Letter

From evolutionarily stable states to eco-evolutionary metastability in evolutionary games with internal mixed equilibrium

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Evolutionary game theory, using deterministic framework, focuses on deriving conditions that describe the evolutionary stability of Nash equilibria, which are the equilibrium points of the replicator equations. Here, we argue that nonasymptotic metastable states can also play a substantial role in evolutionary games, where the evolving trajectory resides in some state for long time; then, without changing any parameter, it exhibits an abrupt transition to a different state. We consider metastates under the demographic games framework settings. This framework explicitly incorporates the payoff matrix of interactions between individual players into death/birth processes, providing a mechanistic (physical) rationale for the abstract concept of fitness, which is a challenge for the classical game theory. We consider games with an internal equilibrium with mixed strategies. As an insightful case study, we consider the demographic version of the Hawk-Dove game, a paradigmatic model of evolution of aggressive behavior. Apart from eco-evolutionary attractors, the system may have metastable states, such as ghost attractors and crawl-by dynamics. Of particular practical importance is the metastate providing a temporal rescue from the eventual evolutionary suicide. We explain why it is necessary to study transients in evolutionary games and point out consequences of ignoring these phenomena.

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Introduction. In models of complex systems, a major focus has long been on asymptotic dynamics. However, the role of transient dynamics, especially long transients, is now being progressively reconsidered. A system can stay in some nonasymptotic state (a metastable state) for a long time, and then it exhibits an abrupt transition to another state: This is not necessarily caused by changes in model parameters or external perturbation, but it is an intrinsic property of the system dynamics [1]. Long transients and metastates have been found in various areas of physics, such as fluid dynamics [2], semiconductor lasers [3], gravitational waves [4], earthquakes [5], and complex networks [6]. The key role of transients has been uncovered in climate models [7] and life sciences: classical ecology [1,8,9], epidemiology [10], and neuroscience [11]. The goal of this Letter is to revisit metastable states in eco-evolutionary game-theoretical models.

In evolutionary models, long-term transient states have been discovered in stochastic games considering fixation of a strategy in a finite-sized population. Mathematically, these games are represented by Markov chains, where a stochastic trajectory quickly approaches some quasistationary set (characterized by its own probability distribution), then remains at this state for a long time, and eventually abruptly switches to a final absorbing state [12–14]. Importantly, however, metastable quasistationary states in stochastic games are sensitive to the population size of players N. Indeed, the lifetime of the state scales up with N, the variance of the probability distribution shrinks, and eventually the state becomes a nontransient Nash equilibrium for $N \to \infty$ [15]. This raises the following fundamental question: Whether metastable states characterized by scaling-free properties (i.e., with the lifetime of the transient being independent of N) can emerge in evolutionary games, in particular, in deterministic games.

The classical evolutionary game theory operating with species densities is based on the replicator equation, which describes time changes of the fractions of subpopulations playing distinct strategies [16–19]. The replicator equation uses the so-called Darwinian fitness, a quantity measuring long-term reproductive success of a subpopulation using a particular strategy. A key advantage of the classical evolutionary game theory is its simplicity. A major disadvantage, however, is the gap between empirical processes occurring in biological systems and the abstract concept of fitness in evolutionary games [20]. This issue becomes especially problematic, when one needs to construct a mechanistic game model from first (physical) principles [21–24]. We should also stress that metastable states are typically not found in classical replicator-based evolutionary games.

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Here, we show that implementing a mechanistic approach to evolutionary game models, known as demographic games [25–27], results in the emergence of nonasymptotic metastable states, which are not the classical attractors. Using the demographic game theory, we revisit the Hawk-Dove game of Maynard Smith, a well-known model of evolution of aggressive behavior [28]. We show that the amended Hawk-Dove game model exhibits metastable states, caused by long transients, such as ghost attractors and crawl-by dynamics. A metastate can be a temporal refuge from eventual evolutionary suicide. Metastates persist under cyclic perturbation of the system, which mimics seasonal variation of parameters in the ecosystem. Overall, this study emphasizes the importance of considering metastable states along the classical evolutionary attractors in game-theoretical models.

