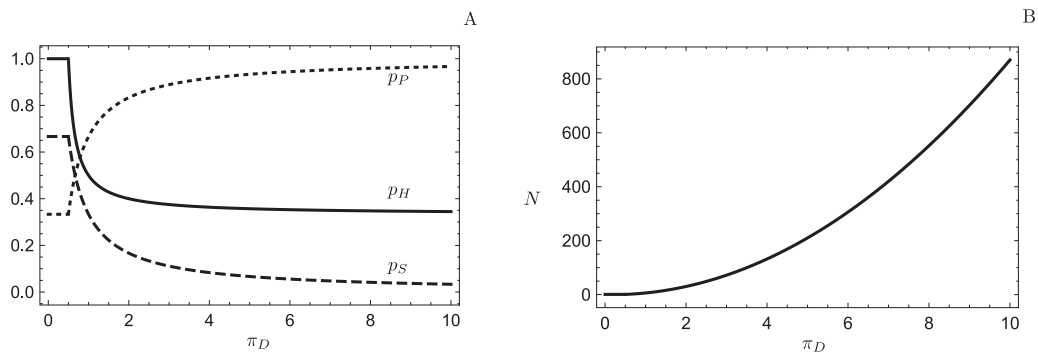

Fig. 3. Dependence on single Dove payoff π_D of the interior equilibrium (24) for Example 2, which exists for $\pi_D > (V/C)\pi_H$. Panel A shows frequency of Hawks (p_H), frequency of single individuals (p_S) and frequency of individuals that are in pairs (p_P) while panel B shows the total population size at the equilibrium. Other parameters are the same as those in Fig. 2, right panels (i.e., $\tau_{HH} = 1$, $\tau_{HD} = 1$, $\tau_{DD} = 1$, $\lambda = 1$, $V = 1$, $C = 2$, $\pi_H = 1$).

row of Fig. 1 shows the case where individuals pair almost instantaneously, because pairing rate λ is high. In this case, there are practically no singles and distributional dynamics converge to (7). Panel B then corresponds with Fig. 3B in Křivan and Cressman (2017) where instantaneous pairing was assumed. When pairing is not instantaneous and singles payoffs are negative but unequal (right panels D, F, H, J), it can be shown for the Hawk–Dove payoffs (12) that there is a finite threshold value such that the all Hawk population is a NE if and only if fighting time τ_{HH} is above this threshold. Moreover, panels D and J with intermediate pairing rate ($\lambda = 1$) document the existence of two interior NE when τ_{HH} is sufficiently large. In this case, one interior NE is stable (indicated by a solid curve) since $\Pi_H - \Pi_D$ is positive (negative) just below (above) the curve and the other is unstable (indicated by a dashed curve). In both panels, all Hawks is then a NE as well since $\Pi_H > \Pi_D$ when $p_H = 1$. Panel F assumes yet lower pairing rate and we observe complex dependence of NEs on interaction times between two Hawks. In particular, it shows that for short interaction times between Hawks, the proportion of Hawks is below $V/C = 1/2$. As this interaction time increases, the proportion of Hawks increases too, and a second NE where initially all individuals are Hawks appears. For intermediate interaction times between Hawks (approx. $4.9 < \tau_{HH} < 9.6$), the only NE is all Hawks. For yet higher interaction times, there are again two interior NE, and the stable lower one decreases with increasing interaction time. Finally, for extremely low pairing rate and $\pi_D > \pi_H$ (panels G and H), the all Dove population is a NE independent of fighting time when population size is small enough since almost all individuals are singles.

2.2. Replicator and population dynamics

The replicator equation of evolutionary game theory is based on a population dynamics that assumes the per capita population growth rate of a strategy's numbers is proportional to its payoff (Taylor and Jonker, 1978). In particular, unlike Section 2.1, total population size N can change. Under the implicit assumptions of classical evolutionary game theory that all interactions take one unit of time and that individuals instantaneously pair at Hardy–Weinberg distribution (2), the replicator equation is independent of N as we will now see. First, the population dynamics becomes

$$\frac{dH}{dt} = \Pi_H H$$
$$\frac{dD}{dt} = \Pi_D D \qquad (14)$$

where the per capita population growth rate is equal to fitness. Moreover, by the second assumption, fitnesses are given by (3) and so population dynamics (14) can be rewritten in terms of the proportion $p_H \equiv H/(H + D)$ of Hawks and the total population size $N \equiv H + D$ as

$$\frac{dp_H}{dt} = p_H(1 - p_H)\left(\Pi_H - \Pi_D\right)$$
$$\frac{dN}{dt} = \overline{\Pi}N, \qquad (15)$$

where $\overline{\Pi} = p_H\Pi_H + p_D\Pi_D$ is the average fitness in the population. Since $\Pi_H = p_H\pi_{HH} + p_D\pi_{HD}$ and $\Pi_D = p_H\pi_{DH} + p_D\pi_{DD}$ where $p_D \equiv 1 - p_H$, the proportion of Hawks evolves according to the replicator equation of classic evolutionary game theory which is independent of total population size. It is well-known (Hofbauer and Sigmund, 1998) that every trajectory of the replicator equation for a two-strategy game evolves to an equilibrium.[3] Depending on whether the average fitness $\overline{\Pi}$ in the population is positive or negative at this equilibrium, the population size will then either grow (in which case the extinction equilibrium $(H, D) = (0, 0)$ is unstable) or decay (the extinction equilibrium is then stable) exponentially and so no positive equilibrium population size exists. Such population dynamics are called density independent.

In the remainder of this section, we generalize the population dynamics approach to evolutionary games where the classic assumptions do not hold. We continue to assume that distributional dynamics (5) operate on a fast time scale so that, in the population dynamics (14), the population distribution tracks instantaneously the unique equilibrium distribution of (5) at current Hawk and Dove numbers.[4] From (6) and (8), population dynamics (14) simplify to

$$\frac{dH}{dt} = (\pi_{HH}\lambda n_H + \pi_{HD}\lambda n_D + \pi_H)n_H$$
$$\frac{dD}{dt} = (\pi_{DH}\lambda n_H + \pi_{DD}\lambda n_D + \pi_D)n_D, \qquad (16)$$

which can be analyzed by rewriting it as a dynamics in n_H and n_D alone. Specifically, using generalized Hardy–Weinberg distribution (6), Hawk and Dove population size at the distributional equilibrium are

$$H = 2n_{HH} + n_{HD} + n_H = n_H(n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD} + 1),$$
$$D = 2n_{DD} + n_{HD} + n_D = n_D(n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD} + 1). \qquad (17)$$

Calculating derivatives of H and D in (17) and substituting them into (16) leads to[5]

$$\frac{dn_H}{dt} = n_H \frac{n_D\lambda(\pi_D + n_D\lambda\pi_{DD} + n_H\lambda\pi_{DH})\tau_{HD} - (\pi_H + n_D\lambda\pi_{HD} + n_H\lambda\pi_{HH})(1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})}{n_Dn_H\lambda^2\tau_{HD}^2 - (1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})(1 + n_D\lambda\tau_{HD} + 2n_H\lambda\tau_{HH})}$$

$$\frac{dn_D}{dt} = n_D \frac{n_H\lambda(\pi_H + n_H\lambda\pi_{HH} + n_D\lambda\pi_{HD})\tau_{HD} - (\pi_D + n_H\lambda\pi_{DH} + n_D\lambda\pi_{DD})(1 + 2n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD})}{n_Dn_H\lambda^2\tau_{HD}^2 - (1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})(1 + n_D\lambda\tau_{HD} + 2n_H\lambda\tau_{HH})}. \qquad (18)$$

In contrast to (14), population dynamics (18) also have non-trivial equilibria. Here we provide conditions (proven in Appendix B) for their local asymptotic stability.

The extinction equilibrium $(n_H, n_D) = (0, 0)$ is locally stable when $\pi_H < 0$ and $\pi_D < 0$. This can be understood intuitively by Fig. 2, where panels C and E (gray lines) show that, as the total population size decreases toward 0, the frequency of singles ($p_S \equiv (n_H + n_D)/N$) in the population increases toward 1. For low population size, individual fitness is then essentially given by the singles payoff, which then determine population dynamics and hence the fate of the population. Thus, when payoffs of singles are negative, the population will go extinct. Fig. 2C also shows that the frequency of Hawks (p_H) in the population does not tend to V/C even in the case that single Hawks and Doves have the same payoff (i.e., $\pi_H = \pi_D$) and all τ's are equal (see the gray solid line

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[3] This equilibrium is a NE of the game (and, generically, an ESS) if initially there are both Hawks and Doves present.

[4] See, however, Section 3, where this assumption is relaxed.

[5] We note that rewriting these dynamics in analogy to (15) where we separated frequency dynamics from population dynamics is cumbersome now, because the analytic expression for the equilibrium of (5) as a function of Hawk and Dove population numbers is a very complex formula (it can be calculated in Mathematica).

in panel C). In fact, the limiting proportion of Hawks depends on the initial conditions that determine the angle with which the corresponding trajectory tends to the origin in Fig. 2, panel A.

The black lines of Fig. 2, panels C and E, show that, as population size increases toward infinity, the frequency of pairs ($p_P \equiv 1 - p_S$) in the population increases toward 1. For large populations, it is the payoffs from interacting pairs that determine population dynamics. For the Hawk–Dove payoff matrix (12), the frequency of Hawks then approaches V/C when all τ's are equal, independently of the initial conditions.

Other boundary equilibria may exist where exactly one strategy is extinct. For instance, the Hawk only boundary equilibrium

$$(n_H, n_D) = \left(-\frac{\pi_H}{\lambda \pi_{HH}}, 0 \right) \tag{19}$$

exists if and only if $\pi_{HH} \neq 0$ and $\pi_H/\pi_{HH} < 0$. Moreover, it is locally stable if and only if $\pi_H > 0$ and $\pi_D \pi_{HH} < \pi_H \pi_{DH}$. Similarly, the Dove only boundary equilibrium

$$(n_H, n_D) = \left(0, -\frac{\pi_D}{\lambda \pi_{DD}} \right) \tag{20}$$

exists if and only if $\pi_{DD} \neq 0$ and $\pi_D/\pi_{DD} < 0$ and is locally stable if and only if $\pi_D > 0$ and $\pi_H \pi_{DD} < \pi_D \pi_{HD}$.

Most importantly, there are payoff parameters for which the interior equilibrium

$$(n_H, n_D) = \left(\frac{\pi_{DD}\pi_H - \pi_D\pi_{HD}}{\lambda(\pi_{DH}\pi_{HD} - \pi_{DD}\pi_{HH})}, \frac{\pi_D\pi_{HH} - \pi_{DH}\pi_H}{\lambda(\pi_{DH}\pi_{HD} - \pi_{DD}\pi_{HH})} \right) \tag{21}$$

exists. It is interesting to note that equilibrium (21) is independent of interaction times. This can also be seen from (16) where the right hand-side is independent of interaction times and, consequently, the values of n_H and n_D at which both Hawks and Doves have zero growth rate are independent of interaction times too. However, due to (17), equilibrium numbers of Hawks and Doves do depend on interaction times. Stability analysis of equilibrium (21) also depends on interaction times and leads to complex expressions. Below we will analyze its stability for the Hawk–Dove game.

Before doing so, we observe two important effects of singles on population dynamics (16) (or (18)). First, when singles do not get any payoff ($\pi_D = \pi_H = 0$), then (0,0) is the only equilibrium. Second, as the pairing rate of singles λ tends to infinity, both boundary and interior equilibria tend to (0,0). These observations clearly show that existence of non-extinction equilibria in these dynamics depends on singles being considered.

