

The Hairy-Downy Game: A Model of Interspecific Social Dominance Mimicry*

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Abstract: The evolution of many forms of mimicry are well understood, but the evolution of mimicry in the absence of aposematic models or third party participants remains poorly understood. This paper presents a model of the evolution of interspecific social dominance mimicry (ISDM), that does not rely on third-party observers, in the context of the *Hairy-Downy* game. Members of a socially dominant species contest a resource by playing the hawk-dove game. Nonmimic members of a subordinate species surrender the resource whenever encountering a member of the dominant species, and split the resource whenever interacting among themselves. Mimicry allows members of the subordinate species to pose as members of the dominant species who play dove, splitting the resource when facing other dominant doves while continuing to surrender the resource to dominant hawks. We characterize the evolutionary dynamics and equilibrium behavior of this game, developing conditions under which evolution will select for mimicry, and under which the subordinate species will consist (almost or even literally) entirely of mimics.

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Contents

1	Introduction	1
1.1	Interspecific Mimicry	1
1.2	Interspecific Social Dominance Mimicry	3
2	Hairy Woodpeckers: The hawk-dove Game	4
3	Downy Nonmimics	6
3.1	The Strategic Interaction	6
3.2	Equilibrium	7
3.3	Summary	11
4	Mimicry: The Hairy-Downy Game	11
4.1	Mimics	11
4.2	Equilibrium Mimicry: Existence	13
4.3	Equilibrium Mimicry: Characterization	14
4.3.1	Assumptions	14
4.3.2	Computation	15
4.3.3	Comparative Statics	18
4.3.4	The Dynamic System	22
4.3.5	Evolution	24
5	When Will Mimics Vanquish Nonmimics?	30
5.1	Unsuccessful Nonmimics	30
5.2	Costless Mimicry	33
5.3	Intraspecific Advantages of Mimicry	33
6	Discussion	34
7	Appendix	37
7.1	Notation	37
7.2	Proof of Proposition 2	38
7.3	Completion of the Proof of Proposition 3: Other Equilibria	39
7.3.1	Monomorphic Equilibria	39
7.3.2	Dimorphic Equilibria	40
7.3.3	Trimorphic Equilibria	40
7.3.4	Completely Mixed Equilibria	42
7.4	Calculations, Example 2	43
7.5	Calculations, Example 3	44
7.5.1	$v_H - 2c_m - c_d > 0$	44
7.5.2	$v_H - 2c_m - c_d < 0$	44
7.5.3	Large c_h	45
7.6	Derivation of the Replicator Dynamics, Section 4.3.4	46
7.7	Asymptotic Stability	48

1 Introduction

1.1 Interspecific Mimicry

Interspecific mimicry is known to evolve through natural selection on appearance to avoid attack (Ruxton, Sherratt and Speed [17], Wickler [26]). Classically, mimicry includes three players: a model, a mimic, and a third party predator/observer. In Müllerian mimicry, two or more toxic/noxious species converge in appearance on each other to share the benefits of a common aposematic warning signal. In Batesian mimicry, a harmless species evolves to mimic the aposematic signals of a toxic, venomous, or noxious model species, and benefits from deceiving predators about itself.

Progress in phylogenetic reconstruction has recently revealed new examples of evolutionary convergence in appearance among species which were originally thought to be closely related to one another. These discoveries have clearly established the need to understand the evolution of non-aposematic mimicry between ecological competitors in the absence of additional third-party observer/participants. However, the evolution of mimicry in the absence of aposematic models or third party participants remains poorly understood.

Wallace [22, 23] proposed several examples of mimicry in non-toxic birds. He hypothesized that smaller subordinate species may gain an evolutionary advantage from mimicking a larger dominant species in order to deceive other small species, frightening them away and thereby gaining access to resources with less competition. Alternatively, Osbert Salvin (cited in Newton and Gadow [13, pp. 572–575]) proposed that a larger species may evolve to mimic a smaller species so that other small species will mistake it for the smaller species, allowing the larger species to more readily prey upon them. Both of these proposals relied on third-party observer/participants.

Moynihan [11] and Cody [1] proposed that interspecific plumage coloration convergence may evolve to facilitate efficiency of social interactions within multi-species foraging flocks and among interspecifically territorial ecological competitors, respectively, but these proposals have not received much empirical support or intellectual enthusiasm. In a re-analysis of Wallace’s classic example of mimicry between clades of the larger bodied friarbirds (*Philemon*, *Meliphagidae*) and the smaller Old World orioles (*Oriolus*, *Oriolidae*) in Indonesia, New Guinea, and Australia, Diamond [3] presented a new hypothesis for the evolution of mimicry in the absence of third party observers. Diamond proposed that a smaller species may evolve to resemble a larger, socially dominant model species in order to deceive the dominant species and reduce aggressive attack. Diamond presented evidence in support of mimicry between the *Oriolus-Philemon* clades, but he remained inconclusive as to whether deception of additional, third-party species, or deception of the dominant



Figure 1: Hairy Woodpecker (*Picoides villosus*, left) and Downy Woodpecker (*Picoides pubescens*, right). The two species are virtually identical in appearance, but Downy Woodpeckers have somewhat less than half the body mass of Hairy Woodpeckers. (Copyright permission requested.)

model was more important in its evolution. More recently, Rainey and Grether [15] reviewed and classified types of mimicry between ecological competitors. They identified competitive mimicry by a subordinate competitor of a dominant ecological competitor as a form of bipolar, antergic, defensive mimicry (following the classification of Vane-Wright [21]). Their brief discussion of this phenomenon was restricted to song sharing between bird species, and did not consider convergence in visual appearance. Rainey and Grether [15] called for theoretical and empirical research on competitive mimicry.

A striking example of unexpected plumage convergence comes from the Hairy Woodpecker (*Picoides villosus*) and Downy Woodpecker (*Picoides pubescens*), two broadly sympatric North American species that are strikingly similar in plumage. Although the two species can be distinguished by bill proportions and very subtle plumage characters, they are virtually identical in appearance (Figure 1). However, the Downy Woodpecker has only 43 percent of the body mass of the Hairy (Dunning [4]). Recently, molecular phylogenetic research has demonstrated that these two species are not close relatives within the genus *Picoides*, and that their plumage similarities are convergently evolved (Weibel and Moore [24, 25]). Attempts to explain such striking patterns of convergent evolution have remained inconclusive because of the lack of a coherent theory about how non-aposematic mimicry evolves (Weibel and Moore [25]).

There is also a rich literature on interspecific mimicry in coral reef fishes (reviewed in Eagle and Jones [5] and Randall [16]). Eagle and Jones [5] raised the possibility that smaller subordinate species are mimicking larger, dominant ecological competitors, but conclude that “this mechanism does not fall within the traditional framework of mimicry theory, and requires further investigation.” Clearly, a detailed mechanism for the evolution of mimicry between socially dominant and subordinate ecological competitors is required.

1.2 Interspecific Social Dominance Mimicry

This paper presents a model of the evolution of interspecific social dominance mimicry (ISDM). Our analysis explores the fitness consequences of mimicry by members of a subordinate species, within the subordinate species as well as within a dominant species. Inspired by the example of Hairy and Downy Woodpeckers, we refer throughout to the species in our model as woodpeckers, though the analysis could just as well apply to the interaction between any dominant and subordinate species incorporating the possibility of mimicry.

The analysis is centered around the *Hairy-Downy game*. The game is played by a dominant species, Hairy Woodpeckers, and a subordinate species, Downy Woodpeckers. The members of these populations interact in contests for the control of a resource. The interaction between two Hairies takes the form of the familiar hawk-dove game, and we thus think of the Hairy population as being comprised of Hairy hawks and Hairy doves.

A Downy Woodpecker who is not a mimic surrenders the resource to a Hairy, whether the latter is a Hairy hawk or Hairy dove. To keep the analysis simple, we assume that two interacting Downies simply split the resource with one another.

We then consider the possibility of a Downy mimic. A Downy mimic resembles a Hairy sufficiently closely as to obtain a split of the resource when encountering a Hairy dove, just as would another Hairy dove. The Downy mimic surrenders the resource to a Hairy hawk, again just as would a Hairy dove, but may pay a cost (dubbed the “cost of mimicry”) in doing so, arising out of the Downy’s smaller size. A Downy mimic thus incurs some (perhaps small) costs of mimicry, in return for being able to act as a dove (rather than surrendering the resource altogether) when encountering Hairy doves.

We develop our main results in Section 4:

- We establish sufficient conditions for the existence of an equilibrium in which Hairy hawks, Hairy doves, Downy mimics and Downy nonmimics coexist. Intuitively, these conditions include that the cost of mimicry be sufficiently small, that the resource not be too valuable to Downies, and that the Downy background fitness be neither too large nor too small. The latter two requirements ensure that Hairies and Downies coexist, though the latter may be nonmimics, with the key requirement for mimicry then being that it not be too costly.
- We characterize the evolutionary dynamics under these conditions, showing that there is a unique interior equilibrium.
- We calculate the equilibrium and derive comparative static results. For example:
 - As the cost of mimicry gets small, the equilibrium frequency of Hairy doves decreases to zero. Hairy hawks decrease in frequency but not to zero. The frequencies of both Downy mimics and Downy nonmimics increase.

- As the cost to a Hairy hawk of fighting with other hairy hawks increases, the equilibrium frequencies of Hairy hawks and Hairy doves decrease, while the ratio of Downy mimics to Downy nonmimics may either increase or decrease, depending on parameters.
- The Downy population (and indeed the entire community of woodpeckers) will be composed almost exclusively of mimics when the cost of mimicry is relatively small, the value of the resource and the background fitness of Downies is relatively small, and the cost of fighting to a Hairy hawk is large.

We often observe cases in which the subordinate species is comprised entirely of mimics. Section 5 examines conditions under which Downy nonmimics will be eliminated entirely, while Hairies and Downy mimics survive. We find that in our basic game, this is generically impossible (though Downy nonmimics may be very rare in equilibrium). However, if Downy mimics enjoy some advantage in contests with Downy nonmimics, perhaps because nonmimics sometimes mistake Downy mimics for Hairies, then mimics may drive nonmimics to elimination.

2 Hairy Woodpeckers: The hawk-dove Game

We begin by considering a population of Hairy Woodpeckers, who play the hawk-dove game,

$$\begin{array}{c} H_h \\ H_d \end{array} \begin{array}{cc} H_h & H_d \\ \hline z_H + \frac{v_H - c_h}{2}, z_H + \frac{v_H - c_h}{2} & z_H + v_H, z_H \\ \hline z_H, z_H + v_H & z_H + \frac{v_H}{2}, z_H + \frac{v_H}{2} \end{array} ,$$

where H_h identifies a Hairy Woodpecker playing hawk and H_d identifies a Hairy Woodpecker playing dove. z_H is the background fitness of a Hairy Woodpecker, v_H is the incremental value of the resource to a Hairy Woodpecker, and c_h is the cost of conflict.

We lose no generality in assuming that background fitnesses are measured in such units that $z_H = 0$, allowing us to write the game more succinctly in traditional form as

$$\begin{array}{c} H_h \\ H_d \end{array} \begin{array}{cc} H_h & H_d \\ \hline \frac{v_H - c_h}{2}, \frac{v_H - c_h}{2} & v_H, 0 \\ \hline 0, v_H & \frac{v_H}{2}, \frac{v_H}{2} \end{array} .$$

As usual, the fitnesses satisfy

$$\frac{v_H - c_h}{2} < 0 < v_H.$$

Winning sole possession of the resource (v_H) or even sharing possession ($v_H/2$) is thus better than nothing (i.e., has a positive incremental effect on fitness), but the cost of

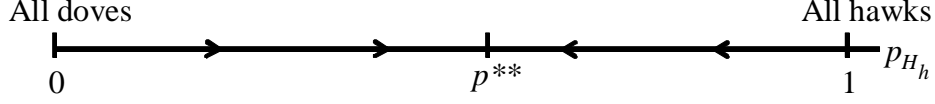


Figure 2: Dynamics in the hawk-dove game. The axis measures p_{H_h} , the frequency of the hawk strategy in the Hairy population, ranging from a population comprised entirely of doves ($p_{H_h} = 0$) to a population comprised entirely of hawks ($p_{H_h} = 1$). The arrows indicate that whenever there are too few hawks ($p_{H_h} < p^{**} = v_H/c_h$), hawks enjoy a higher fitness than do doves and selection pushes the frequency of hawks upward. Whenever there are too many hawks ($p_{H_h} > p^{**}$), hawks enjoy a lower fitness than do doves and selection pushes the frequency of hawks downward. The dynamics have a unique asymptotically stable state in which hawks appear in frequency p^{**} .

fighting c_h is sufficiently high that the expected outcome of a contest $((v_H - c_h)/2)$ is worse than nothing.

The basic dynamics in this game arise out of the fact that it pays to be a hawk in a population of doves (obviating the need to share and giving fitness v_H rather than $v_H/2$), but pays to be a dove in a population of hawks (obviating the need to fight and giving fitness 0 rather than $(v_H - c_h)/2$). As a result, the game has a unique (Nash) equilibrium and evolutionarily stable strategy. Letting p_{H_h} be the frequency of H_h in the Hairy population, the equilibrium condition is that hawk and dove give equal expected fitnesses, or

$$p_{H_h} \frac{v_H - c_h}{2} + (1 - p_{H_h})v_H = (1 - p_{H_h})\frac{v_H}{2},$$

which we solve for

$$\frac{p_{H_h}}{1 - p_{H_h}} = \frac{p_{H_h}}{p_{H_d}} = \frac{v_H}{c_h - v_H} := p^* \quad (1)$$

and hence

$$p_{H_h} = \frac{v_H}{c_h} := p^{**}.$$

The equilibrium features a higher frequency of H_h the higher is the value of the resource v_H and the lower is the cost of fighting c_h . Figure 2 illustrates the resulting dynamics.

3 Downy Nonmimics

3.1 The Strategic Interaction

Now we add Downy Woodpeckers to the game, though at this point without any prospects for mimicry. The Downy Woodpecker is a smaller, socially submissive competitor of the Hairy Woodpecker.

The fitness game is then

	H_h	H_d	D_n
H_h	$\frac{v_H - c_h}{2}, \frac{v_H - c_h}{2}$	$v_H, 0$	v_H, z_D
H_d	$0, v_H$	$\frac{v_H}{2}, \frac{v_H}{2}$	v_H, z_D
D_n	z_D, v_H	z_D, v_H	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$

where D_n denotes a Downy Woodpecker not engaged in mimicry, z_D is the background fitness level of a Downy, and v_D is the value of the resource to a Downy.

It is standard to normalize one's measurement scheme by taking background fitness to be zero, and then interpreting the fitnesses in the game to be incremental fitnesses to be added to background fitness. We did this in the original hawk-dove game by setting $z_H = 0$. However, it need not be the case that Hairies and Downies have the same background fitness, and so once having normalized the Hairy background fitness to be 0, we must explicitly represent the Downy background fitness, denoted here by z_D . In principle, we could have either $z_D > 0$ or $z_D < 0$, meaning that Downies may be either advantaged or disadvantaged, relative to Hairies, in terms of their interactions outside the game in question.

In the game, Downies surrender the resource to both Hairy hawks and Hairy doves, earning only their background fitness z_D from interactions with Hairies of either strategy. Downies on average split the resource in interactions among themselves, earning $z_D + v_D/2$.

We now have two species in the interaction, Hairy Woodpeckers and Downy Woodpeckers. We will refer to the *population* of Hairy Woodpeckers and the *population* of Downy Woodpeckers, and to the *community* of both woodpeckers. We will measure all frequencies as frequencies in the community of woodpeckers, so that p_{H_h} (for example) tells us the frequency of H_h within the entire community of Hairy and Downy Woodpeckers. The frequency of H_h in the Hairy population is given by $p_{H_h}/(p_{H_h} + p_{H_d})$. The frequency of Hairy Woodpeckers in the community is then given by $p_{H_h} + p_{H_d}$, and the frequency of Downies by p_{D_n} . When we add Downy mimics (denoted by D_m) to the community, the frequency of Hairies will remain $p_{H_h} + p_{H_d}$, while the frequency of Downy mimics will be p_{D_m} , the frequency of Downy nonmimics will be p_{D_n} , and the frequency of Downies will be $p_{D_m} + p_{D_n}$.¹

¹We can think of the analysis of Section 2 as examining the community of Hairy and Downy wood-

3.2 Equilibrium

The necessary conditions for an equilibrium include that any strategies appearing with positive frequency yield the same fitness (whether these are strategies from the same species or from different species), and these fitnesses must be at least as large as those that would be earned by any strategy with zero frequency.

