

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

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Abstract

Game theoretic models of evolution such as the Hawk-Dove game assume that individuals gain fitness (which is a proxy of the per capita 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 NE 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.

Keywords: Contest competition, evolutionary game theory, exploitative competition, Hawk-Dove game, pair formation, population dynamics

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1 **1. Introduction**

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

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

17 In Section 2, we start with the replicator equation (Taylor and Jonker, 1978)
18 that has often been used in the context of evolutionary modeling. Replicator
19 dynamics assume that a strategy’s growth rate is given by its average payoff
20 (fitness). The standard approach also assumes that individuals meet at random
21 (which implicitly means that all interaction times must be the same) and that
22 payoff is density independent since it is given by this pairwise interaction. The
23 replicator equation for two-strategy games then predicts that the frequencies of
24 strategies in the population will converge to an evolutionarily stable strategy
25 (ESS) of the game and that the overall population will grow (or decay) expo-
26 nentially thereafter (Hofbauer and Sigmund, 1998; Cressman, 2003). These two
27 properties are captured by saying that replicator dynamics are frequency de-
28 pendent but density independent. Section 2 generalizes the standard replicator
29 equation to the case where interaction times depend on strategies and singles
30 get some (density independent) fitnesses too. We show that the replicator equa-
31 tion can now lead to stable equilibria at finite, positive population size. We
32 document evolutionary outcomes where both strategies coexist at the equilib-
33 rium using generalizations of the Hawk-Dove model and distributional dynamics
34 that evolve on a faster time scale compared to the replicator equation. In other
35 words, it is no longer necessary to assume *a priori* density dependent fitnesses
36 to obtain coexistence.

37 Section 3 considers the effect on the stable evolutionary outcome when dis-
38 tributional and population dynamics operate on a commensurable time scale.
39 To do so, the combined dynamics must model how payoffs translate into chang-
40 ing numbers of singles and pairs. Specifically, we assume that payoffs to singles
41 only influence the number of singles whereas payoffs to pairwise interactions are
42 interpreted in terms of birth and death rates of the individuals in the pair and
43 any newborns increase the number of singles. It is shown that non-zero death

44 rates when in pairs alter the stable evolutionary outcome in the combined dy-
 45 namics. In fact, for our generalized Hawk-Dove game, we find that the stable
 46 coexistence equilibrium when distributional dynamics are fast can disappear
 47 altogether when time scales are similar and, in such cases the Doves go extinct.

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

57 Through the models of Sections 2, 3 and 4, we show how implicit and explicit
 58 density dependence arises naturally when population and evolutionary models
 59 are integrated. The Discussion (Section 5) expands further on this theme by
 60 emphasizing how the Hawk-Dove game, originally developed to model the fre-
 61 quency evolution of aggressive behavior in a biological species, can serve to
 62 understand the effects of competition on the combined evolutionary and popu-
 63 lation outcome.

64 **2. Evolutionary games when distribution dynamics are independent** 65 **of fitness**

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

69 *2.1. Distributional dynamics, fitness, and Nash equilibrium*

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

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

73 These payoffs to the row player result from pairwise interactions between players.
 74 Classic evolutionary game theory interprets the payoffs as changes in individual
 75 fitnesses due to an interaction. To calculate fitness, one then needs to describe
 76 the distribution of interacting pairs in the population.

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

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

80 where n_{ij} is the number of ij pairs ($i, j = H, D$), $H = 2n_{HH} + n_{HD}$, and
81 $D = 2n_{DD} + n_{HD}$, where H is the number of Hawks, D is the number of
82 Doves, and $N = H + D$ is the population size.² In mixed pairs, we do not
83 distinguish between HD and DH pairs, i.e., n_{HD} consists of all mixed pairs.
84 Assuming that the distribution of pairs is at its Hardy–Weinberg equilibrium,
85 the expected payoffs per interaction to a Hawk and to a Dove are

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

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

93 Following Krivan and Cressman (2017), we introduce the (symmetric) inter-
94 action time matrix

$$\begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \left(\begin{array}{cc} \tau_{HH} & \tau_{HD} \\ \tau_{HD} & \tau_{DD} \end{array} \right)\end{array}\tag{4}$$

95 where τ_{ij} is the average interaction time an ij pair takes (with all τ 's positive).
96 Furthermore, contrary to classic evolutionary game theory, we will not assume
97 that all individuals instantaneously pair, i.e., we consider singles in the popula-
98 tion. The problem of finding the distributional equilibrium of pairs and singles
99 is then much more complex when compared to the Hardy–Weinberg distribution
100 (2).

101 Let n_H and n_D denote the numbers of singles in the population. Consider

²Note 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.

102 the distributional dynamics of pairs and singles

$$\begin{aligned}
\frac{dn_H}{dt} &= -\lambda n_H^2 - \lambda n_H n_D + 2 \frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} \\
\frac{dn_D}{dt} &= -\lambda n_D^2 - \lambda n_H n_D + 2 \frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}} \\
\frac{dn_{HH}}{dt} &= -\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2} n_H^2 \\
\frac{dn_{HD}}{dt} &= -\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D \\
\frac{dn_{DD}}{dt} &= -\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2} n_D^2
\end{aligned} \tag{5}$$

103 that leaves the number of Hawks and Doves unchanged. These dynamics model a
104 pair formation process (see also Mylius, 1999) that is based on the mass action
105 law whereby single individuals meet at random with encounter (or pairing)
106 rate λ . The 2's and 1/2's in these equations relate to the fact that two single
107 individuals appear when a pair disbands and that two singles produce one pair
108 when they meet, respectively. Appendix A shows that, given H and D , there
109 exists a unique distributional equilibrium of (5). This distributional equilibrium
110 can be obtained using computer algebra software (Appendix F), but it is too
111 complicated for analysis. We observe that at the distributional equilibrium we
112 have a generalized Hardy–Weinberg distribution

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

113 If individuals instantaneously pair (i.e., λ converges to infinity in distribu-
114 tional dynamics (5)), the pair dynamics are described by (Křivan and Cressman,
115 2017)

$$\begin{aligned}
\frac{dn_{HH}}{dt} &= -\frac{n_{HH}}{\tau_{HH}} + \frac{\left(\frac{2n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}\right)^2}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)} \\
\frac{dn_{HD}}{dt} &= -\frac{n_{HD}}{\tau_{HD}} + \frac{2\left(\frac{2n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}\right)\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)} \\
\frac{dn_{DD}}{dt} &= -\frac{n_{DD}}{\tau_{DD}} + \frac{\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)^2}{4\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}}\right)}.
\end{aligned} \tag{7}$$

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

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

$$\Pi_H = \frac{2n_{HH}}{H} \frac{\pi_{HH}}{\tau_{HH}} + \frac{n_{HD}}{H} \frac{\pi_{HD}}{\tau_{HD}} + \frac{n_H}{H} \pi_H, \quad (8)$$

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

123 We now analyze the game that consists of the Hawk and Dove strategies
 124 together with their fitnesses (8) evaluated at the unique equilibrium distribution
 125 of (5). Substituting equilibrium distribution of pairs (6) in the equation for an
 126 interior Nash equilibrium (NE) $\Pi_H = \Pi_D$ and into the total population size
 127 $N = n_H + n_D + 2n_{HH} + 2n_{HD} + 2n_{DD}$ leads to the following system of equations

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

128 and

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

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

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

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

133 and

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

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

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

136 In particular, the NE depends on population size when there are payoffs to singles.
 137 This contrasts with the classic result of evolutionary game theory whereby
 138 the strategy proportion at NE depends only on the payoff matrix and not on
 139 N . On the other hand, in the special case where the payoff to singles for both

140 strategies are the same (i.e., $\pi_H = \pi_D$),³ we recover the classic result (Hof-
 141 bauer and Sigmund, 1998) of matrix game theory with two strategies and equal
 142 interaction times where the NE proportion of Hawks is

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

143 In the following example, our analysis of the Hawk-Dove model with stan-
 144 dard payoff matrix shows clearly that, in general, interior NE depend both on
 145 population size and on interaction times. This raises the question of the appli-
 146 cability of classic evolutionary game theory to real populations. In particular,
 147 the classic results require that all interactions take the same amount of time
 148 and that all single individuals have the same payoff per unit of time.

149 **Example 1.** The Hawk-Dove model (e.g., Maynard Smith and Price, 1973;
 150 Krivan and Cressman, 2017) has payoff matrix

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

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

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

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

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

³These equal payoffs to singles can be considered a type of strategy-independent back-
 ground 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).

169 When interaction times are not all the same, interior NE can be approxi-
 170 mated by numerically solving equations (9) and (10). The proportion of Hawks
 171 at NE are shown in the right panels of Figure 1 as a function of τ_{HH} when all
 172 other interaction times are 1. The top row of Figure 1 shows the case where
 173 individuals pair almost instantaneously, because pairing rate λ is high. In this
 174 case, there are practically no singles and distributional dynamics converge to
 175 (7). Panel B then corresponds with Figure 3B in Krivan and Cressman (2017)
 176 where instantaneous pairing was assumed. When pairing is not instantaneous
 177 and singles payoffs are negative but unequal (right panels D, F, H, J), it can
 178 be shown for the Hawk-Dove payoffs (12) that there is a finite threshold value
 179 such that the all Hawk population is a NE if and only if fighting time τ_{HH} is
 180 above this threshold. Moreover, panels D and J with intermediate pairing rate
 181 ($\lambda = 1$) document the existence of two interior NE when τ_{HH} is sufficiently
 182 large. In this case, one interior NE is stable (indicated by a solid curve) since
 183 $\Pi_H - \Pi_D$ is positive (negative) just below (above) the curve and the other is
 184 unstable (indicated by a dashed curve). In both panels, all Hawks is then a NE
 185 as well since $\Pi_H > \Pi_D$ when $p_H = 1$. Panel F assumes yet lower pairing rate
 186 and we observe complex dependence of NEs on interaction times between two
 187 Hawks. In particular, it shows that for short interaction times between Hawks,
 188 the proportion of Hawks is below $V/C = 1/2$. As this interaction time increases,
 189 the proportion of Hawks increases too, and a second NE where initially all indi-
 190 viduals are Hawks appears. For intermediate interaction times between Hawks
 191 (approx. $4.9 < \tau_{HH} < 9.6$), the only NE is all Hawks. For yet higher interaction
 192 times, there are again two interior NE, and the stable lower one decreases with
 193 increasing interaction time. Finally, for extremely low pairing rate and $\pi_D > \pi_H$
 194 (panels G and H), the all Dove population is a NE independent of fighting time
 195 when population size is small enough since almost all individuals are singles.