Classical replicator dynamics of the Hawk-Dove game. We start with the classical Hawk-Dove game [28]. In this two-player game, individuals can be either aggressive (the Hawk strategy) or peaceful (the Dove strategy). The corresponding payoff matrix is given by

$$U = \left(\begin{array}{c|cc} & H & D \\ \hline H & \frac{f-d}{2} & f \\ D & 0 & \frac{f}{2} \end{array}\right), \tag{1}$$

where the $i, j = H, D$ entry is the payoff of the first (row) player when it plays strategy i and the second (column) player plays strategy j, f is the reward, and d the cost of the fight.

The dynamics of the frequency of the ith strategy is described by the replicator equation. Let $n_i(t)$ be the number of individuals playing strategy i at time t, $i = H, D$, and $n(t) = n_H(t) + n_D(t)$ the total population size, then the frequency of the ith strategy is given by $q_i = n_i/n$. We denote the frequency of the Dove strategy by $q = q_D$. Then, the Hawk frequency is $q_H = 1 - q$ and the state vector is $\overline{q} = (q_D, q_H)$. The average payoffs of the Hawk and Dove subpopulations are given, respectively, by $U_H = (U\overline{q}^T)_1 = (1-q)(f-d)/2 + qf$, $U_D = (U\overline{q}^T)_2 = q(f/2)$, and $\bar{U} = \overline{q}U\overline{q}^T = (1-q)U_H + qU_D$ (calculated in Sec. 1 of the Supplemental Material [29]). Then, the standard replicator equation for the Hawk-Dove game, which is a rescaled Malthusian equation for population densities $dn_i/dt = n_i(U_i - \mu(n))$ (the neutral, i.e., strategy-independent, adult mortality $\mu(n)$ is explained below), can be derived as [28]

$$\frac{dq}{dt} = q(U_D - \bar{U}) = q(1-q)(U_D - U_H) \tag{2}$$

$$= 0.5q(1-q)((1-q)d - f). \tag{3}$$

From the above equation, it follows that for $f > d$ the Hawks always win. For $f < d$, the game has two Nash equilibria in pure strategies and the mixed one, $q = 1 - f/d$; the latter is globally asymptotically stable. The equation for the total population density n is

$$\frac{dn}{dt} = n(\bar{U} - \mu(n)) = n(0.5f - (1-q)^2 0.5d - \mu(n)), \tag{4}$$

where $\mu(n)$ is the per capita (monotonously increasing) density-dependent mortality. From Eq. (4), one can derive the asymptotically stable population size $\tilde{n}(q) = \mu^{-1}(\bar{U})$.

Despite its seemingly straightforward interpretation, the classical game theory has conceptual limitations. Darwinian fitness (thus a game payoff) is defined as the long-term growth rate, while in the replicator equation, the growth rate is proportional to the payoff (defined as fitness). This is related to the so-called tautology problem in evolutionary theory [30–33] (the survival and reproduction will be greatest for the fittest, and the fittest are those with the greatest survival and reproduction). Another large problem is the lack of clear physical meaning of the cost d and benefit f parameters in the classical payoff matrix: They are introduced as some unspecified increments and decrements of some unspecified growth rate (i.e., the cost describes unborn descendants). Such vague connection to biological realism, in particular, to possible experimental measuring of parameters, limits the quantitative description of models [34].

Demographic replicator dynamics. To address the above criticism, we apply the demographic games approach [25–27], which derives the strategic payoffs from the level of births and deaths resulting from interactions and takes into account the ecological mechanisms of population growth suppression. We split the payoff matrix into two separate matrices: D, the mortality matrix (d_{ij} is the probability of death of ith strategist playing against jth strategist), and V, the fertility matrix. Demographic payoffs V and D describe, respectively, the number of the offspring (benefit) and the death probability (cost) during an average encounter. The payoffs, which describe outcomes of the average encounter, are connected to the demographic parameters, the reproduction rate and mortality. This can be modeled by introducing the intensity rate of the game occurrence r (assumed constant for simplicity) expressed in units of $1/t$. The abstract strategy-based growth rate components U_i in Eqs. (2) and (4) decompose into the birth and death rate's components, which are both products of the encounter intensity and the resulting number of incremental (birth) and decremental (death) events. A key modification is considering juvenile recruitment survival to be dependent on the population density. This is described by multiplying the fertility by the term $(1 - n/K)$, where K is the carrying capacity, interpreted as the maximal population load [35].