The important observation here is that, unlike classic evolutionary game theory, generalization of replicator dynamics that include singles payoff (i.e., π_H or π_D) can lead to density dependence, and so to non-extinction equilibria. For this to happen it is essential that singles receive payoffs. We note that our payoffs (to pairs and to singles) are independent of population size unlike the background fitness approach of Cressman (1992) where payoffs decrease as population size increases or of Argasinski and Broom (2013) who assume density dependent fertility rates.

Example 1 **continued.** For the classic assumptions of evolutionary game theory applied to the parametrization of the Hawk–Dove model (12), the average fitness in the population at its unique NE is

$$\overline{\Pi} = \frac{V}{C}(C - V) > 0$$

when $C > V$ and $\overline{\Pi} = V - C > 0$ when $V > C$. Thus, the population will eventually grow exponentially, i.e., there is no stable population equilibrium. In fact, even if singles do not pair instantaneously, the population will eventually grow exponentially when $\pi_H = \pi_D = 0$.

Now we consider the case where individuals do not pair instantaneously, pair interaction times may differ, and singles receive payoff. Provided $\frac{\pi_H - 2\pi_D}{\lambda(C-V)} > 0$ and $\pi_D < 0$, the interior population equilibrium (21) is

$$(n_H, n_D) = \left(\frac{\pi_H - 2\pi_D}{\lambda(C - V)}, -\frac{\pi_D}{V\lambda} \right) \tag{22}$$

and the population of Hawks and Doves at this equilibrium are

$$H = \frac{(2\pi_D - \pi_H)((C - V)(\pi_D\tau_{HD} - V) + V(2\pi_D - \pi_H)\tau_{HH})}{(C - V)^2 V\lambda}$$

and

$$D = \frac{\pi_D((C - V)(V - \pi_D\tau_{DD}) + V(\pi_H - 2\pi_D)\tau_{HD})}{V^2(V - C)\lambda}.$$

Appendix B gives conditions on parameters that guarantee the stability of this equilibrium. However, these conditions also imply that for $C > V$ the interior equilibrium is always unstable (Fig. 2A). In fact, since $\pi_H < 0$ and $\pi_D < 0$ in this panel, the extinction equilibrium is locally stable and we observe the Allee effect where the population goes extinct when initially at low numbers, but it survives once it overcomes the extinction threshold (Courchamp et al., 2008) and grows to infinity (Fig. 2E).

In order to avoid this Allee effect in Example 1 whenever there is an interior equilibrium and (0,0) is locally stable, we reparametrize the payoff matrix for the Hawk–Dove game as in the following example by decreasing payoffs from pairs (specifically, by subtracting V from each entry of (12)). As we will see, the decrease in population growth rates due to the fitness component based on pairs results in the stability of the interior equilibrium whenever it exists (Fig. 2B and F). Thus, singles payoff can lead to stable interior equilibria for the combined replicator and population dynamics.

Example 2. The second parametrization of the Hawk–Dove model we consider has payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} -C & V \\ -V & 0 \end{pmatrix}. \end{array} \tag{23}$$

Here, two fighting Hawks always pay a cost $C > 0$, while when a Hawk interacts with a Dove, it gets a positive payoff V, e.g., by stealing the resource owned by its opponent. In this parametrization, the payoff a Hawk obtains when interacting with a Dove is the same as the cost a Dove pays when interacting with a Hawk.

For the classic assumptions of evolutionary game theory, this parametrization as a matrix game has the same NE (and ESS) as parametrization (12) in Example 1.[6] On the other hand, the average fitness in the population at the unique NE is now

$$\overline{\Pi} = -\frac{V^2}{C}$$

for $C > V$ and $\overline{\Pi} = -C$ for $V \geq C$. Thus, the population will go extinct.

Now we consider the case where individuals do not pair instantaneously, pair interaction times may differ and singles have fitness consequences. Provided $\pi_D > 0$ and $C\pi_D > V\pi_H$, the interior population equilibrium (21) is

$$(n_H, n_D) = \left(\frac{\pi_D}{\lambda V}, \frac{C\pi_D - V\pi_H}{V^2\lambda} \right). \tag{24}$$

At this equilibrium, the population of Hawks and Doves are

$$H = \frac{\pi_D(\tau_{HD}(C\pi_D - V\pi_H) + V(V + \pi_D\tau_{HH}))}{V^3\lambda}$$

---

[6] This follows from the fact that each entry of the payoff matric (23) differs from the corresponding entry of (12) by the same constant V.

and

$$D = \frac{(C\pi_D - V\pi_H)(\tau_{DD}(C\pi_D - V\pi_H) + V(V + \pi_D\tau_{HD}))}{V^4\lambda}.$$

[Appendix B](#) shows that if this equilibrium exists, it is stable (Fig. 2, right panels). Moreover, if all τ's are equal and $\pi_H = \pi_D$, the equilibrium frequency of Hawks is the unique NE, $p_H = V/C$, of (23) (Fig. 2D).

On the other hand, as illustrated by the dependence of this equilibrium on $\pi_D > 0$ in Fig. 3, $p_H \neq V/C$ if the payoffs to singles are different. From (24), equilibrium population size increases to infinity as π_D increases (Fig. 3B). Moreover, from (6), the proportion of paired individuals converges to 1 (Fig. 3A, see also [Appendix F](#)). Interestingly, the proportion of Hawks does not converge to 0 (for the parameters of Fig. 3, the limiting proportion is 1/3) even when the payoff π_D to single Doves tends to infinity since most of the fitness is due to pair interactions at high population size.

3. Distributional–population dynamics

In the previous section, we assumed distributional dynamics that were independent of population dynamics. In particular, the distributional dynamics reached its equilibrium very fast at given strategy numbers and then the population dynamics acted on this equilibrium distribution. However, this complete separation of time scales need not hold. For example, perceptual constraints (Abrahams, 1986; Berec and Křivan, 2000; Gray and Kennedy, 1994) may prevent individuals from having perfect information about their environment, making them only locally omniscient. In order to model distributional and population dynamics on similar time scales, we split payoffs in (1) as

$$\begin{pmatrix} \pi_{HH} & \pi_{HD} \\ \pi_{DH} & \pi_{DD} \end{pmatrix} = \begin{pmatrix} \beta_{HH} & \beta_{HD} \\ \beta_{DH} & \beta_{DD} \end{pmatrix} - \begin{pmatrix} \mu_{HH} & \mu_{HD} \\ \mu_{DH} & \mu_{DD} \end{pmatrix}, \quad (25)$$

where we assume that all β's and μ's are non-negative. Here we interpret β's as the part of payoff that increase fitness (e.g., birth rate) while μ's decrease fitness (e.g., mortality rate). For example, β_{HD} is the expected number of offspring produced per interaction by a Hawk when it interacts with a Dove. In the following continuous-time distributional-population dynamics (e.g., (26) and (29)), $\delta\frac{\beta_{HD}}{\tau_{HD}}$ is then interpreted as the probability that, over a small time interval δ, this Hawk produces an offspring. Similarly, $\delta\frac{\mu_{DH}}{\tau_{HD}}$ is the probability the Dove dies during this time interval.

We stress here that similarly to π's for pairs, all β's and μ's in (25) are measured per single interaction. To express these per unit of time, we need to divide them by the average pair duration. Then distributional-population dynamics are described by the following set of differential equations[7]

$$\frac{dn_H}{dt} = \nu\left(-\lambda n_H^2 - \lambda n_H n_D + 2\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}\right)$$
$$+ \pi_H n_H + 2\frac{\beta_{HH} + \mu_{HH}}{\tau_{HH}}n_{HH} + \frac{\beta_{HD} + \mu_{DH}}{\tau_{HD}}n_{HD}$$

$$\frac{dn_D}{dt} = \nu\left(-\lambda n_D^2 - \lambda n_H n_D + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}\right)$$
$$+ \pi_D n_D + 2\frac{\beta_{DD} + \mu_{DD}}{\tau_{DD}}n_{DD} + \frac{\beta_{DH} + \mu_{HD}}{\tau_{HD}}n_{HD}$$

$$\frac{dn_{HH}}{dt} = \nu\left(-\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2}n_H^2\right) - 2\frac{\mu_{HH}}{\tau_{HH}}n_{HH}$$

$$\frac{dn_{HD}}{dt} = \nu\left(-\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D\right) - \frac{\mu_{HD} + \mu_{DH}}{\tau_{HD}}n_{HD}$$

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[7] Note that it is unnecessary to write the payoff to singles as a difference (e.g., $\pi_H = \beta_H - \mu_H$) since these births and deaths only affect the number of singles.

$$\frac{dn_{DD}}{dt} = \nu\left(-\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2}n_D^2\right) - 2\frac{\mu_{DD}}{\tau_{DD}}n_{DD}. \quad (26)$$

These equations assume that newborns are singles and that, if a pair disbands due to mortality of one individual, the surviving individual becomes a single. For example, if a Dove paired with a Hawk dies, the surviving Hawk becomes a single Hawk. For this reason there is $\frac{\mu_{DH}}{\tau_{HD}}$ (and not $\frac{\mu_{HD}}{\tau_{HD}}$) in the equation for single Hawks. Thus, we assume that one individual in a pair always survives. Parameter $\nu > 0$ allows us to study changes in the relative time scales of distribution and demographic dynamics. When $\nu < 1$ ($\nu > 1$), then population dynamics are faster (slower) than distributional dynamics.

For arbitrary ν, we observe that

$$\frac{dH}{dt} = \frac{d(2n_{HH} + n_{HD} + n_H)}{dt} = 2\frac{\beta_{HH} - \mu_{HH}}{\tau_{HH}}n_{HH}$$
$$+ \frac{\beta_{HD} - \mu_{HD}}{\tau_{HD}}n_{HD} + \pi_H n_H = \Pi_H H$$

and

$$\frac{dD}{dt} = \frac{d(2n_{DD} + n_{HD} + n_D)}{dt} = 2\frac{\beta_{DD} - \mu_{DD}}{\tau_{DD}}n_{DD}$$
$$+ \frac{\beta_{DH} - \mu_{DH}}{\tau_{HD}}n_{HD} + \pi_D n_D = \Pi_D D$$

where Π_H and Π_D are given by (8) with payoff matrix (25). That is, fitnesses derived from distributional-population dynamics (26) coincide with those of [Section 2](#). What has changed is how these individual fitnesses are divided among singles and pairs.

At the coexistence equilibrium of (26), the HW distribution (2) and (6) generalizes to

$$n_{HH} = \frac{\lambda\nu n_H^2\tau_{HH}}{2\nu + 4\mu_{HH}}, \quad n_{HD} = \frac{\lambda\nu n_D n_H\tau_{HD}}{\nu + \mu_{DH} + \mu_{HD}}, \quad n_{DD} = \frac{\lambda\nu n_D^2\tau_{DD}}{2\nu + 4\mu_{DD}}. \quad (27)$$

These numbers now depend on fitness through the death rates (i.e., the μ's). When μ's are all zero, then the HW distribution (27) and (6) coincide. Moreover, the equilibria for the distributional-population dynamics (26) will then coincide with those of (16). However, when some μ's are positive, equilibrium points of (26) differ from those given by (16). To illustrate these differences at a stable equilibrium, we will parametrize model (26) by payoff matrix (23) because, as we saw in [Example 2](#), this parametrization leads to a stable interior equilibrium of population dynamics (18).