196 2.2. Replicator and population dynamics

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

$$\begin{aligned}
 \frac{dH}{dt} &= \Pi_H H \\
 \frac{dD}{dt} &= \Pi_D D
 \end{aligned}
 \tag{14}$$

205 where the per capita population growth rate is equal to fitness. Moreover, by
 206 the second assumption, fitnesses are given by (3) and so population dynamics

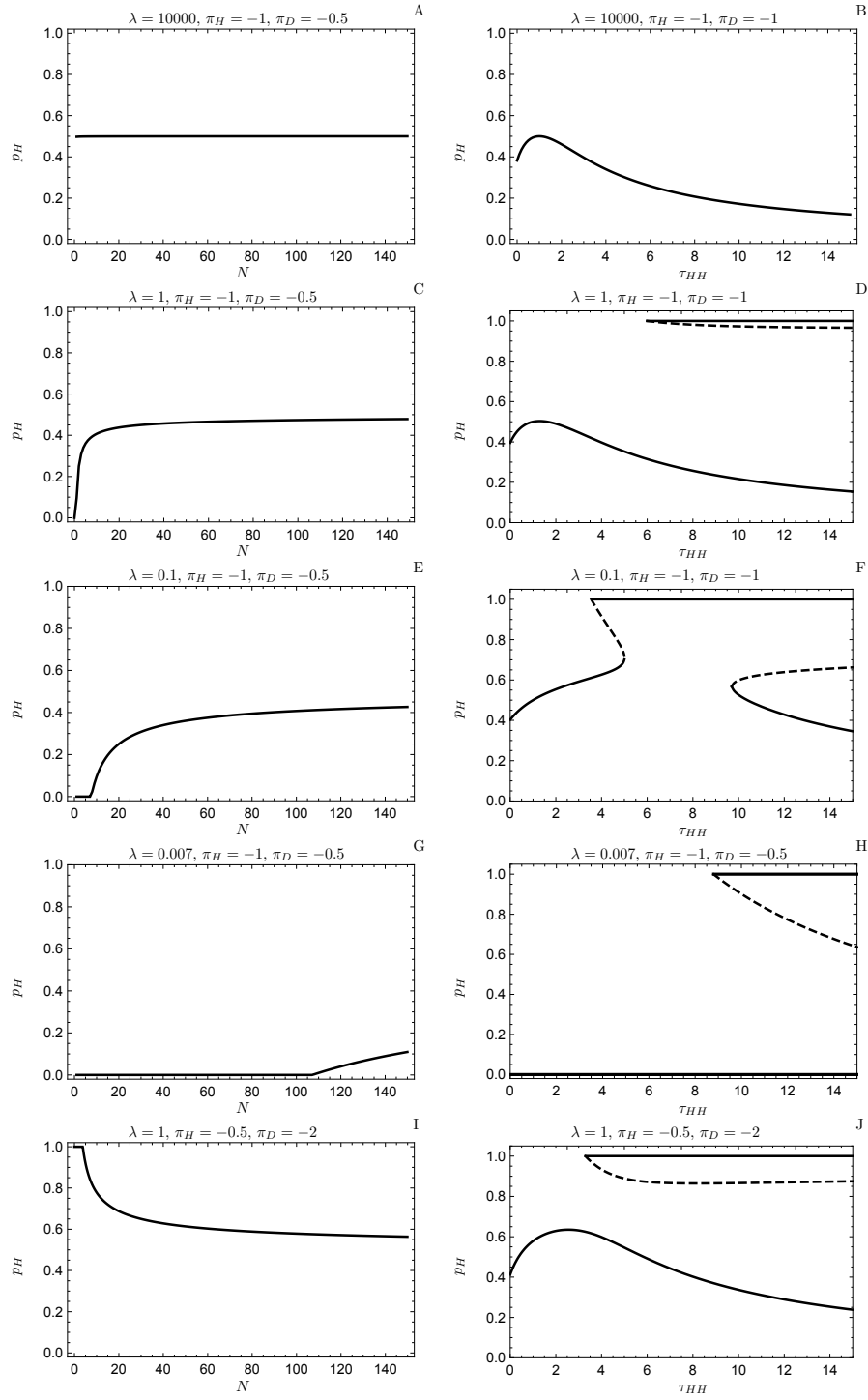


Figure 1:

Figure 1: (Previous page.) 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 ($\lambda = 10000$), the second and fifth rows intermediate pairing rate ($\lambda = 1$), and 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 Figure 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: $\tau_{HD} = 1$, $\tau_{DD} = 1$, $V = 1$, $C = 2$.

207 (14) can be rewritten in terms of the proportion $p_H \equiv H/(H + D)$ of Hawks
 208 and the total population size $N \equiv H + D$ as

$$\begin{aligned} \frac{dp_H}{dt} &= p_H(1 - p_H) \left(\Pi_H - \Pi_D \right) \\ \frac{dN}{dt} &= \bar{\Pi}N, \end{aligned} \quad (15)$$

209 where $\bar{\Pi} = p_H \Pi_H + p_D \Pi_D$ is the average fitness in the population. Since
 210 $\Pi_H = p_H \pi_{HH} + p_D \pi_{HD}$ and $\Pi_D = p_H \pi_{DH} + p_D \pi_{DD}$ where $p_D \equiv 1 - p_H$,
 211 the proportion of Hawks evolves according to the replicator equation of classic
 212 evolutionary game theory which is independent of total population size. It is
 213 well-known (Hofbauer and Sigmund, 1998) that every trajectory of the repli-
 214 cator equation for a two-strategy game evolves to an equilibrium.⁴ Depending
 215 on whether the average fitness $\bar{\Pi}$ in the population is positive or negative at
 216 this equilibrium, the population size will then either grow (in which case the
 217 extinction equilibrium $(H, D) = (0, 0)$ is unstable) or decay (the extinction equi-
 218 librium is then stable) exponentially and so no positive equilibrium population
 219 size exists. Such population dynamics are called density independent.

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

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

⁴This equilibrium is a NE of the game (and, generically, an ESS) if initially there are both Hawks and Doves present.

⁵See, however, Section 3, where this assumption is relaxed.

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

$$\begin{aligned} H &= 2n_{HH} + n_{HD} + n_H = n_H(n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD} + 1), \\ D &= 2n_{DD} + n_{HD} + n_D = n_D(n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD} + 1). \end{aligned} \quad (17)$$

229 Calculating derivatives of H and D in (17) and substituting them into (16) leads
 230 to ⁶

$$\begin{aligned} \frac{dn_H}{dt} &= n_H \frac{n_D\lambda(\pi_D + n_D\lambda\pi_{DD} + n_H\lambda\pi_{DH})\tau_{HD} - (\pi_H + n_D\lambda\pi_{HD} + n_H\lambda\pi_{HH})(1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})}{n_D n_H \lambda^2 \tau_{HD}^2 - (1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})(1 + n_D\lambda\tau_{HD} + 2n_H\lambda\tau_{HH})} \\ \frac{dn_D}{dt} &= n_D \frac{n_H\lambda(\pi_H + n_H\lambda\pi_{HH} + n_D\lambda\pi_{HD})\tau_{HD} - (\pi_D + n_H\lambda\pi_{DH} + n_D\lambda\pi_{DD})(1 + 2n_H\lambda\tau_{HH} + n_D\lambda\tau_{HD})}{n_D n_H \lambda^2 \tau_{HD}^2 - (1 + 2n_D\lambda\tau_{DD} + n_H\lambda\tau_{HD})(1 + n_D\lambda\tau_{HD} + 2n_H\lambda\tau_{HH})}. \end{aligned} \quad (18)$$

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

234 The extinction equilibrium $(n_H, n_D) = (0, 0)$ is locally stable when $\pi_H < 0$
 235 and $\pi_D < 0$. This can be understood intuitively by Figure 2, where panels C
 236 and E (gray lines) show that, as the total population size decreases toward 0, the
 237 frequency of singles ($p_S \equiv (n_H + n_D)/N$) in the population increases toward
 238 1. For low population size, individual fitness is then essentially given by the
 239 singles payoff, which then determine population dynamics and hence the fate
 240 of the population. Thus, when payoffs of singles are negative, the population
 241 will go extinct. Figure 2C also shows that the frequency of Hawks (p_H) in the
 242 population does not tend to V/C even in the case that single Hawks and Doves
 243 have the same payoff (i.e., $\pi_H = \pi_D$) and all τ 's are equal (see the gray solid
 244 line in panel C). In fact, the limiting proportion of Hawks depends on the initial
 245 conditions that determine the angle with which the corresponding trajectory
 246 tends to the origin in Figure 2, panel A.

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

253 Other boundary equilibria may exist where exactly one strategy is extinct.

⁶We 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).