The equilibrium will depend upon the values of the parameters v_H , c_h , v_D , and z_D . We will need to make two comparisons. First, either

$$v_H > z_D + \frac{v_D}{2} \quad \left(\text{or, equivalently, } z_D < v_H - \frac{v_D}{2} \right) \quad (\text{A1})$$

or

$$v_H < z_D + \frac{v_D}{2} \quad \left(\text{or, equivalently, } z_D > v_H - \frac{v_D}{2} \right). \quad (\text{A1}')$$

These inequalities tell us how an invasion by Hairies is likely to fare in a community dominated by nonmimic Downies. Condition (A1) will ensure that Hairies could invade such a community, while (A1') will be sufficient to preclude such invasion. We will derive these implications in the course of proving Proposition 1.

In the second comparison, either

$$z_D > \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2} \quad (\text{A2})$$

or

$$z_D < \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2}. \quad (\text{A2}')$$

These inequalities tell us how an invasion of Downies would fare in a community composed only of Hairies. Condition (A2) will ensure that Downies could invade such a community, while (A2') will be sufficient to preclude such invasion. We again derive these implications in the course of proving Proposition 1.

Recalling that $c_h > v_H$, condition (A2) indicates that Downy nonmimics will be able to invade a community comprised entirely of Hairies only if $z_D > 0$, i.e., only if Downies have a higher background fitness than do Hairies. Behind this is the observation that Downy nonmimics invariably surrender the resource when encountering a Hairy, and hence fare worse in these interactions than do both Hairy doves (who at least secure some of the resource when facing other Hairy doves) and Hairy hawks (whose equilibrium fitness equals that of Hairy doves). The only force that can give Downy nonmimics a toehold in the community is then an advantage in terms of background fitness. Alternatively, we can notice that Hairies earn a positive incremental fitness from the hawk-dove game. Against Hairies, Downies earn only their background fitness. If this background fitness z_D

peckers, but in the special case in which $p_{D_m} = p_{D_n} = 0$. Similarly, we can think of the current section as examining the community in the special case in which $p_{D_m} = 0$.

is below the background fitness of Hairies, the Downies are disadvantaged both in terms of background fitness and in terms of the hawk-dove game, and hence will be unable to invade.

To characterize the community equilibrium, we note that we have a Hairy invasion condition and a Downy invasion condition. If an invasion condition holds, then the relevant species must be present in equilibrium. If an invasion condition fails for species A , then there exists an equilibrium featuring only species B . We then need only keep track of the possibilities, which hinge on the size of the Downy background fitness. The Downy invasion condition holds when the background fitness z_D is sufficiently large, and the hairy invasion condition holds when the background fitness z_D is sufficiently small. We thus have:

Proposition 1

[1.1] Suppose

$$v_H - \frac{v_D}{2} > \frac{c_h - v_H}{c_h} \frac{v_H}{2}.$$

Then there are three possibilities:

- The Hairy invasion condition fails and the Downy invasion condition holds:

$$z_D > v_H - \frac{v_D}{2} > \frac{c_h - v_H}{c_h} \frac{v_H}{2}. \quad ((A1') \text{ and } (A2))$$

Then there is a unique Nash equilibrium featuring only Downies.

- Both invasion conditions hold:

$$v_H - \frac{v_D}{2} > z_D > \frac{c_h - v_H}{c_h} \frac{v_H}{2}. \quad ((A1) \text{ and } (A2))$$

Then there is a unique Nash equilibrium featuring all three strategies, with hawks and doves appearing in the relative frequencies p^* of the hawk-dove game equilibrium.

- The Hairy invasion condition holds and the Downy invasion condition fails:

$$v_H - \frac{v_D}{2} > \frac{c_h - v_H}{c_h} \frac{v_H}{2} > z_D. \quad ((A1) \text{ and } (A2'))$$

Then there is a unique Nash equilibrium featuring only Hairies, with hawks and doves appearing in the relative frequencies p^* of the hawk-dove game equilibrium.

[1.2] Suppose

$$v_H - \frac{v_D}{2} < \frac{c_h - v_H}{c_h} \frac{v_H}{2}.$$

Then there are three possibilities:

- *The Hairy invasion condition fails and the Downy invasion condition holds:*

$$v_H - \frac{v_D}{2} < \frac{c_h - v_H}{c_h} \frac{v_H}{2} < z_D. \quad ((A1') \text{ and } (A2))$$

Then there is a unique Nash equilibrium, featuring only Downies.

- *Both invasion conditions fail:*

$$v_H - \frac{v_D}{2} < z_D < \frac{c_h - v_H}{c_h} \frac{v_H}{2}. \quad ((A1') \text{ and } (A2'))$$

Then there are two Nash equilibria, one featuring only Downies, and one featuring only Hairies (in the relative frequencies p^ of the hawk-dove game equilibrium).*

- *The Hairy invasion condition holds and the Downy invasion condition fails:*

$$z_D < v_H - \frac{v_D}{2} < \frac{c_h - v_H}{c_h} \frac{v_H}{2}. \quad ((A1) \text{ and } (A2'))$$

Then there is a unique Nash equilibrium, featuring only Hairies (in the relative frequencies p^ of the hawk-dove game equilibrium).*

The intuition is straightforward. Condition (A1) ensures that Hairies can invade an exclusively Downy community, while (A2) ensures Downies can invade a community of Hairies. If one condition holds and the other fails, then we have a unique equilibrium featuring only one species. This accounts for four of the cases listed above. If both invasion conditions hold, then we have a unique equilibrium featuring the coexistence of both species. If neither holds, then we have two equilibria, one featuring only Hairies and one featuring only Downies.

Proof The arguments for the various cases are quite similar, and we will go through only one. Suppose (A1) and (A2) hold. We show that there is a unique equilibrium featuring all three strategies.

We first argue that there is no monomorphic equilibrium. The first two steps toward this conclusion are immediate. A community consisting of only H_h would be invaded by H_d , and a community consisting of only H_d would be invaded by H_h . These results follow from the properties of the hawk-dove game. The next step is to use (A1). The right side of (A1) is the fitness to a Downy in a community composed solely of Downies, while the left side is the fitness of H_h and H_d against such a community. The inequality (A1) then implies that a community of only D_n could be invaded by H_h and H_d , and hence that a community of only Downies is not stable.

What about dimorphic equilibria? An equilibrium with only H_h and D_n is impossible, because H_d would earn a higher fitness than H_h in such a community, and would invade,

while a community of H_d and D_n is impossible, because H_h have a higher fitness than H_d and would invade. The nontrivial question here is whether the community could consist of only Hairies. Could D_n invade a community of H_h and H_d ?

If only H_h and H_d are present in the community, then they must appear in the frequencies $p_{H_h} = p^{**}$ and $p_{H_d} = 1 - p^{**}$. D_n will then invade if

$$z_D > p^{**} \frac{v_H - c_h}{2} + (1 - p^{**})v_H = (1 - p^{**}) \frac{v_H}{2},$$

i.e., if the fitness z_D of a Downy nonmimic exceeds the (equal) fitnesses of a Hairy hawk and a Hairy dove. We can substitute for p^{**} to rewrite the inequality between the first and third of these fitnesses as

$$z_D > \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2} > 0,$$

which is condition (A2). The equilibrium must then be one in which all three strategies are present in the community. It is then an immediate calculation that H_h and H_d will have equal fitnesses if and only if their relative frequencies are given by p^* . ■

The Nash equilibrium condition is necessary but not sufficient to be evolutionarily stable. Evolutionary stability is immediate in each case except the most interesting, namely that in which (A1)–(A2) holds. Section 7.2 proves:

Proposition 2 *Let (A1)–(A2) hold. Then if $v_D < v_H$, the unique Nash equilibrium, featuring Hairy hawks, Hairy doves, and Downy nonmimics, is evolutionarily (and hence asymptotically) stable, and every trajectory with an interior initial condition converges to this Nash equilibrium.*

The invasion conditions (A1)–(A2) may both hold but $v_D > v_H$. In this case we still have a unique Nash equilibrium featuring all three strategies, but this state is not evolutionarily stable. Instead, there are mutants who would fare better than the equilibrium strategy when invading the latter.² Nonetheless, as long as (A1)–(A2) hold, the

²For example, suppose $v_H = 80$, $c_H = 160$, $z_D = 22$ and $v_D = 114$. Then the fitness game is

	H_h	H_d	D_n
H_h	−40, −40	80, 0	80, 22
H_d	0, 80	40, 40	80, 22
D_n	22, 80	22, 80	79, 79

.

The equilibrium is $(p_{H_h}, p_{H_d}, p_{D_n}) = (1/6, 1/6, 2/3)$. Now consider a mutant invasion of H_d . Since the equilibrium is completely mixed, strategy H_d is necessarily an alternative best response to the equilibrium strategy, supplying the first (Nash equilibrium) of the usual evolutionary stability conditions. However,

Nash equilibrium is asymptotically stable, and the community will converge to the Nash equilibrium from any interior initial condition.³

3.3 Summary

To summarize, (A1) and (A2) are the conditions for there to be a unique equilibrium including the three strategies H_h , H_d , and D_n . Combining the two conditions, we have

$$v_H - \frac{v_D}{2} > z_D > \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2} \quad (\text{A1})\text{--}(\text{A2})$$

The second inequality requires that Downies have a sufficient edge over Hairies in terms of background fitness. If this does not hold, equilibria will exist in which there are no Downies at all. The first inequality requires that the value of the resource at issue in this interaction to Hairies is sufficiently large relative to its value to Downies, and precludes a population in which there are only Downies.

If these conditions are to hold, the background fitness of Downies must be higher than that of Hairies, but not too high. In order for such a background fitness to exist, it must be that

$$v_H - \frac{v_D}{2} > \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2},$$

putting restrictions on the fitnesses of the hawk-dove game that will hold if the cost of fighting is not too high and if the resource is sufficiently more valuable to Hairies than to Downies.

The stationary state is evolutionarily stable if $v_D < v_H$ but not if $v_D > v_H$, but is asymptotically stable in either case. Figure 3 shows the resulting dynamics.

4 Mimicry: The Hairy-Downy Game

4.1 Mimics

We start the analysis of the evolution of mimicry assuming that (A1) and (A2) hold, maintaining this assumption throughout this section. Hence, Downy nonmimics can co-exist within a community of Hairies. (The evolution of mimicry in the absence of Downy

H_d receives a payoff of 40 against itself, while the equilibrium strategy earns a payoff of only $(1/6)80 + (1/6)40 + (2/3)22 \approx 35$, ensuring that the second (stability) condition for evolutionary stability fails. An invasion of H_d with thus cause the frequency of H_d to initially grow more, leading away from the equilibrium, until the increased prevalence of H_d leads to an increase in the payoff and hence frequency of first H_h and then D_n , leading back to the equilibrium.

³Every converging trajectory with an interior initial condition must converge to a Nash equilibrium, and hence to the unique Nash equilibrium in this case. A straightforward argument exploiting the fact that p_{H_h}/p_{H_d} is increasing (decreasing) if and only if it falls short of (exceeds) p^* allows us to establish asymptotic stability and that there are no nonconverging trajectories.

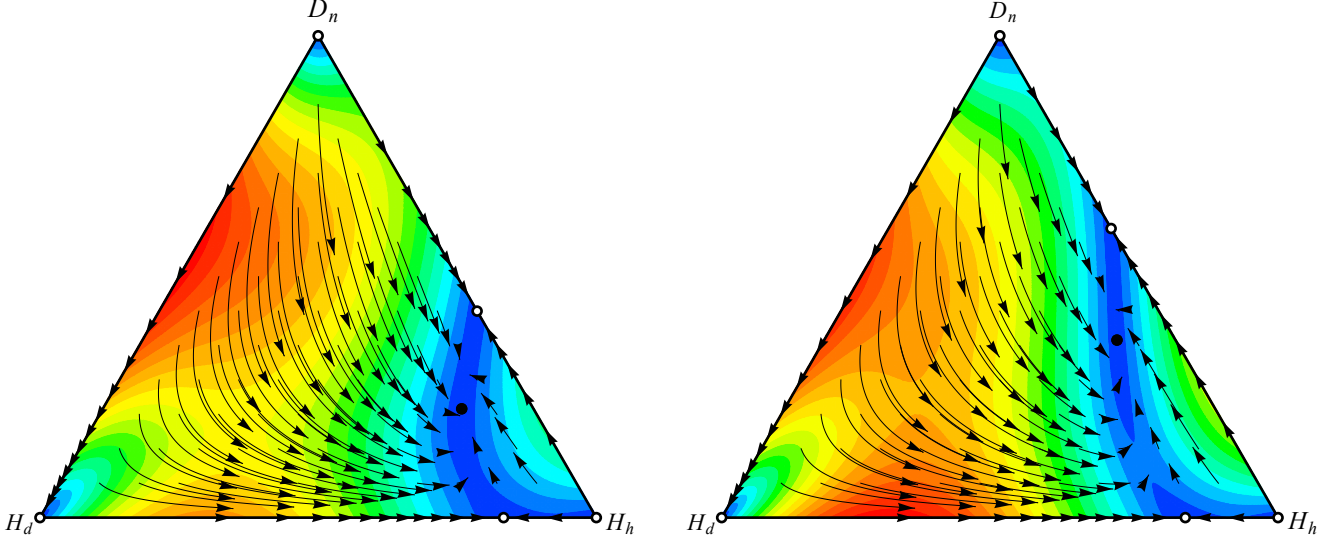


Figure 3: Dynamics in the Hairy hawk-dove game with Downy nonmimics. Points in the triangle describe frequencies in a community, with the top vertex corresponding to a community comprised exclusively of Downy nonmimics, the bottom left vertex a community comprised exclusively of Hairy doves, and the bottom right corner a community comprised exclusively of Hairy hawks. The dynamics on the bottom edge of the triangle duplicate those pictured in Figure 2. The hollow dot on the horizontal axis corresponds to the equilibrium configuration in the hawk-dove game, with $p_{H_h}/p_{H_d} = p^*$. A line connecting the vertex D_n with this point would identify the collection of states in which the ratio p_{H_h}/p_{H_d} is given by $v_H/(c_h - v_H) = p^*$. The dynamics push any state to the right of this line toward the line, and also push any state to the left of this line toward the line. There is unique interior stationary state and Nash equilibrium, marked by the solid dot. Arrows indicate the direction of movement of the dynamics, and lengths indicate speed of movement (as does color, ranging from red (fastest) to blue (slowest)). The left panel is drawn for the values $(v_H, c_h, v_D, z_D) = (5, 6, 4, 1)$, the right for $(v_H, c_h, v_D, z_D) = (5, 6, 6, 1)$. Both specifications satisfy (A1)–(A2). The left panel satisfies $v_D < v_H$, and hence the stationary state is evolutionarily stable. The right panel features $v_D > v_H$, and the stationary state is not evolutionarily stable.

nonmimic co-existence, or conditions (A1) and (A2'), will be discussed in Section 5.) Adding mimics gives us the game

	H_h	H_d	D_m	D_n
H_h	$\frac{v_H - c_h}{2}, \frac{v_H - c_h}{2}$	$v_H, 0$	$v_H, z_D - c_m$	v_H, z_D
H_d	$0, v_H$	$\frac{v_H}{2}, \frac{v_H}{2}$	$\frac{v_H}{2}, z_D + \frac{v_D}{2}$	v_H, z_D
D_m	$z_D - c_m, v_H$	$z_D + \frac{v_D}{2}, \frac{v_H}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$
D_n	z_D, v_H	z_D, v_H	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$

In this full Hairy-Downy game, Downy mimics split the resource in interactions with Hairy doves (earning fitnesses of $z_D + v_D/2$ and $v_H/2$, respectively), but Downy mimics pay an additional cost of mimicry in their interactions with Hairy hawks, yielding fitness $z_D - c_m$. Downy mimics and nonmimics split the resource evenly in their interactions.