[Example 2](#) **continued.** To parametrize model (26) for the Hawk–Dove game given by (23), we follow (25) and write payoff matrix (23) as a difference of two matrices, where the first describes benefits and the second losses, e.g.,

$$\begin{pmatrix} -C & V \\ -V & 0 \end{pmatrix} = \begin{pmatrix} 0 & V \\ 0 & 0 \end{pmatrix} - \begin{pmatrix} C & 0 \\ V & 0 \end{pmatrix}. \quad (28)$$

Here the birth rate of a Hawk from an interaction with a Dove (V) is the same as is the death rate of a Dove when interacting with a Hawk. Distributional-population dynamics (26) are then

$$\frac{dn_H}{dt} = \nu(-\lambda n_H^2 - \lambda n_H n_D + 2\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}})$$
$$+ \pi_H n_H + 2\frac{C}{\tau_{HH}}n_{HH} + \frac{2V}{\tau_{HD}}n_{HD}$$

$$\frac{dn_D}{dt} = \nu(-\lambda n_D^2 - \lambda n_H n_D + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}) + \pi_D n_D$$

$$\frac{dn_{HH}}{dt} = \nu(-\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2}n_H^2) - 2\frac{C}{\tau_{HH}}n_{HH}$$
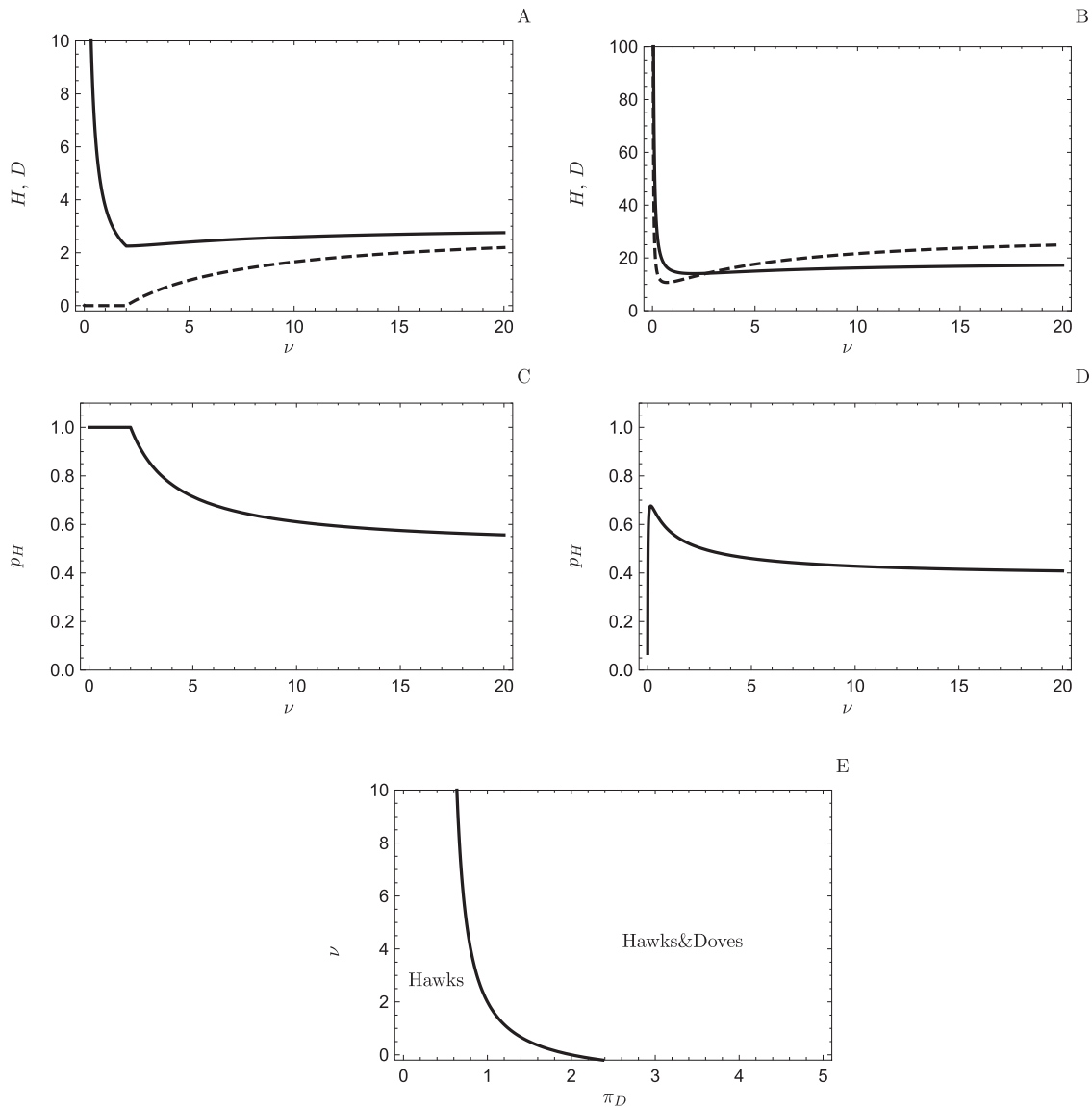
Fig. 4. Dependence of the stable equilibrium of model (29) for Example 2 on the relative speed of distributional dynamics to demographic dynamics. Hawks (Doves) abundance is shown as the solid (dashed) curve in top panels. The middle panels (C and D) show Hawk frequency. Left panels (A, C) assume relatively low payoff to single Doves ($\pi_D = 1$) and as ν increases, population abundances converge to the equilibrium shown in Fig. 2F ($N = H + D = 6$). Right panels (B, D) assume a higher payoff to single Doves ($\pi_D = 2.5$) for which both populations become arbitrarily large as ν decreases toward 0. Panel E shows the critical threshold in the (ν, π_D) phase space, below which Doves go extinct and above which both Hawks and Doves coexist at positive numbers. Other parameters are the same as those used in Fig. 2, right panels (i.e., $\tau_{HH} = 1$, $\tau_{HD} = 1$, $\tau_{DD} = 1$, $\lambda = 1$, $V = 1$, $C = 2$, $\pi_H = 1$).

$$\frac{dn_{HD}}{dt} = \nu\left(-\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D\right) - \frac{V}{\tau_{HD}} n_{HD}$$

$$\frac{dn_{DD}}{dt} = \nu\left(-\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2} n_D^2\right). \tag{29}$$

Provided the interior equilibrium exists, it is

$$(n_H, n_D) = \left(\frac{\pi_D(\nu + V)}{\lambda \nu V}, \frac{(\nu + V)(C\pi_D(\nu + V) - \pi_H V(2C + \nu))}{\lambda \nu V^2(2C + \nu)}\right) \tag{30}$$

and the number of pairs at the equilibrium is given by (27). We note that the equilibrium numbers of singles continue to be independent of the interaction times and, as ν tends to infinity, is given by (24) (see also (21)).

Since equilibrium (30) converges to equilibrium (24) as ν tends to infinity, we assume that equilibrium (24) is in the interior (i.e., $\pi_D > 0$ and $C\pi_D - \pi_H V > 0$) in what follows. We observe that

Doves exist (i.e., $n_D > 0$) at equilibrium (30) if and only if distributional dynamics are fast enough so that

$$\nu > \frac{CV(2\pi_H - \pi_D)}{C\pi_D - \pi_H V}.$$

Fig. 4E shows this bifurcation curve in the $\pi_D - \nu$ parameter space. The curve separates the values such that Doves go extinct (parameter values below the curve) from those where Doves survive (above the curve).

Fig. 4A and B (respectively C and D) show the dependence on ν of Hawk and Dove numbers (respectively, proportion of Hawks) at the stable population equilibrium. For slow distributional dynamics, total population size is increasing as ν tends to 0 since singles have positive payoffs ($\pi_H > 0$, $\pi_D > 0$ in Fig. 4). However, since $\nu = 2$ is the threshold below which Doves go extinct in Panel A where $\pi_D = 1$, this payoff to single Doves is too low to rescue Doves from extinction when ν is small. Panel B with $\pi_D = 2.5$ shows the opposite case where the Dove population does not go extinct for any

$\nu > 0$ and, in fact, as the speed of distributional dynamics decreases toward 0, both Hawk and Dove population numbers become arbitrarily large. As ν tends to infinity in these four panels, the stable interior equilibrium of (29) converges to that of model (16) of Section 2. In particular, for the left panels, this equilibrium approaches that of the right panels in Fig. 2 where $N = H + D = 6$ and $p_H = V/C = 0.5$ since all τ's are equal and $\pi_H = \pi_D$.

4. Contest competition for a limited resource

The Hawk–Dove model, when interpreted as a model of contest competition, can represent competition for resources, such as breeding sites where each site can be owned by at most one individual (Kokko et al., 2014). We represent these K sites as a resource with finite environmental carrying capacity. Individuals are again either Hawks or Doves, and they can be either searching for the resource (n_{H_s}, n_{D_s}), owning the resource (n_{H_o}, n_{D_o}), or interacting with each other when a searcher finds an owner. During the competition for a site there are four possible types of searcher-owner pairs and the numbers of these pairs are denoted as $n_{H_sH_o}$, $n_{H_sD_o}$, $n_{H_oD_s}$, and $n_{D_sD_o}$. Once the competing pair is formed and jointly occupy the site, the individuals are no longer searchers for the site or owners of the site. The notation for competing pairs indicates how the pair formed. In particular, $n_{H_sD_o}$ is the number of occupied sites where a searching Hawk encountered an owning Dove.

4.1. Distributional dynamics

Distributional dynamics at fixed population sizes H and D of Hawks and Doves, respectively, that are based on the mass action principle are

$$\frac{dn_{H_s}}{dt} = -\lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}}$$

$$\frac{dn_{H_o}}{dt} = \lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{D_s}n_{H_o} + \frac{n_{H_sH_o}}{\tau_{HH}} + \frac{n_{H_oD_s}}{\tau_{HD}} + \frac{n_{H_sD_o}}{\tau_{HD}}$$

$$\frac{dn_{D_s}}{dt} = -\lambda n_{D_s}F - \lambda n_{D_s}n_{H_o} - \lambda n_{D_s}n_{D_o} + \frac{n_{D_sD_o}}{\tau_{DD}} + \frac{n_{H_sD_o}}{\tau_{HD}} + \frac{n_{H_oD_s}}{\tau_{HD}}$$

$$\frac{dn_{D_o}}{dt} = \lambda n_{D_s}F - \lambda n_{D_s}n_{D_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{D_sD_o}}{\tau_{DD}}$$

$$\frac{dn_{H_sH_o}}{dt} = -\frac{n_{H_sH_o}}{\tau_{HH}} + \lambda n_{H_s}n_{H_o}$$

$$\frac{dn_{H_sD_o}}{dt} = -\frac{n_{H_sD_o}}{\tau_{HD}} + \lambda n_{H_s}n_{D_o}$$

$$\frac{dn_{H_oD_s}}{dt} = -\frac{n_{H_oD_s}}{\tau_{HD}} + \lambda n_{D_s}n_{H_o}$$

$$\frac{dn_{D_sD_o}}{dt} = -\frac{n_{D_sD_o}}{\tau_{DD}} + \lambda n_{D_s}n_{D_o}$$

(31)

where

$$F \equiv K - n_{H_o} - n_{D_o} - n_{H_sH_o} - n_{H_sD_o} - n_{D_sD_o} - n_{H_oD_s} \tag{32}$$

is the nonnegative number of free sites (i.e., sites that are neither occupied by a single owner or by a pair). Model (31) assumes that individual search rate is λ. If a searching individual encounters a free site, it will occupy it and will become an owning consumer. When a searching Hawk encounters a site owned by a Dove, the Hawk wins the competition and, when the pair disbands, becomes

an owning Hawk while the Dove that lost the site becomes a searching Dove. This assumption leads to the term $\frac{n_{H_sD_o}}{\tau_{HD}}$ in the second and third equations. Once again this shows that distributional dynamics such as (31) may depend on how entries in the payoff matrix are interpreted.