254 For instance, the Hawk only boundary equilibrium

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

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

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

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

260 Most importantly, there are payoff parameters for which the interior equi-
 261 librium

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

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

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

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

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

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

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

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

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

294 and the population of Hawks and Doves at this equilibrium are

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

295 and

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

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

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

311 **Example 2.** The second parametrization of the Hawk-Dove model we consider
 312 has payoff matrix

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

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

318 For the classic assumptions of evolutionary game theory, this parametriza-
 319 tion as a matrix game has the same NE (and ESS) as parametrization (12) in
 320 Example 1.⁷ On the other hand, the average fitness in the population at the
 321 unique NE is now

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

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

323 Now we consider the case where individuals do not pair instantaneously, pair
 324 interaction times may differ and singles have fitness consequences. Provided
 325 $\pi_D > 0$ and $C\pi_D > V\pi_H$, the interior population equilibrium (21) is

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

326 At this equilibrium, the population of Hawks and Doves are

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

327 and

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

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

331 On the other hand, as illustrated by the dependence of this equilibrium on
 332 $\pi_D > 0$ in Figure 3, $p_H \neq V/C$ if the payoffs to singles are different. From (24),
 333 equilibrium population size increases to infinity as π_D increases (Figure 3B).
 334 Moreover, from (6), the proportion of paired individuals converges to 1 (Fig-
 335 ure 3A, see also Appendix F). Interestingly, the proportion of Hawks does not
 336 converge to 0 (for the parameters of Figure 3, the limiting proportion is 1/3)
 337 even when the payoff π_D to single Doves tends to infinity since most of the
 338 fitness is due to pair interactions at high population size.

339 3. Distributional–population dynamics

340 In the previous section, we assumed distributional dynamics that were in-
 341 dependent of population dynamics. In particular, the distributional dynamics
 342 reached its equilibrium very fast at given strategy numbers and then the pop-
 343 ulation dynamics acted on this equilibrium distribution. However, this com-
 344 plete separation of time scales need not hold. For example, perceptual con-
 345 straints (Abrahams, 1986; Gray and Kennedy, 1994; Berec and Křivan, 2000)

⁷This follows from the fact that each entry of the payoff matrix (23) differs from the corresponding entry of (12) by the same constant V .

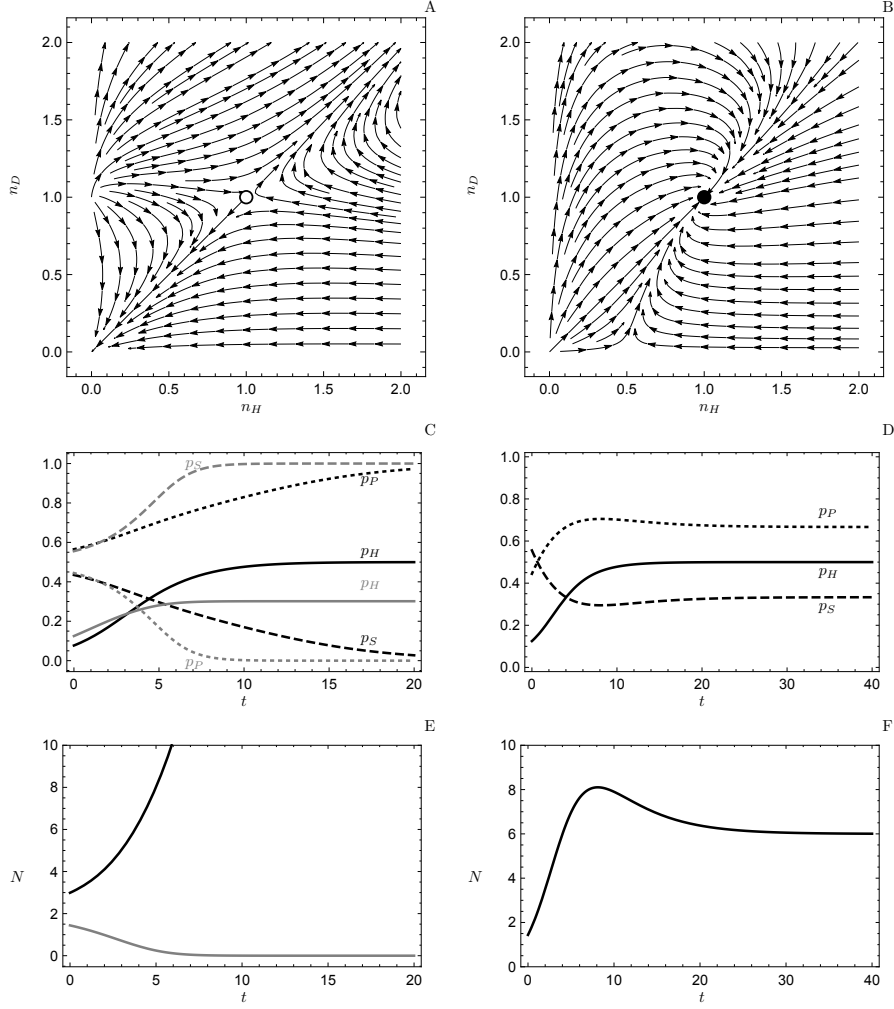


Figure 2: Simulations of Hawk and Dove population dynamics (16). Left panels correspond to Example 1 ($\pi_H = \pi_D = -1$) and right panels to Example 2 ($\pi_H = \pi_D = 1$). Top row shows stream plot of singles population dynamics (18). The middle row shows frequency of Hawks (p_H), frequency of single 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: $\tau_{HH} = 1$, $\tau_{HD} = 1$, $\tau_{DD} = 1$, $\lambda = 1$, $V = 1$, $C = 2$.

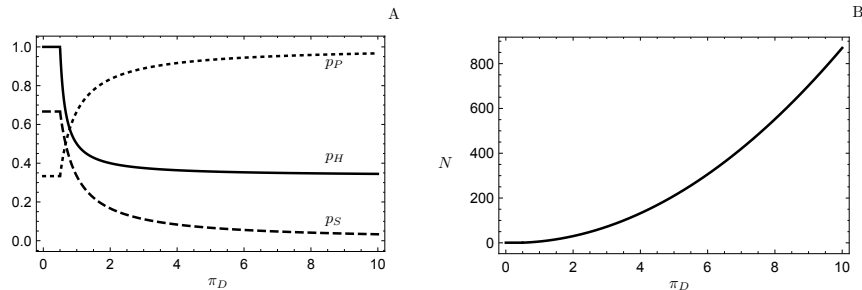


Figure 3: Dependence on single Dove payoff π_D of the interior equilibrium (24) for Example 2, which exists for $\pi_D > (V/C)\pi_H$. Panel A shows frequency of Hawks (p_H), frequency of single individuals (p_S) and frequency of individuals that are in pairs (p_P) while panel B shows the total population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

346 may prevent individuals from having perfect information about their environ-
 347 ment, making them only locally omniscient. In order to model distributional
 348 and population dynamics on similar time scales, we split payoffs in (1) as

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

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

357 We stress here that similarly to π 's for pairs, all β 's and μ 's in (25) are
 358 measured per single interaction. To express these per unit of time, we need
 359 to divide them by the average pair duration. Then distributional-population

360 dynamics are described by the following set of differential equations⁸

$$\begin{aligned}
\frac{dn_H}{dt} &= \nu(-\lambda n_H^2 - \lambda n_H n_D + 2\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}) + \\
&\quad \pi_H n_H + 2\frac{\beta_{HH} + \mu_{HH}}{\tau_{HH}} n_{HH} + \frac{\beta_{HD} + \mu_{DH}}{\tau_{HD}} n_{HD} \\
\frac{dn_D}{dt} &= \nu(-\lambda n_D^2 - \lambda n_H n_D + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}) + \\
&\quad \pi_D n_D + 2\frac{\beta_{DD} + \mu_{DD}}{\tau_{DD}} n_{DD} + \frac{\beta_{DH} + \mu_{HD}}{\tau_{HD}} n_{HD} \quad (26) \\
\frac{dn_{HH}}{dt} &= \nu(-\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2} n_H^2) - 2\frac{\mu_{HH}}{\tau_{HH}} n_{HH} \\
\frac{dn_{HD}}{dt} &= \nu(-\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D) - \frac{\mu_{HD} + \mu_{DH}}{\tau_{HD}} n_{HD} \\
\frac{dn_{DD}}{dt} &= \nu(-\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2} n_D^2) - 2\frac{\mu_{DD}}{\tau_{DD}} n_{DD}.
\end{aligned}$$

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

369 For arbitrary ν , we observe that

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

370 and

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

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

⁸Note 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.

