International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-04-086**

The Dynamics of Public Goods

Christoph Hauert (hauert@zoology.ubc.ca)
Nina Haiden (e9525868@fbma.tuwien.ac.at)
Karl Sigmund (karl.sigmund@univie.ac.at)

Approved by

Ulf Dieckmann
Program Leader, ADN

December 2004

IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 97

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is collected in the IIASA Studies in Adaptive Dynamics series.

No. 1 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS: *Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction.* IIASA Working Paper WP-95-099 (1995). van Strien SJ, Verduyn Lunel SM (eds): Stochastic and Spatial Structures of Dynamical Systems, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen), North Holland, Amsterdam, pp. 183-231 (1996).

No. 2 Dieckmann U, Law R: *The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes.* IIASA Working Paper WP-96-001 (1996). Journal of Mathematical Biology 34:579-612 (1996).

No. 3 Dieckmann U, Marrow P, Law R: *Evolutionary Cycling of Predator-Prey Interactions: Population Dynamics and the Red Queen.* IIASA Preprint (1995). Journal of Theoretical Biology 176:91-102 (1995).

No. 4 Marrow P, Dieckmann U, Law R: *Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective.* IIASA Working Paper WP-96-002 (1996). Journal of Mathematical Biology 34:556-578 (1996).

No. 5 Law R, Marrow P, Dieckmann U: *On Evolution under Asymmetric Competition.* IIASA Working Paper WP-96-003 (1996). Evolutionary Ecology 11:485-501 (1997).

No. 6 Metz JAJ, Mylius SD, Diekmann O: *When Does Evolution Optimize? On the Relation Between Types of Density Dependence and Evolutionarily Stable Life History Parameters.* IIASA Working Paper WP-96-004 (1996).

No. 7 Ferrière R, Gatto M: *Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations.* Theoretical Population Biology 48:126-171 (1995).

No. 8 Ferrière R, Fox GA: *Chaos and Evolution.* IIASA Preprint (1996). Trends in Ecology and Evolution 10:480-485 (1995).

No. 9 Ferrière R, Michod RE: *The Evolution of Cooperation in Spatially Heterogeneous Populations.* IIASA Working Paper WP-96-029 (1996). The American Naturalist 147:692-717 (1996).

No. 10 van Dooren TJM, Metz JAJ: *Delayed Maturation in Temporally Structured Populations with Non-Equilibrium Dynamics.* IIASA Working Paper WP-96-070 (1996). Journal of Evolutionary Biology 11:41-62 (1998).

No. 11 Geritz SAH, Metz JAJ, Kisdi É, Meszéna G: *The Dynamics of Adaptation and Evolutionary Branching.* IIASA Working Paper WP-96-077 (1996). Physical Review Letters 78:2024-2027 (1997).

No. 12 Geritz SAH, Kisdi É, Meszéna G, Metz JAJ: *Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree.* IIASA Working Paper WP-96-114 (1996). Evolutionary Ecology 12:35-57 (1998).

No. 13 Heino M, Metz JAJ, Kaitala V: *Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: The Crucial Role of Dimensionality of Feedback Environment.* IIASA Working Paper WP-96-126 (1996). Philosophical Transactions of the Royal Society of London Series B 352:1647-1655 (1997).

No. 14 Dieckmann U: *Can Adaptive Dynamics Invade?* IIASA Working Paper WP-96-152 (1996). Trends in Ecology and Evolution 12:128-131 (1997).

No. 15 Meszéna G, Czibula I, Geritz SAH: *Adaptive Dynamics in a 2-Patch Environment: A Simple Model for Allopatric and Parapatric Speciation.* IIASA Interim Report IR-97-001 (1997). Journal of Biological Systems 5:265-284 (1997).

No. 16 Heino M, Metz JAJ, Kaitala V: *The Enigma of Frequency-Dependent Selection.* IIASA Interim Report IR-97-061 (1997). Trends in Ecology and Evolution 13:367-370 (1998).