Then, we consider the system of the Malthusian population dynamics equations for the densities n_i:

$$\frac{dn_i}{dt} = n_i\Big[(rV_i + \Phi)\Big(1 - \frac{n}{K}\Big) - rD_i - \Psi\Big], \tag{5}$$

where $i = H, D$, whereas Φ and Ψ are the background fertility and mortality rate, respectively, and they are density independent. In the above equation, $V_i = (V\overline{q}^T)_i$ describes the average number of offspring produced during an average game round (interaction) and $D_i = (D\overline{q}^T)_i$ is the respective probability of death. We assume that the timescale is adjusted such that $r = 1$. Then, the demographic rates are proportional to the game payoffs.

Similarly to the derivation of Eqs. (2) and (4), we obtain

$$\frac{dq}{dt} = q\Big[(V_D - \overline{V})\Big(1 - \frac{n}{K}\Big) - (D_D - \overline{D})\Big], \tag{6}$$

$$\frac{dn}{dt} = n\Big[(\overline{V} + \Phi)\Big(1 - \frac{n}{K}\Big) - \overline{D} - \Psi\Big], \tag{7}$$

where $\overline{V} = \overline{q}V\overline{q}^T$ and $\overline{D} = \overline{q}D\overline{q}^T$ are average payoffs. Unlike the classical game-theoretical framework, the evolutionary attractors now depend on both the frequency of strategies and the population density. The number of individual game interactions per time unit and the resulting births and deaths are empirical observables. This is important from the point of view of experimental verification of the model predictions (very scarce at this moment), which is difficult for the classical models [36], based on the abstract fitness. The demographic approach makes empirical verification easier, and may be useful in the design of the future experimental settings or individual-based simulations [37].

Demographic Hawk-Dove game. In the amended Hawk-Dove game, f denotes the increase in the expected offspring number (as compared to the background fertility) and d is the death probability resulting from an encounter. We assume that the probability of winning a contest is 0.5 for both Hawk-Hawk and Dove-Dove encounters, and that only Hawk losers suffer extra mortality. The fertility V and the death D matrices become

$$V = \left(\begin{array}{c|cc} & H & D \\ \hline H & 0.5f & f \\ D & 0 & 0.5f \end{array}\right), \quad D = \left(\begin{array}{c|cc} & H & D \\ \hline H & 0.5d & 0 \\ D & 0 & 0 \end{array}\right). \tag{8}$$

We substitute matrices (8) into Eqs. (6) and (7) to obtain

$$\frac{dq}{dt} = 0.5q(1-q)\Big((1-q)d - \Big(1-\frac{n}{K}\Big)f\Big), \tag{9}$$

$$\frac{dn}{dt} = n\left(\left(\frac{f}{2}+\Phi\right)\Big(1-\frac{n}{K}\Big) - \left[(1-q)^2\frac{d}{2}+\Psi\right]\right), \tag{10}$$

which describe the demographic Hawk-Dove game (derived in Sec. 1 of the Supplemental Material [29]).

Eco-evolutionary attractors. The demographic Hawk-Dove model possesses equilibrium states, which are intersections of the nullclines. The system has two trivial equilibria (0, 0) and (1, 0), signifying extinction of the population. The stability of the trivial equilibria is determined by the mutual position of the nullclines (derived in Sec. 2 of the Supplemental Material [29]):

$$\tilde{q}(n) = 1 - \frac{f}{d}\Big(1-\frac{n}{K}\Big), \tag{11}$$

$$\tilde{n}(q) = \left[1 - \frac{(1-q)^2 0.5d + \Psi}{0.5f+\Phi}\right]K. \tag{12}$$

From Eq. (11), it follows that for every n, the frequency nullcline provides the equilibrium of the classical Hawk-Dove model with the reward f scaled by juvenile survival $(1-\frac{n}{K})$. Intersection of Eqs. (11) and (12) gives nontrivial stationary states. These nullclines intersect at $q \neq 0, 1$ if

$$\Delta = \left(\frac{\Phi}{f}\right)^2 + \frac{\Phi}{f} - 2\frac{\Psi}{d} + 0.25 \geqslant 0.$$

Then, the nontrivial equilibria of the system are

$$q_{1,2} = 0.5 - \Phi/f \pm \sqrt{\Delta}, \tag{13}$$

where q_1 is a stable node, while q_2 is a saddle. Note that above equilibria depend on the ratios $A = \Phi/f$ and $B = \Psi/d$, rather than on f and d separately. The derivation of the equilibria $q_{1,2}$ is provided in Sec. 3 of the Supplemental Material [29]).