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

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

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

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

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

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

$$\begin{aligned} \frac{dn_H}{dt} &= \nu(-\lambda n_H^2 - \lambda n_H n_D + 2\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}}) + \pi_H n_H + 2\frac{C}{\tau_{HH}} n_{HH} + \frac{2V}{\tau_{HD}} n_{HD} \\ \frac{dn_D}{dt} &= \nu(-\lambda n_D^2 - \lambda n_H n_D + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}) + \pi_D n_D \\ \frac{dn_{HH}}{dt} &= \nu(-\frac{n_{HH}}{\tau_{HH}} + \frac{\lambda}{2} n_H^2) - 2\frac{C}{\tau_{HH}} n_{HH} \\ \frac{dn_{HD}}{dt} &= \nu(-\frac{n_{HD}}{\tau_{HD}} + \lambda n_H n_D) - \frac{V}{\tau_{HD}} n_{HD} \\ \frac{dn_{DD}}{dt} &= \nu(-\frac{n_{DD}}{\tau_{DD}} + \frac{\lambda}{2} n_D^2). \end{aligned} \quad (29)$$

391 Provided the interior equilibrium exists, it is

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

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

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

397 in what follows. We observe that Doves exist (i.e., $n_D > 0$) at equilibrium (30)
 398 if and only if distributional dynamics are fast enough so that

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

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

402 Figure 4A and B (respectively C and D) show the dependence on ν of Hawk
 403 and Dove numbers (respectively, proportion of Hawks) at the stable population
 404 equilibrium. For slow distributional dynamics, total population size is increasing
 405 as ν tends to 0 since singles have positive payoffs ($\pi_H > 0$, $\pi_D > 0$ in Figure 4).
 406 However, since $\nu = 2$ is the threshold below which Doves go extinct in Panel
 407 A where $\pi_D = 1$, this payoff to single Doves is too low to rescue Doves from
 408 extinction when ν is small. Panel B with $\pi_D = 2.5$ shows the opposite case
 409 where the Dove population does not go extinct for any $\nu > 0$ and, in fact, as
 410 the speed of distributional dynamics decreases toward 0, both Hawk and Dove
 411 population numbers become arbitrarily large. As ν tends to infinity in these
 412 four panels, the stable interior equilibrium of (29) converges to that of model
 413 (16) of Section 2. In particular, for the left panels, this equilibrium approaches
 414 that of the right panels in Figure 2 where $N = H + D = 6$ and $p_H = V/C = 0.5$
 415 since all τ 's are equal and $\pi_H = \pi_D$.

416 4. Contest competition for a limited resource

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

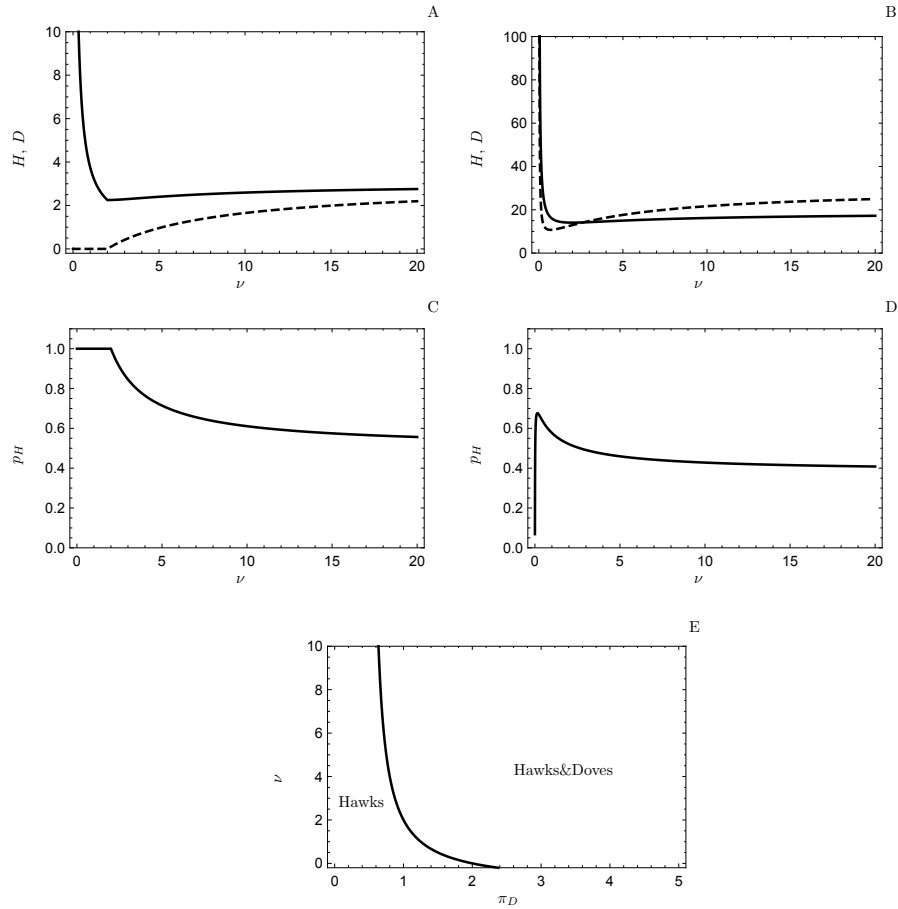


Figure 4: Dependence of the stable equilibrium of model (29) for Example 2 on the relative speed of distributional dynamics to demographic dynamics. Hawks (Doves) abundance is shown as the solid (dashed) curve in top panels. The middle panels (C and D) show Hawk frequency. Left panels (A, C) assume relatively low payoff to single Doves ($\pi_D = 1$) and as ν increases, population abundances converge to the equilibrium shown in Figure 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 Figure 2, right panels (i.e., $\tau_{HH} = 1, \tau_{HD} = 1, \tau_{DD} = 1, \lambda = 1, V = 1, C = 2, \pi_H = 1$).

430 4.1. *Distributional dynamics*

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

$$\begin{aligned}
 \frac{dn_{H_s}}{dt} &= -\lambda n_{H_s} F - \lambda n_{H_s} n_{H_o} - \lambda n_{H_s} n_{D_o} + \frac{n_{H_s} H_o}{\tau_{HH}} \\
 \frac{dn_{H_o}}{dt} &= \lambda n_{H_s} F - \lambda n_{H_s} n_{H_o} - \lambda n_{D_s} n_{H_o} + \frac{n_{H_s} H_o}{\tau_{HH}} + \frac{n_{H_o} D_s}{\tau_{HD}} + \frac{n_{H_s} D_o}{\tau_{HD}} \\
 \frac{dn_{D_s}}{dt} &= -\lambda n_{D_s} F - \lambda n_{D_s} n_{H_o} - \lambda n_{D_s} n_{D_o} + \frac{n_{D_s} D_o}{\tau_{DD}} + \frac{n_{H_s} D_o}{\tau_{HD}} + \frac{n_{H_o} D_s}{\tau_{HD}} \\
 \frac{dn_{D_o}}{dt} &= \lambda n_{D_s} F - \lambda n_{D_s} n_{D_o} - \lambda n_{H_s} n_{D_o} + \frac{n_{D_s} D_o}{\tau_{DD}} \\
 \frac{dn_{H_s H_o}}{dt} &= -\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda n_{H_s} n_{H_o} \\
 \frac{dn_{H_s D_o}}{dt} &= -\frac{n_{H_s D_o}}{\tau_{HD}} + \lambda n_{H_s} n_{D_o} \\
 \frac{dn_{H_o D_s}}{dt} &= -\frac{n_{H_o D_s}}{\tau_{HD}} + \lambda n_{D_s} n_{H_o} \\
 \frac{dn_{D_s D_o}}{dt} &= -\frac{n_{D_s D_o}}{\tau_{DD}} + \lambda n_{D_s} n_{D_o}
 \end{aligned} \tag{31}$$

433 where

$$F \equiv K - n_{H_o} - n_{D_o} - n_{H_s H_o} - n_{H_s D_o} - n_{D_s D_o} - n_{H_o D_s} \tag{32}$$

434 is the nonnegative number of free sites (i.e., sites that are neither occupied by a
 435 single owner or by a pair). Model (31) assumes that individual search rate is λ .
 436 If a searching individual encounters a free site, it will occupy it and will become
 437 an owning consumer. When a searching Hawk encounters a site owned by a
 438 Dove, the Hawk wins the competition and, when the pair disbands, becomes an
 439 owning Hawk while the Dove that lost the site becomes a searching Dove. This
 440 assumption leads to the term $\frac{n_{H_s D_o}}{\tau_{HD}}$ in the second and third equations. Once
 441 again this shows that distributional dynamics such as (31) may depend on how
 442 entries in the payoff matrix are interpreted.

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

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

444 That is, the number of free sites changes at a rate proportional to the number
 445 of searchers encountering them. Equation (33) shows that the system either
 446 converges to a state where there are no searchers (i.e., $n_{H_s} + n_{D_s} = 0$) or to the

447 set of states where there are no free sites (i.e., $F = 0$). Appendix C shows that
 448 for each fixed Hawk and Dove population numbers, system (31) has a unique
 449 equilibrium. It also shows that this equilibrium depends on the abundances of
 450 Hawks and Doves and on the number of sites, K , according to the following
 451 three cases.

- 452 1. When the number of individuals is no larger than the number of sites
 453 ($H + D \leq K$), all Hawks and all Doves own sites, i.e., the equilibrium is
 454 $n_{H_o} = H, n_{D_o} = D$.
- 455 2. When the total number of individuals is larger than the number of sites
 456 ($H + D > K$) while the number of Hawks in the population is no larger
 457 than the number of sites ($H \leq K$), all Hawks occupy sites either as single
 458 owners or in H_oD_s pairs and all other $K - H$ sites are occupied by Doves.
- 459 3. When the number of Hawks in the population is larger than the number
 460 of sites ($H > K$), all sites are occupied by Hawks, either as single owners
 461 or in H_oH_s and H_oD_s pairs.

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

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

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

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

$$\begin{aligned}
 \frac{dn_{H_s}}{dt} &= -\lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} - \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}} \\
 \frac{dn_{H_o}}{dt} &= \lambda n_{H_s}F - \lambda n_{H_s}n_{H_o} + \lambda n_{H_s}n_{D_o} + \frac{n_{H_sH_o}}{\tau_{HH}} \\
 \frac{dn_{D_s}}{dt} &= -\lambda n_{D_s}F + \lambda n_{H_s}n_{D_o} \\
 \frac{dn_{D_o}}{dt} &= \lambda n_{D_s}F - \lambda n_{H_s}n_{D_o} \\
 \frac{dn_{H_sH_o}}{dt} &= -\frac{n_{H_sH_o}}{\tau_{HH}} + \lambda n_{H_s}n_{H_o}
 \end{aligned}
 \tag{35}$$

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

472 In particular, the three cases above simplify to

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

$$(n_{H_s}, n_{H_o}, n_{D_s}, n_{D_o}, n_{H_s H_o}) = (0, H, 0, D, 0) \quad (36)$$

475 (see Figure 5 for $K \geq 100$).

