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On the instability of evolutionary stable strategies in small populations

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Abstract

Evolutionary stable strategies (ESSs) are often used to explain the behaviors of individuals and species. The analysis of ESSs determines which, if any, combinations of behaviors cannot be invaded by alternative strategies. Two assumptions required to generate an ESS (i.e. an infinite population and payoffs described only on the average) do not hold under natural conditions. Previous experiments have indicated that under more realistic conditions of finite populations and stochastic payoffs, populations may evolve in trajectories that are unrelated to an ESS, even in very simple evolutionary games. The simulations are extended here to small populations with varying levels of selection pressure and mixing levels. The results suggest that ESSs may not provide a good explanation of the behavior of small populations even at relatively low levels of selection pressure and even under persistent mixing. The implications of these results are discussed briefly in light of previous literature which claimed that ESSs generated suitable explanations of real-world data. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The concept of evolutionary stable strategies (ESSs) has become increasingly common in explanations of the long-term dynamics of complex adaptive systems. The behavior of such systems is anticipated by examining an evolutionary game with various possible strategies for each player and prescribed payoffs that depend on the simultaneous play of all participants. The equilibrium conditions of the game are determined, and it is assumed that once the players' strategies arrive at such an equilibrium they will tend to remain in that condition, barring external influences. Thus the equilibrium states are the likely resulting be-

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haviors of the complex coevolutionary system with the caveat that such states are accessible (Nowak, 1990; Takada and Kigami, 1991) and that the game provides an adequate description of the real-world conditions.

The most basic game is a mathematical construction involving pairwise contests among an infinite collection of players over resources of specified values. Each competing player can adopt one of two alternative behaviors, A or B. A payoff is defined for each alternative combination of behaviors. The respective worth for a player adopting a certain behavior is determined by the expected payoff for the behavior, given the distribution of behaviors in the population. The payoff for a single pairwise encounter is denoted as

E(A, B),

where the payoff is to the individual adopting strategy A against an opponent adopting strategy B, with a similar notation for other possible pairs of strategies.

For a strategy I to be an ESS, it must satisfy either of the following conditions:

E(I, I) > E(I, J)E(I, I) = E(J, I) and E(I, J) > E(J, J)

where J is any other strategy, $J \neq I$ (Maynard Smith and Price, 1973; Maynard Smith, 1982). Essentially, an ESS is a strategy, or set of strategies, which cannot be invaded by any other strategy. When members of a population adopt an ESS, their expected payoffs are always greater than the payoff awarded by any new member adopting an alternative policy. Analysis by ESSs has been used to predict the behavior and characteristics of naturally evolved organisms (e.g. expected sex ratio (Dawkins, 1989, pp. 144–145), courtship strategies (Dawkins, 1989, pp. 150– 151), searching for suitable feeding areas (Motro, 1991), superparasitism (Visser et al., 1992), mating tactics (Wolf and Waltz, 1993), and many others).

The principal assumption for analyzing systems in terms of their ESSs is an infinite population (Maynard Smith, 1982, p. 20). Under this assumption, if individual payoffs reflect random effects (e.g. when two equivalent strategies meet, one wins and the other loses with equal probability), these effects can be collapsed to their expectation (i.e. the variability of the distribution of the sample mean goes to zero in the limit); however, under a finite population, regardless of population size, these random effects are instead described by a probability mass function. Sampling from such a probability distribution can have a marked effect on the trajectory of a population over the course of many iterations. In an adaptation of the simple hawk-dove game (Dawkins, 1989), simulations that incorporated a finite population and random payoffs demonstrated limit cycle behavior (Fig. 1) and population trajectories that were not associated with the ESS found in the infinite game (Fogel and Fogel, 1995). Fogel et al. (1997) extended these results to include various levels of selection pressure (i.e. the fraction of the population culled by selection at each generation) for populations of size 600 (Fig. 2). The results indicated that the mean fraction of hawks was qualitatively different from the ESS for selection pressures of 16% and above, and was statistically significantly different from the ESS for pressures \geq 7%. The current experiments quantify the relevance of ESSs in the finite population hawk-dove game under smaller populations (size 60) at various levels of selection pressure and random mixing of individuals.