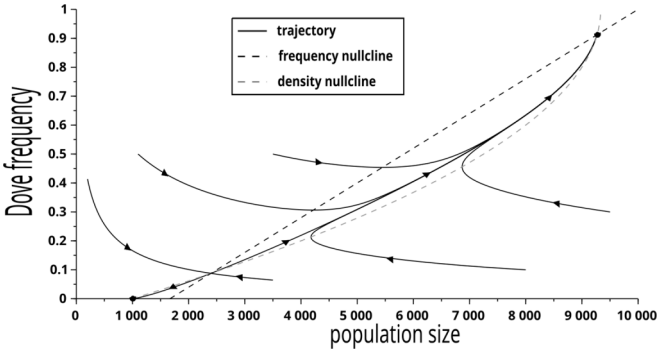


FIG. 1. Phase portrait of the demographic Hawk-Dove model for parameters $f = 1.2$, $d = 1$, $\Phi = 0$, $\Psi = 0.04$, and $K = 10\,000$. Eco-evolutionary attractors are denoted by filled circles.

Note that the frequencies of strategies $q_{1,2}$ are asymptotically stable equilibria of the classical Hawk-Dove model for the fixed corresponding population densities. However, only q_1 is stable in the new framework. Therefore, being an attracting game equilibrium (ESS) in the classical model [3,4] cannot guarantee a general eco-evolutionary stability in the demographic game model.

From mutual positions of the nullclines, it follows that if $q_{1,2} \in [0, 1]$ and $\tilde{n}(0) > 0$, then we have a stable pure Hawk population ($q = 0$) at the population density $\tilde{n}(0) = [1 - \frac{0.5d+\Psi}{0.5f+\Phi}]K$, and an unstable pure Dove population ($q = 1$) at $\tilde{n}(1) = [1 - \frac{\Psi}{0.5f+\Phi}]K$.

Figure 1 shows an example of phase portrait of the demographic Hawk-Dove model with two interior (nontrivial) equilibria given by nullcline intersections. Trajectories are attracted from both sides to the close neighborhood of the stable manifold of the saddle. Importantly, the demographic replicator model is characterized by bistability (not observed in the classical settings): Starting from a different initial condition, the resulting stable equilibrium would be different. In Fig. 2, we present the corresponding time trajectories, where two trajectories are initially attracted to the vicinity of the saddle point, and then they stay for sometime near the saddle, which can be interpreted by an external observer as a possible evolutionary equilibrium. Eventually, the trajectories transfer to their true final attractors: one with mixed strategies, the other one with pure Hawk strategy. This is known as a crawl-by [1,9], and it is an example of long-term transient dynamics.

Metastable eco-evolutionary states. Apart from crawl-by dynamics, due to the saddle point, the system has other types of metastable states. For example, this is related to the so-called ghost attractors [1,9,38]. Ghost attractors occur when the nontrivial nullclines (12) do not intersect, but pass close to each other. The trajectory becomes trapped at the vicinity of the ghost of the equilibrium, which is no more feasible. The nullclines form a narrow channel, where the flow is very slow since in this channel the values of the right-hand sides of both equations are very small. An example of a ghost attractor is shown in Fig. 3: A trajectory is initially attracted by the ghost attractor and spends some time in its vicinity, and then there is a sharp transition from mixed strategies to a pure Hawk state.

