5

⁂

Mathematical Models of Cooperation

CHRISTOPH HAUERT

Cooperation is a conundrum that has challenged researchers across disciplines and over many generations. In mathematical models, cooperation simply refers to behavioral actions that benefit others at some cost to an actor. Prima facie, defectors always outperform cooperators, but groups of cooperating individuals fare better than groups of noncooperating defectors. However, each individual faces the temptation to defect in order to avoid the costs of cooperation while free-riding on the benefits produced by others. This generates a conflict of interest between the individual and the group known as a social dilemma (Dawes 1980; Hauert et al. 2006).

Social dilemmas are abundant in nature. For example, musk oxen create defense formations to protect their young from wolves (Hamilton 1971). However, each ox would be better off and avoid potential injury by standing in the second line—but if every individual behaves in this way, their defense formation breaks down and the group becomes prone to attacks by wolves. A similar conflict of interest occurs in sentinel behavior in meerkats (Clutton-Brock et al. 1999): a few individuals are on the lookout for predators and warn foraging group members of impending danger. Spotting the predators first returns a direct benefit to the sentinels because they get a head start on finding shelter. At the same time, the costs for keeping watch depend on the individuals' hunger. From time to time sentinels abandon their position and get replaced by other individuals. Other prominent examples of social dilemmas occur in predator inspection behavior in fish (Milinski 1987; Magurran and Higham 1988; Pitcher 1992), in phages competing for reproduction (Turner and Chao 1999, 2003), or in microorganisms producing extra cellular products such as enzymes in yeast (Greig and Travisano 2004), biofilms (Rainey and Rainey 2003), or antibiotic resistance (Neu 1992).

Social dilemmas also occurred on an evolutionary scale and life could not have unfolded without the repeated incorporation of entities of lower complexity or degrees of self-organization into higher-level entities. Major transitions such as the formation of chromosomes out of replicating DNA molecules, the transition from single cells to multicellular organisms, or the change from individuals to societies all require cooperation (Maynard-Smith and Szathmáry 1995). Finally, humans have taken the problem of cooperation to yet another level (Hardin 1968) when it comes to social welfare such as health care or pension plans and, even more importantly, to global issues concerning natural resources such as drinking water, clean air, fisheries, or climate change (Milinski et al. 2006).

In order to analyze individual behavior in social dilemmas or other types of interactions, the economist Oscar Morgenstern and the mathematician John von Neumann developed a mathematical framework termed game theory (von Neumann and Morgenstern 1944). The most prominent game to study cooperation in social dilemmas is the prisoner's dilemma (Flood 1958; Axelrod and Hamilton 1981). In the prisoner's dilemma, two individuals decide whether to cooperate or to defect. Cooperation incurs costs, c, to the actor while the benefits of cooperation, b, accrue exclusively to the opponent with $b > c$. Defection does not incur costs to the actor and produces no benefits for the opponent. Thus, if both players cooperate, each receives $b - c$, whereas if both defect, neither receives anything. If only one cooperates and the other defects, the cooperator is left with the costs, $-c$, while the defector receives the full benefit, b. In this situation, defection should dominate because individuals are better off defecting, irrespective of the opponent's decision. Consequently, two rational players will opt for defection and end up with nothing, as opposed to the more favorable reward, $b - c$, for mutual cooperation.

Evolutionary Dynamics

The predicted dominance of defection in social dilemmas, however, contrasts with abundant evidence of cooperation in nature. Ever since Darwin (Darwin 1859), the evolution, and maintenance of cooperation has posed a major challenge to evolutionary biologists and social scientists. The theoretical foundation for addressing the problem of cooperation rests on Hamilton's kin selection theory (Hamilton 1964) and Maynard Smith's adaptation of game theory to evolutionary scenarios (Maynard Smith and Price 1973), by linking game theoretical payoffs with biological fitness. In evolutionary biology, fitness denotes the single determinant of evolutionary success and essentially reflects the reproductive output of individuals over their life span. Thus, under Darwinian selection, behavioral traits (or strategies) of individuals with high fitness are more likely to be passed on to future generations.

REPLICATOR DYNAMICS

Consider a population with a fraction x cooperators (and $1-x$ defectors). If individuals randomly engage in prisoner's dilemma interactions, the average payoffs for defectors is $f_D = xb$ (with probability x the defector interacts with a cooperator and obtains the benefit b); for cooperators it is $f_C = xb - c$ (with probability x the cooperator interacts with another cooperator and receives b but always pays the costs of cooperation c); and for the entire population $\bar{f} = xf_c + (1-x)f_D = x(b-c)$. Selection prescribes that strategies that perform better than the population on average increase in abundance. In the simplest case this leads to the replicator equation (Hofbauer and Sigmund 1998):

$$\dot{x} = x(f_c - \bar{f}) \tag{1}$$

which states that the change in frequency of cooperators ($\dot{x}$ denotes the time derivative of the fraction of cooperators) is proportional to the payoff difference between cooperators and the population average. Since $f_c - \bar{f} = -c(1-x) < 0$, cooperators decrease over time and eventually disappear ($x^\star = 0$ is the only stable fixed point).