4.2 Equilibrium Mimicry: Existence

Now let us ask when we can expect to have an equilibrium in which mimicry exists. The key condition for the success of mimics will be the mimic invasion condition:

$$\frac{v_D(c_h - v_H)}{2c_m} > v_H, \quad (\text{A3})$$

while mimics will not appear in equilibrium if

$$\frac{v_D(c_h - v_H)}{2c_m} < v_H. \quad (\text{A3}')$$

The mimic invasion condition will hold as long as the cost of mimicry c_m is sufficiently low.

Proposition 3 *Let (A1)–(A2) hold. If (A3) holds, then there exists a unique Nash equilibrium, and all four strategies have positive frequency in that equilibrium. If (A3') holds, then there exists a unique Nash equilibrium, and only H_h , H_d and D_n have positive frequency.*

The proof of this proposition begins by deriving (A3). To do so, suppose we have a community of H_h , H_d and D_n . Suppose further that this community is in equilibrium, meaning that H_h and H_d must appear in relative frequencies $p_{H_h}/(p_{H_h} + p_{H_d}) = p^*$ (cf. Proposition 1), and each of the three strategies earns the same expected fitness. To check whether D_m can invade this community, we need only determine whether it earns a higher fitness than any one of the other three strategies. For example, D_m will invade if they earn a higher expected fitness than D_n , or

$$p_{H_h}(z_D - c_m) + (p_{H_d} + p_{D_m} + p_{D_n}) \left(z_D + \frac{z_D}{2} \right) > (p_{H_h} + p_{H_d}) z_D + (p_{D_m} + p_{D_n}) \left(z_D + \frac{v_D}{2} \right).$$

We are considering the case in which $p_{D_m} = 0$, and so we can simplify this to

$$p_{H_h}(z_D - c_m) + p_{H_d}\left(z_D + \frac{v_D}{2}\right) > (p_{H_h} + p_{H_d})z_D.$$

We can eliminate z_D (since all Downies earn background fitness z_D , only increments to this background fitness are relevant in determining whether D_n or D_m earn a higher payoff) to find that D_m will invade if

$$-p_{H_h}c_m + p_{H_d}\frac{v_D}{2} > 0.$$

Rearranging to $v_D/2 > (p_{H_h}/p_{H_d})c_m$, recalling that H_h and H_d must appear in proportion $p_{H_h}/(p_{H_h} + p_{H_d}) = p^*$, and hence using (1) to substitute, this gives (A3).

This argument establishes that if (A3) holds, then D_m can invade a community of H_h , H_d , and D_n . One need only turn the equality signs around to conclude that if (A3') holds, then D_m will be unable to invade. This allows us to conjecture that there are two candidates for equilibria:

- If (A3) holds, there is a unique Nash equilibrium, in which all four strategies are present.
- If (A3) fails, there is a unique Nash equilibrium, in which H_h , H_d , and D_n are present.

We can confirm this conjecture by first systematically eliminating the other possibilities for equilibrium. We do this in Section 7.3. Nash's [12] existence theorem ensures that the game has a Nash equilibrium, in each case, which must coincide with our candidate.

4.3 Equilibrium Mimicry: Characterization

4.3.1 Assumptions

We focus on the case in which all four strategies are present in equilibrium. Our maintained assumptions are thus (A1)–(A3). Condition (A2) ensures that D_n will invade a community of only Hairies; condition (A3) ensures that D_m will invade a community of H_h , H_d and D_n , and condition (A1) ensures that Hairies will invade a community of only Downies. Intuitively, these assumptions will hold when c_m is sufficiently small (including cases in which c_m is very small, so that mimicry is almost free), and that z_D is appropriately mid-ranged. In particular, if c_m is small enough, (A3) is satisfied, ensuring the presence of mimicry. We view the case of low mimicry cost as natural, and hence view (A1) and (A2) as the important conditions.

4.3.2 Computation

We can compute the equilibrium by solving the following system of equations for values of $(\hat{p}_{H_h}, \hat{p}_{H_d}, \hat{p}_{D_m}, \hat{p}_{D_n}, \hat{\pi})$, where $\hat{\pi}$ is interpreted as the equilibrium fitness:

$$\begin{bmatrix} \frac{v_H - c_h}{2} & v_H & v_H & v_H \\ 0 & \frac{v_H}{2} & \frac{v_H}{2} & v_H \\ z_D - c_m & z_D + \frac{v_D}{2} & z_D + \frac{v_D}{2} & z_D + \frac{v_D}{2} \\ z_D & z_D & z_D + \frac{v_D}{2} & z_D + \frac{v_D}{2} \\ 1 & 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} \hat{p}_{H_h} \\ \hat{p}_{H_d} \\ \hat{p}_{D_m} \\ \hat{p}_{D_n} \end{bmatrix} = \begin{bmatrix} \hat{\pi} \\ \hat{\pi} \\ \hat{\pi} \\ \hat{\pi} \\ 1 \end{bmatrix}.$$

This is simply the statement that in equilibrium each strategy must attain the same fitness, and the shares of the various strategies in the community must add to one.

To solve this system, let us begin with the Hairy population. In equilibrium, Hairy hawks and Hairy doves must attain the same fitness, or

$$\hat{p}_{H_h} \frac{v_H - c_h}{2} + \hat{p}_{H_d} v_H + \hat{p}_{D_m} v_H + \hat{p}_{D_n} v_H = \hat{p}_{H_d} \frac{v_H}{2} + \hat{p}_{D_m} \frac{v_H}{2} + \hat{p}_{D_n} v_H,$$

from which we can eliminate the common term involving \hat{p}_{D_n} to obtain

$$\hat{p}_{H_h} \frac{v_H - c_h}{2} + \hat{p}_{H_d} v_H + \hat{p}_{D_m} v_H = \hat{p}_{H_d} \frac{v_H}{2} + \hat{p}_{D_m} \frac{v_H}{2} \quad (2)$$

and then rearrange as

$$\frac{\hat{p}_{H_h}}{\hat{p}_{H_d} + \hat{p}_{D_m}} = \frac{v_H}{c_h - v_H} = p^*. \quad (E1)$$

Hence, in equilibrium, the ratio of Hairy hawks to the sum of Hairy doves and Downy mimics must be the same as the equilibrium hawk-dove ratio in the original hawk-dove game. To put it differently, the ratio of hawk to dove-like behavior must match that of the hawk/dove game. This in turn implies that if there are to be Downy mimics in the community, then

$$\frac{\hat{p}_{H_h}}{\hat{p}_{H_d}} > p^*,$$

so that the ratio of Hairy hawks to Hairy doves must exceed that of the Hawk-Dove game. Hairy hawks fare better against Downy mimics than do Hairy doves, and the presence of Downy mimics thus confers a relative payoff advantage on Hairy hawks. The only way to restore the equilibrium condition that Hairy hawks and Hairy doves receive the same fitness is to increase the proportion of hawks in the Hairy population.⁴

⁴In contrast, Hairy hawks and Hairy doves fare equally well against Downy nonmimics, and so the proportion of nonmimics in the community has no effect on the equilibrium ratio $\hat{p}_{H_h}/\hat{p}_{H_d}$. This is why this ratio equals p^* in the game of Section 3, where there are Downy nonmimics but no mimics.

Let us next consider the Downy population. The equilibrium condition that D_m and D_n receive the same payoff is

$$\hat{p}_{H_h}(z_D - c_m) + \hat{p}_{H_d}\left(z_D + \frac{v_D}{2}\right) = (\hat{p}_{H_h} + \hat{p}_{H_d})z_D,$$

or

$$\hat{p}_{H_d}\frac{v_D}{2} = \hat{p}_{H_h}c_m.$$

and hence

$$\frac{\hat{p}_{H_h}}{\hat{p}_{H_d}} = \frac{v_D}{2c_m}, \quad (\text{E2})$$

Downy mimics and Downy nonmimics split the resource, and hence fare equally well against one another. As a result, their relative payoffs depend only on the ratio of Hairy hawks to Hairy doves. Downy mimics fare relatively well against Hairy doves, and so the proportion of mimics in the Downy community is increasing whenever the proportion of doves in the Hairy community is relatively large.

Our analysis of the Hairy population showed that the equilibrium ratio of hawks to doves must exceed p^* , and (E2) then implies that we can have an equilibrium only if $v_D/2c_m$ exceeds p^* . Using (1), this is

$$\frac{c_D}{2c_m} > \frac{v_H}{c_h - c_H},$$

which is equivalent to the sufficient condition (A3) for the existence of mimicry.

What about the relative sizes of the Hairy and Downy populations? The equilibrium condition that H_h and D_m attain the same fitness, using the fact that $\hat{p}_{H_d} + \hat{p}_{D_m} + \hat{p}_{D_N} = 1 - \hat{p}_{H_h}$, is

$$\hat{p}_{H_h}\frac{v_H - c_h}{2} + (1 - \hat{p}_{H_h})v_H = \hat{p}_{H_h}(z_D - c_m) + (1 - \hat{p}_{H_h})\left(z_D + \frac{v_D}{2}\right). \quad (3)$$

Successive simplifications give

$$\begin{aligned} \hat{p}_{H_h}\left(\frac{v_H - c_h}{2} - v_H\right) + v_H &= \hat{p}_{H_h}\left(-c_m - \frac{v_D}{2}\right) + \frac{v_D}{2} + z_D \\ \hat{p}_{H_h}\left(-\frac{v_H}{2} - \frac{c_h}{2}\right) + v_H &= \hat{p}_{H_h}\left(-c_m - \frac{v_D}{2}\right) + \frac{v_D}{2} + z_D \\ 2v_H - \hat{p}_{H_h}(v_H + c_h) &= v_D - \hat{p}_{H_h}(2c_m + v_D) + 2z_D \end{aligned}$$

and hence

$$\hat{p}_{H_h} = \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D}. \quad (\text{E3})$$

The fitnesses of both Hairy hawks and Downy mimics depend only on whether they are facing hawks or some other strategy, and the equality of their fitnesses thus fixes the proportion of Hairy hawks in the community.⁵

With this calculation of \hat{p}_{H_h} as an anchor, we can obtain explicit solutions for the remaining equilibrium frequencies. We can combine (E2) and (E3) to obtain

$$\hat{p}_{H_d} = \frac{2c_m}{v_D} \hat{p}_{H_h} = \frac{2c_m}{v_D} \cdot \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D}.$$

Then we can rearrange (2) as

$$\hat{p}_{D_m} \frac{v_H}{2} = \hat{p}_{H_d} \left(\frac{v_H}{2} - v_H \right) + \hat{p}_{H_h} \left(\frac{c_h - v_H}{2} \right),$$

and then use our solution for \hat{p}_{H_d} and (E3) to solve for

$$\begin{aligned} \hat{p}_{D_m} &= \frac{2}{v_H} \left(-\frac{2c_m}{v_D} \frac{v_H}{2} + \frac{c_h - v_H}{2} \right) \hat{p}_{H_h} \\ &= \frac{1}{v_H} \left(c_h - v_H \left(1 + \frac{2c_m}{v_D} \right) \right) \hat{p}_{H_h} \\ &= \frac{1}{v_H} \left(c_h - v_H \left(1 + \frac{2c_m}{v_D} \right) \right) \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D}. \end{aligned}$$

Finally, we can immediately identify the remaining probability:⁶

$$\hat{p}_{D_n} = 1 - (\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m}).$$

⁵We can confirm that $\hat{p}_{H_h} \in [0, 1]$. The payoff condition (3) is a linear equation in \hat{p}_{H_h} . When $\hat{p}_{H_h} = 0$, condition (A1) ensures that the left side of (3) exceeds the right side. We then need only show that when $\hat{p}_{H_h} = 1$, the right side exceeds the left, or $2(z_D - c_m) > v_H - c_h$. Replacing z_D by the minimum value consistent with (A2) and c_m by the maximum value consistent with (A3) and successively simplifying, it suffices to show (replacing v_D with the maximum allowed by (A1)–(A2) to progress from the third line to the fourth)

$$\begin{aligned} (c_h - v_H) \frac{v_H}{c_h} - (c_h - v_H) \frac{v_D}{v_H} &\geq v_H - c_h \\ \frac{v_H}{c_h} - \frac{v_D}{v_H} &\geq -1 \\ v_H^2 + c_h v_H &\geq c_h v_D \\ v_H^2 + c_h v_H &\geq 2c_h v_H - c_h v_H + v_H^2. \end{aligned}$$

which is obvious. Conditions (E1), (E2) and (A3) then ensure that \hat{p}_{H_d} and \hat{p}_{D_m} are also positive.

⁶We can confirm that $\hat{p}_{D_n} > 0$. This is equivalent to $\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m} < 1$, or, making the relevant substitutions,

$$\frac{c_h}{v_H} \cdot \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} < 1.$$

Let us collect these as

$$\hat{p}_{H_h} = \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \quad (4)$$

$$\hat{p}_{H_d} = \frac{2c_m}{v_D} \hat{p}_{H_h} = \frac{2c_m}{v_D} \cdot \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \quad (5)$$

$$\hat{p}_{D_m} = \left(\frac{c_h - v_H}{v_H} - \frac{2c_m}{v_D} \right) \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \quad (6)$$

$$\hat{p}_{D_n} = 1 - \hat{p}_{H_h} - \hat{p}_{H_d} - \hat{p}_{D_m}. \quad (7)$$

4.3.3 Comparative Statics

We can use these calculations to obtain equilibrium comparative statics. We illustrate here a few of the many possibilities, investigating variations in the parameters that preserve (A1)–(A3).

Example 1. Large mimicry cost. As the cost of mimicry c_m approaches its upper bound of $(v_D(c_h - v_H))/2v_H$:

- $\hat{p}_{D_m} \rightarrow 0$. Mimics disappear (from (6)).
- $\frac{\hat{p}_{H_h}}{\hat{p}_{H_d}} \rightarrow p^*$. Hairy hawks and Hairy doves appear in the equilibrium proportions of the hawk-dove game (from (E1)).
- The equilibrium approaches that of Section 3.3, giving a limiting population consisting only of Hairy hawks, Hairy doves, and Downy nonmimics.

We thus have a continuity result. As mimicry gets increasingly costly, mimics disappear, and the community converges to the equilibrium derived for the case in which the mimicry is impossible. ■

The denominator is positive (since \hat{p}_{H_h} is), and we can simplify to obtain

$$\begin{aligned} 2c_h v_H - c_h v_D - 2z_D c_h &< v_h^2 + c_h v_H - 2c_m v_H - v_H v_D \\ c_h v_H + 2c_m v_H + v_H v_D &< c_h v_D + 2z + Dc_h + v_H^2. \end{aligned}$$

It suffices to replace c_m with the maximum value consistent with (A3) and z_D with the minimum value consistent with (A2), and then to verify the resulting inequality

$$c_h v_H + v_D(c_h - v_H) + v_H v_D \leq c_h v_D + (c_h - v_H)v_H + v_H^2,$$

which is immediate.

Example 2. Small mimicry cost. As the cost of mimicry c_m approaches zero:

- \hat{p}_{H_h} decreases (from (4)). The frequency of Hairy hawks declines, but Hairy hawks do not disappear from the population.
- $\hat{p}_{H_d} \rightarrow 0$. The frequency of hairy doves becomes arbitrarily small (from (5)).
- $\frac{\hat{p}_{H_h}}{\hat{p}_{D_m}} \rightarrow p^*$. Hairy hawks and Downy mimics appear in proportions equal to the hawk-dove proportions of the original hawk-dove game (from (E1)).
- \hat{p}_{D_n} increases (because \hat{p}_{H_h} decreases and hence, since $\frac{\hat{p}_{H_h}}{\hat{p}_{H_d} + \hat{p}_{D_m}}$ is constant, so does $\hat{p}_{H_d} + \hat{p}_{D_m}$). Downy nonmimics thus become more frequent.
- \hat{p}_{D_m} increases. The frequency of Downy mimics increases, though this seemingly obvious implication requires some calculation, done in Section 7.4.
- The equilibrium approaches a limit consisting only of Hairy hawks, Downy mimics, and Downy nonmimics.