2. Background

The hawk-dove game involves two players who may choose between strategies of hawk or dove. A hawk is always aggressive and only retreats when injured. A dove, in contrast, merely adopts a threatening posture but never causes physical harm to an opponent. If a hawk fights a dove, the dove flees. If a hawk fights another hawk, they continue to fight until one of them is injured. If a dove meets a dove, neither is harmed; both adopt threatening positions for a long time until one retires. It is assumed that there are no recognition mechanisms that would enable either player to discern the opponent's strategy before an encounter.



Fig. 1. The results of a typical simulation (Fogel and Fogel, 1995) of the hawk-dove game with a finite population and random payoffs. A population of 600 individuals was initialized at the ESS (350 hawks). At each generation, all individuals met in a round-robin competition (all possible pairs) and the 300 individuals with the lowest scores were replaced by copies of the 300 individuals with the highest scores (50% selection). The population did not remain at the ESS, but instead diverged away from it and fell into an apparent limit cycle for an indeterminate length of time. The particular cycle of (560, 520, 440, 280) shown above, describing the number of hawks in the population over successive generations, occurred in each of ten trials. The mean of this cycle is 450 hawks, which does not correspond well with the ESS. A variety of other results were generated for populations of 60 and 6000 individuals, but in no case did the ESS provide a useful description of the population's trajectory.

Points are awarded for encounters as follows. A win is worth 50 points, a loss is worth 0 points, being injured is worth -100 points, and wasting time in a long contest is worth -10 points. These values are taken from Dawkins (1989)(p. 70), and are somewhat arbitrary but are meant to reflect the reproductive potential in light of the above descriptions. Encounters between a hawk and

dove always yield 50 points for the hawk and 0 for the dove. Encounters between doves yield 40 points to one dove (50 points for the win and -10 for wasting time) and -10 to the other, with the winner chosen with equal probability. Encounters between hawks yield 50 points to the victor and -100 to the vanquished, again with the winner chosen with equal probability (Table 1



Fig. 2. A scatterplot of the mean fraction of hawks after replication for each of 100 trials at each level of selection pressure (i.e. the fraction of the population that is eliminated at each generation) using a population of 600 players (from Fogel et al., 1997 with greater detail displayed here). Coincident points are represented by larger star symbols. As the selection pressure was increased, the mean behavior of the population after replication tended to diverge away from the ESS (which is depicted by a horizontal line). For selection pressure up to $\approx 15\%$, hawks comprised the majority of individuals both eliminated and replicated (i.e. they possessed scores in both tails of the distribution). After 15% selection, the distribution of individuals selected against diversified, and the mean behavior of the population tended to drift sharply away from the ESS until it was ultimately dominated by limit cycles. At very high selection pressure, the data suggest that the probability distribution of the mean fraction of hawks may be bimodal.

where H and D are the respective hawk and dove

strategies, and the payoff is the mean payoff for

provides a summary). Thus the expected payoffs for encounters are:

E(H, H) = -25the strategy listed first in parentheses. Operating
on these expected values, the ESS for the game is
a population consisting of 5/12 doves and 7/12
hawks. In the infinite population game, if the
fraction of hawks started to increase above 7/12,
doves would begin to gain an extra advantage,
and the stable 7:5 ratio of hawks to doves would

Table 1									
A summary	of the	payoffs	for th	e various	encounters	in the	hawk-	dove g	ame

		Player B			
Player A	Hawk	Hawk $50/-100$ or $-100/50$		Dove 50/0	
	Dove	0/50		40/-10 or $-10/40$	

The payoff for each encounter in the table is described by A/B, where A is the payoff to player A and B is the payoff to player B. If two hawks meet, they fight. One wins and receives 50 points, while the other is injured and receives -100 points. Both hawks have equal probabilities for winning. If a hawk meets a dove, the dove flees and receives no points, while the hawk receives 50 points. If two doves meet, they both posture and waste time, both earning -10 points, but then one dove outlasts the other and is compensated with 50 points, for a total of 40 points. Both doves have equal probabilities for winning. The payoffs in the classic hawk–dove game are taken as the mean payoffs (or expectations) of these circumstances.

reappear. But under more realistic conditions of a finite population, with high selection pressure (i.e. the fraction of the population that is eliminated), where the payoffs for individual encounters are not taken as the expected payoffs but rather are sampled as random variables, the ratio of hawks to doves can diverge from the ESS and may exhibit limit cycles (Fig. 1).