In order to model the promotion and maintenance of cooperation among unrelated individuals, a variety of approaches have been proposed over the last few decades. In particular, cooperation can be established through conditional behavioral rules in repeated encounters (Trivers 1971). If behavioral actions are reflected in an individual's reputation, repeated interactions are not required to establish cooperation (Nowak and Sigmund 1998). Moreover, punishment of defectors (Yamagishi 1986; Sigmund, Hauert, and Nowak 2001), or voluntary interactions (Hauert et al. 2002, 2007), also promote and sustain cooperation. Finally, spatial extension and limited local interactions can enhance cooperation, which is the topic of the second part of this chapter.

Another complementary approach to address the problem of cooperation is to reconsider the mathematical implementation of the social dilemma. In contrast to the theoretical effort expended on studying the prisoner's dilemma, it receives surprisingly little support from empirical evidence in biological systems. In fact, in all of the prominent examples of social dilemmas listed above, it remains largely unresolved whether individuals indeed engage in prisoner's dilemma type interactions. Instead, another game, called the snowdrift game (Sugden 1986; Hauert and Doebeli 2004), seems to be a biologically appealing alternative to the prisoner's dilemma (Doebeli and Hauert 2005). The anecdotal story behind the snowdrift game states that two drivers are caught in a blizzard and trapped on either side of a snowdrift. Each driver has the option to remove the snowdrift and start shoveling or to remain in the cozy warmth of the car. If both cooperate and shovel, they both get home while sharing the labor, but if only one shovels, again both get home, but the cooperator has to do all the work. If no one shovels, neither gets anywhere, and they have to wait for spring to melt the snowdrift. In contrast to the prisoner's dilemma, the best strategy now depends on the co-player's decision: if the other driver shovels, it is best to shirk, but when facing the potential for a lazy counterpart, it is better to start shoveling instead of remaining stuck in the snow.

The snowdrift game potentially seems to apply whenever individuals generate a valuable public resource. For example, in antibiotic resistance (Neu 1992) bacteria *(Staphylococci)* secrete an enzyme, β-lactamase, that destroys penicillin. The production of this enzyme is costly to the bacterium, while the resulting protection represents a public resource that benefits not only the enzyme-producing bacterium but also its fellow bacteria. Thus, in the vicinity of enzyme producers it pays for a bacterium to throttle enzyme production and increase replication, but in the absence of the enzyme, protection against penicillin becomes vital.

The evolutionary dynamics of the snowdrift game can again be analyzed using the replicator equation. For mutual cooperation the costs are shared and each individual receives $b - c/2$, whereas a cooperator facing a defector obtains $b - c$. The payoffs for defectors remain the same as in the prisoner's dilemma, with b against a cooperator and zero for mutual defection. Thus, the average payoff of cooperators becomes $f_C = b - c(1 - x/2)$, and the average payoff for defectors remains $f_D = xb$. A short calculation shows that, in the snowdrift game, the replicator equation admits another fixed point that is stable (obtained by setting $f_C = \bar{f}$) at $x^\star = 1 - r$, where $r = c/(2b - c)$ denotes the cost-to-net-benefit ratio of mutual cooperation. Consequently, cooperators and defectors coexist in the snowdrift game. Nevertheless, the conflict of interest persists because a population at $x^\star$ is still worse off than if everybody had cooperated. Hence, the snowdrift game represents a relaxed social dilemma as compared to the prisoner's dilemma.

Adaptive Dynamics

In nature, the problem of cooperation may not always be adequately addressed by limiting the analysis to two distinct strategic types—the cooperators and the defectors. Instead, in many situations, it might be more appropriate to consider continuous degrees of cooperation such as time and effort expended in producing a public resource. In such continuous games, the strategy or trait u of an individual denotes its cooperative investment and can vary between zero and an upper limit u_{max}. The fitness costs and benefits are determined by the increasing functions $C(u)$ and $B(u)$, respectively, such that an increase in the cooperative trait u both raises costs and increases benefits. Moreover, no cooperation ($u = 0$) neither provides benefits nor incurs costs, $C(0) = B(0) = 0$.

In the continuous prisoner's dilemma, the payoff of an individual with trait u interacting with a trait v individual is written as $Q(u,v) = B(v) - C(u)$. This means that the benefits are determined by the opponent's trait, whereas the costs are determined by the individual's own trait. Thus, the only way to improve the payoff is to lower the costs, and hence the degree of cooperation, because $C(u) < C(u + \Delta u)$ for $\Delta u > 0$. Consequently, evolution, when modeled on the dynamics of continuous prisoner's dilemma interactions, selects lower investors such that cooperation gradually declines and eventually disappears.