As mimicry cost gets very small, Downy mimics and Downy nonmimics both increase in frequency. Hairy hawks diminish in frequency, though they persist, while the frequency of Hairy doves becomes negligible.⁷

The potential surprise here is that Downy nonmimics increase in frequency as the cost of mimicry declines. Why don't Downy mimics take over at least the Downy population, if not the entire community, as mimicry becomes costless? As c_m declines, the cost that Downy nonmimics pay against Hairy hawks declines, eliminating the advantage that Downy nonmimics have over Downy mimics. However, Hairy doves are disappearing from the population, eliminating the one opportunity for Downy mimics to secure an advantage over Downy nonmimics. The net effect of these two forces is to increase the frequencies of both D_m and D_n . ■

Figure 4 illustrates the effects of variations in the cost of mimicry.

Example 3. Costly combat. As the cost c_h to a Hairy woodpecker of being involved in a conflict increases,

- \hat{p}_{H_h} decreases (from (4)). Combat is costly for H_h , and so increasing costs lead to a lower frequency of H_h .

⁷As long as $c_m > 0$, there will remain some Hairy doves in the population. This follows from Section 7.3.3, which shows that there are no trimorphic equilibria for $c_m > 0$. However, as c_m gets close to zero, the frequency of Hairy doves also approaches zero.

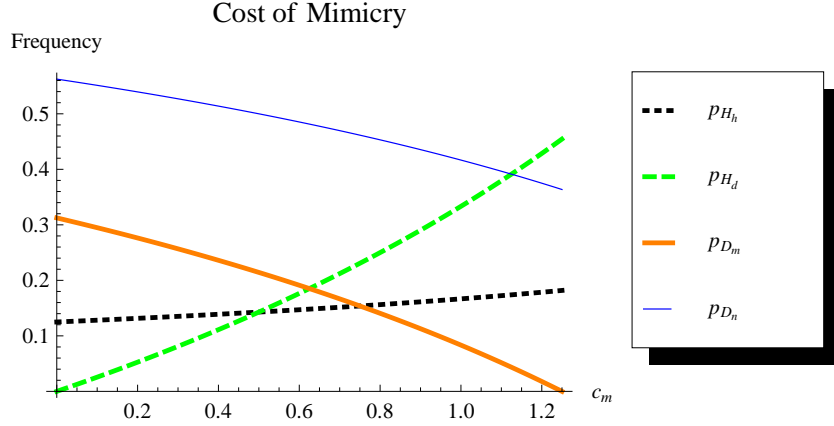


Figure 4: The effects of the cost of mimicry c_m on the equilibrium frequencies \hat{p}_{H_h} , \hat{p}_{H_d} , \hat{p}_{D_m} and \hat{p}_{D_n} . We set $(v_H, c_h, v_D, z_D) = (2, 7, 1, 1)$. The cost of mimicry ranges from 0 to its maximum value (consistent with (A3)) of $(v_D(c_h - v_H))/(2v_H) = 5/4$.

- \hat{p}_{H_d} decreases (from (5)).
- If $v_H - 2c_m - v_D > 0$, then \hat{p}_{D_m} increases and \hat{p}_{D_n} decreases. This requires some calculation, done in Section 7.5.
- If $v_H - 2c_m - v_D < 0$, then \hat{p}_{D_m} may either increase or decrease, and \hat{p}_{D_n} increases. This again requires some calculation, done in Section 7.5, in the course of which we identify the determinants of whether \hat{p}_{D_m} increases or decreases.
- If $z_D < \frac{v_H}{2}$, the solution remains interior (i.e., all four frequencies remain positive) as c_h approaches the finite upper limit imposed by (A2). If $z_D > \frac{v_H}{2}$, there is no upper limit on c_h , and the frequency of Hairies in the community declines to zero as c_h increases. The limiting community includes only Downy mimics and Downy nonmimics. This is again established in Section 7.5.

Figure 5 illustrates the effects of variations in the cost of combat.

Example 4. Rare Nonmimics. We investigate here the conditions under which Downy nonmimics will be rare. Our point of departure is the relationship

$$1 - \hat{p}_{D_n} = \hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m} = \frac{c_h}{v_H} \cdot \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D},$$

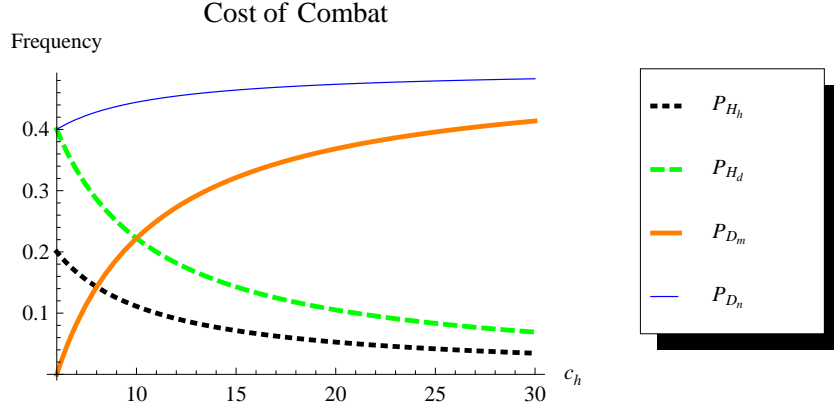


Figure 5: The effects of the cost of combat c_h on the equilibrium frequencies \hat{p}_{H_h} , \hat{p}_{H_d} , \hat{p}_{D_m} and \hat{p}_{D_n} . We set $(v_H, v_D, z_D) = (2, 1, 1)$ and $c_m = 1$. c_h is drawn as ranging from its lower bound of 6 (satisfying $(v_D(c_h - v_H))/2c_m = v_H$) to a maximum of 30, but has no upper bound.

obtained from adding (4)–(6). We are interested in cases in which Downy mimics are not rare, and so we focus on the case in which $c_m \approx 0$. The frequency of Downy nonmimics is small as z_D is small, and so we set z_D equal to the lower bound imposed by (A2), and then substitute to obtain

$$1 - \hat{p}_{D_n} = \hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m} = \frac{c_h}{v_H} \cdot \frac{c_h(2v_H - v_D) - (c_h - v_H)v_H}{c_h(v_H + c_h - v_D)}. \quad (8)$$

We now note that as c_h increases, the product on the right in (8) approaches

$$\frac{v_H - v_D}{v_H}.$$

If v_H is large relative to v_D , then this limit will be very close to one, and hence Downy nonmimics will disappear from the community. At the same time, the first term in the product on the right in (8) is getting large (and the second term, and hence \hat{p}_{H_h} , is getting small), indicating that the Downy mimics are becoming a large proportion of the community.

In summary, Downy mimics will be common and Downy nonmimics will be rare if

- c_m , the cost of mimicry, is quite small.
- z_D , the background fitness of Downies, is near the lower limit necessary for Downy nonmimics to be able to invade a community comprised entirely of Hairies.

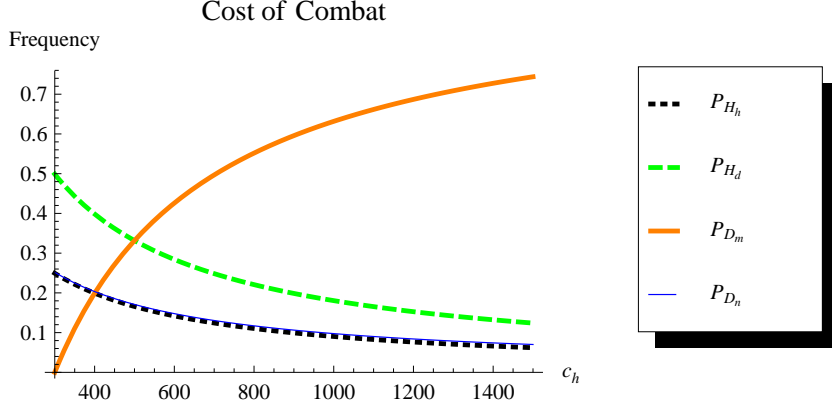


Figure 6: Illustration of conditions under which the Downy population is dominated by mimics. The figure shows the equilibrium frequencies \hat{p}_{H_h} , \hat{p}_{H_d} , \hat{p}_{D_m} and \hat{p}_{D_n} . We set $(v_H, v_D, z_D) = (100, 1, 50)$ and $c_m = 1$. c_h is drawn as ranging from its lower bound of 300 (satisfying $(v_D(c_h - v_H))/2c_m = v_H$) to a maximum of 1500, but has no upper bound. The equilibrium frequencies of Hairy doves and Downy nonmimics are virtually identical.

- v_D is not too large and c_h is large.

Figure 6 illustrates these conditions. ■

4.3.4 The Dynamic System

Now let us examine the dynamics of this system. Let $p_{H_h}(t)$, $p_{H_d}(t)$, $p_{D_m}(t)$, and $p_{D_n}(t)$ denote the frequencies of H_h , H_d , D_m and D_n at time t . Then the replicator dynamics are given by:

$$\frac{dp_{H_h}(t)}{dt} = p_{H_h}(t)(\pi_{H_h}(t) - \bar{\pi}(t)) \quad (9)$$

$$\frac{dp_{H_d}(t)}{dt} = p_{H_d}(t)(\pi_{H_d}(t) - \bar{\pi}(t)) \quad (10)$$

$$\frac{dp_{D_m}(t)}{dt} = p_{D_m}(t)(\pi_{D_m}(t) - \bar{\pi}(t)) \quad (11)$$

$$\frac{dp_{D_n}(t)}{dt} = p_{D_n}(t)(\pi_{D_n}(t) - \bar{\pi}(t)). \quad (12)$$

The terms $\pi_{H_h}(t)$, $\pi_{H_d}(t)$, $\pi_{D_m}(t)$, and $\pi_{D_n}(t)$ are the average fitnesses of the four

strategies, given $p_{H_h}(t)$, $p_{H_d}(t)$, $p_{D_m}(t)$, and $p_{D_n}(t)$, and are given by

$$\begin{aligned}
\pi_{H_h} &= p_{H_h} \frac{v_H - c_h}{2} + (p_{H_d} + p_{D_m} + p_{D_n}) v_H \\
&= p_{H_h} \frac{v_H - c_h}{2} + (1 - p_{H_h}) v_H \\
\pi_{H_d} &= (p_{H_d} + p_{D_m}) \frac{v_H}{2} + p_{D_n} v_H \\
\pi_{D_m} &= z_D - p_{H_h} c_m + (p_{H_d} + p_{D_m} + p_{D_n}) \frac{v_D}{2} \\
&= z_D - p_{H_h} c_m + (1 - p_{H_h}) \frac{v_D}{2} \\
\pi_{D_n} &= z_D + (p_{D_m} + p_{D_n}) \frac{v_D}{2}.
\end{aligned}$$

The term $\bar{\pi}$ is the average fitness of a strategy in the woodpecker community, and is given by

$$\bar{\pi} = p_{H_h} \pi_{H_h} + p_{H_d} \pi_{H_d} + p_{D_m} \pi_{D_m} + p_{D_n} \pi_{D_n}.$$

We thus have the familiar replicator-dynamic relationship that the growth rate of a strategy is given by the difference between its fitness and the average fitness in the community. Section 7.6 provides the derivation of these conditions. We then have:

Proposition 4 *Let (A1)–(A3) hold. The unique Nash equilibrium calculated in (4)–(7) is not evolutionarily stable, but it is the limit of any converging trajectory with an interior initial condition.*

Proof If $v_D > v_H$, the proof of Proposition 2 is readily adapted to show that the equilibrium strategy \hat{p} calculated in (4)–(7) is not evolutionarily stable.⁸ Suppose $v_D < v_H$. We must find an alternative best response q that fares better against itself than does \hat{p} . Let $(q_{H_h}, q_{H_d}, q_{D_m}, q_{D_n}) = (\hat{p}_{H_h}, 0, \hat{p}_{H_d} + \hat{p}_{D_m} + \hat{p}_{D_n}, 0)$. Hence, q differs from \hat{p} in that q shifts Hairy doves and Downy nonmimics to Downy mimics. Strategies q and \hat{p} are both best responses to \hat{p} . Next, notice that q earns the same fitness against q as it does against \hat{p} . We need then only show that \hat{p} earns a lower payoff against q than against \hat{p} . This inequality is

$$\hat{p}_{H_d} \hat{p}_{D_n} \frac{v_H}{2} + \hat{p}_{D_n} \hat{p}_{H_d} \left(z_D + \frac{v_D}{2} \right) < \hat{p}_{H_d} \hat{p}_{D_n} v_H + \hat{p}_{D_n} \hat{p}_{H_d} v_H z_D,$$

which is negative if $v_D < v_H$.

Samuelson [18, Proposition 2, p. 219] shows that converging trajectories must have Nash equilibria as their limits. ■

⁸In particular, (19) is again a requirement for evolutionary stability.

This result leaves open the question of the dynamic stability of the interior equilibrium. Section 7.7 explains how we establish that it is asymptotically stable.

4.3.5 Evolution

How will the frequencies of the various strategies in the community evolve? Figure 7 illustrates the state space for the dynamics in this game. A state identifies the proportion of the community comprised of each of H_h , H_d , D_m and D_n , and hence consists of four nonnegative numbers $(p_{H_h}, p_{H_d}, p_{D_m}, p_{D_n})$ that sum to one. The simplex, or tetrahedron, shown in Figure 7 contains all possible community configurations. To translate a point in this simplex into frequencies $(p_{H_h}, p_{H_d}, p_{D_m}, p_{D_n})$, we think of the frequency of p_{H_h} (for example) as being the normal distance between the point and the surface of the simplex opposite the vertex labeled H_h . We take this vertex itself to be distance one from the opposite surface. The frequency of H_h thus increases as we move away from the opposite surface towards H_h , and is maximized (and equal to one) at the vertex H_h . This vertex thus corresponds to a community consisting entirely of H_h . The other vertices similarly identify states in which the community is composed of a single strategy. Interior states correspond to communities in which all four strategies are present, with any particular strategy increasing in frequency as we move toward its vertex.

States on a line connecting two vertices represent communities in which only two strategies are present. Along the bottom, front edge of the simplex, for example, there are only H_h and H_d , in proportions ranging from all H_h at the right vertex to all H_d at the left vertex. This front edge of the simplex is equivalent to the state space of the classic hawk-dove game shown in Figure 2. States on the bottom surface of the simplex correspond to communities including Hairy hawks, Hairy doves, and Downy nonmimics, studied in Section 3. States near the front surface of the tetrahedron represent communities consisting of Hairy hawks, Hairy doves, and Downy mimics, with very rare Downy nonmimics.

To describe the dynamics in this state space, we can associate with each state (or equivalently, with each possible community configuration) a collection of three vectors, corresponding to our three equilibrium conditions (E1)–(E3). One vector describes the structure of the Hairy population, indicating whether the ratio p_{H_h}/p_{H_d} is increasing or decreasing. The second vector describes the structure of the Downy population, indicating whether the ratio p_{D_m}/p_{D_n} is increasing or decreasing. The third describes the relative population sizes, indicating whether the ratio p_{H_h}/p_{D_m} is increasing or decreasing. There is nothing special about these three ratios—any combination of three such ratios would suffice to describe the dynamics—and we choose these three to emphasize interesting biological forces.⁹

⁹More precisely, the dynamics are completely described by associating with each state three vectors, each of which describes the direction and magnitude of change of a distinct ratio of probabilities drawn

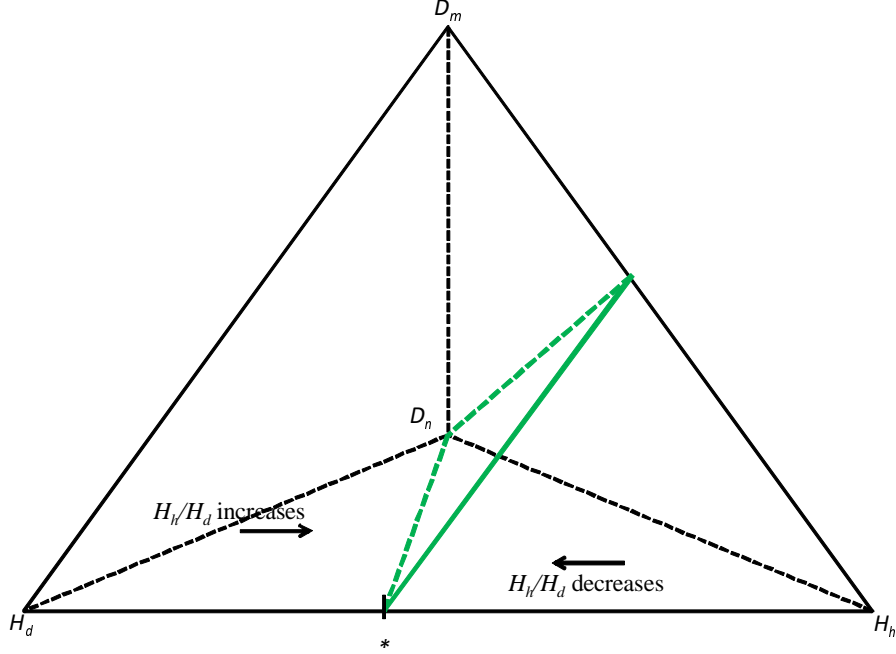


Figure 7: State space for the woodpecker community. The simplex, or equilateral tetrahedron, is the space of all possible community configurations. Any given point in the tetrahedral state space describes a unique combination of the frequencies of strategies in the community, all summing to one. Each vertex of the tetrahedron is a distance one from the opposite side of the tetrahedron. Given a point in the tetrahedron, the frequency of strategy H_h (for example) is given by the normal distance from the point to the side of the tetrahedron opposite the vertex labeled H_h . This distance takes on its maximum of one at the point corresponding to the vertex labeled H_h , where the community consists entirely of H_h . The point marked $*$ on the front edge of the simplex identifies the equilibrium proportion of hawks and doves in the hawk-dove game, as illustrated in Figure 2.