From (31), the number of free sites evolves according to

$$\frac{dF}{dt} = -\lambda(n_{H_s} + n_{D_s})F. \tag{33}$$

That is, the number of free sites changes at a rate proportional to the number of searchers encountering them. Eq. (33) shows that the system either converges to a state where there are no searchers (i.e., $n_{H_s} + n_{D_s} = 0$) or to the set of states where there are no free sites (i.e., $F = 0$). Appendix C shows that for each fixed Hawk and Dove population numbers, system (31) has a unique equilibrium. It also shows that this equilibrium depends on the abundances of Hawks and Doves and on the number of sites, K, according to the following three cases.

1. When the number of individuals is no larger than the number of sites ($H + D \leq K$), all Hawks and all Doves own sites, i.e., the equilibrium is $n_{H_o} = H, n_{D_o} = D$.
2. When the total number of individuals is larger than the number of sites ($H + D > K$) while the number of Hawks in the population is no larger than the number of sites ($H \leq K$), all Hawks occupy sites either as single owners or in H_oD_s pairs and all other $K - H$ sites are occupied by Doves.
3. When the number of Hawks in the population is larger than the number of sites ($H > K$), all sites are occupied by Hawks, either as single owners or in H_oH_s and H_oD_s pairs.

As the distributional equilibrium is quite complicated in the last two cases, the next example considers distributional dynamics (31) when only Hawk–Hawk interactions are time consuming.

Example 3. In this example, we will assume that τ_{HD} and τ_{DD} tend to 0. As τ_{HD} and τ_{DD} tend to 0, the number of pairs, except $n_{H_sH_o}$, will quickly equilibrate with the number of singles, i.e.,

$$n_{H_sD_o} = \lambda\tau_{HD}n_{H_s}n_{D_o}$$
$$n_{H_oD_s} = \lambda\tau_{HD}n_{D_s}n_{H_o}$$
$$n_{D_sD_o} = \lambda\tau_{DD}n_{D_s}n_{D_o}. \tag{34}$$

We substitute this pseudo-equilibrium into distributional dynamics (31) to get

$$\frac{dn_{H_s}}{dt} = -\lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}}$$

$$\frac{dn_{H_o}}{dt} = \lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} + \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}}$$

$$\frac{dn_{D_s}}{dt} = -\lambda n_{D_s}F + \lambda n_{H_s}n_{D_o}$$

$$\frac{dn_{D_o}}{dt} = \lambda n_{D_s}F - \lambda n_{H_s}n_{D_o}$$

$$\frac{dn_{H_sH_o}}{dt} = -\frac{n_{H_sH_o}}{\tau_{HH}} + \lambda n_{H_s}n_{H_o} \tag{35}$$

where $F = K - (n_{H_o} + n_{D_o} + n_{H_oH_s})$. Appendix D analyzes the unique distributional equilibrium of (35) and proves that it is globally asymptotically stable at any Hawk and Dove population abundances.

In particular, the three cases above simplify to

1. When the number of individuals is no larger than the number of sites ($H + D \leq K$), all Hawks and all Doves own sites, i.e., the equilibrium is

$$(n_{H_s}, n_{H_o}, n_{D_s}, n_{D_o}, n_{H_sH_o}) = (0, H, 0, D, 0) \tag{36}$$
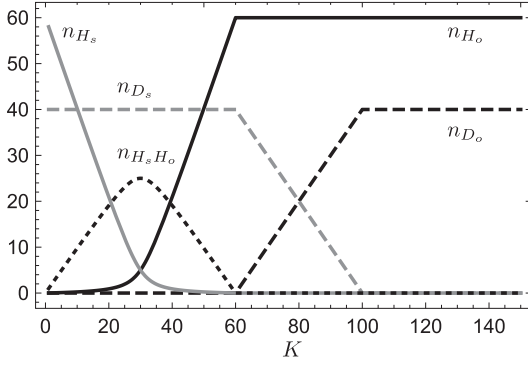
(see Fig. 5 for $K \geq 100$).

A

Fig. 5. Dependence of the number of searchers (n_{H_o} and n_{D_s}) and number of owners (n_{H_o} and n_{D_o}) at the distributional equilibrium of model (35) as a function of K. The overall number of individuals is fixed at $H = 60$ and $D = 40$. Hawks are described by solid lines, Doves are described by dashed lines. Black lines denote owning individuals and gray lines denote searching individuals. The dotted line denotes the number of Hawk pairs, i.e, $n_{H_sH_o}$. Parameters: $\lambda = 1$, $\tau_{HH} = 1$, $\tau_{HD} = 0$, $\tau_{DD} = 0$.

2. When the total number of individuals is larger than the number of sites ($H + D > K$) while the number of Hawks in the population is no larger than the number of sites ($H \leq K$), all Hawks own sites while Doves occupy the rest of the sites and some Doves are searching, i.e., the equilibrium is

$$(n_{H_s}, n_{H_o}, n_{D_s}, n_{D_o}, n_{H_sH_o}) = (0, H, H + D - K, K - H, 0),\qquad (37)$$

(see Fig. 5 for $60 \leq K < 100$).

3. When the number of Hawks in the population is larger than the number of sites ($H > K$), all sites are occupied by Hawks and all Doves are single searchers.

$$n_{H_s} = \frac{-1 + (H - 2 K)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2 K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}}$$

$$n_{H_o} = \frac{-1 - (H - 2 K)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2 K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}}$$

$$n_{D_s} = D$$

$$n_{D_o} = 0$$

$$n_{H_sH_o} = \frac{1 + H\lambda\tau_{HH} - \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2 K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}}.\qquad (38)$$

(see Fig. 5 for $K < 60$).

4.2. Distributional–population dynamics

To combine distributional dynamics (31) with changing population size, we must include fitness effects (cf. Section 3). Single Hawk and Dove searchers (owners) gain payoffs π_{H_s} (π_{H_o}) and π_{D_s} (π_{D_o}) per unit of time, respectively. When in pairs, payoffs are given by a payoff bi-matrix

$$\begin{array}{cc} & \begin{array}{cc} H_o & D_o \end{array} \\ \begin{array}{c} H_s \\ D_s \end{array} & \left(\begin{array}{cc} \pi_{H_sH_o}, \pi_{H_oH_s} & \pi_{H_sD_o}, \pi_{D_oH_s} \\ \pi_{D_sH_o}, \pi_{H_oD_s} & \pi_{D_sD_o}, \pi_{D_oD_s} \end{array} \right) \end{array} \qquad (39)$$

where the first (second) payoff in each entry of the matrix is that of the row (column) player. With fitness defined as the average payoff per unit of time (cf. (8)), we now have

$$\Pi_H = \frac{n_{H_sH_o}\left(\frac{\pi_{H_sH_o}}{\tau_{HH}} + \frac{\pi_{H_oH_s}}{\tau_{HH}}\right) + n_{H_sD_o}\frac{\pi_{H_sD_o}}{\tau_{HD}} + n_{H_oD_s}\frac{\pi_{H_oD_s}}{\tau_{HD}} + n_{H_o}\pi_{H_o} + n_{H_s}\pi_{H_s}}{H}$$

and

$$\Pi_D = \frac{n_{D_sD_o}\left(\frac{\pi_{D_sD_o}}{\tau_{DD}} + \frac{\pi_{D_oD_s}}{\tau_{DD}}\right) + n_{H_oD_s}\frac{\pi_{D_sH_o}}{\tau_{HD}} + n_{H_sD_o}\frac{\pi_{D_oH_s}}{\tau_{HD}} + n_{D_o}\pi_{D_o} + n_{D_s}\pi_{D_s}}{D}$$

$$\qquad (40)$$

where $H = 2n_{H_sH_o} + n_{H_sD_o} + n_{H_oD_s} + n_{H_s} + n_{H_o}$ and $D = 2n_{D_sD_o} + n_{H_sD_o} + n_{D_sH_o} + n_{D_s} + n_{D_o}$ are the total number of Hawks and Doves, respectively.

To add the fitness terms in (40) to the distributional dynamics (31) in order to produce a distributional-population dynamics in analogy to model (26), we again split payoffs for pairs into birth and death rates, i.e., $\pi_{ij} = \beta_{ij} - \mu_{ij}$. Distributional-population dynamics are then

$$\frac{dn_{H_s}}{dt} = \nu\left(- \lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}}\right) + (\beta_{H_s} - \mu_{H_s})$$

$$n_{H_s} + \beta_{H_o}n_{H_o} + \frac{\beta_{H_sH_o} + \beta_{H_oH_s}}{\tau_{HH}}n_{H_sH_o} + \frac{\beta_{H_sD_o}}{\tau_{HD}}n_{H_sD_o}$$

$$+ \frac{\beta_{H_oD_s}}{\tau_{HD}}n_{H_oD_s}$$

$$\frac{dn_{H_o}}{dt} = \nu\left(\lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{D_s}n_{H_o} + \frac{n_{H_sH_o}}{\tau_{HH}} + \frac{n_{H_oD_s}}{\tau_{HD}} + \frac{n_{H_sD_o}}{\tau_{HD}}\right)$$

$$- \mu_{H_o}n_{H_o} + \frac{\mu_{H_sH_o} + \mu_{H_oH_s}}{\tau_{HH}}n_{H_sH_o} + \frac{\mu_{D_oH_s}}{\tau_{HD}}n_{H_sD_o} + \frac{\mu_{D_sH_o}}{\tau_{HD}}n_{H_oD_s}$$

$$\frac{dn_{D_s}}{dt} = \nu\left(- \lambda n_{D_s}F - \lambda n_{D_s}n_{H_o} - \lambda n_{D_s}n_{D_o} + \frac{n_{D_sD_o}}{\tau_{DD}} + \frac{n_{H_sD_o}}{\tau_{HD}} + \frac{n_{H_oD_s}}{\tau_{HD}}\right)$$

$$+ (\beta_{D_s} - \mu_{D_s})n_{D_s} + \beta_{D_o}n_{D_o} + \frac{\beta_{D_sD_o} + \beta_{D_oD_s}}{\tau_{DD}}n_{D_sD_o}$$

$$+ \frac{\beta_{D_oH_s}}{\tau_{HD}}n_{H_sD_o} + \frac{\beta_{D_sH_o}}{\tau_{HD}}n_{H_oD_s}$$

$$\frac{dn_{D_o}}{dt} = \nu\left(\lambda n_{D_s}F - \lambda n_{D_s}n_{D_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{D_sD_o}}{\tau_{DD}}\right)$$

$$- \mu_{D_o}n_{D_o} + \frac{\mu_{D_sD_o} + \mu_{D_oD_s}}{\tau_{DD}}n_{D_sD_o} + \frac{\mu_{H_sD_o}}{\tau_{HD}}n_{H_sD_o} + \frac{\mu_{H_oD_s}}{\tau_{HD}}n_{H_oD_s}$$

$$\frac{dn_{H_sH_o}}{dt} = \nu\left(- \frac{n_{H_sH_o}}{\tau_{HH}} + \lambda n_{H_s}n_{H_o}\right) - \frac{\mu_{H_sH_o} + \mu_{H_oH_s}}{\tau_{HH}}n_{H_sH_o}$$

$$\frac{dn_{H_sD_o}}{dt} = \nu\left(- \frac{n_{H_sD_o}}{\tau_{HD}} + \lambda n_{H_s}n_{D_o}\right) - \frac{\mu_{H_sD_o} + \mu_{D_oH_s}}{\tau_{HD}}n_{H_sD_o}$$

$$\frac{dn_{H_oD_s}}{dt} = \nu\left(- \frac{n_{H_oD_s}}{\tau_{HD}} + \lambda n_{D_s}n_{H_o}\right) - \frac{\mu_{H_oD_s} + \mu_{D_sH_o}}{\tau_{HD}}n_{H_oD_s}$$