No. 17 Heino M: *Management of Evolving Fish Stocks.* IIASA Interim Report IR-97-062 (1997). Canadian Journal of Fisheries and Aquatic Sciences 55:1971-1982 (1998).

No. 18 Heino M: *Evolution of Mixed Reproductive Strategies in Simple Life-History Models.* IIASA Interim Report IR-97-063 (1997).

No. 19 Geritz SAH, van der Meijden E, Metz JAJ: *Evolutionary Dynamics of Seed Size and Seedling Competitive Ability.* IIASA Interim Report IR-97-071 (1997). Theoretical Population Biology 55:324-343 (1999).

No. 20 Galis F, Metz JAJ: *Why Are There So Many Cichlid Species? On the Interplay of Speciation and Adaptive Radiation.* IIASA Interim Report IR-97-072 (1997). Trends in Ecology and Evolution 13:1-2 (1998).

No. 21 Boerlijst MC, Nowak MA, Sigmund K: *Equal Pay for all Prisoners/ The Logic of Contrition.* IIASA Interim Report IR-97-073 (1997). American Mathematical Society Monthly 104:303-307 (1997). Journal of Theoretical Biology 185:281-293 (1997).

No. 22 Law R, Dieckmann U: *Symbiosis Without Mutualism and the Merger of Lineages in Evolution.* IIASA Interim Report IR-97-074 (1997). Proceedings of the Royal Society of London Series B 265:1245-1253 (1998).

No. 23 Klinkhamer PGL, de Jong TJ, Metz JAJ: *Sex and Size in Cosexual Plants.* IIASA Interim Report IR-97-078 (1997). Trends in Ecology and Evolution 12:260-265 (1997).

No. 24 Fontana W, Schuster P: *Shaping Space: The Possible and the Attainable in RNA Genotype-Phenotype Mapping.* IIASA Interim Report IR-98-004 (1998). Journal of Theoretical Biology 194:491-515 (1998).

No. 25 Kisdi É, Geritz SAH: *Adaptive Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment.* IIASA Interim Report IR-98-038 (1998). Evolution 53:993-1008 (1999).

No. 26 Fontana W, Schuster P: *Continuity in Evolution: On the Nature of Transitions.* IIASA Interim Report IR-98-039 (1998). Science 280:1451-1455 (1998).

No. 27 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity by Image Scoring/ The Dynamics of Indirect Reciprocity.* IIASA Interim Report IR-98-040 (1998). Nature 393:573-577 (1998). Journal of Theoretical Biology 194:561-574 (1998).

No. 28 Kisdi É: *Evolutionary Branching Under Asymmetric Competition.* IIASA Interim Report IR-98-045 (1998). Journal of Theoretical Biology 197:149-162 (1999).

No. 29 Berger U: *Best Response Adaptation for Role Games.* IIASA Interim Report IR-98-086 (1998).

No. 30 van Dooren TJM: *The Evolutionary Ecology of Dominance-Recessivity.* IIASA Interim Report IR-98-096 (1998). Journal of Theoretical Biology 198:519-532 (1999).

No. 31 Dieckmann U, O'Hara B, Weisser W: *The Evolutionary Ecology of Dispersal.* IIASA Interim Report IR-98-108 (1998). Trends in Ecology and Evolution 14:88-90 (1999).

No. 32 Sigmund K: *Complex Adaptive Systems and the Evolution of Reciprocation.* IIASA Interim Report IR-98-100 (1998). Ecosystems 1:444-448 (1998).

No. 33 Posch M, Pichler A, Sigmund K: *The Efficiency of Adapting Aspiration Levels.* IIASA Interim Report IR-98-103 (1998). Proceedings of the Royal Society London Series B 266:1427-1435 (1999).

No. 34 Mathias A, Kisdi É: *Evolutionary Branching and Coexistence of Germination Strategies.* IIASA Interim Report IR-99-014 (1999).