The situation is rather different in the continuous snowdrift game (Doebeli, Hauert, and Killingback 2004). In the previous section the snowdrift game was introduced by assuming constant benefits and costs that are shared among cooperators. Mathematically, this is equivalent to assuming that costs are constant and benefits depend on the number of cooperators. In the continuous snowdrift game, the payoff to an individual with trait u interacting with a trait v individual then becomes $P(u,v) = B(u+v) - C(u)$. If $B(u) > C(u)$ holds at least for small u, it seems that evolution should select intermediate degrees of cooperation. However, it turns out that the evolutionary dynamics of the continuous snowdrift game are much richer.

The evolution of the trait u can be analyzed using the adaptive dynamics framework (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998). This assumes a homogeneous resident population with trait u. Occasionally, an initially rare mutant trait v appears and attempts to invade. The fitness of the mutant type is given by $P(v, u)$—interactions with its own type, $P(v,v)$, can be neglected because the mutant is rare. According to the replicator equation, the mutant increases in abundance if $P(v, u)$ exceeds the average population payoff—namely, the fitness of the resident, $P(u, u)$—interactions of the resident with the mutant are again neglected because the mutant is rare. Thus, the growth rate of the mutant v is given by $f_u(v) = P(v, u) - P(u, u)$ and is called the invasion fitness because for $f_u(v) > 0$ invasion succeeds, but fails for $f_u(v) < 0$. If mutations are small, such that v is close to u, it follows that whenever invasion succeeds ($f_u(v) > 0$), the mutant v eventually takes over and becomes the new resident (Geritz et al. 1998). Mutations are assumed to be rare, such that mutants always face a homogeneous resident population. Under these assumptions, the selection gradient $D(u)$ determines whether more or less cooperative mutants can invade.[1] For $D(u) > 0$ mutants with $v > u$ can invade and cooperation increases, but it decreases for $D(u) < 0$. Thus, the evolutionary change of cooperation is given by the canonical equation of adaptive dynamics, $\dot{u} = D(u)$ (Metz et al. 1996). Of particular interest are singular traits $u^\star$, for which the selection gradient vanishes, $D(u^\star) = 0$, and hence denote fixed points of the adaptive dynamics ($\dot{u} = 0$). If no singular trait $u^\star$ exists in the interval $(0, u_{\max})$, then either cooperation

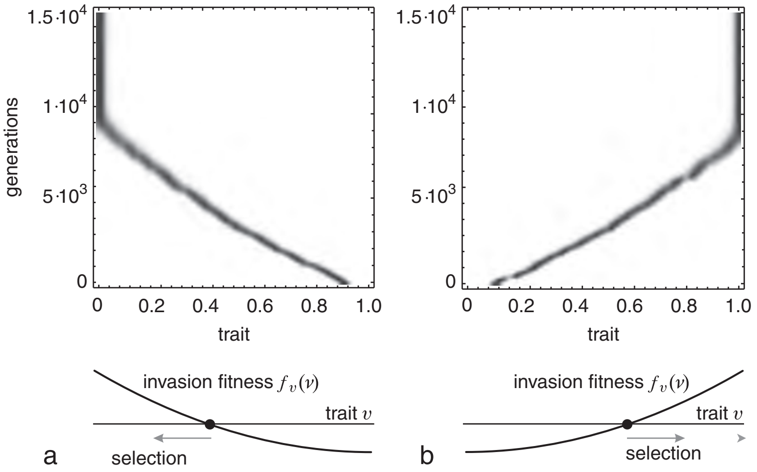

Figure 5.1 Dynamics in the continuous snowdrift game in the absence of singular traits. Simulation results for the trait distribution in the population over time (top row) and schematic illustration of the fitness profile in the population (bottom row). The benefit and cost functions are quadratic, $B(u)=b_2u^2+b_1u$, $C(u)=c_2u^2+c_1u$, such that $C(u)$, $B(u)$ are saturating and strictly increasing over the trait interval [0,1]. **a** The selection gradient is always negative, $D(u)<0$, and evolution always favors less cooperative individuals until cooperation vanishes. The qualitative features of the invasion fitness $f_u(v)$ do not change as u changes over time. **b** Counterpart to **a**: $D(u)>0$ always holds and evolution selects more cooperative individuals until the upper bound is reached. Parameters: $b_2=-1{:}5$, $b_1=7, c_2=-1$ and **a** $c_1=8$; **b** $c_1=2$.

keeps decreasing, $D(u)<0$, as in the continuous prisoner's dilemma, or it keeps increasing until $u_{\max}$ is reached. The latter refers to situations where the social dilemma is fully relaxed and cooperation merely evolves as a by-product (Connor, 1996). Both cases are possible in continuous snowdrift games (see Figure 5.1).