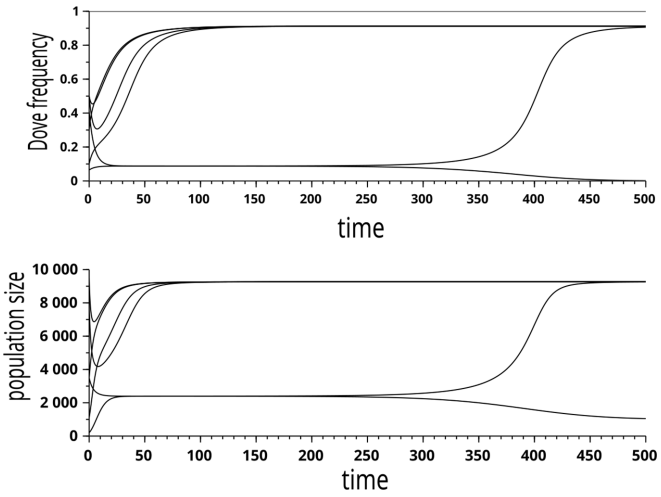


FIG. 2. Time trajectories corresponding to the phase portrait in Fig. 1. There is a nontrivial equilibrium with mixed strategies ($q_1 = 0.9123, n_1 = 9269$) and a saddle point ($q_2 = 0.0877, n_2 = 2397$). The other stable equilibrium is a pure Hawk population $q = 0$ with the density of $n = 1000$. The crawl-by transients are due to the presence of the saddle point.

This metastable state can be mistakenly understood as being the final eco-evolutionary attractor of the model, especially, if the observation is limited in time. Mathematically, the ghost attractor shown in Fig. 3 is due to vicinity of a saddle-node bifurcation, which occurs for $\Delta = 0$ (the possibility of this bifurcation is discussed in Sec. 4 of the Supplemental Material [29]). The condition of disconnection of the nullclines is $A < \sqrt{2B} - 0.5$ (then $\Delta < 0$, but the value of A should be close to $\sqrt{2B} - 0.5$, to keep the nullclines close to each other). We found that our results are generic, in the sense that metastates of the given type can emerge in any game with a stable internal mixed equilibrium (which becomes a nullcline under juvenile recruitment survival). For a two-strategy case, in models based on Refs. [6,7], no more than two internal equilibria can exist. When this happens, the change of the parameters may lead to their collision and annihilation, and a ghost attractor (metastate) emerges. The underlying mechanism is explained in Sec. 4 of the Supplemental Material [29].

A metastable state can be a temporal rescue from population collapse and extinction. This is shown in Figs. 4 and 5, where a trajectory is initially attracted to a state characterized by mixture of strategies (and nonzero population density), whereas after long time the population collapses and goes extinct. This is an example of delayed eco-evolutionary suicide: A semitrivial state with zero population density is the global attractor. From Figs. 4 and 5, one can see that this metastable state has its own basin of attraction: Starting the trajectory outside the basin results in a quick extinction of the population.

Finally, we found that the presented metastable states are robust to periodic forcing in the system, which mimics the effects of seasonality. For example, metastability is observed in the model for the periodic mortality term given by $\alpha(1 + \sin(\frac{2\Pi}{\theta}t))$, which acts as a perturbation to the background mortality Ψ in Eq. (10), where α describes mortality amplitude and θ is the duration of the season. Figure 6 shows a periodic ghost attractor for the parameters $\alpha = 0.0875$ and period $\theta = 1.7$, the other parameters are the same as in Fig. 3. This pattern demonstrates resilience of metastate of the demographic Hawk-Dove model to perturbations.

Concluding remarks. In the classical evolutionary game theory (in models operating with large number of players), the main focus has been long on the stability of Nash equilibria constituting the equilibria of the corresponding replicator equation. Here, we highlight the importance of considering metastable states in evolutionary game theory,