No. 35 Dieckmann U, Doebeli M: *On the Origin of Species by Sympatric Speciation.* IIASA Interim Report IR-99-013 (1999). Nature 400:354-357 (1999).

No. 36 Metz JAJ, Gyllenberg M: *How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies.* IIASA Interim Report IR-99-019 (1999). Proceedings of the Royal Society of London Series B 268:499-508 (2001).

No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations.* IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).

No. 38 Meszéna G, Metz JAJ: *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality.* IIASA Interim Report IR-99-045 (1999).

No. 39 Kisdi É, Geritz SAH: *Evolutionary Branching and Sympatric Speciation in Diploid Populations.* IIASA Interim Report IR-99-048 (1999).

No. 40 Ylikarjula J, Heino M, Dieckmann U: *Ecology and Adaptation of Stunted Growth in Fish.* IIASA Interim Report IR-99-050 (1999). Evolutionary Ecology 13:433-453 (1999).

No. 41 Nowak MA, Sigmund K: *Games on Grids.* IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).

No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation.* IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).

No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction.* IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).

No. 44 Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics.* IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).

No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity.* IIASA Interim Report IR-00-035 (2000). Journal of Evolutionary Biology 16:143-153 (2003).

No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions.* IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).

No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model.* IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).

No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations.* IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).

No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable.* IIASA Interim Report IR-00-048 (2000). Evolution 54: 1899-1914 (2000).

No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game.* IIASA Interim Report IR-00-57 (2000). Science 289:1773-1775 (2000).

No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling.* IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).

No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola.* IIASA Interim Report IR-01-018 (2001). Oikos 94:525-532 (2001).

No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames.* IIASA Interim Report IR-01-031 (2001). Proceedings of the National Academy of Sciences of the USA 98:10757-10762 (2001).

No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games.* IIASA Interim Report IR-01-036 (2001).

No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models.* IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): Dispersal, Oxford University Press, pp. 57-79 (2001).

No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism.* IIASA Interim Report IR-01-053 (2001). The American Naturalist 158: 109-123 (2001).

No. 57 Claessen D, Dieckmann U: *Ontogenetic Niche Shifts and Evolutionary Branching in Size-Structured Populations.* IIASA Interim Report IR-01-056 (2001). Evolutionary Ecology Research 4:189-217 (2002).

No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes.* IIASA Interim Report IR-01-058 (2001).

No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interacations.* IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).

No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes.* IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).

No. 61 Sabelis MW, Metz JAJ: *Perspectives for Virulence Management: Relating Theory to Experiment.* IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).

No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations .* IIASA Interim Report IR-02-024 (2002). Proceedings of the Royal Society of London Series B 269:1177-1186 (2002).

No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study.* IIASA Interim Report IR-02-013 (2002). Theoretical Population Biology 61:197-213 (2002).

No. 64 Hauert C, De Monte S, Hofbauer J, Sigmund K: *Volunteering as Red Queen Mechanism for Co-operation in Public Goods Games.* IIASA Interim Report IR-02-041 (2002). Science 296:1129-1132 (2002).

No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition.* IIASA Interim Report IR-02-053 (2002). Evolution 56:1081-1090 (2002).

No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics.* IIASA Interim Report IR-02-054 (2002). Theoretical Population Biology 62:365-374 (2002).

No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation.* IIASA Interim Report IR-02-058 (2002). Genetical Research 80:31-46 (2002).

No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection.* IIASA Interim Report IR-02-062 (2002). Amer. Natur. 160:661-682 (2002).

No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients.* IIASA Interim Report IR-02-079 (2002). Nature 421:259-264 (2003).

No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model.* IIASA Interim Report IR-02-078 (2002). SIAM Journal on Applied Mathematics 63:1378-1391 (2003).