The Origin of Cooperators and Defectors

The dynamics of cooperation become more interesting if the continuous snowdrift game admits singular traits. A singular trait $u^\star$ can be convergent stable such that traits in the vicinity of $u^\star$ converge to $u^\star$ (see Figure 5.2a and b), or unstable and traits near $u^\star$ evolve away (see Figure 5.2c). Interestingly, convergent stability of $u^\star$ does not necessarily imply that $u^\star$ represents

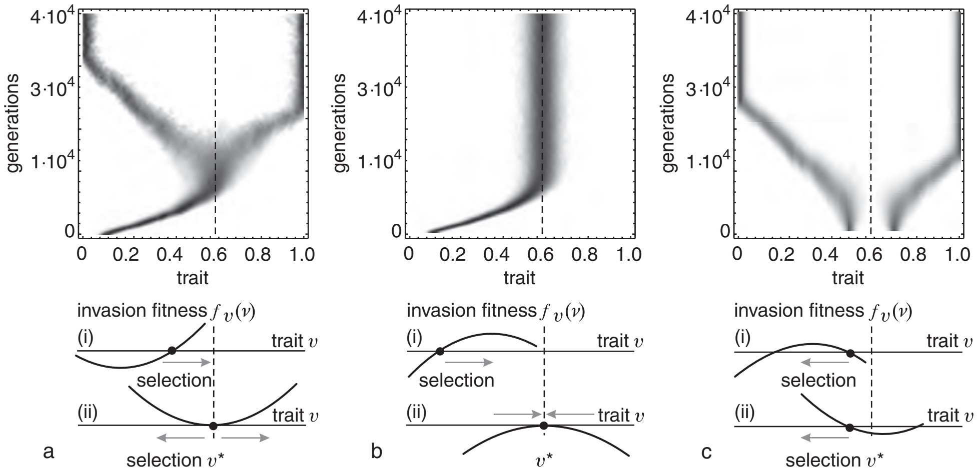

Figure 5.2 Dynamics in the continuous snowdrift game in the presence of a unique singular trait $u^\star$. Simulation results for the trait distribution in the population over time (top row) and schematic illustration of the fitness profile in the population (bottom row). $u^\star$ is marked by a vertical dashed line. As in Figure 5.1, the benefit and cost functions are quadratic, saturating and strictly increasing in [0, 1]. **a** *Evolutionary branching*—the singular strategy is convergent stable and the trait distribution approaches $u^\star$ but it is not evolutionarily stable and the population branches into two distinct phenotypic clusters. Evolution selects individuals with higher fitness [bottom panel (i)], which in turn changes the profile of the invasion fitness $f_u(v)$ such that the fitness minimum catches up at $u^\star$ [bottom panel (ii)] and mutants with both higher and lower v can invade. **b** *Evolutionary stability*—the singular strategy is not only convergent stable but also evolutionarily stable. As the population converges to $u^\star$ [bottom panel (i)] the profile of $f_u(v)$ changes and at $u^\star$ the trait catches up with the maximum of $f_u(v)$ [bottom panel (ii)] and no mutants are able to invade. **c** *Evolutionary repellor*—the singular strategy is an evolutionary repellor such that the traits evolve away from $u^\star$. Two separate simulation runs are shown: when starting below $u^\star$ cooperation disappears but if initial cooperative contributions are sufficiently high they keep increasing until the maximum is reached. In this case it is irrelevant whether $u^\star$ is evolutionarily stable [bottom panel (i)] or an evolutionary branching point [bottom panel (ii)] because evolution never reaches $u^\star$. Parameters: **a** $b_2=-1.4$, $b_1=6$, $c_2=-1.6$, $c_1=4.56$; **b** $b_2=-1.5$, $b_1=7$, $c_2=-1$, $c_1=4.6$; **c** $b_2=-0.5$, $b_1=3.4$, $c_2=-1.5$, $c_1=4$.

an evolutionary end state because $u^\star$ either represents a maximum or a minimum of the invasion fitness.[2] If it is a maximum, then $u^\star$ is not only convergent stable but also evolutionarily stable and $u^\star$ indeed denotes stable intermediate degrees of cooperation (see Figure 5.2b). If, however, $u^\star$ denotes a fitness minimum, then both, more *and* less cooperative mutants can invade. In this case $u^\star$ is called an evolutionary branching point and the population undergoes a spontaneous division into two distinct trait groups of cooperators and defectors (see Figure 5.2a). Thus, the evolutionary dynamics recovers the original snowdrift game discussed above. The continuous snowdrift game therefore suggests an evolutionary pathway for social diversification and for the origin of cooperators and defectors (Doebeli, Hauert, and Killingback 2010). All scenarios can be further explored using the *EvoLudo* (Hauert 2012), a growing collection of interactive tutorials on evolutionary dynamics.