The plane outlined in green identifies community states at which the strategies H_h and H_d have the same fitness. This plane includes all community states at which $p_{H_h}(v_N - c_h) + (p_{H_d} + p_{D_m})v_H = 0$. Only points on the green plane are candidate equilibria. To the right and below the green plane, H_d has a higher fitness than H_h and the dynamics push the system to the left, i.e., the vector corresponding to the p_{H_h}/p_{H_d} component of the dynamics points toward lower values of this ratio. To the left and above the green plane, the opposite is the case.

To describe these vectors, first consider the composition of the Hairy population, and hence the strategies H_h and H_d . We know that the fitness of H_h will equal that of H_d when (E1) holds. Figure 7 illustrates the plane, outlined in green, that identifies the states satisfying (E1). This plane passes through the vertex corresponding to strategy D_n , and identifies all states that fix the ratio $p_{H_h}/(p_{H_d} + p_{D_m})$ so as to satisfy (E3). At those states to the right and below the plane, the fitness of H_d exceeds that of H_h , and the dynamics push toward lower values of p_{H_h}/p_{H_d} . Above and to the left of the green plane, the fitness of H_d falls short of that of H_h , and the dynamics push toward higher values of p_{H_h}/p_{H_d} .¹⁰ Notice that the green plane hits the lower front edge of the simplex at $*$, the point marking a ratio $p_{H_h}/p_{H_d} = p^*$. This edge corresponds to the state space of the hawk-dove game, shown in Figure 2, and p^* is the ratio of hawks to doves that equalizes the fitness of the two strategies in this game. The equilibrium in the Hairy-Downy game must lie in the interior of the green plane, and hence must feature a ratio $\hat{p}_{H_h}/\hat{p}_{H_d}$ exceeding p^* .

Next consider the Downy population, and hence the strategies D_m and D_n . The fitness of D_m will equal the fitness of D_n when (E2) holds. Figure 8 illustrates the plane, outlined in red, that identifies the states satisfying (E2). This plane contains the D_m/D_n edge of the simplex. Rotating the plane leftward would decrease the ratio $\frac{p_{H_h}}{p_{H_d}}$, rotating to the right would increase it. To the left of this plane, the fitness of D_m is higher and the dynamics push toward increasing the ratio p_{D_m}/p_{D_n} . To the right, the fitness of D_n is higher and the dynamics push toward decreasing the ratio p_{D_m}/p_{D_n} .¹¹

Finally, let us consider the relative population sizes, and hence H_h and D_m . Figure 9 illustrates the implications of this relationship. This figure contains a plane outlined in blue that is parallel to the surface of the tetrahedron opposite the vertex H_h . Being parallel to this surface, this blue plane consists of states characterized by a common value

from $\{p_{H_h}, p_{H_d}, p_{D_m}, p_{D_n}\}$, as long as each of these probabilities appears in at least one of the ratios and no two ratios are reciprocals of one another. The ability to choose different descriptions of the dynamics is analogous to the ability to choose different bases for a vector space.

¹⁰We can be more precise about what it means in the tetrahedron of Figure 7 to increase the ratio p_{H_h}/p_{H_d} . States with a common ratio p_{H_h}/p_{H_d} lie on a plane, with one such plane for each possible ratio in $[0, \infty]$. For a fixed ratio, the corresponding plane cuts the edge connecting H_h and H_d at a single point, with this point being closer to the right end of the edge the higher is the ratio in question. The plane also includes the entire edge connecting D_n and D_m . A higher ratio p_{H_h}/p_{H_d} corresponds to a rightward rotation of the plane, with the plane continuing to contain the edge connecting D_m and D_n , but rotating to hit the edge connecting H_h and H_d at a point further to the right. As the ratio p_{H_h}/p_{H_d} approaches ∞ , the corresponding plane approaches the right face of the tetrahedron, where $p_{H_d} = 0$. As the ratio p_{H_h}/p_{H_d} approaches zero, the plane approaches the left face of the tetrahedron, where $p_{H_h} = 0$.

¹¹States with a common ratio p_{D_m}/p_{D_n} lie on a plane, with one such plane for each possible ratio in $[0, \infty]$. For a fixed ratio, the corresponding plane cuts the edge connecting D_m and D_n at a single point, with this point being closer to the top of the simplex the higher is the ratio in question. The plane also includes the entire edge connecting H_d and H_h . A higher ratio p_{D_m}/p_{D_n} thus corresponds to an upward rotation of the plane, with the plane continuing to contain the edge connecting H_d and H_h , but rotating to hit the edge connecting D_n and D_m at a higher point.

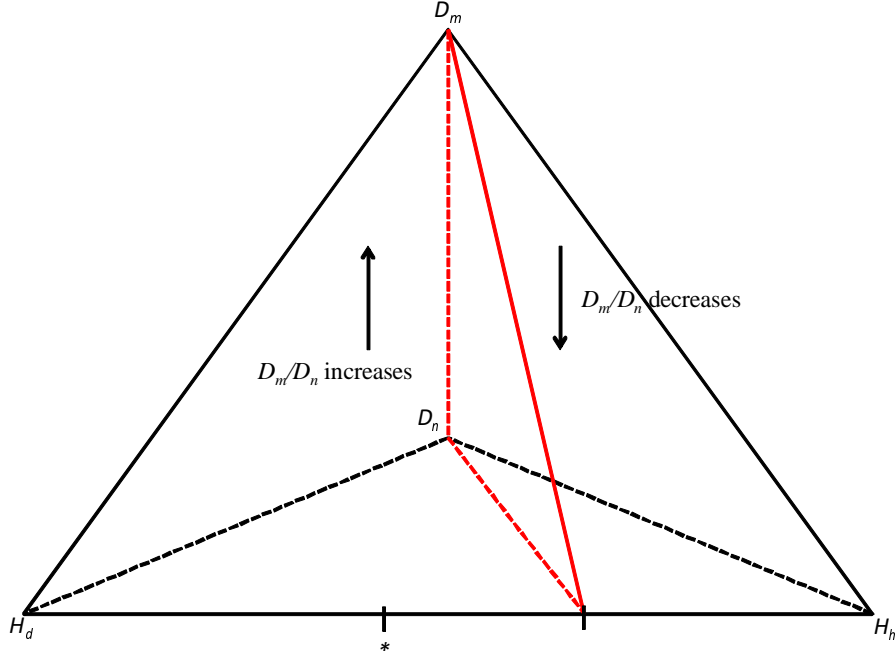


Figure 8: The plane outlined in red identifies community states at which the strategies D_m and D_n have the same fitness, and hence at which there is no selection pressure on the ratio p_{D_m}/p_{D_n} . This plane includes all community states at which $p_{H_h}/p_{H_d} = v_D/(2c_m)$. Only points on the red plane are candidate equilibria. To the left of the red plane, D_m has a higher fitness than D_n and the dynamics push the system upward, i.e., the vector corresponding to the p_{D_m}/p_{D_n} component of the dynamics points toward higher values of this ratio. To the right of the red plane, the opposite is the case.

of p_{H_h} , namely that satisfying (E1), or $p_{H_h} = (2v_H - v_D - 2z_D)/(v_H + c_h - 2c_m - v_D)$. On this plane, H_h and D_m have the same fitness. At those states in the front right of the plane, the fitness of D_m exceeds that of H_h , and the dynamics push toward higher values of p_{D_m}/p_{H_h} . Behind and to the left of the blue plane, the fitness of D_m falls short of that of H_h , and the dynamics push toward lower values of p_{D_m}/p_{H_h} .¹²

Figure 10 combines the planes corresponding to the three equilibrium conditions (E1)–(E3). Each pair of planes intersects to form a line segment, indicated on the figure. These three line segments in turn intersect to identify a single state, which satisfies (E1)–(E3) and is the unique equilibrium. Moreover, we can trace the dynamics that lead to this equilibrium. To the right of the red plane, the dynamics push downward, decreasing the

¹²States with a common ratio p_{D_m}/p_{H_h} again lie on a plane. For a fixed ratio, the corresponding plane cuts the edge connecting D_m and H_h at a single point, with this point being closer to the bottom end of the edge the lower is the ratio in question. The plane also includes the entire edge connecting H_d and D_n . A lower ratio p_{D_m}/p_{H_h} thus corresponds to a downward rotation of the plane, with the plane continuing to contain the edge connecting H_d and D_n , but rotating to hit the edge connecting D_m and H_h at a point closer to the bottom right.

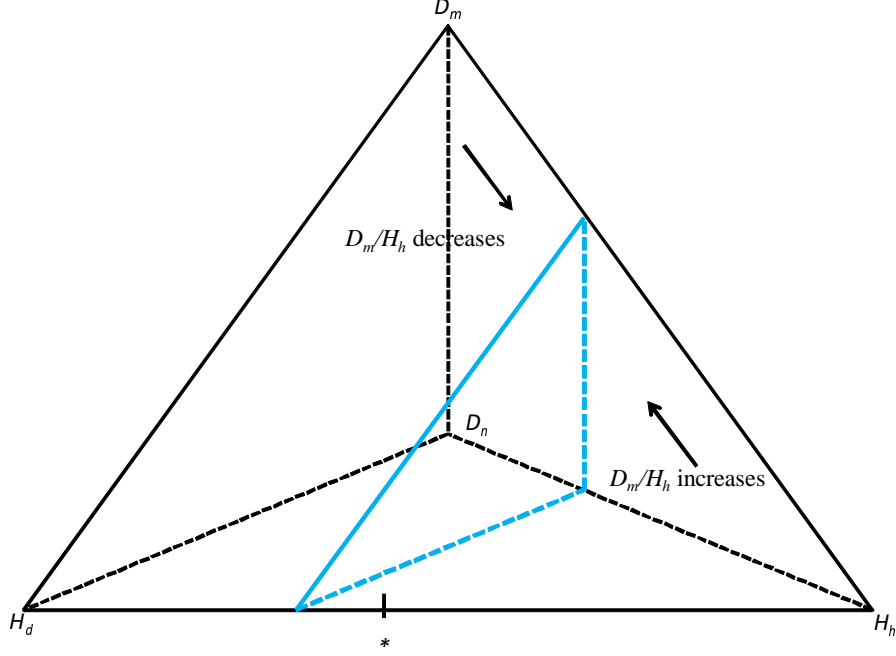


Figure 9: The plane outlined in blue identifies community states at which the strategies H_h and D_m have the same fitness. This plane includes all community states at which $p_{H_h} = (2v_H - v_D - 2z_D)/(v_H + c_h - 2c_m - v_D)$. Only points on the blue plane are candidate equilibria. To the right front of the blue plane, D_m has a higher fitness than H_h and the dynamics push the system backward, i.e., the vector corresponding to the p_{D_m}/p_{H_h} component of the dynamics points toward higher values of this ratio. To the back left of the blue plane, the opposite is the case.

ratio p_{D_m}/p_{D_n} , with the reverse holding to the left. At those states in the front right of the blue plane, the dynamics push backward toward higher values of p_{D_m}/p_{H_h} , with the reverse holding to the back left of the blue plane. At those states to the right and below the green plane, the dynamics push toward lower values of p_{H_h}/p_{H_d} , with the reverse holding to the left and above the green plane.

Figure 11 illustrates the resulting dynamics. In each case, a collection of interior initial community configurations are randomly generated, and then the trajectories showing the subsequent evolution of the community are shown. These trajectories converge to the equilibrium, denoted by the black dot. Evolution rather quickly pushes the frequency of Hairy hawks to the vicinity of its equilibrium value, and then the community winds its way to equilibrium. Moving from the top left to the top right panel decreases the cost

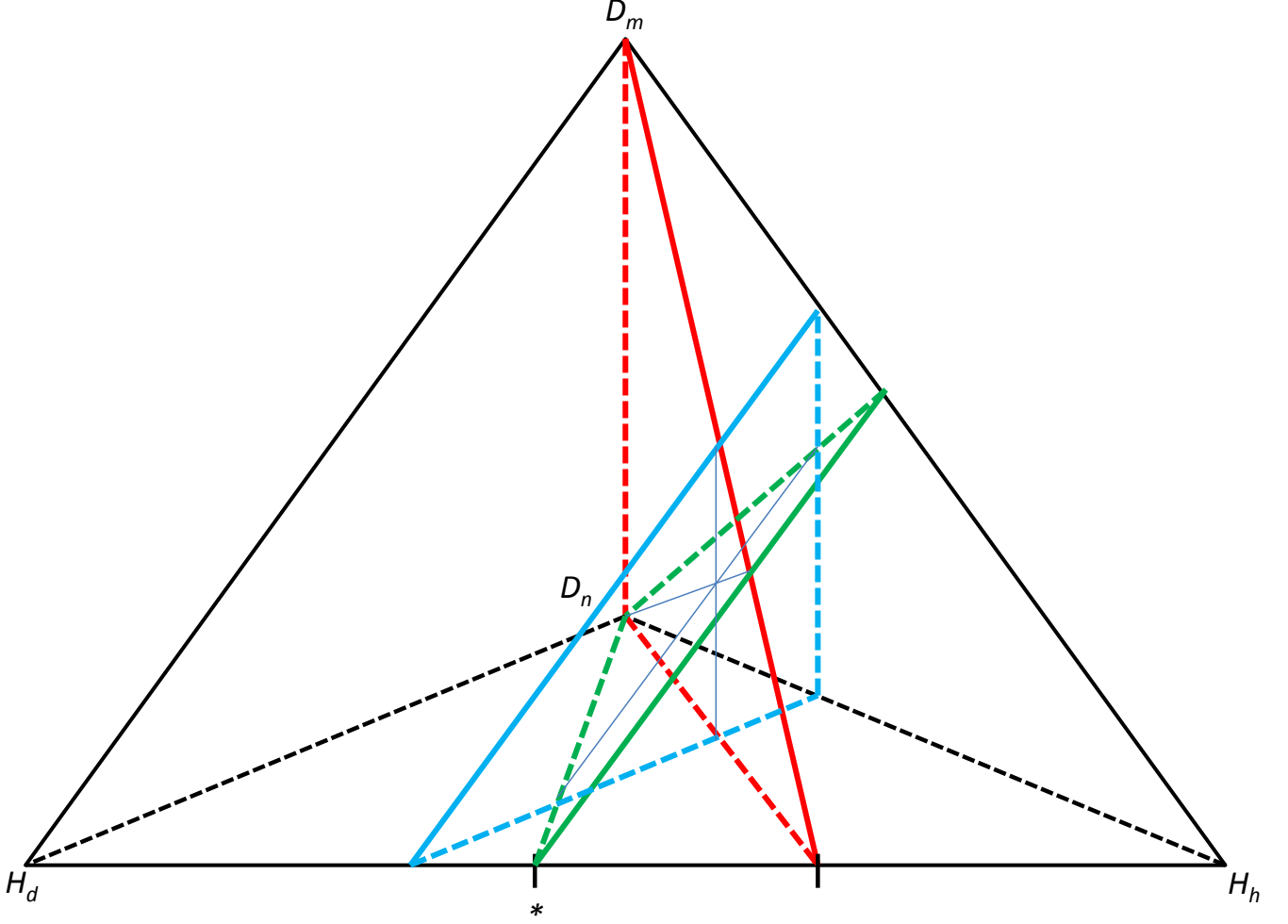


Figure 10: The blue plane identifies community states satisfying equilibrium condition (E1), the red plane identifies community states satisfying equilibrium condition (E2), and the green plane community states satisfying (E3). Each pair of planes intersects to form a line segment, indicated on the figure. These three line segments in turn intersect to identify a single state, which satisfies (E1)–(E3) and is the unique equilibrium. The heel of the blue plane, lying on the edge connecting D_n and H_h , identifies the equilibrium frequency \hat{p}_{H_h} of hairy hawks. The green plane intersects the front edge at point $*$, indicating that the equilibrium proportion $\hat{p}_{H_h}/(\hat{p}_{H_d} + \hat{p}_{D_m})$ of hawk to dove-like behavior (i.e., Hairy doves and Downy mimics) is fixed at the proportion p^* that would prevail in a community comprise solely of Hairies, while the ratio $\hat{p}_{H_h}/\hat{p}_{H_d}$ exceeds p^* .

of mimicry c_m , leading to an equilibrium with more Downy mimics and nonmimics, but fewer Hairy hawks and doves (as indicated by Figure 4). Moving from the top left to the bottom left and then bottom right figure successively increases the cost of combat c_h , in the process increasing the frequency of Downy mimics and ultimately reducing Hairies to a negligible proportion of the community.