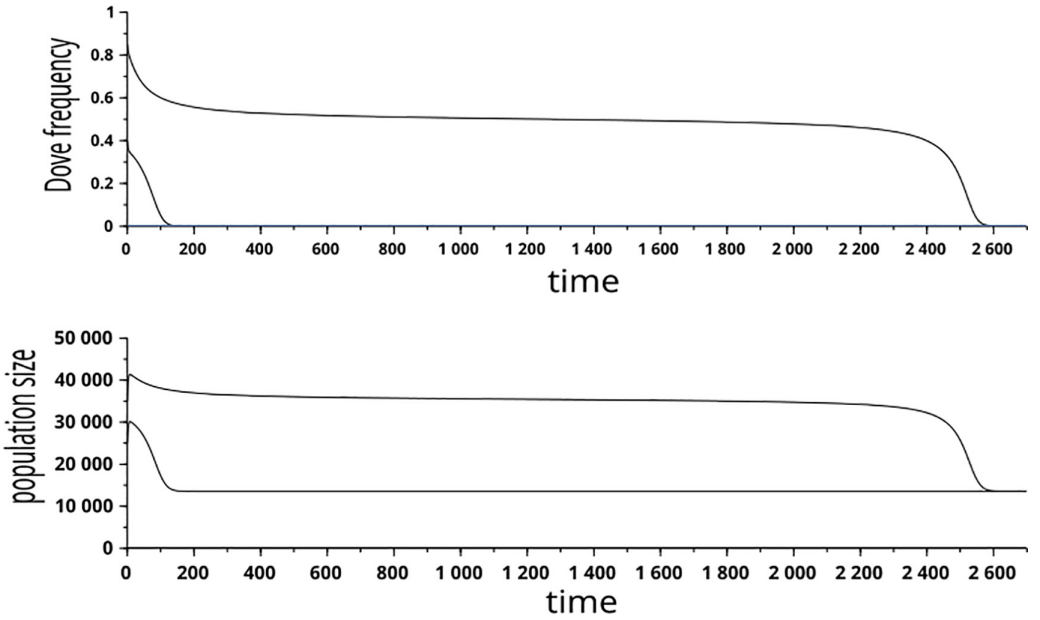


FIG. 3. Example of dynamics for a metastable state in the demographic Hawk-Dove model due to the ghost attractor. A trajectory, starting in the vicinity of the metastate, is initially trapped by the ghost attractor, before a quick shift to another regime occurs without any parameter change. The parameters are $f = 1.2$, $d = 0.7$, $\Phi = 0$, $\Psi = 0.0876$, and $K = 50\,000$.

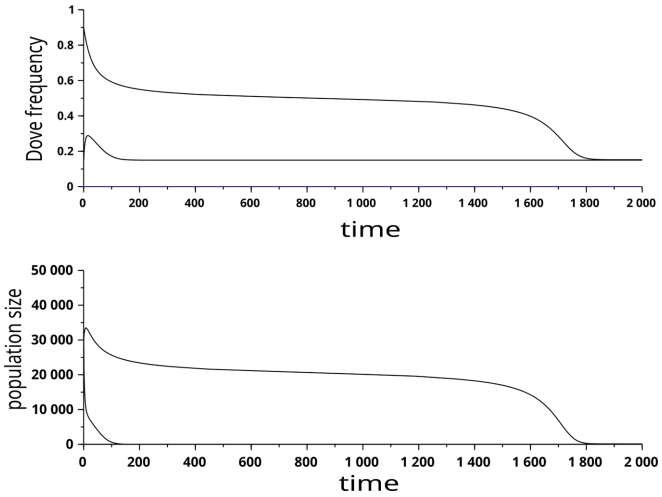


FIG. 4. Example of dynamics for a temporal evolutionary rescue in the demographic Hawk-Dove game. A trajectory, within the basin of attraction of the metastate, initially converges to the ghost attractor, and then eventually collapses to the evolutionary suicide state after a long transient phase. The other trajectory shows a rapid extinction. The model parameters are $f = 0.85$, $d = 1$, $\Phi = 0$, $\Psi = 0.1253$, and $K = 50\,000$.

along with asymptotic dynamics. We stress that metastable states have been recognized to play a key role in physics and geophysics (e.g., fluid dynamics, semiconductor lasers, gravitational waves, earthquakes, climatology [2–7]) and life sciences (e.g., ecology, epidemiology, neural and brain sciences [1,8–11]). However, so far the transient scenarios are almost ignored in evolutionary games (apart from quasistationary probabilistic distributions in stochastic games with absorbing states and boundary heteroclinic cycles in deterministic models in more than two strategies [17,39]).

In modeling in ecology and evolution, a large number of definitions of stability have been introduced so far to cover different aspects of system's behavior [40–43]. A short, but not exhaustive summary of stability definitions is provided in Sec. 6 of the Supplemental Material [29]). Most definitions