Two Tragedies

Social dilemmas potentially occur whenever individuals supply a public resource, such as in the case of antibiotic resistance (Neu 1992), or whenever individuals consume a public resource, such as in Hardin's *Tragedy of the Commons* (Hardin 1968). Individual interests cause public resources to become overexploited. In the context of humans, this is hardly surprising—Aristotle (384–322 BC) already drew the same conclusion: "That which is common to the greatest number has the least care bestowed upon it." The continuous snowdrift game serves as a model of social dilemmas and may equally apply to communal enterprises in humans. However, the spontaneous separation into coexisting cooperators and defectors could additionally raise a *Tragedy of the Commune* (Doebeli, Hauert, and Killingback 2004), which states that evolution may not favor egalitarian contributions to the common good but instead promote highly asymmetric commitments. However, differences in cooperative contributions bear a formidable risk for escalating conflicts based on the accepted notion of fairness.

Spatial Games

According to the replicator equation, Eq. (1), cooperators are doomed and disappear in the prisoner's dilemma in the absence of supporting mechanisms, whereas in the snowdrift game coexistence of cooperators and defectors is expected. These predictions are based on the assumption that individuals randomly interact with other members of the population. This is a convenient assumption because it admits a full analysis. However, more realistic scenarios should take spatial extension and local interactions into account. In order to model this, individuals are arranged on a rectangular lattice and each individual interacts only with neighbors on its four adjacent sites. The population is then updated according to a spatial analogue of the replicator equation: first, a focal individual is randomly selected and its payoff, f_f, is determined through interactions with all its neighbors. Second, a neighbor of the focal individual is randomly chosen and its payoff, f_n, is determined in the same way. Third, the focal individual adopts the strategy of the neighbor with a probability proportional to the payoff difference, provided that the neighbor performs better, and sticks to its own strategy otherwise. This procedure is repeated many times in order to determine the equilibrium frequency and configuration of cooperators and defectors. Note that for increasing population and neighborhood sizes, this microscopic update rule recovers the replicator equation (Traulsen, Claussen, and Hauert 2005). Unfortunately, the dynamics of spatial systems is no longer analytically accessible, and results are either based on a technique called pair approximation (Matsuda et al. 1992; van Baalen and Rand 1998; Szabó and Hauert 2002a), or, as in the following, on simulation data.

In the spatial prisoner's dilemma, cooperators are able to survive by forming clusters (Nowak and May 1992; Ohtsuki et al. 2006; Taylor, Day, and Wild 2007). Compact clusters increase interactions with other cooperators, while reducing exploitation by defectors . However, the clustering advantages are limited, and the equilibrium fraction of cooperators decreases when costs are increased or benefits are lowered (see Figure 5.3a). Eventually, cooperators are unable to survive and go extinct. Effects of spatial structure, and hence the characteristic features of spatial configurations, are most pronounced near the extinction threshold of cooperators (see Figure 5.3b).

Upon approaching the extinction threshold, the population exhibits interesting dynamical features as it undergoes a critical phase transition (Szabó & Hauert 2002b)—a well-studied phenomenon in statistical mechanics. Critical phase transitions are exciting for physicists but may not seem exceedingly important in biologically relevant scenarios. However, they do

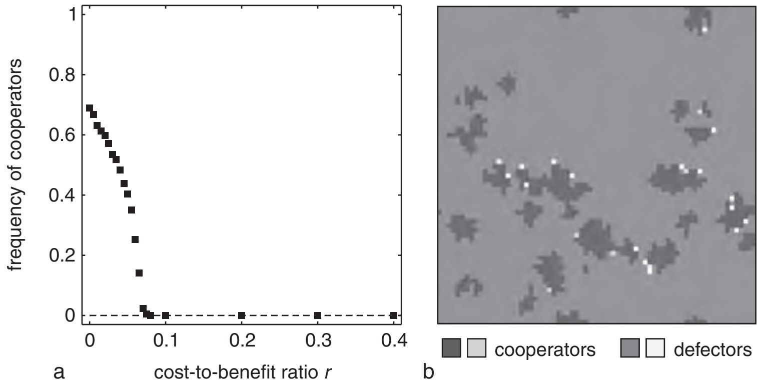

Figure 5.3 Spatial prisoner's dilemma on a square 100-x-100 lattice with four neighbors. **a** Equilibrium fraction of cooperators (solid squares) as a function of the cost-to-benefit ratio of mutual cooperation $r = c/(b - c)$. For small r cooperators persist but disappear for $r > r_c \approx 0.076$. In unstructured populations, cooperators cannot survive (dotted line). **b** Snapshot of a typical lattice configuration near the extinction threshold r_c. Spatial clustering enables cooperators to persist through more frequent interactions with other cooperators while reducing exploitation by defectors.

have substantial implications with far reaching consequences. For example, small changes in the costs or benefits can have disastrous effects on the equilibrium state of the population. Figure 5.3a illustrates that variations in the cost-benefit ratio r near the extinction threshold of cooperators result in big changes in their equilibrium frequency. Moreover, for populations that are prone to extinction, this indicates intrinsic difficulties for the empirical assessment of the current state because spatial and temporal variation increases when approaching the critical threshold.