5 When Will Mimics Vanquish Nonmimics?

Section 4 describes a community in which Downy mimics coexist with Hairy woodpeckers and Downy nonmimics. Conditions (A1)–(A3) ensure that all four strategies will be present in equilibrium.

We often observe mimics in communities with either very few or no nonmimics. Example 4 develops conditions under which nonmimics will be rare, in the context of parameters that satisfy (A1)–(A3), finding that this will be the case when the cost of mimicry c_m is small, the Downy background fitness z_D is near the lower limit consistent with (A3), the resource value v_D is small, and the cost of fighting c_h is large.

It may then simply be that cases in which all of the subordinate species appear to be mimics are cases in which these conditions hold. Such communities will typically include some, though perhaps very few, nonmimics. Alternatively, we might ask when mimics will eliminate nonmimics entirely. This section explores three possibilities.

5.1 Unsuccessful Nonmimics

First, we consider the case in which (A1)–(A3) do not hold, opening the possibility of communities that do not contain all four strategies. The obvious suspect for relaxation here is (A2). This condition ensures that D_n will invade a population of Hairies. Suppose that (A2) fails, so that Downy nonmimics by themselves are not viable. Downy mimics may still be viable, and it then seems natural that the result will be a community consisting only of Hairies (in some mixture of H_h and H_d) and Downy mimics.

Generically, such a community will not occur, no matter what the status of (A1)–(A3). Except for a knife-edge specification of parameters identified below, there are no parameter values that will allow the coexistence of Hairies and Downy mimics, without Downy nonmimics also appearing.

To establish this result, let us consider the possible community configurations that include Hairies and Downy mimics, but no Downy nonmimics:

- We could have a community comprised of D_m and H_d . This cannot be an equilibrium, because H_d would earn a fitness of $\frac{v_H}{2}$, while H_h earns a fitness of v_H against both H_d and D_m , and hence H_h could invade.

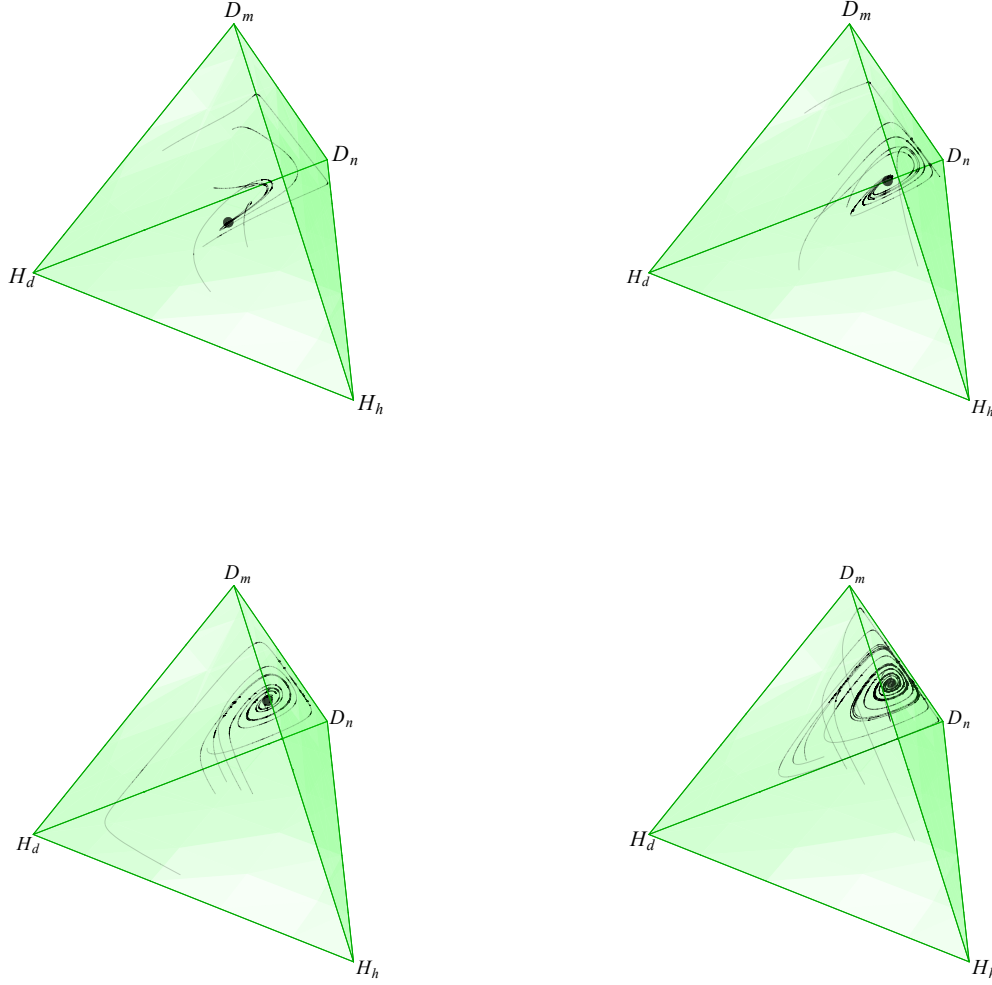


Figure 11: Four illustrations of the equilibrium dynamics. In each panel, solution trajectories are illustrated, beginning from a handful of randomly-selected initial conditions. These trajectories converge to the black dot, corresponding to the equilibrium. The value of p_{H_h} moves close to its equilibrium value relatively quickly, after which the community winds its way to equilibrium. The parameter values $(v_H, c_h, v_D, z_D, c_m)$ are $(2, 7, 1, 1, 1)$ in the top left, a parameter configuration that appears in both Figure 4 and Figure 5. The top right illustrates the reducing the mimicry costs, with parameter values $(2, 7, 1, 1, 0.5)$. As in Figure 4, the result is an equilibrium with more Downy mimic and nonmimics, coupled with fewer Hairy hawks and especially fewer Hairy doves. The bottom left panel increases the cost of conflict, with parameters $(2, 20, 1, 1, 1)$. As expected from Figure 5, the result is a community with fewer Hairy hawks and Doves, with more Downy mimics. The bottom right panel increases the cost of combat yet further, with parameters, $(2, 35, 1, 1, 1)$, at which point Hairies essentially disappear from the community.

- We could have a community comprised of H_h and D_m . This cannot be an equilibrium, because D_n fares as well as D_m against D_m , and fares better than D_m against H_h , and so could invade.
- The final possibility is a community comprised of H_h , H_d and D_m . Let \tilde{p}_{H_h} , \tilde{p}_{H_d} , \tilde{p}_{D_m} and \tilde{p}_{D_n} be the equilibrium strategies in such a community. We have taken $\tilde{p}_{D_n} = 0$, and so are effectively examining the three-strategy game given by

	H_h	H_d	D_m
H_h	$\frac{v_H - c_h}{2}, \frac{v_H - c_h}{2}$	$v_H, 0$	$v_H, z_D - c_m$
H_d	$0, v_H$	$\frac{v_H}{2}, \frac{v_H}{2}$	$\frac{v_H}{2}, z_D + \frac{v_D}{2}$
D_m	$z_D - c_m, v_H$	$z_D + \frac{v_D}{2}, \frac{v_H}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$

It is apparent that in equilibrium, we must again have a version of (E1), or

$$\frac{\tilde{p}_{H_h}}{\tilde{p}_{H_d} + \tilde{p}_{D_m}} = \frac{v_H}{c_h - v_H} = p^*. \quad (13)$$

The equilibrium will thus include H_h and some mixture of H_d and D_m . This mixture will include both of H_d and D_m , only if the two strategies have identical fitnesses, i.e., only if

$$\tilde{p}_{H_h}(z_D - c_m) + (\tilde{p}_{H_d} + \tilde{p}_{D_m}) \left(z_D + \frac{v_D}{2} \right) = (\tilde{p}_{H_d} + \tilde{p}_{D_m}) \frac{v_H}{2}. \quad (14)$$

Generically, (13) will ensure that (14) fails, and hence that the candidate equilibrium will include only one of H_d or D_m .¹³ But we have already noted that there cannot

¹³To determine which, notice that the equilibrium will feature D_m if D_m has the higher expected payoff, i.e., if the left side of (14) exceeds the right side. Using (1) and (13), this is

$$\frac{v_H}{c_h}(z_D - c_m) + \frac{c_h - v_H}{c_h} \left(z_D + \frac{v_D}{2} \right) > \frac{c_h - v_H}{c_h} \cdot \frac{v_H}{2}. \quad (15)$$

It is immediately obvious that if c_m is too large, the equilibrium will feature only H_h and H_d , and hence will feature no mimicry and indeed no Downies. We then need to examine the other extreme. Will we see D_m if c_m is sufficiently small? To answer this we examine the case in which $c_m = 0$, finding a condition for D_m to exist of

$$\frac{v_H}{c_h} z_D + \frac{c_h - v_H}{c_h} \left(z_D + \frac{v_D - v_H}{2} \right) > 0$$

or

$$\frac{v_H}{c_h} \left(\frac{v_H - v_D}{2} \right) + z_D + \frac{v_D - v_H}{2} > 0$$

and hence

$$z_D > \left(1 - \frac{v_H}{c_h} \right) \frac{v_H - v_D}{2} = \frac{c_h - v_H}{c_h} \cdot \frac{v_H - v_D}{2},$$

which will hold as long as z_D is sufficiently large.

be an equilibrium with only H_h and D_m , and an equilibrium composed solely of H_h and H_d contains no Downies.

5.2 Costless Mimicry

We are often interested in the case in which c_m is very small. Suppose $c_m = 0$, so that there are no costs of being a mimic against a Hairy hawk. We could then have a stationary state of the equilibrium dynamics consisting only of H_h and D_m . This state is stable, in the sense that there is no evolutionary pressure pushing the community away from this state, but it is not asymptotically stable. Instead, D_n can drift into the community, as D_m and D_n have identical fitnesses. The community will then drift within a connected component of stationary states, with each state featuring the same frequency of H_h but distinguished by the relative mix of D_m and D_n in the Downy population. The states in this component in which the relative frequency of D_n is small are stable, but the states in which the relative frequency of D_n is large are not stable. In the latter states, H_d has a higher fitness than H_h and hence can invade.

5.3 Intraspecific Advantages of Mimicry

So far we have modeled the potential advantages of mimicry as arising solely out of the ability to deceive a socially dominant species. However, there is also the possibility of an additional intraspecific advantage to mimicry that comes from deceiving other conspecifics about your identity. In this case, we may well have equilibrium communities in which all Downies are mimics.

Consider the following game, in which an interaction between a Downy mimic and Downy nonmimic allows the mimic to capture an additional amount b of the resource v_D at the expense of the nonmimic.

	H_h	H_d	D_m	D_n
H_h	$\frac{v_H - c_h}{2}, \frac{v_H - c_h}{2}$	$v_H, 0$	$v_H, z_D - c_m$	v_H, z_D
H_d	$0, v_H$	$\frac{v_H}{2}, \frac{v_H}{2}$	$\frac{v_H}{2}, z_D + \frac{v_D}{2}$	v_H, z_D
D_m	$z_D - c_m, v_H$	$z_D + \frac{v_D}{2}, \frac{v_H}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$	$z_D + \frac{v_D}{2} + b, z_D + \frac{v_D}{2} - b$
D_n	z_D, v_H	z_D, v_H	$z_D + \frac{v_D}{2} - b, z_D + \frac{v_D}{2} + b$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$

We are interested in whether the mimic advantage in contests between D_m and D_n can lead to communities in which all Downies are mimics. We will assume that (A1)–(A2) hold, and hence a community comprised of H_h , H_d , and D_n will have a unique equilibrium in which all three strategies are represented in the population. These conditions depend only on the fitnesses in contests involving nonmimics, and are unaffected by the addition of the advantage b of a D_m against a D_n . However, it will now be easier for D_m to

invade, since it garners an extra fitness advantage against D_m , and hence (A3) is no longer required for a successful D_m invasion.

Could we have an equilibrium comprised of H_h , H_d and D_m ? The analysis of Section 5.1 is again relevant. Only in nongeneric cases can these three strategies (only) coexist, a conclusion that is again unaffected by the appearance of the advantage b of a D_m against a D_n . The question is then when we will have an equilibrium consisting of H_h and D_m . There are two conditions. First, it must be that in equilibrium, D_m fares better than H_d against H_h . We have derived this condition in (15), which we can rearrange to give:

$$z_D > \left(1 - \frac{v_H}{c_h}\right) \left(\frac{v_H - v_D}{2}\right) + \frac{v_H}{c_h} c_m. \quad (16)$$

Second, it must be that D_n cannot invade, which requires D_m earn a higher fitness than D_n , or, letting \check{p}_{H_h} and \check{p}_{D_m} denote the equilibrium frequencies of H_h and D_m ,

$$\check{p}_{H_h}(z_D - c_m) + \check{p}_{D_m}(z_D + \frac{v_D}{2}) > \check{p}_{H_h}(z_D) + \check{p}_{D_m}(z_D + \frac{v_D}{2} - b),$$

or, simplifying,

$$\check{p}_{H_h} c_m < \check{p}_{D_m} b.$$

We can rewrite this as

$$\frac{b}{c_m} > \frac{\check{p}_{H_h}}{\check{p}_{D_m}}. \quad (17)$$

This is still not a complete solution, because \check{p}_{H_h} and \check{p}_{D_m} are themselves endogenous. However, we know that as long as (16) holds, then $\frac{\check{p}_{H_h}}{\check{p}_{D_m}} < p^*$.¹⁴ This allows us to conclude that communities consisting of H_h and D_m will exist (in equilibrium) if z_D is relatively large and C_m relatively small (ensuring (16)), and if b is sufficiently large (ensuring (17)).

A community of this composition was impossible in Section 5 because there we had $b = 0$, ensuring that (17) fails and that D_n would be able to invade a population of H_h and D_m . Here, these Downy nonmimics pay a cost of b when interacting against Downy mimics, and this suffices to preclude their invasion when b is large.

6 Discussion

Why should mimicry evolve between unrelated, non-aposematic species? Most reviews of mimicry provide no insight into this question (Ruxton, Sherratt and Speed [17], Wickler [26]). Recently, Rainey and Grether [15] discussed mimicry between ecological competitors, and called for further research into the possible mechanisms for its evolution.

¹⁴Condition (16) ensures that D_m earns a higher payoff than both H_d and H_h when H_h and D_m appear in frequencies p^{**} and $1 - p^{**}$, respectively and hence in relative frequencies p^* . In equilibrium, H_h and D_m must earn the same payoff, which requires a smaller relative frequency of H_h .