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

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

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

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

$$\begin{aligned} n_{H_s} &= \frac{-1 + (H - 2K)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}} \\ n_{H_o} &= \frac{-1 - (H - 2K)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}} \\ n_{D_s} &= D \\ n_{D_o} &= 0 \\ n_{H_s H_o} &= \frac{1 + H\lambda\tau_{HH} - \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}}. \end{aligned} \quad (38)$$

484 (see Figure 5 for $K < 60$).

485 4.2. Distributional–population dynamics

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

$$\begin{array}{cc} & \begin{array}{cc} H_o & D_o \end{array} \\ \begin{array}{c} H_s \\ D_s \end{array} & \left(\begin{array}{cc} \pi_{H_s H_o}, \pi_{H_o H_s} & \pi_{H_s D_o}, \pi_{D_o H_s} \\ \pi_{D_s H_o}, \pi_{H_o D_s} & \pi_{D_s D_o}, \pi_{D_o D_s} \end{array} \right) \end{array} \quad (39)$$

490 where the first (second) payoff in each entry of the matrix is that of the row
 491 (column) player. With fitness defined as the average payoff per unit of time (cf.

A

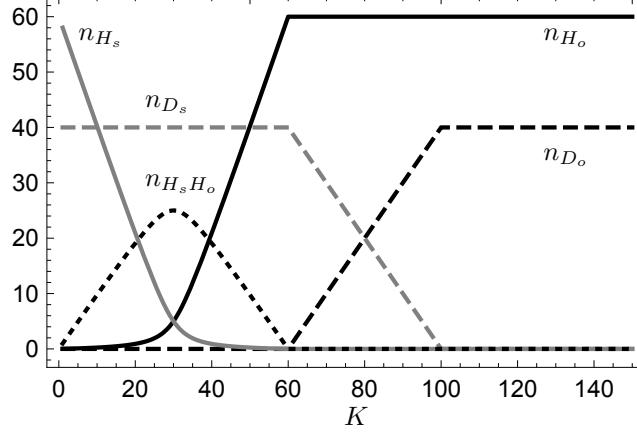


Figure 5: Dependence of the number of searchers (n_{H_s} and n_{D_s}) and number of owners (n_{H_o} and n_{D_o}) at the distributional equilibrium of model (35) as a function of K . The overall number of individuals is fixed at $H = 60$ and $D = 40$. Hawks are described by solid lines, Doves are described 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. $n_{H_s H_o}$. Parameters: $\lambda = 1$, $\tau_{HH} = 1$, $\tau_{HD} = 0$, $\tau_{DD} = 0$.

492 (8)), we now have

$$\Pi_H = \frac{n_{H_s H_o} \left(\frac{\pi_{H_s H_o}}{\tau_{HH}} + \frac{\pi_{H_o H_s}}{\tau_{HH}} \right) + n_{H_s D_o} \frac{\pi_{H_s D_o}}{\tau_{HD}} + n_{H_o D_s} \frac{\pi_{H_o D_s}}{\tau_{HD}} + n_{H_o} \pi_{H_o} + n_{H_s} \pi_{H_s}}{H}$$

and

$$\Pi_D = \frac{n_{D_s D_o} \left(\frac{\pi_{D_s D_o}}{\tau_{DD}} + \frac{\pi_{D_o D_s}}{\tau_{DD}} \right) + n_{H_o D_s} \frac{\pi_{D_s H_o}}{\tau_{HD}} + n_{H_s D_o} \frac{\pi_{D_o H_s}}{\tau_{HD}} + n_{D_o} \pi_{D_o} + n_{D_s} \pi_{D_s}}{D} \quad (40)$$

493 where $H = 2n_{H_s H_o} + n_{H_s D_o} + n_{H_o D_s} + n_{H_s} + n_{H_o}$ and $D = 2n_{D_s D_o} + n_{H_s D_o} +$
 494 $n_{D_s H_o} + n_{D_s} + n_{D_o}$ are the total number of Hawks and Doves, respectively.

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

498 Distributional-population dynamics are then

$$\begin{aligned}
\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_s H_o}}{\tau_{HH}} \right) + (\beta_{H_s} - \mu_{H_s}) n_{H_s} + \\
&\quad \beta_{H_o} n_{H_o} + \frac{\beta_{H_s H_o} + \beta_{H_o H_s}}{\tau_{HH}} n_{H_s H_o} + \frac{\beta_{H_s D_o}}{\tau_{HD}} n_{H_s D_o} + \frac{\beta_{H_o D_s}}{\tau_{HD}} n_{H_o D_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_s H_o}}{\tau_{HH}} + \frac{n_{H_o D_s}}{\tau_{HD}} + \frac{n_{H_s D_o}}{\tau_{HD}} \right) - \\
&\quad \mu_{H_o} n_{H_o} + \frac{\mu_{H_s H_o} + \mu_{H_o H_s}}{\tau_{HH}} n_{H_s H_o} + \frac{\mu_{D_o H_s}}{\tau_{HD}} n_{H_s D_o} + \frac{\mu_{D_s H_o}}{\tau_{HD}} n_{H_o D_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_s D_o}}{\tau_{DD}} + \frac{n_{H_s D_o}}{\tau_{HD}} + \frac{n_{H_o D_s}}{\tau_{HD}} \right) + \\
&\quad (\beta_{D_s} - \mu_{D_s}) n_{D_s} + \beta_{D_o} n_{D_o} + \frac{\beta_{D_s D_o} + \beta_{D_o D_s}}{\tau_{DD}} n_{D_s D_o} + \frac{\beta_{D_o H_s}}{\tau_{HD}} n_{H_s D_o} + \frac{\beta_{D_s H_o}}{\tau_{HD}} n_{H_o D_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_s D_o}}{\tau_{DD}} \right) - \\
&\quad \mu_{D_o} n_{D_o} + \frac{\mu_{D_s D_o} + \mu_{D_o D_s}}{\tau_{DD}} n_{D_s D_o} + \frac{\mu_{H_s D_o}}{\tau_{HD}} n_{H_s D_o} + \frac{\mu_{H_o D_s}}{\tau_{HD}} n_{H_o D_s} \\
\frac{dn_{H_s H_o}}{dt} &= \nu \left(-\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda n_{H_s} n_{H_o} \right) - \frac{\mu_{H_s H_o} + \mu_{H_o H_s}}{\tau_{HH}} n_{H_s H_o} \\
\frac{dn_{H_s D_o}}{dt} &= \nu \left(-\frac{n_{H_s D_o}}{\tau_{HD}} + \lambda n_{H_s} n_{D_o} \right) - \frac{\mu_{H_s D_o} + \mu_{D_o H_s}}{\tau_{HD}} n_{H_s D_o} \\
\frac{dn_{H_o D_s}}{dt} &= \nu \left(-\frac{n_{H_o D_s}}{\tau_{HD}} + \lambda n_{D_s} n_{H_o} \right) - \frac{\mu_{H_o D_s} + \mu_{D_s H_o}}{\tau_{HD}} n_{H_o D_s} \\
\frac{dn_{D_s D_o}}{dt} &= \nu \left(-\frac{n_{D_s D_o}}{\tau_{DD}} + \lambda n_{D_s} n_{D_o} \right) - \frac{\mu_{D_s D_o} + \mu_{D_o D_s}}{\tau_{DD}} n_{D_s D_o}
\end{aligned} \tag{41}$$

499 where F is given by (32). Here the model assumes that newborns are single
500 searchers. This makes it important to also write payoffs to singles as differences
501 (e.g., $\pi_{H_o} = \beta_{H_o} - \mu_{H_o}$). Population demography is given by two processes.
502 First, the model assumes demographic changes associated with singles. For ex-
503 ample, in the first equation in (41), the term $(\beta_{H_s} - \mu_{H_s}) n_{H_s}$ describes changes
504 due to birth and death among single Hawk searchers. Note that, in the simula-
505 tions below, we assume that only individuals who are on a site either as singles
506 or in pairs can give birth (and so $\beta_{H_s} = \beta_{D_s} = 0$). Term $\beta_{H_o} n_{H_o}$ describes birth
507 for those Hawks that own a site. Second, (41) considers demographic changes
508 due to contests between individuals. For example, term $\frac{\beta_{H_s H_o} + \beta_{H_o H_s}}{\tau_{HH}} n_{H_s H_o}$ de-
509 scribes newborns produced as a consequence of a contest between two Hawks,
510 i.e., when a searching Hawk is paired with an owning Hawk. One of the two
511 Hawks will win the site and will gain fitness by the opportunity of reproducing
512 in the site. The probability of winning the contest and reproducing is cap-
513 tured by terms $\beta_{H_s H_o}$ in the case it is the searching Hawk that wins the contest
514 and $\beta_{H_o H_s}$ when the owning Hawk retains the site after the contest. Term
515 $\frac{\beta_{H_s D_o}}{\tau_{HD}} n_{H_s D_o}$ represents newborn Hawks produced when a searching Hawk is

516 paired with an owning Dove, because in this case we assume that with probabil-
 517 ity one the Hawk will win the contest. In the second equation for owning Hawks,
 518 term $\frac{\mu_{D_o H_s}}{\tau_{HD}} n_{H_s D_o}$ represents the situation where the owning Dove paired with
 519 a searching Hawk dies and the searching Hawk becomes a single owning Hawk.
 520 The other terms follow the same logic.