Based on the results of the prisoner's dilemma in spatially extended settings, it has become widely accepted that spatial extension with limited local interactions is beneficial for cooperation. However, this does not necessarily apply to social dilemmas in general (Hauert and Doebeli 2004; Hauert 2006). In particular, in the spatial snowdrift game, the equilibrium proportion of cooperators tends to be lower than in unstructured settings with random interactions (see Figure 5.4a). Only for very low costs or high benefits does spatial structure support cooperation, but for most values cooperation is reduced and even gets eliminated altogether if costs are high or benefits are low.

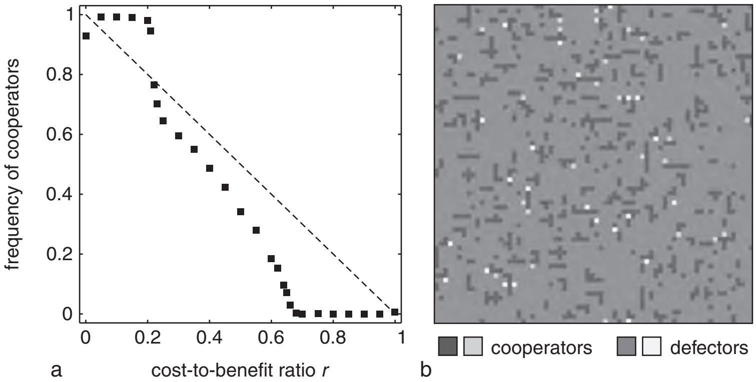

Figure 5.4 Spatial snowdrift game on a square 100-x-100 lattice with four neighbors. **a** Equilibrium fraction of cooperators (solid squares) as a function of the cost-to-benefit ratio of mutual cooperation $r = c/(2b - c)$. In unstructured populations, cooperators and defectors coexist (dotted line). With the exception of small r, spatial structure inhibits cooperation and for $r > r_c \approx 0.68$ cooperators even disappear. **b** Snapshot of a typical lattice configuration near the extinction threshold r_c. The equilibrium fraction of cooperators lies around 20% as compared to 40% cooperation in the absence of spatial structure.

The fact that in the snowdrift game the best option of one individual depends on the opponent's behavior, such that it is best to choose a strategy that is different from the opponent, often prevents cooperators from forming compact clusters as in the spatial prisoner's dilemma. Instead of minimizing the boundary between cooperators and defectors to avoid exploitation, the characteristics of the snowdrift game tend to maximize this boundary, which results in dendritic or filament-like cluster shapes. These cluster shapes become most apparent near the extinction threshold of cooperators (see Figure 5.4b). An intuitive approximation of the extinction threshold is obtained by considering the payoff of a single isolated cooperator in the spatial snowdrift game. As soon as the cooperator's payoff drops below the payoff of its defecting neighbors it perishes. Note, however, that this scenario underestimates the actual extinction threshold because of larger patches of cooperators. On average, the filament-like structures generate an advantage for defectors because of increased exploitation along the fractal-like boundary between cooperators and defectors. This results in an overall reduction of cooperators when compared to unstructured populations.

The *EvoLudo* site (Hauert 2012) encourages further interactive explorations and comparisons of the fascinating spatiotemporal dynamics in different types of spatial games.

Conclusions

The most prominent mathematical model to study the evolution of cooperation is the prisoner's dilemma. Only more recently has the snowdrift game attracted increasing attention as a viable and biologically interesting alternative for modeling cooperation dynamics. For example, *RNA* phages engage in prisoner's dilemma interactions in cells (Turner and Chao 1999), but selection alters the payoff structure, leading to the stable coexistence of cooperating and defecting types in a snowdrift game (Turner and Chao 2003). Unfortunately, differentiating between the two games can be challenging in real populations because the determination of payoffs is notoriously difficult. For example, predator inspection in sticklebacks is an often-cited application of the prisoner's dilemma (Milinski 1987). Sophisticated experimental setups confirmed the payoff ranking for three out of the four possible behavioral outcomes (Milinski et al. 1997). However, only the missing ranking of the payoff for mutual defection would enable one to discriminate between the prisoner's dilemma and snowdrift games. Other well-known examples of potential snowdrift games include alarm calls in meerkats (Clutton-Brock et al. 1999), and fighting in large ungulates (Wilkinson and Shank 1977). Cooperation is ubiquitous in meerkats, whereas serious escalations of fights seem to be common in musk ox. Because the costs of alarm calls are small, whereas the costs of forgoing reproduction are high, both observations are in agreement with the spatial snowdrift game, which promotes cooperation for low cost-to-benefit ratios but suggests more frequent escalations for high ratios of cost-to-benefit (Hauert and Doebeli 2004).