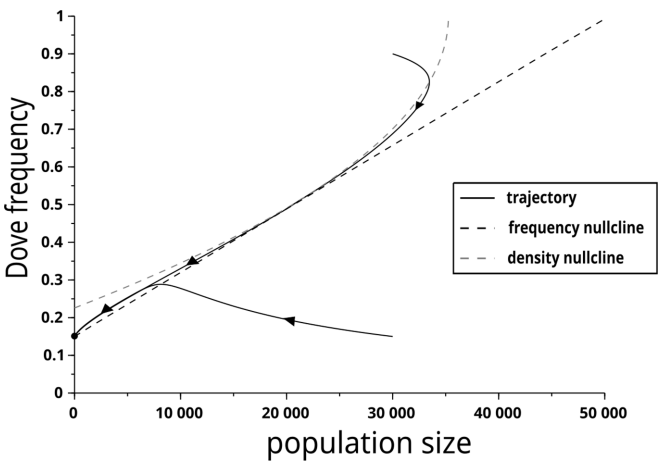


FIG. 5. The corresponding phase portrait for the evolutionary rescue metastate in Fig. 4. The ghost attractor traps trajectories within the narrow channel formed by nonintersecting nullclines.

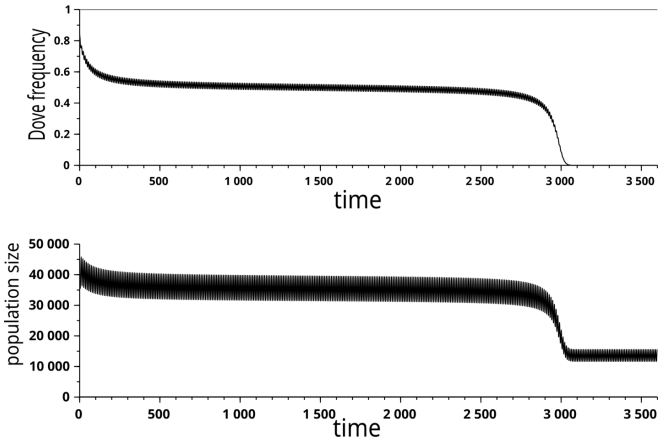


FIG. 6. A periodic ghost attractor in the demographic Hawk-Dove game with periodic mortality. The parameters are $f = 1.2$, $d = 0.7$, $\Phi = 0$, $K = 50\,000$, amplitude $\alpha = 0.0875$, and period $\theta = 1.7$.

explicitly require separation of timescales to distinguish between short-term and long-term processes [41,44]. A typical assumption is that ecological processes are much faster than evolutionary ones; however, there is also separation of timescales between different levels of evolutionary processes. For example, a short-term evolutionary stability (described by the replicator equation) can be considered with respect to phenotype frequencies corresponding to a fixed set of possible phenotypes (often defined as the Lyapunov stability), whereas a long-term evolutionary stability (described by adaptive dynamics modeling the movement in the phenotypic trait space) considers noninvadability with respect to any biologically feasible mutants [41]. Importantly, for each of considered modeling timescales, we expect to have some asymptotic dynamics: After some long time, the state of the system will stop changing. For large timescale, evolutionary models' asymptotic dynamics is related to the so-called convergence stability, where the final state is achieved by gradual substitution of resident strategies by close mutant strategies [44–47]. In contrast, metastable states have an opposite meaning to asymptotic dynamics, and they can occur on any timescale. The trajectory is initially attracted to a narrow part of the phase space, then it remains trapped for long (but finite) time, and, eventually, it leaves the state without an external perturbation [1]. Another feature of a metastable state is that such a state is not mathematically a manifold, but is characterized by an ensemble of trajectories located within some narrow region of the phase space.

There are two major reasons for including metastable phenomena in consideration. First, modeling any realistic biological (as well as a physical) system implies a finite time horizon. Therefore, for a system currently functioning in a metastable regime for a long transient time, the "classical" predictions using asymptotic dynamics (the Nash equilibrium) will be invalid. This should have drastic consequences from the practical point of view: Delayed extinction of species due to temporary evolutionary rescue would provide time for taking conservation measures [48]. Second, unexpected regime shift in the system (e.g., population extinction) can be falsely attributed to some external factors, whereas it is

only a consequence of intrinsic mechanisms signifying that the system leaves the metastable state after a long stay. For regime shift anticipation theory, the home-taking message is the following: Sudden regime shifts can occur even in a constant environment.