No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations.* IIASA Interim Report IR-03-006 (2003). Evolution 57:1-17 (2003).

No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality.* IIASA Interim Report IR-03-004 (2003). Proceedings of the Royal Society of London Series B 270:713-721 (2003).

No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation.* IIASA Interim Report IR-03-008 (2003). Evolutionary Ecology Research 5:239-257 (2003).

No. 74 Mizera F, Meszéna G: *Spatial Niche Packing, Character Displacement and Adaptive Speciation Along an Environmental Gradient.* IIASA Interim Report IR-03-062 (2003). Evolutionary Ecology Research 5: 363-382 (2003).

No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles.* IIASA Interim Report IR-03-075 (2003). Journal of Mathematical Biology 47: 569-580 (2003).

No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics.* IIASA Interim Report IR-03-078 (2003). Bulletin of the American Mathematical Society 40: 479-519 (2003).

No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation.* IIASA Interim Report IR-03-058 (2003). Proceedings of the Royal Society of London Series B-Biological Sciences, 271: 415-423 (2004).

No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes.* IIASA Interim Report IR-03-028 (2003). Theoretical Population Biology 63:309-338 (2003).

No. 79 van Doorn G, Dieckmann U, Weissing FJ: *Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation.* IIASA Interim Report IR-04-003 (2004). American Naturalist 163: 709-725 (2004).

No. 80 Egas M, Dieckmann U, Sabelis MW: *Evolution Restricts the Coexistence of Specialists and Generalists - the Role of Trade-off Structure.* IIASA Interim Report IR-04-004 (2004).

No. 81 Ernande B, Dieckmann U: *The Evolution of Phenotypic Plasticity in Spatially Structured Environments: Implications of Intraspecific Competition, Plasticity Costs, and Environmental Characteristics.* IIASA Interim Report IR-04-006 (2004). Journal of Evolutionary Biology 17 (3): 613-628 (2004).

No. 82 Cressman R, Hofbauer J: *Measure Dynamics on a One-Dimensional Continuous Trait Space: Theoretical Foundations for Adaptive Dynamics.* IIASA Interim Report IR-04-016 (2004).

No. 83 Cressman R: *Dynamic Stability of the Replicator Equation with Continuous Strategy Space.* IIASA Interim Report IR-04-017 (2004).

No. 84 Ravigné V, Olivieri I, Dieckmann U: *Implications of Habitat Choice for Protected Polymorphisms.* IIASA Interim Report IR-04-005 (2004). Evolutionary Ecology Research 6: 125-145 (2004).

No. 85 Nowak MA, Sigmund K: *Evolutionary Dynamics of Biological Games.* IIASA Interim Report IR-04-013 (2004). Science 303: 793-799 (2004).

No. 86 Vukics A, Asbóth J, Meszéna G: *Speciation in Multidimensional Evolutionary Space.* IIASA Interim Report IR-04-028 (2004). Physical Review E 68 4 (2003).

No. 87 de Mazancourt C, Dieckmann U: *Trade-off Geometries and Frequency-dependent Selection.* IIASA Interim Report IR-04-039 (2004).

No. 88 Cadet CR, Metz JAJ, Klinkhamer PGL: *Size and the Not-So-Single Sex: disentangling the effects of size on sex allocation.* IIASA Interim Report IR-04-084 (2004). American Naturalist, 164: 779-792 (2004).

No. 89 Rueffler C, van Dooren TJM, Metz JAJ: *Adaptive Walks on Changing Landscapes: Levins' Approach Extended.* IIASA Interim Report IR-04-083 (2004). Theoretical Population Biology, 65: 165-178 (2004).

No. 90 de Mazancourt C, Loreau M, Dieckmann U: *Understanding Mutualism When There is Adaptation to the Partner.* IIASA Interim Report IR-05-016 (2005).