3. Method

Two experimental designs were employed. In the first, 100 trials were conducted for each of a variety of selection pressures (see Fig. 2) within a finite population of 60 individuals playing a hawk-dove game. In each trial, the population was initialized at the ESS: 35 hawks and 25 doves. All individuals in the population competed in a round-robin tournament (i.e. each individual pairs with each other individual one time), and payoffs were awarded in each encounter by sampling from the appropriate random variable, rather than using its expected value. For example, if two hawks met, one would receive a payoff of 50 for the win while the other would receive -100 for fighting and losing, instead of assigning both hawks the statistical expectation of -25. The results of any encounter did not affect the probabilities of winning or losing in subsequent encounters (i.e. encounters between like individuals were always decided with equal chances for each to win). After all pairwise contests were completed and point totals accumulated, a selected percentage of the population with the lowest scores was removed from the population and replaced by copies of the corresponding percentage of highest scoring individuals. For example, if the selection pressure were 10% then the six lowest scoring individuals would be replaced by replicas of the six highest scoring individuals. Selection levels (percentage to be culled) covered the range [1-50] by single percentage points. Each trial was executed for 200 iterations of replication and selection, this being chosen so as to minimize any initial transient effects on the mean population trajectory.

The second experiment broadly followed the design of the first except that the round-robin pairing was replaced by a randomized mixing procedure. Rather than compute all pairwise encounters, a random mixing level was described as a percentage of the population size. The expected number of encounters for each individual per iteration was determined by multiplying the mixing percentage by the population size. For example, if the mixing level were 5% and the chosen population size consisted of 60 individuals then this would indicate that each individual should be expected to engage in three encounters. The expected number of encounters per individual was multiplied by the total population size to determine a total number of encounters for each iteration. Individuals were then selected completely at random for each encounter up to the prescribed maximum number. Thus it was possible for an individual to have more than the expected number of engagements, or even no engagements. Each individual was initialized with zero points at the



Fig. 3. A scatterplot of the mean fraction of hawks after replication for each of 100 trials at each level of selection pressure (i.e. the fraction of the population that is eliminated at each generation) using a population of 60 players. Coincident points are represented by larger star symbols. As the selection pressure was increased, the mean behavior of the population after replication tended to diverge away from the ESS (the horizontal line). At and above 5% selection, the mean behavior of the population tended to drift sharply away from the ESS.

start of each round of competition, and selection was imposed based on the number of points per individual after all pairwise competitions had been completed. The mixing level was stepped over the range [5, 100] by five percentage points and the selection percentage was simultaneously stepped over [5, 50] percent (i.e. 100 trials for 200 iterations for each pair of settings for mixing level and selection pressure). In addition, a selection pressure of 1% (which was set equal to one individual) was also executed.

4. Results

Conceptually, the simulation operated in discrete phases of selection and replication, thus consideration should be given to the mean fraction or number of hawks in the population at the completion of both phases. Previous experiments with 600 individuals indicated that the ESS was not qualitatively relevant to the fraction of hawks after selection (Fogel et al., 1997), and attention was therefore focused on the fraction or number of hawks in the population after replication. For the first experiment, this is displayed in Fig. 3 (Table 2 summarizes these statistics across all trials). The mean fraction of hawks after replication was statistically significantly different from the ESS (P < 0.01) at all selection levels $\geq 5\%$. The mean fraction of hawks after replication moved increasingly away from the ESS at successively higher levels of selection pressure. None of the sets of 100 trials for any selection pressure above 10% generated a distribution of the mean fraction of hawks that bounded the ESS, nor did the ESS appear to be a useful point estimate of the distribution of trials for selection pressure at $\geq 5\%$.

For the second experiment, Fig. 4 shows the combined effects of varying the selection percentage and the mixing level (noted as encounter percentage). When the mixing level is held constant and selection percentage is varied, systematic deviations away from the ESS are observed. These deviations are exaggerated for a mixing level of only 5%, where the mean number of hawks after replication in 100 trials of 200 iterations appears to take on a decidedly non-linear pattern as selection percentage is varied from 1-30 individuals (i.e. 1-50%). For any particular mixing level, the ESS did not serve as a useful point estimate of the population's mean behavior at any selection percentage greater than 5%. There was often considerable variability even at only 5% selection. For constant selection pressure of 5, 25 and 50% (as shown in Fig. 4), as the encounter percentage is increased, the distribution of the mean number of hawks after replication (across all iterations) appears to stabilize. But the ESS served as a potentially useful point estimate of the mean population behavior only for the relatively slight selection pressure of 5%. Note that as the mixing level was reduced the results typically became more variable (as might be expected). Moreover, the directionality of the variability was not consistent (i.e. low mixing at low selection pressure generated a low mean number of hawks, while low mixing and medium and high selection pressures generated a high mean numbers of hawks).