The significance and scientific value of game theoretical models for understanding the evolution of cooperation does not primarily lie in their predictive power for particular applications to specific scenarios. Instead, these games represent a conceptual framework to highlight and to emphasize the rich and often-unexpected dynamics generated by simple models that capture the essence of biologically and socially relevant interaction patterns. For example, the snowdrift game demonstrates that spatial structure may not be as universally beneficial for cooperation as previously thought, based on results of the spatial prisoner's dilemma. Similarly, evolutionary branching in the continuous snowdrift game illustrates that distinct behavioral traits may easily originate in a continuum of behavioral options. Game theoretical results delineate evolutionary constraints that are critical in resolving the problem of cooperation.

In theoretical and evolutionary biology, the ambiguity and limited consensus on the usage of the terms "cooperation," "altruism" and "helping" can cause some disputes but generally pose less severe problems than in the interdisciplinary discourse of this book. In all theoretical investigations, the starting point as well as the concluding results are unambiguous mathematical statements. Misunderstandings are readily averted by resorting to the mathematics. Instead, the core challenge lies in the proper translation of biological questions into tractable mathematical models as well as in interpreting the mathematical results in meaningful biological terms.

Notes

1. The selection gradient $D(u)$ denotes the slope of the invasion fitness $f_u(v)$ at $v=u$ and is defined as $D(u)=\partial f_u(v)/\partial v\big|_{v=u}=B'(2u)-C'(u)$ where the primes indicate the derivatives with respect to u (for details see Doebeli, Hauert, and Killingback 2004).
2. $u^\star$ is convergent stable if $dD(u)/du\big|_{u=u^\star}=B''(2u^\star)-C''(u^\star)<0$ and evolutionarily stable if the invasion fitness $f_u\cdot(v)$ has a fitness maximum at $v=u^\star$, i.e. if the second derivative $\partial^2 f_{u^\star}(v)/\partial v^2\;\big|_{v=u^\star}=2B''\,(2u^\star)-C''(u^\star)<0$ is negative. Hence the two stability criteria are not identical.

References

Axelrod, R., and W. D. Hamilton. 1981. "The Evolution of Cooperation." *Science* 211: 1390–96.

Clutton-Brock, T. H., M. J. O'Riain, P. N. M. Brotherton, D. Gaynor, R. Kansky, A. S. Griffin, and M. Manser. 1999. "Selfish Sentinels in Cooperative Mammals." *Science* 284: 1640–44.

Connor, R. C. 1996. "Partner Preferences in By-Product Mutualisms and the Case of Predator Inspection in Fish." *Animal Behaviour* 51: 451–54.

Darwin, C. 1859. *The Origin of Species*. Cambridge, MA: Harvard University Press. Reprinted in 1964.

Dawes, R. M. 1980. "Social Dilemmas." *Annual Review of Psychology* 31: 169–93.

Dieckmann, U., and R. Law. 1996. "The Dynamical Theory of Co-Evolution: A Derivation from Stochastic Ecological Processes." *Journal of Mathematical Biology* 34: 579–612.

Doebeli, M., and C. Hauert. 2005. "Models of Cooperation Based on the Prisoner's Dilemma and the Snowdrift Game." *Ecology Letters* 8: 748–66.

Doebeli, M., C. Hauert, and T. Killingback. 2004. "The Evolutionary Origin of Cooperators and Defectors." *Science* 306: 859–62.

Flood, M. 1958. "Some Experimental Games." *Management Science* 5: 5–26.

Geritz, S. A. H., E. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. "Evolutionarily Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree." *Evolutionary Ecology* 12: 35–57.

Greig, D., and M. Travisano. 2004. "The Prisoner's Dilemma and Polymorphism in Yeast SUC Genes." *Biology Letters* 271: S25–26.

Hamilton, W. D. 1964. "The Genetical Evolution of Social Behaviour." *Journal of Theoretical Biology* 7: 1–16.

———. 1971. "The Geometry of the Selfish Herd." *Journal of Theoretical Biology* 31: 295–311.

Hardin, G. 1968. "The Tragedy of the Commons." *Science* 162: 1243–48.

Hauert, C. 2006. "Spatial Effects in Social Dilemmas." *Journal of Theoretical Biology* 240: 627–36.

———. 2012. *EvoLudo: Interactive Tutorials on Evolutionary Game Theory,* http://www.evoludo.org.

Hauert, C., S. De Monte, J. Hofbauer, and K. Sigmund. 2002. "Volunteering as Red Queen Mechanism for Cooperation in Public Goods Games." *Science* 296: 1129–32.

Hauert, C., and M. Doebeli. 2004. "Spatial Structure often Inhibits the Evolution of Cooperation in the Snowdrift Game." *Nature* 428: 643–46.

Hauert, C., F. Michor, M. Nowak, and M. Doebeli. 2006. "Synergy and Discounting of Cooperation in Social Dilemmas." *Journal of Theoretical Biology* 239: 195–202.

Hauert, C., A. Traulsen, H. Brandt, M. Nowak, and K. Sigmund. 2007. "Via Freedom to Coercion: The Emergence of Costly Punishment." *Science* 316: 1905–7.