The Hairy-Downy game supports an evolutionary mechanism for the origin of inter-specific social dominance mimicry (ISDM). In this game, a subordinate species evolves to mimic a dominant species, to deceive the dominant species into misidentifying the mimic as an individual of its own species, and thus to overestimate the mimic’s size and the costs of combat. These mechanistic details are lacking from previous proposals on non-aposematic mimicry between species pairs (Cody [1], Diamond [3], Moynihan [11], Newton and Gadow [13], Wallace [22, 23]).

The models presented here are new in several ways. First, we model a form of mimicry in which a subordinate species takes advantage of the dynamics of aggressive social interactions of a dominant ecological competitor. The model explores the traditional hawk-dove game with a new component of interspecific interactions. It extends the literature on social dominance to interspecific dominance and its deceptive exploitation. We also model the social component of the ecological interactions between the species both with and without the possibility of mimicry.

We apply game theory to the coevolution of subordinate mimicry and dominant aggression, and establish the coevolutionary dynamics of the evolution toward equilibrium. Gavrillets and Hastings [6] have presented haploid genetic models of the coevolution of two species of Batesian and Müllerian mimics assuming constant population densities. They documented a diversity of coevolutionary cycles and “arms races” between species when both species are allowed to evolve. Holen and Johnstone [9] used game theory to model the evolution of mimetic resemblance under various perceptual constraints within a single population of a Batesian or aggressive mimic. The model was not coevolutionary.

We have established conditions under which mimics and nonmimics will coexist in the subordinate population of nonmimics. These include that the cost of mimicry not be too large, that the contested resource not be too valuable for the subordinate species, and that the subordinate background fitness be neither too large nor too small. These conditions are intuitive. Mimicry will not bring fitness benefits if it is too costly. We will also not see mimicry if the resource is too valuable for the subordinate species, for the simple reason that in this case the subordinate species will be sufficiently fit as to drive out the socially dominant species. We will have a similar result if the background fitness of the subordinate species is too large, while the reverse will be the case (with the subordinates driven out) if the subordinate background fitness is too small. Given coexistent species, the key condition for successful mimicry is thus that it not be too costly.

We obviously cannot expect these conditions to be universal, and nor is mimicry ubiquitous. However, we view them as being quite plausible. In particular, we expect mimicry to often be virtually costless, allowing mimicry to flourish.

The condition that the background fitness of the subordinate species not be too small requires in particular that it be larger than the background fitness of the dominant species. This is consistent with the general biological principal that smaller species within an ecological guild can maintain higher densities in a given habitat than can larger species,

merely due to the scaling of body mass and home range size (cf. Damuth [2], Hasker, Ritchie and Olff [7] and Kelt and Van Vuren [10]).

The dominant populations in our Hairy/Downy game contains aggressive individuals (hawks) as well as submissive individuals (doves). Mimics effectively function as doves of the dominant species. The existence of mimicry then creates a coevolutionary feedback on the hawk-dove equilibrium within the dominant species, increasing the fitness of the hawk strategy, and lowering the fitness of both the dove and mimic strategies. The mix of behavior in the dominant species is thus partially shaped by the incidence of mimicry among subordinates.

Mimics will comprise a relatively larger proportion of the subordinate species the smaller the cost of mimicry (clearly making mimicry more advantageous), the smaller is the subordinate background fitness (enhancing the relative advantage of mimicry), and the larger is the cost of combat to the dominant species (so that a larger proportion of that species are doves, against which mimics fare well).

What if there were no possibility for aggressive behavior in the dominant species, so that the latter necessarily consisted only of doves? In this case, there would be no cost to mimics in the subordinate population, and mimics would necessarily fare strictly better than nonmimics. We would then have an outcome featuring only dominant doves and subordinate mimics.

Because the dominant and subordinate species compete for the same resource, a strategy (such as mimicry in the subordinate species) can provide fitness benefits, even though it confers no fitness advantages in interactions within the individual's own species, because it fares well in interactions with the other species. As a result, understanding coevolution among species at the level of the community is required to fully understand the evolutionary dynamics of interspecific social dominance mimicry. Furthermore, the three-party, Hairy and Downy mimic models in Section 3 demonstrate that the cost of aggression within one species can affect its total population fitness relative to an ecological competitor. Thus, the evolutionary consequences of intraspecific social interactions, such as aggression, may have to be understood in the context of ecological competition.

Many examples of evolutionary convergent in appearance between non-aposematic ecological competitors remain to be explained, implying a potentially important role for ISDM in nature. Avian mimicry between ecological competitors has yet to be satisfactorily explained (Diamond [3], Weibel and Moore [24, 25]). Experimental studies of interspecific mimicry in coral reef fishes have concentrated on the deception of third party observers, but support for this hypothesis is not very strong (Eagle and Jones [5]) and is not consistent geographically (Rainey [14]). Thus, this common evolutionary phenomenon in marine fishes has yet to be satisfactorily explained. Further, there are many more likely cases of ISDM in birds that are waiting to be identified because the evolutionary mechanism was so unclear. Thus, there is an exciting opportunity to pursue tests of ISDM in marine fishes, birds, and other species in which visual detection of conspecifics is common.

7 Appendix

7.1 Notation

Notation	Interpretation
b	Fitness advantage of Downy mimic against Downy nonmimic
c_h	Cost incurred by Hairy hawk contesting with Hairy hawk
c_m	Cost of mimicry
D_m	Downy mimic
D_n	Downy nonmimic
H_d	Hairy dove
H_h	Hairy hawk
p^*	Equilibrium ratio $p_{H_h}/(1 - p_{H_h})$ in hawk-dove game
p^{**}	Equilibrium value of p_{H_h} in hawk-dove game
p_{D_m}	Proportion of Downy mimics in woodpecker community
p_{D_n}	Proportion of Downy nonmimics in woodpecker community
p_{H_d}	Proportion of Hairy doves in woodpecker community
p_{H_h}	Proportion of Hairy hawks in woodpecker community
\hat{p}_{D_m}	Equilibrium proportion of Downy mimics, (A1)–(A3) hold
\hat{p}_{D_n}	Equilibrium proportion of Downy nonmimics, (A1)–(A3) hold
\hat{p}_{H_d}	Equilibrium proportion of Hairy doves, (A1)–(A3) hold
\hat{p}_{H_h}	Equilibrium proportion of Hairy hawks, (A1)–(A3) hold
\tilde{p}_{D_m}	Proportion of Downy mimics, (A1)–(A3) need not hold
\tilde{p}_{D_n}	Proportion of Downy nonmimics, (A1)–(A3) need not hold
\tilde{p}_{H_d}	Proportion of Hairy doves, (A1)–(A3) need not hold
\tilde{p}_{H_h}	Proportion of Hairy hawks, (A1)–(A3) need not hold
\check{p}_{D_m}	Proportion of Downy mimics, $b > 0$
\check{p}_{D_n}	Proportion of Downy nonmimics, $b > 0$
\check{p}_{H_d}	Proportion of Hairy doves, $b > 0$
\check{p}_{H_h}	Proportion of Hairy hawks, $b > 0$
π_{H_h}	Fitness of Hairy hawk
π_{H_d}	Fitness of Hairy dove
π_{D_m}	Fitness of Downy mimic
π_{D_n}	Fitness of Downy nonmimic
$\bar{\pi}$	Average fitness in woodpecker community
v_D	Value of resource for Downy woodpecker
v_H	Value of resource for Hairy woodpecker
z_D	Background fitness, Downy woodpecker
z_H	Background fitness, Hairy woodpecker, normalized to 0

7.2 Proof of Proposition 2

Let q and p denote community configurations, so that $q = (q_{H_h}, q_{H_D}, q_{D_n})$ and $p = (p_{H_h}, p_{H_D}, p_{D_n})$ are 3-tuples of numbers that are nonnegative and sum to one, and that denote the frequencies of H_h , H_d , and D_n in the community. When writing simply q and p , we will think of these as column vectors. We refer to q and p as strategies. A strategy is pure if it contains only one nonzero element, and otherwise is mixed. We let p^\dagger similarly be a column vector $(p_{H_h}^\dagger, p_{H_d}^\dagger, p_{D_n}^\dagger)$, denoting the Nash equilibrium. The strategy p^\dagger is completely mixed, in the sense that every element of the vector p^\dagger is positive.

Let A denote the payoff matrix

$$\begin{bmatrix} \frac{v_H - c_h}{2} & v_H & v_H \\ 0 & \frac{v_H}{2} & v_H \\ z_D & z_D & z_D + \frac{v_D}{2} \end{bmatrix}.$$

Then the expected fitness of a strategy p , in a population composed of members playing strategy q is given by $p^T A q$, where p^T denotes the transpose of the vector p . An arbitrary strategy p is evolutionarily stable if and only if there exists a neighborhood $N(p)$ such that (cf. Sandholm [19, Condition 8.2, p. 276]):

$$q A q < p A q \quad \forall q \in N(p). \quad (18)$$

Hence, p must be a better response to q than is q itself, for all q in a neighborhood of p .¹⁵

Let us define the function $\pi(q) = q^T A q - p^{\dagger T} A q$. This gives the difference in the expected fitnesses of strategies q and p^\dagger , in a community comprised of strategy q . Note that $\pi(p^\dagger) = 0$.

The evolutionary stability condition (18), applied to p^\dagger , is equivalent to the statement that p^\dagger is a strict local maximizer of $\pi(q)$ on some neighborhood $N(p^\dagger)$. It is immediate that p^\dagger satisfies the first-order condition for a maximum. We then need to check the second order conditions, which requires verifying three inequalities (Sundaram [20, Theorems 5.4 and 5.4, pp. 118–120]), concerning the three principal minors of the bordered Hessian of $\pi(p^\dagger)$. The Hessian of the function π is given by $A^T + A$, and hence we need to examine the matrix:

$$\begin{bmatrix} 0 & 1 & 1 & 1 \\ 1 & v_H - c_h & v_H & z_D + v_H \\ 1 & v_H & v_H & z_D + v_H \\ 1 & z_D + v_H & v_D + z_H & 2z_D + v_D \end{bmatrix}.$$

The requirement is that the determinant of the first principal minor be negative, or,

$$\begin{vmatrix} 0 & 1 \\ 1 & \frac{v_H - c_h}{2} \end{vmatrix} < 0,$$

¹⁵This implies the familiar conditions that p must be a Nash equilibrium (Sandholm [19, Proposition 8.3.4, p. 277]) and that p must be a better response to any alternative best response q than is q itself.

which is obvious.

The second requirement is that the determinant of the second principal minor be positive, or (obtaining the first equality by subtracting v_H times the first row from the second and third row),

$$\begin{vmatrix} 0 & 1 & 1 \\ 1 & v_H - c_H & v_H \\ 1 & v_H & c_H \end{vmatrix} = \begin{vmatrix} 0 & 1 & 1 \\ 1 & -c_H & 0 \\ 1 & 0 & 0 \end{vmatrix} = c_H > 0.$$

The third requirement is that the determinant of the third principal minor be negative, or

$$\begin{vmatrix} 0 & 1 & 1 & 1 \\ 1 & v_H - c_h & v_H & z_D + v_H \\ 1 & v_H & v_H & z_D + v_H \\ 1 & z_D + v_H & z_D + v_H & 2z_D + v_D \end{vmatrix} < 0. \quad (19)$$

Subtracting a multiple of the first row from each of the next three this is

$$\begin{vmatrix} 0 & 1 & 1 & 1 \\ 1 & -c_h & 0 & z_D \\ 1 & 0 & 0 & z_D \\ 1 & v_H & v_H & z_D + v_D \end{vmatrix} < 0.$$

Now subtracting the third row from the second and fourth, we have

$$\begin{vmatrix} 0 & 1 & 1 & 1 \\ 0 & -c_h & 0 & 0 \\ 1 & 0 & 0 & z_D \\ 0 & v_H & v_H & v_D \end{vmatrix} = c_H(v_D - v_H) < 0,$$

as required. Asymptotic stability then follows immediately from the fact that evolutionarily stable strategies are asymptotically stable (Sandholm [19, Theorem 8.4.1, p. 283]). Hofbauer and Sigmund [8, pp. 127–128] show that if there exists an interior evolutionarily stable strategy, then every solution trajectory with an interior initial condition converges to this strategy.

7.3 Completion of the Proof of Proposition 3: Other Equilibria

7.3.1 Monomorphic Equilibria

We first argue that given (A1), (A2), and $c_m > 0$, but regardless of the status of (A3), there is no monomorphic equilibrium, in four steps:

- There is no equilibrium consisting only of H_h . The maintained assumption $v_H < c_h$ on the payoffs of the hawk-dove game ensures that doves would then invade. This is the familiar statement that the hawk-dove game has no pure equilibria.
- There is no equilibrium consisting only of H_d . The maintained assumption $v_H > 0$ on the payoffs of the hawk-dove game ensures that hawks would then invade. This is again the familiar statement that the hawk-dove game has no pure equilibria.
- There is no equilibrium consisting only of D_m . Condition (A1) ensures that hawks would invade.
- There is no equilibrium consisting only of D_n . Condition (A1) ensures that both hawks and doves would invade.

7.3.2 Dimorphic Equilibria

We now argue that, regardless of the status of (A3), there is no dimorphic equilibrium, in six steps:

- There is no equilibrium consisting of H_h and H_d . Condition (A2) ensures that D_n could invade such a community.
- There is no equilibrium consisting of H_h and D_m . D_n would invade such a community, faring better than D_m because it pays no cost when facing H_h .
- There is no equilibrium consisting of H_h and D_n . H_d would invade such a community, saving the cost of fighting against H_h .
- There is no equilibrium consisting of H_d and D_m . H_h would invade such a community, exploiting both of the existing strategies.
- There is no equilibrium consisting of H_d and D_n . Again, H_h could invade, exploiting H_d .
- There is no equilibrium consisting of D_n and D_m . Condition (A1) ensures that H_h could invade such a community.

7.3.3 Trimorphic Equilibria

We now consider trimorphic equilibria. Here, the status of (A3) plays a role. We have four possibilities to consider:

- Consider an equilibrium consisting of H_h , H_d , and D_n . Our calculations in Section 4.2 ensure that if condition (A3) holds, then D_m will invade such a population, ensuring that we do not have an equilibrium. Alternatively, if (A3') holds, then D_m will be unable to invade, establishing the existence of an equilibrium.
- Regardless of the status of (A3), there is no equilibrium consisting of H_h , D_m and D_n . In any community consisting of these three strategies, D_n would earn a higher payoff than D_m (since mimics pay a cost against H_h that nonmimics do not, while D_m and D_n fare equally well against D_m and D_n). As a result, the relative frequency p_{D_n}/p_{D_m} must be increasing in any community consisting of H_h , D_m and D_n , and hence there is no stationary state featuring these three frequencies.
- Similarly, regardless of the status of (A3), there is no equilibrium consisting of H_d , D_m and D_n . In any community consisting of these three strategies, D_m would earn a higher payoff than D_n (since mimics reap a benefit against H_d that nonmimics do not, while D_m and D_n fare equally well against D_m and D_n). As a result, the relative frequency p_{D_m}/p_{D_n} must be increasing in any community consisting of H_h , D_m and D_n , and hence there is no stationary state featuring these three frequencies.
- Regardless of the status of (A3), there is no equilibrium consisting of H_h , H_d , and D_m . This argument is a bit more involved. Let us consider the truncated version of the game that would characterize such a community:

	H_h	H_d	D_m	
H_h	$\frac{v_H - c_h}{2}, \frac{v_H - c_h}{2}$	$v_H, 0$	$v_H, z_d - c_m$,
H_d	$0, v_H$	$\frac{v_H}{2}, \frac{v_H}{2}$	$\frac{v_H}{2}, z_D + \frac{v_D}{2}$	
D_m	$z_D - c_m, v_H$	$z_D + \frac{v_D}{2}, \frac{v_H}{2}$	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$	
D_n	z_D, v_H	z_D, v_H	$z_D + \frac{v_D}{2}, z_D + \frac{v_D}{2}$	

where D_n do not appear as a column, since they are absent from the population, but are included as a row to indicate their status as potential entrants.