5. Discussion and conclusions

The results provide further evidence that the equilibrium conditions associated with ESSs may not be stable in simple evolutionary games involving a finite population and random payoffs based on individual encounters. The simulations demonstrate the potential for generating qualitatively different results than would be expected under the assumption of an infinite population simply by varying fundamental characteristics such as the selection pressure and mixing rate. Cavalieri and Kocak (1995) have shown that in a model simulation study with parameter values based on field data, a population undergoing regular periodic cycles can become chaotic in the absence of changes in environmental factors. Analysis by Dieckmann et al. (1995) also indicates that evolutionary limit cycles may be a natural outcome to coevolutionary dynamics and they suggest "Clearly, there is no general rule in nature to say that phenotypic evolution would lead to an equilibrium point in the absence of external changes in the environment". It may be more useful to view populations in terms of chaotic behavior, limit cycles, and stochastic disturbances than in terms of fixed point equilibria.

The payoffs in the classic hawk-dove game describe changes in fitness, where fitness is defined in terms of the expected number of offspring (or surviving offspring, or offspring that survive to reproduce). The simulations conducted here do not explicitly assign payoffs as changes in fitness under this definition. Instead, accumulated payoffs are used to determine which individuals to remove from a population under selection. Although the specifics differ, each pairwise payoff is "taken as a measure of the contribution the contest has made to reproductive success of the individual" (Maynard Smith and Price, 1973). The reproductive success of an individual under the current simulations can only be as great as one offspring. Objection might therefore be raised that the above study is truly analyzing the stability of an ESS.

If attention is given to the long-term behavior in equilibrium of the game under the framework of the simulations above, however, there is an



Fig. 4. A series of scatterplots of the mean number of hawks after replication for each of 100 trials with either the mixing level or selection pressure held constant while the other parameter is allowed to vary. Each data point is the mean of 200 iterations in independent trials. Plots (a)–(e) are for mixing levels (encounter percentage) of 100, 75, 50, 25 and 5% respectively, with selection percentage ranging from [1, 50] in increments of five units. Plots (f)–(h) are for selection percentages of 5, 25 and 50% respectively, with encounter percentage varying over [5, 100] percent in increments of five units. At mixing levels of 75% (b) and 100% (a), for selection pressure greater than 5%, the distribution of results drifts away from the ESS. At mixing levels of 25% (d) and 50% (c), the ESS is not a useful point estimate of the distribution of results even at selection pressures of only 5%. When the mixing level is lowered to 5% (e), the distribution of results takes on a non-monotonic characteristic as selection pressure is increased. Note that in plots (a)–(d), a vast majority of trials at the 1% selection level never deviated from the ESS (e.g. for the case of a mixing level of 100% (a), 99 of 100 trials remained at the ESS). For the cases where selection pressure is held constant (f)–(h), as the mixing level is increased the distribution of trials appears to stabilize, but the ESS is only useful as a point estimate in the case of 5% selection pressure (f). For low mixing levels, none of the results show reasonable agreement with the ESS.



Fig. 4. (Continued)

obvious congruence between the equilibrium conditions and the ESS for the classic game. Indeed, the definition of an ESS follows the concept of putting strategies into equilibrium conditions (Maynard Smith and Parker, 1976, p. 162). The ergodic equilibrium conditions for the simulations conducted here can be determined in a manner similar to Maynard Smith and Parker (1976).

Given H hawks in a population of size N, and therefore N - H doves, the expected payoff to each hawk and dove under panmictic conditions is:

$$E(H) = -25(H-1) + 50(N-H)$$
$$E(D) = 0(H) + 15(N-H-1)$$

Note that each individual cannot play against itself. At equilibrium:

$$-25H + 25 + 50N - 50H = 15N - 15H - 15$$
$$-60H = -35N - 40$$
$$H/N = 7/12 + 2/(3N).$$

H/N defines the proportion of hawks in the population, and as N tends to infinity, this ratio tends to 7/12, which is the ESS for the infinite population case.