$$\frac{dn_{D_sD_o}}{dt} = \nu\left(- \frac{n_{D_sD_o}}{\tau_{DD}} + \lambda n_{D_s}n_{D_o}\right) - \frac{\mu_{D_sD_o} + \mu_{D_oD_s}}{\tau_{DD}}n_{D_sD_o}$$

$$\qquad (41)$$

where F is given by (32). Here the model assumes that newborns are single searchers. This makes it important to also write payoffs to singles as differences (e.g., $\pi_{H_o} = \beta_{H_o} - \mu_{H_o}$). Population demography is given by two processes. First, the model assumes demographic changes associated with singles. For example, in the first equation in (41), the term $(\beta_{H_s} - \mu_{H_s})n_{H_s}$ describes changes due to birth and death among single Hawk searchers. Note that, in the simulations below, we assume that only individuals who are on a site either as singles or in pairs can give birth (and so $\beta_{H_s} = \beta_{D_s} = 0$). Term $\beta_{H_o}n_{H_o}$ describes birth for those Hawks that own a site. Second, (41) considers demographic changes due to contests between individuals. For example, term $\frac{\beta_{H_sH_o} + \beta_{H_oH_s}}{\tau_{HH}}n_{H_sH_o}$ describes newborns produced as a consequence of a contest between two Hawks, i.e., when a searching Hawk is paired with an owning Hawk. One of the two Hawks will win the site and will gain fitness by the opportunity of reproducing in the site. The probability of winning the contest and reproducing is captured by terms $\beta_{H_sH_o}$ in the case it is the searching Hawk that wins the contest and $\beta_{H_oH_s}$ when the owning Hawk retains the site after the contest. Term $\frac{\beta_{H_sD_o}}{\tau_{HD}}n_{H_sD_o}$ represents newborn Hawks produced when a searching Hawk is paired with an owning Dove, because in this case we assume that with probability one the Hawk will win the contest. In the second equation for owning Hawks, term

$\frac{\mu_{D_oH_s}}{\tau_{HD}} n_{H_sD_o}$ represents the situation where the owning Dove paired with a searching Hawk dies and the searching Hawk becomes a single owning Hawk. The other terms follow the same logic.

A lengthy but straightforward calculation based on (41) yields

$$\frac{dH}{dt} = \frac{d(2n_{H_sH_o} + n_{H_sD_o} + n_{H_oD_s} + n_{H_s} + n_{H_o})}{dt} = \Pi_H H$$

and

$$\frac{dD}{dt} = \frac{d(2n_{D_sD_o} + n_{H_sD_o} + n_{H_oD_s} + n_{D_s} + n_{D_o})}{dt} = \Pi_D D$$

where Π_H and Π_D are given by (40). Thus, when distributional dynamics are fast (i.e., ν tends to infinity), H and D evolve according to this dynamical system where Π_H and Π_D in (40) are evaluated at the unique equilibrium of (31) for current population sizes.

Since the notation for pairs only indicates how the pair was formed (i.e., there is no owner or searcher when in a pair), we assume that once two individuals occupy a site, their payoffs do not depend on who was the owner and who was the searcher when they encountered each other. In particular, payoffs to Hawks in all Hawk-Hawk pairs are equal as are those in Hawk–Dove pairs. That is $\pi_{HH} = \pi_{H_sH_o} = \pi_{H_oH_s}$, $\pi_{DD} = \pi_{D_sD_o} = \pi_{D_oD_s}$, $\pi_{HD} = \pi_{H_sD_o} = \pi_{H_oD_s}$, and $\pi_{DH} = \pi_{D_sH_o} = \pi_{D_oH_s}$ in (39). Fitnesses (40) then simplify to

$$\Pi_H = \frac{2n_{H_sH_o} \frac{\pi_{HH}}{\tau_{HH}} + (n_{H_sD_o} + n_{H_oD_s}) \frac{\pi_{HD}}{\tau_{HD}} + n_{H_o}\pi_{H_o} + n_{H_s}\pi_{H_s}}{H},$$

$$\Pi_D = \frac{2n_{D_sD_o} \frac{\pi_{DD}}{\tau_{DD}} + (n_{D_sH_o} + n_{D_oH_s}) \frac{\pi_{DH}}{\tau_{HD}} + n_{D_o}\pi_{D_o} + n_{D_s}\pi_{D_s}}{D}. \quad (42)$$

However, population dynamics (41) are too complex for mathematical analysis even when we assume fast distributional dynamics. We thus restrict our attention to the case where τ_{DD} and τ_{HD} tend to 0 as in Example 3 for the remainder of this section.

Example 3 continued. We first derive population dynamics for Hawks and Doves when ν tends to infinity by assuming that distributional dynamics track the unique equilibrium of the simplified model (35) instantaneously. Substituting distributional equilibria (36), (37), and (38) to (42), we obtain

$$\frac{dH}{dt} = \pi_{H_o}H$$

$$\frac{dD}{dt} = \pi_{D_o}D \quad (43)$$

when $H + D \leq K$,

$$\frac{dH}{dt} = H((D + H - K)\lambda\pi_{HD} + \pi_{H_o})$$

$$\frac{dD}{dt} = (K - H)(2(D + H - K)\lambda\pi_{DD} + \pi_{D_o})$$
$$+ (D + H - K)(H\lambda\pi_{DH} + \pi_{D_s}) \quad (44)$$

when $H + D > K$ and $H \leq K$, and

$$\frac{dH}{dt} = \frac{(-2\pi_{HH} + (D\lambda\pi_{HD} + \pi_{H_o} + \pi_{H_s})\tau_{HH})\sqrt{1 + \lambda\tau_{HH}(2H + (H-2K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}^2} -$$
$$\frac{-2\pi_{HH}(1 + H\lambda\tau_{HH}) + \tau_{HH}(D\lambda\pi_{HD} + \pi_{H_o} + \pi_{H_s} + (H-2K)\lambda(D\lambda\pi_{HD} + \pi_{H_o} - \pi_{H_s})\tau_{HH})}{2\lambda\tau_{HH}^2}$$

$$\frac{dD}{dt} = D\left(\pi_{D_s} + \frac{\pi_{DH}\left(-1 + (2K-H)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H-2K)^2\lambda\tau_{HH})}\right)}{2\tau_{HH}}\right) \quad (45)$$

when $H > K$.

To analyze models (43)–(45), we will assume that owners obtain positive payoffs ($\pi_{H_o} > 0$, $\pi_{D_o} > 0$) and searching individuals obtain negative payoffs ($\pi_{H_s} < 0$ and $\pi_{D_s} < 0$). There is then no non-zero equilibrium for (43) in region $H + D \leq K$ because both Hawks and Doves increase exponentially and so all trajectories with initial positive population sizes for Hawks and Doves leave this region. If, in addition, Hawks gain payoff in their Hawk–Dove interacting pairs ($\pi_{HD} \geq 0$), Eq. (44) shows that Hawks are always increasing in the region where $H + D > K$ and $H < K$, and so these trajectories must enter the region where $H > K$. Furthermore, if $\pi_{DH} \leq 0$, [8]Appendix E shows that Eq. (45) has a unique globally asymptotically stable equilibrium. Altogether, this implies that the system of Eqs. (43)–(45) has a globally asymptotically stable equilibrium given by

$$(H, D) = \left(\frac{2 K\lambda(2\pi_{HH}^2 - \pi_{HH}(\pi_{H_o} + 3\pi_{H_s})\tau_{HH} + 2\pi_{H_o}\pi_{H_s}\tau_{HH}^2) + \pi_{H_s}(2\pi_{HH} - (\pi_{H_o} + \pi_{H_s})\tau_{HH})}{2\lambda \, \pi_{H_s}\tau_{HH}(\pi_{H_o}\tau_{HH} - 2\pi_{HH})}\right.$$
$$\left. + \frac{(2\pi_{HH} - (\pi_{H_o} + \pi_{H_s})\tau_{HH})\sqrt{(2 K\lambda\pi_{HH} + \pi_{H_s})^2 - 4 K\lambda\pi_{H_o}\pi_{H_s}\tau_{HH}}}{2\lambda \, \pi_{H_s}\tau_{HH}(\pi_{H_o}\tau_{HH} - 2\pi_{HH})}, 0\right) \quad (46)$$

provided that $2\pi_{HH} \neq \pi_{H_o}\tau_{HH}$, and

$$(H, D) = \left(K\left(\frac{\pi_{H_s}}{\lambda K\pi_{H_o}\tau_{HH} - \pi_{H_s}} - \frac{\pi_{H_o}}{\pi_{H_s}} + 2\right), 0\right)$$

if $2\pi_{HH} = \pi_{H_o}\tau_{HH}$.

Fig. 6 shows the population equilibrium based on simulations of the dynamics (41) applied to the simplified model of Example 3 without assuming fast distributional dynamics. Panel A uses the classic Hawk–Dove payoff matrix

$$\begin{pmatrix} V - C & 2V \\ 0 & V \end{pmatrix} = \begin{pmatrix} V & 2V \\ 0 & V \end{pmatrix} - \begin{pmatrix} C & 0 \\ 0 & 0 \end{pmatrix} \quad (47)$$

(see also (12)) whereas panel B uses (28). The simulations suggest that there is a unique equilibrium for each set of parameters used in this figure. When distributional dynamics are on a similar time scale as population dynamics, we see that there are significant differences in the equilibrium for the two payoff matrices. For classic payoffs, we observe that both Hawks and Doves coexist at the equilibrium (panel A) for all ν's. For the other payoff matrix (28) (panel B), we observe that the range of ν's for which Doves coexist with Hawks is much smaller. As ν tends to infinity, we see in Fig. 6, that the total numbers of Hawks and the total numbers of Doves tends to the equilibrium given by (46).

5. Discussion

Motivated by genetics, where players are alleles, the classical theory of two-strategy, two-player symmetric evolutionary games assumes that all individuals get payoffs only when paired, pairing is random and instantaneous, and the number of pairs is given by the Hardy–Weinberg distribution. With an individual's fitness equated to its expected payoff, the population growth rate (which is assumed to be proportional to the mean fitness of the population) is then frequency dependent but density independent. For the classical Hawk–Dove game, population growth is exponential as in Eq. (15). On the other hand, growth in natural populations is rarely exponential. Density dependent growth is universal. This calls into question the degree to which results of two-player matrix games may be extended to make predictions about natural populations.