No. 91 Dieckmann U, Doebeli M: *Pluralism in Evolutionary Theory.* IIASA Interim Report IR-05-017 (2005).

No. 92 Doebeli M, Dieckmann U, Metz JAJ, Tautz D: *What We Have Also Learned.* IIASA Interim Report IR-05-018 (2005).

No. 93 Egas M, Sabelis MW, Dieckmann U: *Evolution of Specialization and Ecological Character Displacement of Herbivores Along a Gradient of Plant Quality.* IIASA Interim Report IR-05-019 (2005).

No. 94 Le Galliard J, Ferrière R, Dieckmann U: *Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility.* IIASA Interim Report IR-05-020 (2005).

No. 95 Doebeli M, Dieckmann U: *Adaptive Dynamics as a Mathematical Tool for Studying the Ecology of Speciation Processes.* IIASA Interim Report IR-05-022 (2005).

No. 96 Brandt H, Sigmund K: *The logic of reprobation: assessment and action rules for indirect reciprocity.* IIASA Interim Report IR-04-085 (2004). Journal of Theoretical Biology 231: 475-486 (2004).

No. 97 Hauert C, Haiden N, Sigmund K: *The dynamics of public goods.* IIASA Interim Report IR-04-086 (2004). Discrete and Continuous Dynamical Systems - Series B, 4:575-587 (2004).

Issues of the IIASA Studies in Adaptive Dynamics series can be obtained at www.iiasa.ac.at/Research/ADN/Series.html or by writing to adn@iiasa.ac.at.

Contents

THE DYNAMICS OF PUBLIC GOODS

CHRISTOPH HAUERT

Departments of Zoology and Mathematics
University of British Columbia
Vancouver, Canada V6T 1Z4

NINA HAIDEN

Department of Mathematics
University of Vienna
Strudlhofgasse 4, A 1090 Vienna, Austria

KARL SIGMUND

Department of Mathematics
University of Vienna
Strudlhofgasse 4, A 1090 Vienna, Austria

International Institute for Applied Systems Analysis (IIASA)
A 2361 Laxenburg, Austria

ABSTRACT. We analyse the replicator equation for two games closely related with the social dilemma occurring in public goods situations. In one case, players can punish defectors in their group. In the other case, they can choose not to take part in the game. In both cases, interactions are not pairwise and payoffs non linear. Nevertheless, the qualitative dynamics can be fully analysed. The games offer potential solutions for the problem of the emergence of cooperation in sizeable groups of non-related individuals – a basic question in evolutionary biology and economics.

1. **Introduction.** The replicator equation describes important dynamics occurring in many parts of biomathematics. Let us assume that a (ideally, infinitely large) population consists of n distinct types, and that the frequency of type i at time t is given by $x_i(t)$. The state of the population is thus described by appoint x in the unit simplex S_n spanned by the standard basis vectors $\mathbf{e}_i$, i=1,...,n. If $F_i(x)$ describes the average payoff (or fitness, or reproductive success) of type i in a population whose composition is given by **x**, then the replicator equation postulates that

$$\dot{x}_i = x_i(F_i(x) - \overline{F}(x)) \tag{1}$$

where $\overline{F}(x) := \sum x_i F_i(x)$ is the average payoff within the population. The state space S_n as well as its boundary faces are left in variant by the dynamics.

This type of equation occurs in many problems in mathematical ecology, epidemiology, immunology, evolutionary biology and economics [11]. Most examples which have been analysed deal only with the case of linear functions $F_i(x) = \sum a_{ij} x_j$.

2000 Mathematics Subject Classification. 91A06, 91A10, 91A22, 92D25.

Keywords and phrases. Evolutionary game theory, public goods games, replicator dynamics.

This is a reasonable assumption if the interactions within the population are pairwise. However, important types of interactions occur in larger groups, and are described by non-linear terms.