521 A lengthy but straightforward calculation based on (41) yields

$$\frac{dH}{dt} = \frac{d(2n_{H_s H_o} + n_{H_s D_o} + n_{H_o D_s} + n_{H_s} + n_{H_o})}{dt} = \Pi_H H$$

522 and

$$\frac{dD}{dt} = \frac{d(2n_{D_s D_o} + n_{H_s D_o} + n_{H_o D_s} + n_{D_s} + n_{D_o})}{dt} = \Pi_D D$$

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

527 Since the notation for pairs only indicates how the pair was formed (i.e., there
 528 is no owner or searcher when in a pair), we assume that once two individuals
 529 occupy a site, their payoffs do not depend on who was the owner and who was
 530 the searcher when they encountered each other. In particular, payoffs to Hawks
 531 in all Hawk-Hawk pairs are equal as are those in Hawk-Dove pairs. That is
 532 $\pi_{HH} = \pi_{H_s H_o} = \pi_{H_o H_s}$, $\pi_{DD} = \pi_{D_s D_o} = \pi_{D_o D_s}$, $\pi_{HD} = \pi_{H_s D_o} = \pi_{H_o D_s}$, and
 533 $\pi_{DH} = \pi_{D_s H_o} = \pi_{D_o H_s}$ in (39). Fitnesses (40) then simplify to

$$\begin{aligned} \Pi_H &= \frac{2n_{H_s H_o} \frac{\pi_{HH}}{\tau_{HH}} + (n_{H_s D_o} + n_{H_o D_s}) \frac{\pi_{HD}}{\tau_{HD}} + n_{H_o} \pi_{H_o} + n_{H_s} \pi_{H_s}}{H}, \\ \Pi_D &= \frac{2n_{D_s D_o} \frac{\pi_{DD}}{\tau_{DD}} + (n_{D_s H_o} + n_{D_o H_s}) \frac{\pi_{DH}}{\tau_{HD}} + n_{D_o} \pi_{D_o} + n_{D_s} \pi_{D_s}}{D}. \end{aligned} \quad (42)$$

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

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

$$\begin{aligned} \frac{dH}{dt} &= \pi_{H_o} H \\ \frac{dD}{dt} &= \pi_{D_o} D \end{aligned} \quad (43)$$

542 when $H + D \leq K$,

$$\begin{aligned}\frac{dH}{dt} &= H((D + H - K)\lambda\pi_{HD} + \pi_{H_o}) \\ \frac{dD}{dt} &= (K - H)(2(D + H - K)\lambda\pi_{DD} + \pi_{D_o}) + (D + H - K)(H\lambda\pi_{DH} + \pi_{D_s})\end{aligned}\quad (44)$$

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

$$\begin{aligned}\frac{dH}{dt} &= \frac{(-2\pi_{HH} + (D\lambda\pi_{HD} + \pi_{H_o} + \pi_{H_s})\tau_{HH})\sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})}}{2\lambda\tau_{HH}^2} - \\ &\quad \frac{-2\pi_{HH}(1 + H\lambda\tau_{HH}) + \tau_{HH}(D\lambda\pi_{HD} + \pi_{H_o} + \pi_{H_s} + (H - 2K)\lambda(D\lambda\pi_{HD} + \pi_{H_o} - \pi_{H_s})\tau_{HH})}{2\lambda\tau_{HH}^2} \\ \frac{dD}{dt} &= D\left(\pi_{D_s} + \frac{\pi_{DH}(-1 + (2K - H)\lambda\tau_{HH} + \sqrt{1 + \lambda\tau_{HH}(2H + (H - 2K)^2\lambda\tau_{HH})})}{2\tau_{HH}}\right)\end{aligned}\quad (45)$$

544 when $H > K$.

545 To analyze models (43)–(45), we will assume that owners obtain positive
546 payoffs ($\pi_{H_o} > 0$, $\pi_{D_o} > 0$) and searching individuals obtain negative payoffs
547 ($\pi_{H_s} < 0$ and $\pi_{D_s} < 0$). There is then no non-zero equilibrium for (43) in region
548 $H + D \leq K$ because both Hawks and Doves increase exponentially and so all
549 trajectories with initial positive population sizes for Hawks and Doves leave this
550 region. If, in addition, Hawks gain payoff in their Hawk-Dove interacting pairs
551 ($\pi_{HD} \geq 0$), equation (44) shows that Hawks are always increasing in the region
552 where $H + D > K$ and $H < K$, and so these trajectories must enter the region
553 where $H > K$. Furthermore, if $\pi_{DH} \leq 0$,⁹ Appendix E shows that equation (45)
554 has a unique globally asymptotically stable equilibrium. Altogether, this implies
555 that the system of equations (43), (44), (45) has a globally asymptotically stable
556 equilibrium given by

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

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

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

⁹We 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.

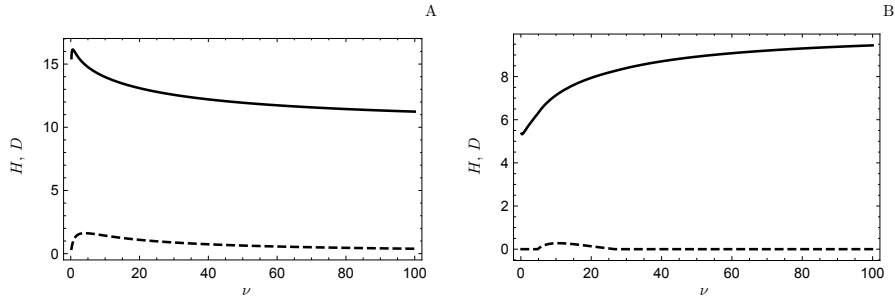


Figure 6: The dependence of the equilibrium of distributional-population dynamics (41) on ν ($\nu > 0.2$) when interaction times between Hawks (solid line) and Doves (dashed line) and between Doves are very short (i.e., $\tau_{HD} = \tau_{DD} = 0.0001$). Left (respectively, right) panel is for the Hawk-Dove game with payoff matrix (47) (respectively, (28)). Other parameters: $\lambda = 1$, $\tau_{HH} = 1$, $V = 1$, $C = 4$, $K = 10$, $\beta_{H_o} = \beta_{D_o} = 0.2$, $\mu_{H_o} = \mu_{D_o} = 0.1$, $\beta_{H_s} = \beta_{D_s} = 0$, $\mu_{H_s} = \mu_{D_s} = 0.1$.

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

559 Figure 6 shows the population equilibrium based on simulations of the dy-
 560 namics (41) applied to the simplified model of Example 3 without assuming fast
 561 distributional dynamics. Panel A uses the classic Hawk-Dove payoff matrix

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

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

571 5. Discussion

572 Motivated by genetics, where players are alleles, the classical theory of two-
 573 strategy, two-player symmetric evolutionary games assumes that all individuals
 574 get payoffs only when paired, pairing is random and instantaneous, and the
 575 number of pairs is given by the Hardy–Weinberg distribution. With an individ-
 576 ual’s fitness equated to its expected payoff, the population growth rate (which
 577 is assumed to be proportional to the mean fitness of the population) is then
 578 frequency dependent but density independent. For the classical Hawk-Dove
 579 game, population growth is exponential as in equation (15). On the other hand,
 580 growth in natural populations is rarely exponential. Density dependent growth

581 is universal. This calls into question the degree to which results of two-player
582 matrix games may be extended to make predictions about natural populations.

583 The above assumptions on pairs make sense when considering for example
584 mating between sexes, but fitness is also gained/lost when individuals are sin-
585 gles. For example, fitness may increase when an individual forages through an
586 increase in its survival probability, or an increase in egg production. In this
587 article, we develop a new theoretical approach that relaxes these assumptions:
588 (i) individuals do not pair instantaneously so that there are singles in the popu-
589 lation, (ii) individuals gain/lose fitness not only when paired, but also as singles,
590 and (iii) duration of encounters between individuals depends on their strategies.
591 We find that including singles can regulate population growth which allows the
592 study of both frequency and density of strategies.

593 Our approach builds on that developed by Krivan and Cressman (2017) who
594 assumed that individuals pair instantaneously, but interactions between differ-
595 ent strategies take different time. As a result, the rate (per unit of time) that
596 individuals are paired with each other depends on the strategies of the players.
597 This idea that interaction rates might be strategy-dependent was incorporated
598 into evolutionary game dynamics by Taylor and Nowak (2006). In their analysis
599 of the evolutionary stability of strategy dynamics, the fitness of a strategy is
600 given in units of payoff per interaction (Argasinski and Broom, 2018), and the
601 interaction rates refer to the intensity with which certain strategies will assort
602 with other strategies. This mirrors the classical theory in which the number of
603 interactions determines overall fitness. Our models include the length of time a
604 game is played, so our approach differs fundamentally from Taylor and Nowak
605 (2006) and is more closely related to that of Argasinski and Broom (2018) where
606 the number of games that are played in a period of time is taken into account¹⁰.
607 This approach allows one to study the fitness of a strategy when fitness includes
608 more than game payoffs, e.g., singles payoff. In Section 2, we see that when
609 singles payoff does not depend on strategy, and interaction times are equal,
610 then the Nash equilibrium of the game is unchanged from classical predictions.
611 Under these assumptions, including singles is equivalent to adding background
612 fitness (Cressman, 1992). However, if singles payoffs depend on strategy, then
613 under the aforementioned assumptions, we see (Figure 2, panels C and E) that
614 these payoffs contribute more to average fitness because the proportion of sin-
615 gles tends to 1 (respectively, 0) when the total population size, N , tends to zero
616 (respectively, infinity).

617 In Sections 2 and 3, where payoffs to singles and pairs are density inde-
618 pendent, we show that non-instantaneous pair formation can induce density
619 dependence in the population growth where the population growth rate is still
620 given by the average fitness in the population.¹¹ The existence of a coexistence

¹⁰These approaches are equivalent when all interactions take the same amount of time and fitness is accrued only through the game.