The above assumptions on pairs make sense when considering for example mating between sexes, but fitness is also gained/lost

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[8] We will assume that $\pi_{HD} \geq 0$ and $\pi_{DH} \leq 0$ from now on. These conditions are satisfied by both parametrizations of the Hawk–Dove payoff matrices given by (12) and (23) (see also (47) and (28)) that have been used throughout the article.
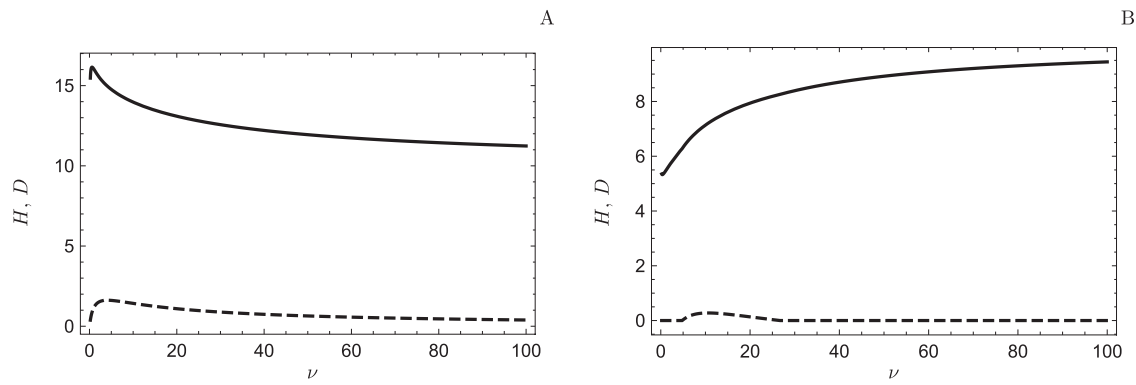
Fig. 6. The dependence of the equilibrium of distributional-population dynamics (41) on ν ($\nu > 0.2$) when interaction times between Hawks (solid line) and Doves (dashed line) and between Doves are very short (i.e., $\tau_{HD} = \tau_{DD} = 0.0001$). Left (respectively, right) panel is for the Hawk–Dove game with payoff matrix (47) (respectively, (28)). Other parameters: $\lambda = 1$, $\tau_{HH} = 1$, $V = 1$, $C = 4$, $K = 10$, $\beta_{H_o} = \beta_{D_o} = 0.2$, $\mu_{H_o} = \mu_{D_o} = 0.1$, $\beta_{H_s} = \beta_{D_s} = 0$, $\mu_{H_s} = \mu_{D_s} = 0.1$.

when individuals are singles. For example, fitness may increase when an individual forages through an increase in its survival probability, or an increase in egg production. In this article, we develop a new theoretical approach that relaxes these assumptions: (i) individuals do not pair instantaneously so that there are singles in the population, (ii) individuals gain/lose fitness not only when paired, but also as singles, and (iii) duration of encounters between individuals depends on their strategies. We find that including singles can regulate population growth which allows the study of both frequency and density of strategies.

Our approach builds on that developed by Křivan and Cressman (2017) who assumed that individuals pair instantaneously, but interactions between different strategies take different time. As a result, the rate (per unit of time) that individuals are paired with each other depends on the strategies of the players. This idea that interaction rates might be strategy-dependent was incorporated into evolutionary game dynamics by Taylor and Nowak (2006). In their analysis of the evolutionary stability of strategy dynamics, the fitness of a strategy is given in units of payoff per interaction (Argasinski and Broom, 2018), and the interaction rates refer to the intensity with which certain strategies will assort with other strategies. This mirrors the classical theory in which the number of interactions determines overall fitness. Our models include the length of time a game is played, so our approach differs fundamentally from Taylor and Nowak (2006) and is more closely related to that of Argasinski and Broom (2018) where the number of games that are played in a period of time is taken into account.[9] This approach allows one to study the fitness of a strategy when fitness includes more than game payoffs, e.g., singles payoff. In Section 2, we see that when singles payoff does not depend on strategy, and interaction times are equal, then the Nash equilibrium of the game is unchanged from classical predictions. Under these assumptions, including singles is equivalent to adding background fitness (Cressman, 1992). However, if singles payoffs depend on strategy, then under the aforementioned assumptions, we see (Fig. 2, panels C and E) that these payoffs contribute more to average fitness because the proportion of singles tends to 1 (respectively, 0) when the total population size, N, tends to zero (respectively, infinity).

In Sections 2 and 3, where payoffs to singles and pairs are density independent, we show that non-instantaneous pair formation can induce density dependence in the population growth where the population growth rate is still given by the average fit-

ness in the population.[10] The existence of a coexistence equilibrium (i.e., an interior equilibrium where both strategies have positive density) relies on a balance between the positive payoff of singles and the negative average payoff from the game (or vice versa). Moreover, the stability of an interior equilibrium for the Hawk–Dove model depends on the parametrization of its payoff matrix, as seen in Fig. 3 of Section 2, where distributional dynamics act on a fast time-scale compared to population dynamics. For instance, an interior population equilibrium may exist for the Hawk–Dove model with classic payoff matrix (12) when the payoffs to singles are negative. However, this equilibrium is never stable (Example 1).[11] On the other hand, when the payoffs to interacting pairs are all decreased by the same amount as in payoff matrix (23) of Example 2,[12] a stable interior equilibrium often emerges if payoffs to singles are positive. Thus, the eco-evolutionary dynamics depend on where fitness is accrued, as remarked in Argasinski and Broom (2013, 2017, 2018) (see also McNamara, 2013).

The population dynamics (16) of Section 2 serve to frame our thinking around relating ecological parameters to V and C from the Hawk–Dove payoff matrix. When these model equations have a stable interior equilibrium (in Example 2), it can be shown using (24) that the proportion of Hawks at equilibrium will increase with increases in V and decrease with increases in C. This is consistent with the classical Hawk–Dove game at the interior ESS where the proportion of Hawks equals $\frac{V}{C}$. On the other hand, in the classical game, Hawks and Doves coexist if and only if the cost when two Hawks fight is higher than their expected gain (i.e., $V < C$) whereas, in Example 2, we show that coexistence may also occur when $V > C$ due to singles receiving payoff. The same result (i.e., coexistence when $V > C$) was shown by Křivan and Cressman (2017) at fixed population size. Specifically, when pairs form instantaneously and interactions between two Hawks take long enough compared to other interactions, they showed that non-aggressiveness can evolve even when $V > C$. Similarly, in the repeated Prisoner's Dilemma game, cooperation evolves when individuals can control how many rounds to continue an interaction (i.e., they can opt-out; Zhang et al., 2016). These models are the limit cases of the model investigated in Section 2 when the mean

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[9] These approaches are equivalent when all interactions take the same amount of time and fitness is accrued only through the game.

[10] Other approaches (e.g., Argasinski and Broom, 2013; Cressman, 1992) to get convergence to non-zero population numbers typically assume some explicit density dependent mechanisms in individual payoff/fitness.

[11] The intuitive reason for this is that the negative payoffs to singles locally stabilizes the extinction equilibrium whereas the positive payoffs from interacting pairs at the distributional equilibrium drives the population to infinity once its size is large enough.

[12] This does not change the evolutionary outcome (i.e., ESS) of the classic Hawk–Dove game (Hofbauer and Sigmund, 1998).

time between encounters tends to zero and the number of singles tends to zero too. Once again, we see that including singles and/or including interaction times can influence the evolutionary predictions.

Although the parameters V and C from the Hawk–Dove game are not well-defined ecological parameters, we show in Section 3 that it is possible to decompose the payoffs from the Hawk–Dove game into payoffs that increase fitness and payoffs that decrease fitness. This allows us to examine population–distributional dynamics when relaxing the assumption that distributional dynamics are fast compared to population dynamics. In particular, non-aggressiveness can evolve when the distributional and population dynamics are on similar time scales. This result does not depend on the amount of time that individuals are paired but only on the relative time scales of the two dynamics. This is illustrated in Fig. 4 where we see that coexistence depends on the speed of distributional dynamics relative to population dynamics.

Our final model (Section 4) includes an explicit density-dependent mechanism in the Hawk–Dove game through competition over a fixed number of breeding sites. With the usual assumption that a Hawk gains the resource (i.e., the site) when interacting with a Dove, Hawks always win at the equilibrium of the distributional dynamics in the sense that Doves can only own breeding sites when there is an insufficient number of Hawks to occupy all sites (Fig. 5). Not surprisingly, Doves are then driven to extinction when population sizes also evolve and the distributional dynamics are fast (i.e., ν is large). Coexistence of Hawks and Doves now requires that the combined population and distributional dynamics operate on a similar time scale (Fig. 6). In particular, as ν increases, Doves go extinct. Interestingly, this effect of increasing ν in the density dependent model of Section 4 is opposite to the coexistence outcome for large ν in Section 3 (Fig. 4) where the model has no *a priori* density dependence.

In sum, we have shown that including singles can induce density dependence into the game's population dynamics. This allows one to study not only the frequency but also the density of strategies. We have been able to study how singles and the relative time scales of the distributional and population dynamics affect the evolutionary predictions of the classical game. Although we have assumed here density independent payoffs to both singles and pairs, it will be interesting to examine in future work how our predictions may be affected by payoffs that can change with the environmental condition.

Appendix A. Uniqueness of distributional equilibrium of (5)

Fix H and D and define $q_H \equiv \frac{n_H}{H}$ (and $q_D \equiv \frac{n_D}{D}$) as the proportion of single Hawks (Doves) in the Hawk (Dove) population. Then, at an equilibrium of (5),

$$
\begin{aligned}
q_H &= \frac{1}{1 + \lambda \tau_{HH} H q_H + \lambda \tau_{HD} D q_D} \\
q_D &= \frac{1}{1 + \lambda \tau_{HD} H q_H + \lambda \tau_{DD} D q_D}
\end{aligned}
\tag{A.1}
$$

since, for example,

$$
\begin{aligned}
q_H(1 + \lambda \tau_{HH} H q_H + \lambda \tau_{HD} D q_D) &= \frac{n_H}{H}\left(1 + \lambda \tau_{HH} H \frac{n_H}{H} + \lambda \tau_{HD} D \frac{n_D}{D}\right) \\
&= \frac{1}{H}(n_H + 2n_{HH} + n_{HD}) = 1
\end{aligned}
$$

by (6).

By Lemma 2 in Garay et al. (2017), there is a unique solution of (A.1) with q_H and q_D between 0 and 1 (in fact, both q_H and q_D will be strictly between 0 and 1) for each fixed H and D. The equilibrium solution of (5) is then

$$
\begin{aligned}
n_H &= H q_H \\
n_D &= D q_D \\
n_{HH} &= \frac{1}{2}\lambda \tau_{HH} n_H^2 \\
n_{HD} &= \lambda \tau_{HD} n_H n_D \\
n_{DD} &= \frac{1}{2}\lambda \tau_{DD} n_D^2
\end{aligned}
$$

which, from (A.1), will satisfy $H = n_H + 2n_{HH} + n_{HD}$ and $D = n_D + n_{HD} + 2n_{DD}$. This will be the only equilibrium solution of (5) for a given H and D.

Appendix B. Stability of equilibria for model (18)

Because eigenvalues of linearized model (18) at extinction equilibrium $(n_H, n_D) = (0, 0)$ are π_H, and π_D, this equilibrium is locally stable when $\pi_H < 0$ and $\pi_D < 0$.

Eigenvalues of linearized model (18) at equilibrium (19) are $(\pi_H \pi_{HH})/(2\pi_H \tau_{HH} - \pi_{HH})$, and $(\pi_{DH}\pi_H - \pi_D \pi_{HH})/(\pi_H \tau_{HD} - \pi_{HH})$. The boundary equilibrium exists (i.e., the Hawk only equilibrium is positive) and is locally stable if and only if $\pi_{HH} < 0$, $\pi_H > 0$, and $\pi_{DH}\pi_H < \pi_D \pi_{HH}$.[13]

Similarly, eigenvalues of linearized model (18) at equilibrium (20) are $\pi_D \pi_{DD}/(2\pi_D \tau_{DD} - \pi_{DD})$, and $(\pi_{DD}\pi_H - \pi_D \pi_{HD})/(\pi_{DD} - \pi_D \tau_{HD})$. This equilibrium exists (i.e., the Dove equilibrium is positive) and locally stable when $\pi_{DD} < 0$, $\pi_D > 0$, and $\pi_D \pi_{HD} < \pi_{DD}\pi_H$.

Stability analysis of the interior equilibrium (21) leads to complex expressions. Instead, we analyze its stability for the Hawk–Dove parametrizations in Examples 1 and 2.