The question at hand is, under conditions of the framework of the simulations, is the equilibrium condition for an infinite population relevant in describing the long-term dynamics of the population? The consistent answer is no, except at extremely low levels of selection pressure. The populations did not exhibit stability ever under modest levels of selection pressure (where stability is defined in the conventional mathematical fashion of returning to a point after a perturbation of less than a specified magnitude). Instead the populations wandered above and below the ESS in an apparently chaotic manner (this remains to be determined precisely), and their mean behavior did not coincide well with the ESS. Thus the ESS was not useful as a predictor of the ultimate state of the population in our simulations.

The simulations incorporated a number of somewhat arbitrarily determined parameters and procedures, including: (1) only the highest-scoring individuals were allowed to reproduce, (2) each contest was independent of previous contests, (3) no spatial influences were imposed on the individuals (i.e. any individual could potentially meet any other), and (4) none of the individuals varied their strategy based on previous encounters. The choice of only reproducing the observed best individuals deserves further consideration, but it is difficult to imagine the introduction of randomly selected parents generating a sudden transformation to greater stability. Factors (2)-(4) were chosen so as to be close to the original formulation of an infinite population with random mixing and fixed strategies. It might be appropriate to modify any or all of these procedures if the model were intended to abstract a particular real-world circumstance, or if the relevance of equilibrium theory were to be tested in a model such as the

Table 2

The mean fraction of hawks after replication averaged over 100 trials at each level of selection pressure (percentage of population eliminated by selection) using a population of 60 individuals

Selection pressure	Mean fraction of hawks after replication	Sample S.D.	t-statistic	P-value
	0.50222	-		
1	0.58355	0 00051	-	-
2	0.58558	0.00031	0.98039	> 0.1
3	0.58355	0.00114	-0.02032	> 0.3
4	0.58349	0.00103	2 42282	>0.1
5	0.58460	0.00447	5.42262 8.41216	< 0.01
0	0.58031	0.00392	0.75260	< 0.001
0	0.50327	0.00009	9.75509	< 0.001
0	0.59375	0.00385	10.25254	< 0.001
9	0.59291	0.00495	19.33334	< 0.001
10	0.59439	0.00413	27.15255	< 0.001
11	0.59441	0.00205	42.12928	< 0.001
12	0.59493	0.00300	38.0000/	< 0.001
13	0.59423	0.00268	40.6/164	< 0.001
14	0.59411	0.00254	42.44094	< 0.001
15	0.59433	0.00208	52.88462	< 0.001
16	0.59529	0.00181	66.07/35	< 0.001
1/	0.59471	0.00187	60.85561	< 0.001
18	0.59609	0.00160	79.75000	< 0.001
19	0.59582	0.00152	82.17105	< 0.001
20	0.59636	0.00127	102.59843	< 0.001
21	0.59668	0.00121	110.33058	< 0.001
22	0.59682	0.00110	122.63636	< 0.001
23	0.59692	0.00121	112.31405	< 0.001
24	0.59697	0.00118	115.59322	< 0.001
25	0.59691	0.00131	103.66412	< 0.001
26	0.59771	0.00117	122.90598	< 0.001
27	0.59783	0.00115	126.08696	< 0.001
28	0.59928	0.00119	134.03361	< 0.001
29	0.59904	0.00134	117.23881	< 0.001
30	0.60052	0.00132	130.22727	< 0.001
31	0.60278	0.00152	127.96053	< 0.001
32	0.60275	0.00158	122.91139	< 0.001
33	0.60436	0.00169	124.43787	< 0.001
34	0.60453	0.00157	135.03185	< 0.001
35	0.60553	0.00179	124.02235	< 0.001
36	0.60707	0.00184	129.02174	< 0.001
37	0.60703	0.00186	127.41935	< 0.001
38	0.60856	0.00177	142.54237	< 0.001
39	0.60840	0.00214	117.14953	< 0.001
40	0.60982	0.00181	146.35359	< 0.001
41	0.61020	0.00200	134.35000	< 0.001
42	0.61062	0.00197	138.52792	< 0.001
43	0.61108	0.00243	114.19753	< 0.001
44	0.61105	0.00213	130.14085	< 0.001
45	0.61156	0.00219	128.90411	< 0.001
46	0.61142	0.00253	111.02767	< 0.001
47	0.61167	0.00200	141.70000	< 0.001
48	0.61169	0.00237	119.66245	< 0.001
49	0.61158	0.00264	107.00758	< 0.001
50	0.61143	0.00255	110.19608	< 0.001