¹¹Other approaches (e.g., Cressman (1992); Argasinski and Broom (2013)) to get convergence to non-zero population numbers typically assume some explicit density dependent mechanisms in individual payoff/fitness.

621 equilibrium (i.e., an interior equilibrium where both strategies have positive den-
622 sity) relies on a balance between the positive payoff of singles and the negative
623 average payoff from the game (or vice versa). Moreover, the stability of an inter-
624 rior equilibrium for the Hawk-Dove model depends on the parametrization of its
625 payoff matrix, as seen in Figure 3 of Section 2, where distributional dynamics
626 act on a fast time-scale compared to population dynamics. For instance, an
627 interior population equilibrium may exist for the Hawk-Dove model with classic
628 payoff matrix (12) when the payoffs to singles are negative. However, this equi-
629 librium is never stable (Example 1).¹² On the other hand, when the payoffs to
630 interacting pairs are all decreased by the same amount as in payoff matrix (23)
631 of Example 2,¹³ a stable interior equilibrium often emerges if payoffs to singles
632 are positive. Thus, the eco-evolutionary dynamics depend on where fitness is
633 accrued, as remarked in Argasinski and Broom (2013, 2018, In press) (see also
634 McNamara, 2013).

635 The population dynamics (16) of Section 2 serve to frame our thinking
636 around relating ecological parameters to V and C from the Hawk-Dove pay-
637 off matrix. When these model equations have a stable interior equilibrium (in
638 Example 2), it can be shown using (24) that the proportion of Hawks at equi-
639 librium will increase with increases in V and decrease with increases in C . This
640 is consistent with the classical Hawk-Dove game at the interior ESS where the
641 proportion of Hawks equals $\frac{V}{C}$. On the other hand, in the classical game, Hawks
642 and Doves coexist if and only if the cost when two Hawks fight is higher than
643 their expected gain (i.e., $V < C$) whereas, in Example 2, we show that coex-
644 istence may also occur when $V > C$ due to singles receiving payoff. The same
645 result (i.e., coexistence when $V > C$) was shown by Křivan and Cressman (2017)
646 at fixed population size. Specifically, when pairs form instantaneously and in-
647 teractions between two Hawks take long enough compared to other interactions,
648 they showed that non-aggressiveness can evolve even when $V > C$. Similarly,
649 in the repeated Prisoner's Dilemma game, cooperation evolves when individuals
650 can control how many rounds to continue an interaction (i.e., they can opt-out;
651 Zhang et al., 2016). These models are the limit cases of the model investigated
652 in Section 2 when the mean time between encounters tends to zero and the
653 number of singles tends to zero too. Once again, we see that including singles
654 and/or including interaction times can influence the evolutionary predictions.

655 Although the parameters V and C from the Hawk-Dove game are not well-
656 defined ecological parameters, we show in Section 3 that it is possible to de-
657 compose the payoffs from the Hawk-Dove game into payoffs that increase fit-
658 ness and payoffs that decrease fitness. This allows us to examine population-
659 distributional dynamics when relaxing the assumption that distributional dy-
660 namics are fast compared to population dynamics. In particular, non-aggressiveness

¹²The 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.

¹³This does not change the evolutionary outcome (i.e., ESS) of the classic Hawk-Dove game (Hofbauer and Sigmund, 1998).

661 can evolve when the distributional and population dynamics are on similar time
662 scales. This result does not depend on the amount of time that individuals
663 are paired but only on the relative time scales of the two dynamics. This is
664 illustrated in Figure 4 where we see that coexistence depends on the speed of
665 distributional dynamics relative to population dynamics.

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

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

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695 **Appendix A. Uniqueness of distributional equilibrium of (5)**

696 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
697 Hawks (Doves) in the Hawk (Dove) population. Then, at an equilibrium of (5),

$$\begin{aligned} q_H &= \frac{1}{1 + \lambda\tau_{HH}Hq_H + \lambda\tau_{HD}Dq_D} \\ q_D &= \frac{1}{1 + \lambda\tau_{HD}Hq_H + \lambda\tau_{DD}Dq_D} \end{aligned} \quad (\text{A.1})$$

since, for example,

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

698 by (6).

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

$$\begin{aligned} n_H &= Hq_H \\ n_D &= Dq_D \\ n_{HH} &= \frac{1}{2}\lambda\tau_{HH}n_H^2 \\ n_{HD} &= \lambda\tau_{HD}n_Hn_D \\ n_{DD} &= \frac{1}{2}\lambda\tau_{DD}n_D^2 \end{aligned}$$

702 which, from (A.1), will satisfy $H = n_H + 2n_{HH} + n_{HD}$ and $D = n_D + n_{HD} +$
703 $2n_{DD}$. This will be the only equilibrium solution of (5) for a given H and D .

704 **Appendix B. Stability of equilibria for model (18)**

705 Because eigenvalues of linearized model (18) at extinction equilibrium $(n_H, n_D) =$
706 $(0, 0)$ are π_H , and π_D , this equilibrium is locally stable when $\pi_H < 0$ and $\pi_D < 0$.

707 Eigenvalues of linearized model (18) at equilibrium (19) are $(\pi_H\pi_{HH})/(2\pi_H\tau_{HH} -$
708 $\pi_{HH})$, and $(\pi_{DH}\pi_H - \pi_D\pi_{HH})/(\pi_H\tau_{HD} - \pi_{HH})$. The boundary equilibrium ex-
709 exists (i.e., the Hawk only equilibrium is positive) and is locally stable if and only
710 if $\pi_{HH} < 0$, $\pi_H > 0$, and $\pi_{DH}\pi_H < \pi_D\pi_{HH}$.¹⁴

711 Similarly, eigenvalues of linearized model (18) at equilibrium (20) are $\pi_D\pi_{DD}/(2\pi_D\tau_{DD} -$
712 $\pi_{DD})$, and $(\pi_{DD}\pi_H - \pi_D\pi_{HD})/(\pi_{DD} - \pi_D\tau_{HD})$. This equilibrium exists (i.e.,
713 the Dove equilibrium is positive) and locally stable when $\pi_{DD} < 0$, $\pi_D > 0$, and
714 $\pi_D\pi_{HD} < \pi_{DD}\pi_H$.

¹⁴We ignore degenerate cases with eigenvalue 0.

715 Stability analysis of the interior equilibrium (21) leads to complex expres-
716 sions. Instead, we analyze its stability for the Hawk-Dove parametrizations in
717 Examples 1 and 2.

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

$$\text{tr}(J) = \frac{V(V-C)}{A} (V(\pi_D^2(-4\tau_{DD} + 9\tau_{HD} - 4\tau_{HH}) + 2\pi_D\pi_H(\tau_{DD} - 3\tau_{HD} + \tau_{HH})) + \\ \pi_H^2\tau_{HD} + V(\pi_D - \pi_H)) - C(\pi_D(\pi_D(\tau_{HD} - 4\tau_{DD}) + 2\pi_H\tau_{DD}) + V(\pi_D - \pi_H))$$

718 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

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

719 Using the **Reduce** command of Mathematica (Appendix F) under the as-
720 sumptions that equilibrium (22) is interior and parameters $V, C, \tau_{HH}, \tau_{HD}, \tau_{DD},$
721 λ are all positive, we found that $\text{tr}(J) < 0$ and $\det J > 0$ (i.e., the equilibrium
722 is locally asymptotically stable) if and only if¹⁵

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

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

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

723 In particular, these conditions imply that the interior equilibrium cannot be
724 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

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

725 and determinant

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

¹⁵Here, we ignore the degenerate cases where $3\pi_D = \pi_H$ or $C\pi_D^2 = V(\pi_H - 3\pi_D)^2$.

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

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

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

731 **Appendix C. Unique equilibrium solution to distributional dynam-** 732 **ics (31)**

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

736 Equation (33) shows that the system either converges to a state where there
 737 are no searchers ($n_{H_s} + n_{D_s} = 0$) or to the set of states where there are no
 738 free sites ($F = 0$).¹⁶ We show that at the distributional equilibrium there are
 739 no searchers if and only if $H + D \leq K$. If there are no searchers, there are
 740 no pairs and so all individuals are owners (i.e., $n_{H_o} = H$ and $n_{D_o} = D$) and,
 741 consequently, the total population size cannot be larger than the number of
 742 sites, i.e., $H + D \leq K$. Conversely, suppose that the total number of individ-
 743 uals satisfies $H + D \leq K$. If there were some searchers at the distributional
 744 equilibrium, there would be no free sites (i.e., all sites would be occupied) and
 745 so $H + D = K$. As we assumed there were some searchers, the total population
 746 would be larger than K , a contradiction. Thus, all individuals are owners if
 747 and only if $H + D \leq K$ and in this case, $n_{H_o} = H$, and $n_{D_o} = D$ is the unique
 748 equilibrium.