First we consider the parametrization of the Hawk–Dove model given by (12). Using Mathematica (Appendix F), we calculated trace

$$
\begin{aligned}
\mathrm{tr}(J) &= \frac{V(V-C)}{A}\Big(V\big(\pi_D{}^2(-4\tau_{DD} + 9\tau_{HD} - 4\tau_{HH}) \\
&\quad + 2\pi_D \pi_H(\tau_{DD} - 3\tau_{HD} + \tau_{HH}) + \pi_H{}^2 \tau_{HD} + V(\pi_D \\
&\quad - \pi_H)\big) - C(\pi_D(\pi_D(\tau_{HD} - 4\tau_{DD}) + 2\pi_H \tau_{DD}) + V(\pi_D - \pi_H))\Big)
\end{aligned}
$$

and determinant

$$
\det J = \frac{\pi_D V^2(C-V)^2(\pi_H - 2\pi_D)}{A}
$$

of the Jacobian matrix evaluated at the interior equilibrium (22) where

$$
\begin{aligned}
A &= (C-V)\big(V(C-V)(V - 2\pi_D \tau_{DD}) - \tau_{HD}\big(2\pi_D{}^2\tau_{DD}(V-C) \\
&\quad + V(\pi_D(C+V) - \pi_H V))\big) + 2\tau_{HH}V(2\pi_D - \pi_H)((V-C) \\
&\quad (V - 2\pi_D \tau_{DD}) + \tau_{HD}V(2\pi_D - \pi_H)).
\end{aligned}
$$

Using the Reduce command of Mathematica (Appendix F) under the assumptions that equilibrium (22) is interior and parameters V, C, τ_{HH}, τ_{HD}, τ_{DD}, λ are all positive, we found that $\mathrm{tr}(J) < 0$

---

[13] We ignore degenerate cases with eigenvalue 0.

and $\det J > 0$ (i.e., the equilibrium is locally asymptotically stable) if and only if[14]

$$0 < C < V < \frac{C\pi_D{}^2}{(\pi_H - 3\pi_D)^2},$$

$$0 < \tau_{HH} <$$
$$\frac{\tau_{HD}\left(V(\pi_H - 3\pi_D)^2 - C\pi_D{}^2\right) + (V - C)(2\pi_D\tau_{DD}(\pi_H - 2\pi_D) + V(\pi_D - \pi_H))}{2\pi_D V(2\pi_D - \pi_H)},$$

$$\tau_{HD} > \frac{(V - C)(2\pi_D\tau_{DD}(\pi_H - 2\pi_D) + V(\pi_D - \pi_H))}{C\pi_D{}^2 - V(\pi_H - 3\pi_D)^2}.$$

In particular, these conditions imply that the interior equilibrium cannot be stable for the case where $C > V$.

Second we consider the parametrization of the Hawk–Dove model given by (23). From (24), there is an interior equilibrium if and only if $\pi_D > 0$ and $V\pi_H < C\pi_D$. Using Mathematica, we calculated trace

$$\text{tr}(J) = - \frac{C\pi_D V(2C\pi_D\tau_{DD} + V(\pi_D\tau_{HD} - 2\pi_H\tau_{DD} + V))}{B}$$

and determinant

$$\det J = \frac{\pi_D V^3(C\pi_D - \pi_H V)}{B}$$

of the Jacobian matrix evaluated at the interior equilibrium (24) where

$$B = 2C^2\pi_D{}^2\tau_{DD}\tau_{HD} + \pi_D V(-4C\pi_H\tau_{DD}\tau_{HD} + CV(2\tau_{DD} + \tau_{HD})$$
$$+ V^2(\tau_{HD} + 2\tau_{HH}) - 4\pi_H\tau_{DD}\tau_{HH}V) + 2\pi_D{}^2\tau_{HH}V$$
$$(2C\tau_{DD} + \tau_{HD}V) + V^2(V - 2\pi_H\tau_{DD})(V - \pi_H\tau_{HD}).$$

Using the `Reduce` command of Mathematica (Appendix F) under the assumptions that equilibrium (24) is interior and parameters V, C, τ_{HH}, τ_{HD}, τ_{DD}, λ are all positive, we found that $\text{tr}(J) < 0$ and $\det J > 0$ (i.e., the equilibrium is locally asymptotically stable) whenever it exists. Note that these conditions can hold both when $V > C$ as well as when $C < V$.

Appendix C. Unique equilibrium solution to distributional dynamics (31)

We want to show that, given H and D, there exists a unique distributional equilibrium of system (31), for which the number of occupied sites is at most K.

Eq. (33) shows that the system either converges to a state where there are no searchers ($n_{H_s} + n_{D_s} = 0$) or to the set of states where there are no free sites ($F = 0$).[15] We show that at the distributional equilibrium there are no searchers if and only if $H + D \leq K$. If there are no searchers, there are no pairs and so all individuals are owners (i.e., $n_{H_o} = H$ and $n_{D_o} = D$) and, consequently, the total population size cannot be larger than the number of sites, i.e., $H + D \leq K$. Conversely, suppose that the total number of individuals satisfies $H + D \leq K$. If there were some searchers at the distributional equilibrium, there would be no free sites (i.e., all sites would be occupied) and so $H + D = K$. As we assumed there were some searchers, the total population would be larger than K, a contradiction. Thus, all individuals are owners if and only if $H + D \leq K$ and in this case, $n_{H_o} = H$, and $n_{D_o} = D$ is the unique equilibrium.

Now we assume that $H + D > K$. Thus, there must be searchers at the equilibrium and (33) implies that $F = 0$, i.e., all sites are occupied (i.e., $K = n_{H_o} + n_{D_o} + n_{H_sH_o} + n_{H_sD_o} + n_{D_sD_o} + n_{H_oD_s}$). Then,

by adding the first and fifth equations of (31), an equilibrium of (31) must satisfy $n_{H_s}(F + n_{D_o}) = 0$. Also, if $n_{H_s} > 0$, then $F = n_{D_o} = 0$ and so all sites are occupied by Hawks and $H > K$. When $H > K$ then $n_{H_s} > 0$, thus, $n_{H_s} = 0$ if and only if $H \leq K$.

First we assume that $H \leq K$. Then all Hawks occupy sites as owners or in H_oD_s pairs (i.e., $H = n_{H_o} + n_{H_oD_s}$) and all other $K - H$ sites are occupied by Doves as owners or in D_sD_o pairs. As there are no Hawks searching, we have $n_{H_sH_o} = n_{H_sD_o} = 0$. Under these assumptions, equations for equilibrium of model (31) are

$$K = n_{H_o} + n_{D_o} + n_{D_sD_o} + n_{H_oD_s} = H + n_{D_o}(1 + \lambda\tau_{DD}n_{D_s}) \quad \text{(C.1a)}$$

$$H = n_{H_o}(1 + \lambda\tau_{HD}n_{D_s}) \quad \text{(C.1b)}$$

$$D = n_{D_s} + n_{D_o} + 2n_{D_sD_o} + n_{D_sH_o}$$
$$= n_{D_o} + n_{D_s} + 2\lambda\tau_{DD}n_{D_s}n_{D_o} + \lambda\tau_{HD}n_{D_s}n_{H_o}. \quad \text{(C.1c)}$$

From (C.1a) and (C.1b), solve for n_{D_o} and n_{H_o} in terms of n_{D_s}. Then system (C.1) can be re-written as a cubic equation for unknown n_{D_s}

$$n_{D_s}^3\lambda^2\tau_{DD}\tau_{HD} +$$
$$\lambda n_{D_s}^2(\lambda\tau_{DD}\tau_{HD}(2K - D - H) + \tau_{DD} + \tau_{HD}) +$$
$$n_{D_s}(-D\lambda(\tau_{DD} + \tau_{HD}) - 2H\lambda\tau_{DD} + \lambda K(2\tau_{DD} + \tau_{HD}) + 1)$$
$$-D - H + K = 0. \quad \text{(C.2)}$$

Since this cubic has positive leading coefficient and negative constant term, there is exactly one nonnegative root if the coefficient of n_{D_s} is negative whenever the coefficient of $n_{D_s}^2$ is negative by Descartes' rule of signs. To see this, suppose that

$$\lambda\tau_{DD}\tau_{HD}(2K - D - H) + \tau_{DD} + \tau_{HD} < 0.$$

That is

$$2K\lambda\tau_{DD}\tau_{HD} + \tau_{DD} + \tau_{HD} < \lambda D\tau_{DD}\tau_{HD} + \lambda H\tau_{DD}\tau_{HD}.$$

Then

$$2K\lambda\tau_{DD} + 1 < \lambda D\tau_{DD} + \lambda H\tau_{DD}.$$

Since $D > K$,

$$2K\lambda\tau_{DD} + \lambda K\tau_{HD} + 1 < \lambda D\tau_{DD} + \lambda H\tau_{DD}$$
$$+ \lambda D\tau_{HD} < \lambda D(\tau_{DD} + \tau_{HD}) + 2H\lambda\tau_{DD}.$$

Thus, the coefficient of n_{D_s},

$$-\lambda D(\tau_{DD} + \tau_{HD}) - 2\lambda H\tau_{DD} + \lambda K(2\tau_{DD} + \tau_{HD}) + 1,$$

is negative. Thus, the cubic (C.2) has exactly one positive root for n_{D_s}. We see from (C.1a) that $K - H = n_{D_o}(1 + \lambda\tau_{DD}n_{D_s})$. Since $H \leq K$, it follows that $n_{D_o} \geq 0$ and so we have a solution with $n_{H_o}, n_{D_sD_o}$ and $n_{H_oD_s}$ all nonnegative.

Second, if $H > K$, then $n_{H_s} > 0$ and all K sites are occupied by Hawks (since $F = n_{D_o} = 0$) either as owners or in H_oH_s and H_oD_s pairs. As there are no Dove owners, we have the following three equations

$$K = n_{H_o} + n_{H_sH_o} + n_{H_oD_s} = n_{H_o} + \lambda\tau_{HH}n_{H_s}n_{H_o} + \lambda\tau_{HD}n_{D_s}n_{H_o} \quad \text{(C.3a)}$$

$$H = n_{H_o} + n_{H_s} + 2\lambda\tau_{HH}n_{H_s}n_{H_o} + \lambda\tau_{HD}n_{D_s}n_{H_o} \quad \text{(C.3b)}$$

$$D = n_{D_s} + n_{D_sH_o} = n_{D_s} + \lambda\tau_{HD}n_{D_s}n_{H_o}. \quad \text{(C.3c)}$$

System (C.3) can be re-written as a cubic equation for unknown n_{H_o}

$$\lambda^2\tau_{HD}\tau_{HH}n_{H_o}^3 + \lambda n_{H_o}^2(\lambda\tau_{HH}\tau_{HD}(H + D - 2K) + (\tau_{HD} + \tau_{HH}))$$
$$+ (1 + \lambda(\tau_{HD}(D - K) + \tau_{HH}(H - 2K)))n_{H_o} - K = 0.$$

$$\text{(C.4)}$$

---

[14] Here, we ignore the degenerate cases where $3\pi_D = \pi_H$ or $C\pi_D{}^2 = V(\pi_H - 3\pi_D)^2$.

[15] This equation is also important in that it guarantees that model (31) is ecologically well-defined. That is, all state variables (i.e., the number of singles and pairs) as well as the number of free sites must stay non-negative when initially non-negative.