Each trial consisted of 200 generations of selection and replication. At 1% selection, the population never deviated from the ESS. But for all levels of selection pressure \geq 5%, the hypothesis that the mean fraction of hawks after replication correspond with the ESS can be rejected at *P* < 0.01 using an approximate *t*-test. At selection pressures of 6% or greater, the *P*-values are consistently < 0.001.

iterated prisoner's dilemma (Axelrod, 1984; Fogel, 1993) where previous encounters can shape future behaviors.

The relative failure of equilibrium theory to describe the behavior of the simulated hawkdove game calls into question the robustness of the theory to describe behavior in naturally evolved settings. Certainly, such settings are orders of magnitude more complex and subject to many potential influences that might be expected to lead to chaotic oscillations. In fact, such conditions have been observed even in the light of expected frequency-dependent selection but under a time delay (Hori, 1993). The true applicability of ESSs as explanations of real-world conditions may be less than commonly believed. Much of the work in ESSs relates only to the mathematical problems posed under a variety of factors, such as mate desertion (Grafen and Sibly, 1978), individual condition and tactic frequency (Repka and Gross, 1995), renewing resources (Houston et al., 1995), learning rules (Tracy and Seaman, 1995), and others. Many of these efforts make analogies to real organisms, but no real data is offered in support of the derived models.

Two examples where data have been offered and tested are Davies and Halliday (1979) and Sinervo and Lively (1996). Davies and Halliday (1979) studied competitive mate searching in male toads (Bufo bufo). During migration to a spawning pond, 363 males and 77 females were obfemales served. Males obtained by (1)encountering an available female and pairing up (riding her back), or (2) dislodging a paired male. Consideration was given to modeling the likelihoods for successful pairing by searching at a spawn site or away from the spawn site, with the belief that the individuals act to equalize these probabilities. Predictions from the equilibrium model suggest the percentage of males to utilize either location on a daily basis over 12 days. Davies and Halliday (1979) recognized the ability of the model to predict the seasonal trend for an increase in the percentage of males searching at the spawn site, yet also described the overall fit to the observed data as 'reasonably good,' despite three or four of the 12 observations undershooting and overshooting the actual percentages in the range of 10-25%.

Sinervo and Lively (1996) studied male sideblotched lizards (Uta stansburiana) in the inner Coast Range of California. Territorial defense by males is dependent on throat color: orange throated males are aggressive and defend large territories, blue throated males are less aggressive and defend smaller territories, and yellow-stripe throated males are 'sneakers' that do not defend territories. It was shown that each morph could invade another morph when rare, but was itself invadable by another morph when common. An ESS model predicted cyclic behavior and indeed an apparent 6-year cycle in morph frequency was observed (apparent because only 6 years of data were obtained and twice this data must be obtained to confirm a 6-year cycle). But the ESS model is described as predicting a 12-year cycle (yet the plotted data from their model shows in fact a 16-year cycle), which does not agree with the observed data (i.e. the model suggests a different cycle). The observed data may in fact be the first example of a population cycle caused by frequency-dependent selection (Maynard Smith, 1996), but it is not clear that an ESS model predicted the data with sufficient fidelity to justify the statement: "There is a special pleasure when a curious piece of natural history fits a theoretical prediction" (Maynard Smith, 1996).

Although mathematical models may be useful tools to explore the potential behavioral strategies of individuals in populations, their results must be interpreted with care. There is significant dissonance between the observed results in the simple hawk-dove simulation offered here and the results that would be expected under equilibrium theory based on infinite populations. This result provides evidence extending preliminary efforts in (Fogel and Fogel, 1995). The greater recognition of the potential for coevolutionary dynamics to lead to chaotic behavior (see also Cavalieri and Kocak, 1995; Dieckmann et al., 1995) and the appearance that ESSs may have been accepted too easily as explanations of observed data in the past, suggests a careful reevaluation of the relevance of ESS theory in general, and of its assumptions in particular.

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