749 Now we assume that $H + D > K$. Thus, there must be searchers at the
 750 equilibrium and (33) implies that $F = 0$, i.e., all sites are occupied (i.e., $K =$
 751 $n_{H_o} + n_{D_o} + n_{H_s H_o} + n_{H_s D_o} + n_{D_s D_o} + n_{H_o D_s}$). Then, by adding the first and
 752 fifth equations of (31), an equilibrium of (31) must satisfy $n_{H_s}(F + n_{D_o}) = 0$.
 753 Also, if $n_{H_s} > 0$, then $F = n_{D_o} = 0$ and so all sites are occupied by Hawks and
 754 $H > K$. 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
 $H_o D_s$ pairs (i.e., $H = n_{H_o} + n_{H_o D_s}$) and all other $K - H$ sites are occupied
 by Doves as owners or in $D_s D_o$ pairs. As there are no Hawks searching, we
 have $n_{H_s H_o} = n_{H_s D_o} = 0$. Under these assumptions, equations for equilibrium

¹⁶This 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.

of model (31) are

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

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

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

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

$$\begin{aligned} &n_{D_s}^3 \lambda^2 \tau_{DD} \tau_{HD} + \lambda n_{D_s}^2 (\lambda \tau_{DD} \tau_{HD} (2K - D - H) + \tau_{DD} + \tau_{HD}) + n_{D_s} (-D \lambda (\tau_{DD} + \tau_{HD}) - \\ 757 &2H \lambda \tau_{DD} + \lambda K (2\tau_{DD} + \tau_{HD}) + 1) - D - H + K = 0. \end{aligned} \quad (\text{C.2})$$

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

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

762 That is

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

763 Then

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

764 Since $D > K$,

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

765 Thus, the coefficient of n_{D_s} ,

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

766 is negative. Thus, the cubic (C.2) has exactly one positive root for n_{D_s} . We see
767 from (C.1a) that $K - H = n_{D_o}(1 + \lambda\tau_{DD}n_{D_s})$. Since $H \leq K$, it follows that
768 $n_{D_o} \geq 0$ and so we have a solution with $n_{H_o}, n_{D_s D_o}$ and $n_{H_o D_s}$ 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 $H_o H_s$ and $H_o D_s$ pairs. As there are
no Dove owners, we have the following three equations

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

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

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

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

$$\lambda^2 \tau_{HD} \tau_{HH} n_{H_o}^3 + \lambda n_{H_o}^2 (\lambda \tau_{HH} \tau_{HD} (H + D - 2K) + (\tau_{HD} + \tau_{HH})) + \quad (\text{C.4})$$

$$(1 + \lambda(\tau_{HD}(D - K) + \tau_{HH}(H - 2K)))n_{H_o} - K. \quad (\text{C.5})$$

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

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

770 Then $H + D < 2K$ and

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

771 Thus

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

772 Since $H > K$,

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

773 and

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

774 since $H < 2K$. That is, the coefficient of n_{H_o} is negative and so the cubic (C.5)
 775 has exactly one positive root for n_{H_o} by Descartes' rule of signs. It follows
 776 from (C.3c) that $n_{D_s} > 0$. Moreover, from (C.3a) and (C.3b), we see that
 777 $K = H - n_{H_s}(1 + \lambda\tau_{HH}n_{H_o})$. Since $H \geq K$, we have $n_{H_s}, n_{H_s H_o}, n_{H_o D_s}$ are all
 778 nonnegative.

779 Appendix D. Global stability of the unique distributional equilib- 780 rium of (35) for Example 3

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

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

788 **Case 1 ($n_{H_s} + n_{D_s}$ converges to 0).** By the last equation of (35), $n_{H_s H_o}$ con-
 789 verges to 0. Thus $n_{H_o} = H - 2n_{H_o H_s} - n_{H_s}$ converges to H and $n_{D_o} =$
 790 $D - n_{D_s}$ converges to D . That is, $H + D \leq K$ and the trajectory converges
 791 to equilibrium (36).

792 **Case 2 ($n_{H_s} + n_{D_s}$ does not converge to 0).** Since F converges to 0, $H +$
 793 $D \geq K$ with equality if and only if $n_{H_s} = 0$ and $n_{D_s} = 0$. Thus, $H + D >$
 794 K .

795 From (35),

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

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

797 **Case 2(i) ($n_{H_s} + n_{H_s H_o}$ converges to 0).** Then n_{H_o} converges to H (and
798 so $H \leq K$) and $n_{H_o} + n_{D_o}$ converges to K (and so n_{D_o} converges to
799 $K - H$). The trajectory converges to equilibrium (37).

800 **Case 2(ii) ($n_{H_s} + n_{H_s H_o}$ does not converge to 0).** From (D.1), $n_{H_s} +$
801 $n_{H_s H_o}$ is decreasing and so converges to $C > 0$. Also, $n_{H_o} + n_{H_s H_o} =$
802 $H - (n_{H_s} + n_{H_s H_o})$ is increasing to $H - C > 0$. Then $n_{D_o} =$
803 $K - F - (n_{H_o} + n_{H_s H_o})$ converges to $K - (H - C)$ since F con-
804 verges to 0. We claim that n_{D_o} converges to 0 (i.e., $K = H - C$).
805 Otherwise, n_{H_s} converges to 0 (since $n_{H_s} n_{D_o}$ converges to 0) and
806 $n_{H_s H_o}$ converges to $C > 0$. But $\frac{dn_{H_s H_o}}{dt} = -\frac{n_{H_s H_o}}{\tau_{HH}} + \lambda n_{H_s} n_{H_o} < 0$
807 when $n_{H_s} = 0$ and $n_{H_s H_o} = C > 0$ and so $n_{H_s H_o}$ cannot converge
808 to C . Thus, n_{D_o} converges to 0 and n_{D_s} converges to D . Also,
809 $n_{H_s} + n_{H_s H_o}$ converges to K and so $H > K$. Furthermore, for large
810 t ,

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

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

817 We now show that the unique equilibrium is locally asymptotically stable.
818 As the number of Doves that jointly occupy sites tends to 0,¹⁷ all Doves are
819 singles ($D = n_{D_s} + n_{D_o}$), and Hawks are either singles or in Hawk-Hawk pairs
820 ($H = n_{H_s} + n_{H_o} + 2n_{H_s H_o}$). Substituting $n_{H_s H_o} = (H - n_{H_s} - n_{H_o})/2$ and
821 $n_{D_o} = D - n_{D_s}$ into (35) leads to simplified distributional dynamics

$$\begin{aligned} \frac{dn_{H_s}}{dt} &= -\frac{1}{2}\lambda n_{H_s}(2K + n_{H_o} + n_{H_s} - H) + \frac{H - n_{H_o} - n_{H_s}}{2\tau_{HH}} \\ \frac{dn_{H_o}}{dt} &= \frac{H - n_{H_o} - n_{H_s} + n_{H_s}\lambda\tau_{HH}(2K - H - 3n_{H_o} + n_{H_s})}{2\tau_{HH}} \\ \frac{dn_{D_s}}{dt} &= \frac{1}{2}\lambda n_{D_s}(H - 2K - 2n_{D_s} + n_{H_o} - 3n_{H_s}) + \lambda D(n_{D_s} + n_{H_s}). \end{aligned} \quad (\text{D.3})$$

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

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

¹⁷For 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.

(36) are

$$\begin{aligned}\lambda_1 &= \lambda(H + D - K), \\ \lambda_2 &= -\frac{\sqrt{4H\lambda\tau_{HH} + (\lambda K\tau_{HH} - 1)^2} + \lambda K\tau_{HH} + 1}{2\tau_{HH}}, \\ \lambda_3 &= \frac{\sqrt{4H\lambda\tau_{HH} + (\lambda K\tau_{HH} - 1)^2} - \lambda K\tau_{HH} - 1}{2\tau_{HH}}.\end{aligned}$$

824 These eigenvalues are real and they are all negative when $H + D < K$.
The eigenvalues at equilibrium (37) are

$$\begin{aligned}\lambda_1 &= \lambda(K - H - D), \\ \lambda_2 &= -\frac{\sqrt{4H\lambda\tau_{HH} + (\lambda K\tau_{HH} - 1)^2} + \lambda K\tau_{HH} + 1}{2\tau_{HH}}, \\ \lambda_3 &= \frac{\sqrt{4H\lambda\tau_{HH} + (\lambda K\tau_{HH} - 1)^2} - \lambda K\tau_{HH} - 1}{2\tau_{HH}}.\end{aligned}$$

825 These eigenvalues are real and they are all negative when $H + D > K$ and
826 $H < K$.

The eigenvalues at equilibrium (38) are

$$\begin{aligned}\lambda_1 &= \frac{1 - 2D\lambda\tau_{HH} + \lambda\tau_{HH}(2K - H) - \sqrt{\lambda\tau_{HH}(\lambda\tau_{HH}(2K - H)^2 + 2H) + 1}}{2\tau_{HH}} \\ \lambda_2 &= -\frac{\sqrt{\lambda\tau_{HH}(\lambda\tau_{HH}(2K - H)^2 + 2H) + 1}}{\tau_{HH}} \\ \lambda_3 &= \frac{1 + \lambda\tau_{HH}(2K - H) - \sqrt{\lambda\tau_{HH}(\lambda\tau_{HH}(2K - H)^2 + 2H) + 1}}{2\tau_{HH}}.\end{aligned}$$

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

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

830 Appendix E. Unique equilibrium solution of (45)

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

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

833 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

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

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

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

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

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

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

835 Using Mathematica (with assumptions $K > 0$, $\lambda > 0$, $\tau_{HH} > 0$, $\pi_{H_s} < 0$,
 836 $\pi_{H_o} > 0$, $\pi_{D_s} < 0$, $\pi_{D_o} > 0$, see Appendix F) we show that condition (E.2)
 837 evaluated at H_- cannot hold when $H_- > K$ and so $(H, D) = (H_-, 0)$ is not
 838 an equilibrium of (45). H_+ is the only solution that satisfies both conditions
 839 (provided we assume $2\pi_{HH} \neq \pi_{H_o}\tau_{HH}$).

840 Moreover, if $D = 0$ in the right-hand side of (45), then dH/dt is positive when
 841 $H = K$ and tends to minus infinity as the number of Hawks increases to infinity
 842 (because $\pi_{H_s} < 0$). Thus, the equilibrium $(H_+, 0)$ is globally asymptotically
 843 stable for Example 3.

844 Appendix F. Mathematica notebook

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

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