Again, suppose the coefficient of $n_{H_o}^2$ is negative. That is,

$$\lambda \tau_{HH} \tau_{HD}(H + D - 2K) + (\tau_{HD} + \tau_{HH}) < 0.$$

Then $H + D < 2K$ and

$$\lambda H \tau_{HD} + \lambda D \tau_{HD} + 1 < 2\lambda K \tau_{HD}.$$

Thus

$$\lambda \tau_{HD}(H - K) + \lambda D \tau_{HD} + 1 < \lambda K \tau_{HD}.$$

Since $H > K$,

$$\lambda D \tau_{HD} + 1 < \lambda K \tau_{HD}$$

and

$$1 + \lambda D \tau_{HD} + \lambda H \tau_{HH} < \lambda K \tau_{HD} + 2\lambda K \tau_{HH}$$

since $H < 2K$. That is, the coefficient of n_{H_o} is negative and so the cubic (C.4) has exactly one positive root for n_{H_o} by Descartes' rule of signs. It follows from (C.3c) that $n_{D_s} > 0$. Moreover, from (C.3a) and (C.3b), we see that $K = H - n_{H_s}(1 + \lambda \tau_{HH} n_{H_o})$. Since $H \geq K$, we have $n_{H_s}, n_{H_s H_o}, n_{H_o D_s}$ are all nonnegative.

Appendix D. Global stability of the unique distributional equilibrium of (35) for Example 3

To prove global asymptotic stability, we first show that trajectories of (35) converge to an equilibrium point. Since there is a unique equilibrium point in each of the three regions in the main text, the equilibrium is globally asymptotically stable if it is locally asymptotically stable (we show this local stability second).

From (33), either F converges to 0 or $n_{H_s} + n_{D_s}$ converges to 0 for a fixed trajectory of (35).

Case 1 ($n_{H_s} + n_{D_s}$ **converges to 0**). By the last equation of (35), $n_{H_s H_o}$ converges to 0. Thus $n_{H_o} = H - 2n_{H_o H_s} - n_{H_s}$ converges to H and $n_{D_o} = D - n_{D_s}$ converges to D. That is, $H + D \leq K$ and the trajectory converges to equilibrium (36).

Case 2 ($n_{H_s} + n_{D_s}$ **does not converge to 0**). Since F converges to 0, $H + D \geq K$ with equality if and only if $n_{H_s} = 0$ and $n_{D_s} = 0$. Thus, $H + D > K$.

From (35),

$$\frac{d(n_{H_s} + n_{H_s H_o})}{dt} = -\lambda n_{H_s}(F + n_{D_o}). \tag{D.1}$$

Thus either $n_{H_s} + n_{H_s H_o}$ converges to 0 or $n_{H_s}(F + n_{D_o})$ converges to 0.

Case 2(i) ($n_{H_s} + n_{H_s H_o}$ **converges to 0**). Then n_{H_o} converges to H (and so $H \leq K$) and $n_{H_o} + n_{D_o}$ converges to K (and so n_{D_o} converges to $K - H$). The trajectory converges to equilibrium (37).

Case 2(ii) ($n_{H_s} + n_{H_s H_o}$ **does not converge to 0**). From (D.1), $n_{H_s} + n_{H_s H_o}$ is decreasing and so converges to $C > 0$. Also, $n_{H_o} + n_{H_s H_o} = H - (n_{H_s} + n_{H_s H_o})$ is increasing to $H - C > 0$. Then $n_{D_o} = K - F - (n_{H_o} + n_{H_s H_o})$ converges to $K - (H - C)$ since F converges to 0. We claim that n_{D_o} converges to 0 (i.e., $K = H - C$). Otherwise, n_{H_s} converges to 0 (since $n_{H_s} n_{D_o}$ converges to 0) and $n_{H_s H_o}$ converges to $C > 0$. But

$$\frac{dn_{H_s H_o}}{dt} = -\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda n_{H_s} n_{H_o} < 0$$ when $n_{H_s} = 0$ and $n_{H_s H_o} = C > 0$ and so $n_{H_s H_o}$ cannot converge to C. Thus, n_{D_o} con-

verges to 0 and n_{D_s} converges to D. Also, $n_{H_s} + n_{H_s H_o}$ converges to K and so $H > K$. Furthermore, for large t,

$$\frac{dn_{H_s H_o}}{dt} = -\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda n_{H_s} n_{H_o} \approx -\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda(C - n_{H_s H_o})(H - C - n_{H_s H_o}).$$
$$\tag{D.2}$$

The approximation gets better as t increases along the trajectory. Thus, the dynamics on the (omega) limit set of this trajectory for (35) is described by the one-dimensional differential equation for $n_{H_s H_o}$. Since trajectories are bounded, $n_{H_s H_o}(t)$ must converge to an equilibrium value for the given trajectory. That is, all components of the trajectory converge to the equilibrium given by (38).

We now show that the unique equilibrium is locally asymptotically stable. As the number of Doves that jointly occupy sites tends to 0,[16] all Doves are singles ($D = n_{D_s} + n_{D_o}$), and Hawks are either singles or in Hawk-Hawk pairs ($H = n_{H_s} + n_{H_o} + 2n_{H_s H_o}$). Substituting $n_{H_s H_o} = (H - n_{H_s} - n_{H_o})/2$ and $n_{D_o} = D - n_{D_s}$ into (35) leads to simplified distributional dynamics

$$\frac{dn_{H_s}}{dt} = -\frac{1}{2}\lambda n_{H_s}(2K + n_{H_o} + n_{H_s} - H) + \frac{H - n_{H_o} - n_{H_s}}{2\tau_{HH}}$$
$$\frac{dn_{H_o}}{dt} = \frac{H - n_{H_o} - n_{H_s} + n_{H_s}\lambda \tau_{HH}(2K - H - 3n_{H_o} + n_{H_s})}{2\tau_{HH}}$$
$$\frac{dn_{D_s}}{dt} = \frac{1}{2}\lambda n_{D_s}(H - 2K - 2n_{D_s} + n_{H_o} - 3n_{H_s}) + \lambda D(n_{D_s} + n_{H_s}).$$
$$\tag{D.3}$$

Finally, as shown below, the equilibrium points (36), (37), and (38) are locally asymptotically stable.

Using Mathematica (Appendix F), we calculated eigenvalues of the Jacobian matrix of (35) evaluated at equilibria (36)–(38). The eigenvalues at equilibrium (36) are

$$\lambda_1 = \lambda(H + D - K),$$

$$\lambda_2 = -\frac{\sqrt{4H\lambda \tau_{HH} + (\lambda K \tau_{HH} - 1)^2} + \lambda K \tau_{HH} + 1}{2\tau_{HH}},$$

$$\lambda_3 = \frac{\sqrt{4H\lambda \tau_{HH} + (\lambda K \tau_{HH} - 1)^2} - \lambda K \tau_{HH} - 1}{2\tau_{HH}}.$$

These eigenvalues are real and they are all negative when $H + D < K$.

The eigenvalues at equilibrium (37) are

$$\lambda_1 = \lambda(K - H - D),$$

$$\lambda_2 = -\frac{\sqrt{4H\lambda \tau_{HH} + (\lambda K \tau_{HH} - 1)^2} + \lambda K \tau_{HH} + 1}{2\tau_{HH}},$$

$$\lambda_3 = \frac{\sqrt{4H\lambda \tau_{HH} + (\lambda K \tau_{HH} - 1)^2} - \lambda K \tau_{HH} - 1}{2\tau_{HH}}.$$

These eigenvalues are real and they are all negative when $H + D > K$ and $H < K$.

The eigenvalues at equilibrium (38) are

$$\lambda_1 = \frac{1 - 2D\lambda \tau_{HH} + \lambda \tau_{HH}(2K - H) - \sqrt{\lambda \tau_{HH}(\lambda \tau_{HH}(2K - H)^2 + 2H) + 1}}{2\tau_{HH}}$$

$$\lambda_2 = -\frac{\sqrt{\lambda \tau_{HH}(\lambda \tau_{HH}(2K - H)^2 + 2H) + 1}}{\tau_{HH}}$$

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[16] For example, from (31), $\frac{dn_{H_s D_o}}{dt} \leq -\frac{n_{H_s D_o}}{\tau_{HD}} + \lambda n_{H_s} n_{D_o} < 0$ if $n_{H_s D_o} > 0$ and τ_{HD} is small enough.

$$\lambda_3 = \frac{1 + \lambda\tau_{HH}(2K - H) - \sqrt{\lambda\tau_{HH}(\lambda\tau_{HH}(2K - H)^2 + 2H) + 1}}{2\tau_{HH}}.$$

All three eigenvalues are negative when $H > K$.

Thus, in all three cases, the unique distributional equilibrium of (D.3) is locally asymptotically stable.

Appendix E. Unique equilibrium solution of (45)

To find equilibria of (45), notice that $dD/dt < 0$ if $D > 0$ under our assumptions that $\pi_{D_s} < 0$ and $\pi_{DH} \leq 0$ since

$$-1 + (2K - H)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})} > 0$$

when $H > K$. Thus, any equilibrium of (45) satisfies $D = 0$.

Substituting $D = 0$ into the right hand-side of the equation for Hawks in (45), an equilibrium $(H, 0)$ satisfies

$$\frac{-2\pi_{HH}(1 + H\lambda\tau_{HH}) + \tau_{HH}(\pi_{H_o} + \pi_{H_s} + (H - 2K)\lambda(\pi_{H_o} - \pi_{H_s})\tau_{HH})}{-2\pi_{HH} + (\pi_{H_o} + \pi_{H_s})\tau_{HH}} =$$

$$\sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})}. \quad \text{(E.1)}$$

We note that every solution H of the above equation must satisfy

$$\frac{-2\pi_{HH}(1 + H\lambda\tau_{HH}) + \tau_{HH}(\pi_{H_o} + \pi_{H_s} + (H - 2K)\lambda(\pi_{H_o} - \pi_{H_s})\tau_{HH})}{-2\pi_{HH} + (\pi_{H_o} + \pi_{H_s})\tau_{HH}} \geq 0.$$
$$\text{(E.2)}$$

Solving (E.1) by squaring both sides leads to two expressions

$$H_{\pm} = \frac{2K\lambda(2\pi_{HH}^2 - \pi_{HH}(\pi_{H_o} + 3\pi_{H_s})\tau_{HH} + 2\pi_{H_o}\pi_{H_s}\tau_{HH}^2) + \pi_{H_s}(2\pi_{HH} - (\pi_{H_o} + \pi_{H_s})\tau_{HH})}{2\lambda\pi_{H_s}\tau_{HH}(\pi_{H_o}\tau_{HH} - 2\pi_{HH})} \pm$$

$$\frac{(2\pi_{HH} - (\pi_{H_o} + \pi_{H_s})\tau_{HH})\sqrt{(2K\lambda\tau_{HH} + \pi_{H_s})^2 - 4K\lambda\pi_{H_o}\pi_{H_s}\tau_{HH}}}{2\lambda\pi_{H_s}\tau_{HH}(\pi_{H_o}\tau_{HH} - 2\pi_{HH})}. \quad \text{(E.3)}$$

Using Mathematica (with assumptions $K > 0$, $\lambda > 0$, $\tau_{HH} > 0$, $\pi_{H_s} < 0$, $\pi_{H_o} > 0$, $\pi_{D_s} < 0$, $\pi_{D_o} > 0$, see Appendix F) we show that condition (E.2) evaluated at H_- cannot hold when $H_- > K$ and so $(H, D) = (H_-, 0)$ is not an equilibrium of (45). H_+ is the only solution that satisfies both conditions (provided we assume $2\pi_{HH} \neq \pi_{H_o}\tau_{HH}$).

Moreover, if $D = 0$ in the right-hand side of (45), then dH/dt is positive when $H = K$ and tends to minus infinity as the number of Hawks increases to infinity (because $\pi_{H_s} < 0$). Thus, the equilibrium $(H_+, 0)$ is globally asymptotically stable for Example 3.

Appendix F. Mathematica notebook

This appendix contains Mathematica notebook with symbolic calculations used in the text.

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