Hofbauer, J., and K. Sigmund. 1998. *Evolutionary Games and Population Dynamics.* Cambridge, MA: Cambridge University Press.

Killinback, T., M. Doebeli, and C. Hauert. 2010. "Diversity of Cooperation in the Tragedy of the Commons." *Biological Theory* 5/1: 3–6.

Magurran, A. E., and A. Higham. 1988. "Information Transfer Across Fish Shoals under Predator Threat." *Ethology* 78: 153–58.

Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. 1992. "Statistical Mechanics of Populations." *Progress of Theoretical Physics* 88(6): 1035–49.

Maynard-Smith, J., and G. Price. 1973. "The Logic of Animal Conflict." *Nature* 246: 15–18.

Maynard-Smith, J., and E. Szathmáry. 1995. *The Major Transitions in Evolution.* Oxford: W. H. Freeman and Co.

Metz, J. A. J., S. A. H. Geritz, G. Meszena, F. J. A. Jacobs, and J. S. van Heerwaarden. 1996. "Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction." In *Stochastic and Spatial Structures of Dynamical Systems,* ed. S. J. van Strien and S. M. Verduyn Lunel. Amsterdam: North Holland, 183–231.

Milinski, M. 1987. "Tit for Tat in Sticklebacks and the Evolution of Cooperation." *Nature* 325: 433–35.

Milinski, M., J. H. Lüthi, R. Eggler, and G. A. Parker. 1997. "Cooperation under Predation Risk: Experiments on Costs and Benefits." *Proceedings of the Royal Society B* 264: 831–37.

Milinski, M., D. Semmann, H. Krambeck, and M. Marotzke. 2006. "Stabilizing the Earth's Climate Is Not a Losing Game: Supporting Evidence from Public Goods Experiments." *Proceedings of the National Academy of Sciences of the USA* 103: 3994–98.

Neu, H. C. 1992. "The Crisis in Antibiotic Resistance." *Science* 257: 1064–73.

Nowak, M. A., and R. M. May. 1992. "Evolutionary Games and Spatial Chaos." *Nature* 359: 826–29.

Nowak, M. A., and K. Sigmund. 1998. "Evolution of Indirect Reciprocity by Image Scoring." *Nature* 393: 573–77.

Ohtsuki, H., C. Hauert, E. Lieberman, and M. Nowak. 2006. "A Simple Rule for the Evolution of Cooperation on Graphs and Social Networks." *Nature* 441: 502–5.

Pitcher, T. 1992. "Who Dares, Wins—The Function and Evolution of Predator Inspection Behavior in Shoaling Fish." *Netherlands Journal of Zoology* 42: 371–91.

Rainey, P. B., and K. Rainey. 2003. "Evolution of Cooperation and Conflict in Experimental Bacterial Populations." *Nature* 425: 72–74.

Sigmund, K., C. Hauert, and M. Nowak. 2001. "Reward and Punishment." *Proceedings of the National Academy of Sciences of the USA* 98: 10757–62.

Sugden, R. 1986. *The Economics of Rights, Cooperation and Welfare.* Oxford and New York: Blackwell.

Szabó, G., and C. Hauert. 2002a. "Evolutionary Prisoner's Dilemma with Optional Participation." *Physical Review E* 66: 062903.

———. 2002b. "Phase Transitions and Volunteering in Spatial Public Goods Games." *Physical Review Letters* 89: 118101.

Taylor, P. D., T. Day, and G. Wild. 2007. "Evolution of Cooperation in a Finite Homogeneous Graph." *Nature* 447: 469–72.

Traulsen, A., J. C. Claussen, and C. Hauert. 2005. "Coevolutionary Dynamics: From Finite to Infinite Populations." *Physical Review Letters* 95: 238701.

Trivers, R. L. 1971. "The Evolution of Reciprocal Altruism." *Quarterly Review of Biology* 46: 35–57.

Turner, P. E., and L. Chao. 1999. "Prisoner's Dilemma in an RNA Virus." *Nature* 398: 441–43.

———. 2003. "Escape from Prisoner's Dilemma in RNA phage Φ6." *American Naturalist* 161: 497–505.

van Baalen, M., and D. A. Rand. 1998. "The Unit of Selection in Viscous Populations and the Evolution of Altruism." *Journal of Theoretical Biology* 193: 631–48.

von Neumann, J., and O. Morgenstern. 1944. *Theory of Games and Economic Behaviour.* Princeton, NJ: Princeton University Press.

Wilkinson, G. S., and C. C. Shank. 1977. "Rutting-Fight Mortality among Musk Oxen on Banks Island, Northwest Territories, Canada." *Animal Behaviour* 24: 756–58.

Yamagishi, T. 1986. "The Provision of a Sanctioning System as a Public Good." *Journal of Personality and Social Psychology* 51: 110–16.