The first observation is that

- H_h earns the same payoff against H_d as against D_m (a payoff of v_H in each case,
- H_d earns the same payoff against H_d as against D_m (a payoff of $\frac{v_H}{2}$ in each case,

The first equality implies that from a fitness point of view, it does not matter whether H_h plays against H_d or D_m . All that matters is the balance between H_h opponents on the one hand and the sum of H_d and D_m opponents on the other. The

next equality tells us that the same is true for H_d . Hence, if H_h and H_d are to have the same expected payoff, as equilibrium requires, then it must be that H_h are the same proportion of this three-strategy community as they are in the equilibrium of the original hawk-dove game. (In particular, from the point of view of H_h , it is as if we are in the original hawk-dove game, but some doves have been relabeled as D_m . The total equilibrium proportion of dove-like behavior must remain unchanged, some of it now done by H_d and some by D_m .) Hence, in equilibrium, we must have

$$p_{H_h} = p^{**} \quad (20)$$

$$p_{H_d} + p_{D_m} = 1 - p^{**} \quad (21)$$

For D_n to invade, it must be that a mutant playing strategy D_n would earn a higher payoff than the existing strategies H_h , H_d , and D_m . We are examining a putative equilibrium in which the three existing strategies earn the same payoff, so it suffices to compare the payoff of D_n against any one of them. Takeing the case of H_h , it suffices for D_n to invade that

$$(p_{H_h} + p_{H_d})z_D + (p_{D_m} + p_{D_n})\left(z_D + \frac{v_D}{2}\right) > p_{H_h}\frac{v_H - c_h}{2} + (p_{H_d} + p_{D_m} + p_{D_n})v_H,$$

where the left side is the payoff to D_n and the right side is the payoff to H_h . Because we are examining a small mutant invasion of strategy D_n , we can take $p_{D_n} = 0$, and hence rewrite this condition as

$$(p_{H_h} + p_{H_d})z_D + p_{D_m}\left(z_D + \frac{v_D}{2}\right) > p_{H_h}\frac{v_H - c_h}{2} + (p_{H_d} + p_{D_m})v_H.$$

The left side of this inequality clearly exceeds z_D , so it suffices that

$$z_D > p_{H_h}\frac{v_H - c_h}{2} + (p_{H_d} + p_{D_m})v_H.$$

Now using our observation that p_{H_h} , p_{H_d} and p_{D_m} must satisfy (20)–(21), we can write this as

$$z_D > p^{**}\frac{v_H - c_h}{2} + (1 - p^{**})v_H + p_{D_n}v_H.,$$

which is implied by (A2).

7.3.4 Completely Mixed Equilibria

Finally, we need to show that if (A3') holds, there is no equilibrium in which all four strategies coexist. This is straightforward. The failure of (A3) implies that when the ratio of H_h to H_d is given by p^* , then D_n have a higher fitness than do D_m , and hence there is selection pressure against D_m , precluding the existence of a completely mixed equilibrium. We will see in Section 4.3.5 that in any completely mixed equilibrium, the ratio of H_h to $H_h + H_d$ must exceed p^* , ensuring the D_m has a lower fitness than D_n .

7.4 Calculations, Example 2

We need to show that for small values of c_m , the frequency of D_m increases as c_m declines. Using (E1) and then (5), we have

$$\begin{aligned}\hat{p}_{H_h} &= p^* (\hat{p}_{H_d} + \hat{p}_{D_m}) \\ &= p^* \frac{2c_m}{v_D} \hat{p}_{H_h} + p^* \hat{p}_{D_m}\end{aligned}$$

and hence

$$\hat{p}_{H_h} \left(1 - p^* \frac{2c_m}{v_D} \right) = p^* \hat{p}_{D_m}.$$

It thus suffices to show that the left side of this equality has a negative derivative, or

$$\frac{d\hat{p}_{H_h}}{dc_m} \left(1 - p^* \frac{2c_m}{v_D} \right) - \hat{p}_{H_h} p^* \frac{2}{v_D} < 0.$$

We examine this inequality for the limiting case of $c_m = 0$, or

$$\frac{d\hat{p}_{H_h}}{dc_m} < \hat{p}_{H_h} p^* \frac{2}{v_D}.$$

Using (4) to take the derivative $\frac{d\hat{p}_{H_h}}{dc_m}$ and then using the definition of p^* from (1), this is

$$\hat{p}_{H_h} \frac{2}{v_H + c_h - v_D} < \hat{p}_{H_h} \frac{v_H}{c_h - v_H} \frac{2}{v_D}$$

or

$$(c_h - v_H)v_D < v_H(v_H + c_h - v_D)$$

and hence

$$c_h v_D < v_H^2 + v_H c_h. \tag{22}$$

We now note that the two sides of this equation are linear in c_h , with the inequality holding for $c_h = 0$. We thus need only verify the inequality for the maximal value of c_h . This maximal value is set by the requirement that (A1)–(A2) be feasible, or

$$v_H - \frac{v_D}{2} > \frac{c_h - v_H}{c_h} \frac{v_H}{2}.$$

Successive manipulations of this condition give:

$$\begin{aligned}2v_H c_h - v_D c_h &> c_h v_H - v_H^2 \\ c_h(v_H - v_D) &> -v_H^2.\end{aligned}$$

If $v_H > v_D$, then this inequality is satisfied for all c_h , and there is no upper bound on c_h . In this case, the right side of (22) has a larger slope (as well as intercept) than the left side, and so (22) holds for all c_h . If $v_H < v_D$, then we can calculate the upper bound on c_h as

$$c_h < \frac{v_H^2}{v_D - v_H}.$$

Inserting the maximal value $c_h = \frac{v_H^2}{v_D - v_H}$ in (22) and manipulating, we need:

$$\begin{aligned} \frac{v_H^2}{v_D - v_H} v_D &\leq v_H^2 + v_H \frac{v_H^2}{v_D - v_H} \\ \frac{v_D}{v_D - v_H} &\leq 1 + \frac{v_H}{v_D - v_H} \\ v_D &\leq v_D - v_H + v_H, \end{aligned}$$

which is obvious.

7.5 Calculations, Example 3

We have

$$\begin{aligned} \hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m} &= \left(1 + \frac{2c_m}{c_D} + \frac{c_h - v_H}{v_H} - \frac{2c_m}{c_D}\right) \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \\ &= \frac{c_h}{v_H} \cdot \frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \\ &= \frac{c_h}{v_H + c_h - 2c_m - v_D} \cdot \frac{2v_H - v_D - 2z_D}{v_H}. \end{aligned} \tag{23}$$

7.5.1 $v_H - 2c_m - c_d > 0$

The derivative of the first fraction in (23) with respect to c_h is

$$\frac{[v_H + c_h - 2c_m - v_D] - c_h}{[v_H + c_h - 2c_m - v_D]^2}$$

which is positive if $v_H - 2c_m - c_d > 0$. This ensures that the sum $\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m}$ is increasing in c_h . Since the first two terms are decreasing in c_h , it must be that \hat{p}_{D_m} is increasing in c_h . Since $\hat{p}_{D_n} = 1 - (\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m})$, \hat{p}_{D_n} must be decreasing in c_h .

7.5.2 $v_H - 2c_m - c_d < 0$

The derivative of the first fraction in (23) with respect to c_h is now negative. This ensures that \hat{p}_{D_n} is increasing in c_h . To ascertain the effect on \hat{p}_{D_m} , we differentiate (6)

to find

$$\frac{d\hat{p}_{D_m}}{dc_h} = \frac{1}{v_H} \left(\frac{2v_H - v_D - 2z_D}{v_H + c_h - 2c_m - v_D} \right) - \left(\frac{c_h - v_H}{v_H} - \frac{2c_m}{v_D} \right) \left(\frac{2v_H - v_D - 2z_D}{[v_H + c_h - 2c_m - v_D]^2} \right).$$

This derivative has the sign of

$$\left(v_H - \frac{v_D}{2} \right) - c_m \left(1 - \frac{v_H}{v_D} \right). \quad (24)$$

We now note that we can find examples where this expression takes either sign. If $(v_H, v_D, z_D, c_h, c_m) = (2, 1, 1, 7, 1)$, then (A1)–(A3) hold and $v_H - 2c_m - c_d < 0$, and (24) is positive. Alternatively, if $(v_H, v_D, z_D, c_h, c_m) = (21/4, 10, 1/8, 27/5, 1)$, then (A1)–(A3) hold and $v_H - 2c_m - c_d < 0$, and (24) is negative.

7.5.3 Large c_h

Now we examine what happens as c_h becomes large. There are two cases to consider. First, it may be that

$$z_D \geq \frac{v_H}{2}. \quad (25)$$

In this case, c_h can increase without bound, while still satisfying (A1)–(A3). This ensures that \hat{p}_{H_h} and \hat{p}_{H_d} converge to zero. The limiting frequencies of both Downy mimics and Downy nonmimics is positive. This follows from the fact that

$$\lim_{c_h \rightarrow \infty} \frac{c_h}{v_H + c_h - 2c_m - v_D} \cdot \frac{2v_H - v_D - 2z_D}{v_H} = \frac{2v_H - v_D - 2z_D}{v_H} \in (0, 1).$$

This ensures that the sum of the limiting frequencies $\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m}$ is greater than zero but less than one, and hence that we have a positive frequencies of both D_m and D_n . To verify the inequality

$$\frac{2v_H - v_D - 2z_D}{v_H} < 1,$$

we note that this is

$$2v_H - v_D - 2z_D < v_H,$$

which is hardest to satisfy if we set z_D at its minimum of (from (25)) $\frac{v_H}{2}$, in which case the preceding inequality is

$$v_H - v_D < v_H,$$

which is immediate.

Alternatively, we may have

$$z_D < \frac{v_H}{2}.$$

Then c_h has a finite upper limit at which (A2) holds with equality. At this upper limit, \hat{p}_{H_h} , \hat{p}_{H_d} , and \hat{p}_{D_m} are all nonzero. To show that D_n is as well, we show that $\hat{p}_{H_h} + \hat{p}_{H_d} + \hat{p}_{D_m}$ is less than one, or

$$\frac{c_h}{v_H + c_h - 2c_m - v_D} \cdot \frac{2v_H - v_D - 2z_D}{v_H} < 1.$$

We are interested in the case in which c_h is such that (A2) binds, allowing us to substitute for z_D :

$$\frac{c_h}{v_H + c_h - 2c_m - v_D} \cdot \frac{2v_H - v_D - \frac{v_H}{c_h}(c_h - v_H)}{v_H} < 1.$$

Multiplying by the denominator of the left side, this is equivalent to

$$2c_h v_H - c_h v_D - c_h v_H + v_H^2 < v_H^2 + c_h v_H - 2v_H c_m - v_H v_D.$$

Eliminating common terms, this is

$$c_h v_D > v_H v_D + 2v_H c_m,$$

which is equivalent to (A3).

7.6 Derivation of the Replicator Dynamics, Section 4.3.4

The replicator dynamics are derived as follows. We think of a very large population. Formally, we treat the population as a continuum, so that the law of large numbers smooths out all of the randomness, giving us deterministic dynamics. There are approximation theorems showing that with arbitrarily high probability the actual dynamics of a finite population will lie arbitrarily close to these deterministic dynamics for arbitrarily long time, with each arbitrarily in this statement becoming sharper as the population becomes larger.

Fix a time t , and consider a very small interval of time τ . We assume that in the interval $[t, t + \tau]$, proportion τ of the of the agents in the community are selected to reproduce. (We could assume that proportion $\alpha\tau$ of the population is selected, for any $\alpha > 0$, and it is simply a rescaling time to take $\alpha = 1$.) The individuals chosen to reproduce are selected randomly from each population in the community, and so we can assume that proportion τ of each strategy in the community is selected to reproduce. Each individual selected to reproduce gives rise to offspring characterized by the same strategy. Hence, Hairies only have Hairy offspring and Downies only have Downy offspring, and in addition H_h only have H_h offspring, H_d only have H_d , and so on. The number of offspring an individual has is given by their fitness in the game. (It is again equivalent to rescaling the way time is measured to let the offspring be any common multiple of this fitness.)

There is no death in the population, but we would get the same result if we assumed that parents die immediately upon giving birth, or a variety of intermediate assumptions.

Let us choose our units of measurement so that at time t , the population size is 1. Then the number and frequency of H_h is $p_{H_h}(t)$. The number of H_h at time $t + \tau$ is given by

$$p_{H_h}(t + \tau) = p_{H_h}(t) + \tau p_{H_h}(t) \pi_{H_h}(t),$$

where π_{H_h} is the average fitness of H_h . The proportion of H_h at time t_τ is then given by

$$\begin{aligned} & p_{H_h}(t + \tau) \\ = & \frac{p_{H_h}(t) + \tau p_{H_h}(t) \pi_{H_h}(t)}{p_{H_h}(t) + \tau p_{H_h}(t) \pi_{H_h}(t) + p_{H_d}(t) + \tau p_{H_d}(t) \pi_{H_d}(t) + p_{D_m}(t) + \tau p_{D_m}(t) \pi_{D_m}(t) + p_{D_n}(t) + \tau p_{D_n}(t) \pi_{D_n}(t)} \\ = & \frac{p_{H_h}(t) + \tau p_{H_h}(t) \pi_{H_h}(t)}{1 + \tau \bar{\pi}(t)}, \end{aligned}$$

where π_{H_d} , π_{D_m} and π_{D_n} are similarly average payoffs to the various strategies, the second equality uses our convention that the current population size is 1, and $\bar{\pi}$ is the average fitness across the community of both Hairies and Downies.

We now subtract $p_{H_h}(t)$ from both sides to get

$$\begin{aligned} p_{H_h}(t + \tau) - p_{H_h}(t) &= \frac{p_{H_h}(t) + \tau p_{H_h}(t) \pi_{H_h}(t) - p_{H_h}(t)(1 + \tau \bar{\pi}(t))}{1 + \tau \bar{\pi}(t)} \\ &= \tau \frac{p_{H_h}(t)(\pi_{H_h}(t) - \bar{\pi}(t))}{1 + \tau \bar{\pi}(t)} \end{aligned}$$

and then divide by τ to get

$$\frac{p_{H_h}(t + \tau) - p_{H_h}(t)}{\tau} = \frac{p_{H_h}(t)(\pi_{H_h}(t) - \bar{\pi}(t))}{1 + \tau \bar{\pi}(t)}$$

and then take the limit as τ gets small to obtain

$$\frac{dp_{H_h}(t)}{dt} = p_{H_h}(t)(\pi_{H_h}(t) - \bar{\pi}(t)).$$

We can repeat this for each of the other three strategies, giving the dynamic system:

$$\begin{aligned} \frac{dp_{H_h}(t)}{dt} &= p_{H_h}(t)(\pi_{H_h}(t) - \bar{\pi}(t)) \\ \frac{dp_{H_d}(t)}{dt} &= p_{H_d}(t)(\pi_{H_d}(t) - \bar{\pi}(t)) \\ \frac{dp_{D_m}(t)}{dt} &= p_{D_m}(t)(\pi_{D_m}(t) - \bar{\pi}(t)) \\ \frac{dp_{D_n}(t)}{dt} &= p_{D_n}(t)(\pi_{D_n}(t) - \bar{\pi}(t)) \end{aligned}$$

where the fitnesses are given by (suppressing time arguments)

$$\begin{aligned}
\pi_{H_h} &= p_{H_h} \frac{v_H - c_h}{2} + (1 - p_{H_h}) v_H \\
\pi_{H_d} &= (p_{H_d} + p_{D_m}) \frac{v_H}{2} + p_{D_n} v_H \\
\pi_{D_m} &= z_D + p_{H_h} (-c_m) + (1 - p_{H_h}) \frac{v_D}{2} \\
\pi_{D_n} &= z_D + (p_{D_m} + p_{D_n}) \frac{v_D}{2}
\end{aligned}$$

and

$$\bar{\pi} = p_{H_h} \pi_{H_h} + p_{H_d} \pi_{H_d} + p_{D_m} \pi_{D_m} + p_{D_n} \pi_{D_n}.$$

7.7 Asymptotic Stability

Our point of departure is the replicator dynamics specified by (9)–(12). Let p be a the vector of community frequencies $(p_{H-H}, p_{H_d}, p_{D_m}, p_{D_n})$, and let \hat{p} denote the equilibrium. We can denote the replicator dynamics by

$$\frac{dp}{dt} = F(p).$$

Let DF denote the Jacobian matrix of F . Then a sufficient condition for the asymptotic stability of the equilibrium \hat{p} is that the matrix $DF(\hat{p})$ have eigenvalues with negative real parts ([8, pp. 52–55]). We have turned to numerical methods to establish that the eigenvalues have negative real parts.

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