We found metastable states in the demographic eco-evolutionary Hawk-Dove game, which is a game with an internal mixed equilibrium. The observed metastates are of different nature, such as a crawl-by, ghost attractor related to saddle-node bifurcation, or a more complicated periodic ghost pattern. Unlike the previous studies, where saddle points were located in the vertices of the simplex (signifying extinction of species, in realistic biological systems), we report crawl-by dynamics in the interior of the phase portrait [17,39]. Arguably, from a biological point of view, the most interesting metastate is the one providing temporal evolutionary rescue followed by a further population collapse (Figs. 4 and 5). This metastate is related to a ghost attractor, and the "mechanistic" explanation of this type of long transients is the following. The two nullclines of system (9)–(10) are attracting. The frequency nullcline represents the selection equilibria (meaning the equality of the growth rates of the competing strategies), while the density nullcline represents the set of states with zero growth rate of the whole population. When these nullclines are close to each other, but without intersection, the system does not possess an internal equilibrium. The trajectory is initially attracted to the region of close mutual location of the nullclines, so both the frequency and population size change rates are very small (often referred to as a weak selection limit), and the system gets trapped. Then, gradual slow variation of both variables results in escaping from the trap, and the trajectory eventually approaches to the extinction state. From the biological point of view, both the shape of nullclines and the occurrence of the trap in the model are possible due to the density dependence of the juvenile growth rate.

Available literature provides examples of eco-evolutionary suicide in various natural systems, caused by many different mechanisms (such as selective pressure on life history traits); this includes fish, plants, insects, and microorganisms [49–53] (for details, see Sec. 5 of the Supplemental Material [29]). Our model suggests possible explanation of eco-evolutionary population collapse. This occurs because of disconnection of the selection equilibrium (defined by a zero selection gradient) from the ecological equilibrium (defined as a zero population growth rate), as a system parameter changes. For example, a small variation of the background mortality (the parameter Ψ in our model), due to harvesting, can trigger a delayed extinction of the population. Also, our findings can shed light on the "extinction debt" problem, which is a delayed extinction of a population (or community) due to an event in the past [54,55]. Previously, the extinction debt was considered to be a purely ecological phenomenon, and possible explanations were centered on ecological interactions, for example, intraspecific competition (our model fits this aspect) or degradation of the environment. Our study highlights the importance of including into consideration internal heterogeneity of population (e.g., Hawks and Doves) and interactions between individuals, so we argue that the biomass-based approaches might be too simplistic. The importance of considering variation (i.e., evolution) of vital rates has been mentioned in the extinction debt literature [54–56], and here we model this using the game-theoretical framework.

A central question is how ubiquitous metastable long-term states in evolutionary models are. We show the existence of long transients in demographic games. Demographic games propose a mechanistic connection of the abstract concept of fitness to physical processes, such as demography and competition for resources [25–27]. Including demography creates features that are impossible in classical games. For example, in the demographic variant of the Hawk-Dove game there are multiple equilibria, each of them having its own basin of attraction, which is not observed in the classical game. No metastable states with long transients are possible in the classical Hawk-Dove model. Metastable states can be found in other replicator-based models, for example, in a hypercycle model (a cycle of linked, self-replicating macromolecules) [57,58]. There is also the possibility for metastable states in eco-evolutionary games with environmental feedback [59] (however, metastable states have not be formally reported for those models yet). Note that certain economic models, which incorporate environmental feedback as the by-product of the actions of economic agents [60,61], can generate long-living metastates as well. Thus, the concept of long transients is not limited to strictly eco-evolutionary games.

Importantly, the existence of metastable states gives another argument in the long discussion on the equivalence of two main approaches in game theory working with deterministic models: the static and dynamic (replicator-based) approaches. Unlike the replicator-based approach, the static approach considers the algebraic expression for the expected gain using the elements of the payoff matrix [28,62,63]. Our study demonstrates a clear advantage of utilizing the dynamic approach, since it captures metastates, which arguably might be more biologically/physically relevant to describe evolution over some long (but finite) time.

Finally, our study sheds light on the concept of (eco-evolutionary) resilience, which is the propensity to absorb perturbations of a system state while maintaining system's functioning [64–68]. We reconsider interpretation of resilience in biological (and, generally, in physical) systems, which is being debated in the literature [69,70]. Metastates generally occur when the model parameters are perturbed in a way that the system's attractor does not exist anymore for the new parameters. However, the system still "remembers" its preperturbation state; thus, the corresponding attracting metastate can provide a temporal resilience (refuge) by trapping the trajectory near the ghost state for long time. Also, we found that the metastate can be resilient itself to the system perturbation as for external periodic forcing, which describes seasonal variation of the background mortality.

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