In this paper we survey two such examples which are of great interest for the evolution of cooperation, an essential problem in biology and economics. They deal with public goods. Such public goods are crucial, indeed defining elements for every society: sheltering, foraging, hunting, or defense are often collective enterprises. In many such situations, it is possible that individuals profit from the public good without contributing to it in full measure. Such 'defectors' do better than cooperators within every group. Selection should therefore eliminate the cooperators, and the public good should vanish.

Economists, psychologists and students of animal behaviour have studied such situations in experiments with humans [4, 13, 3]. To give a simple example, each member of a group of six players (who do not know each other and will not meet again) is given ten dollars and offered the possibility to invest some part of the money in a common pool. The players are told that the experimenter will triple the total amount in the pool, and distribute it equally among all players, irrespective of their contributions. If all players contribute fully, each earns thirty dollars. But note that all contributors receive only half of their own investments. Hence players are tempted to withhold their contribution. But if all decline to contribute, there is no pool to share. Such a public goods game describes neatly the social dilemma caused by the discrepancy between individual and social welfare [2]. In reality, many players contribute; but experiments show that if the game is repeated for a few rounds, the contributions will decline and eventually stop.

More generally, we shall consider games where each individual in a group of N players has the option to cooperate or to defect. Cooperation means to contribute a certain amount c to the common pool. The sum of all contributions is multiplied by a certain factor r, and divided equally among all N players. If n_c of the players cooperate, then the payoff for a defector will be

$$P_d = rc\frac{n_c}{N}, \tag{2}$$

whereas the payoff for a cooperator will be

$$P_c = P_d - c \tag{3}$$

because the cooperator bears the burden of the contribution. It is obvious that the replicator dynamics implies that the frequency of cooperators converges to 0. This is also, of course, the prediction from classical game theory, which is based on the assumption that players are selfish individuals trying rationally to maximise their own income.

There have been many attempts to explain why, in spite of this result, collaboration prevails. In this mathematical survey, we only describe two approaches [15, 8, 7]. In the first part, we investigate the effect of punishing defectors, and in the second part, the effect of withdrawing altogether from such games. Both models lead to interesting replicator dynamics which can be fully analysed in spite of being based on non-linear payoff functions.

2. **Public Goods with Punishment.** There are two options for the public goods game. Option $\mathbf{e}_1$ contributes to the public good, whereas option $\mathbf{e}_2$ does not. In the public goods game with punishment, this decision is followed by a second round where players have the option to punish the defectors, or not. Option $\mathbf{f}_1$ consists

in punishing non-contributors, option $\mathbf{f}_2$ in not punishing them. We assume that each act of punishment reduces the payoff of the punished player by the amount β, but also reduces the payoff of the punishing player by an amount γ (with $\beta, \gamma > 0$). Thus, punishing is a costly activity: a selfish player should refrain from it. In the resulting game (first, contribute or not; then punish or not), there are four distinct strategies.

$G_1 = \mathbf{e}_1\mathbf{f}_1$: contributes and punishes, this is the social strategy.

$G_2 = \mathbf{e}_2\mathbf{f}_1$: is the paradoxical strategy which does not contribute, but punishes all co-players who do not contribute.

$G_3 = \mathbf{e}_2\mathbf{f}_2$: is the selfish strategy of players who neither contribute nor punish.

$G_4 = \mathbf{e}_1\mathbf{f}_2$: is the strategy of mild players who contribute, but do not punish.

All players receive as a result of the contributions of their $(N-1)$ co-players an average payoff

$$B = \frac{rc}{N}(N-1)(x_1 + x_4). \tag{4}$$

The costs arising from their own contribution (if any), their punishing activities and the fines incurred from the punishers result in a net average payoff P_i for type G_i, with

$$P_1 = B - c(1 - \frac{r}{N}) - (N-1)\gamma(x_2 + x_3) \tag{5}$$

$$P_2 = B - (N-1)\beta(x_1 + x_2) - (N-1)\gamma(x_2 + x_3) \tag{6}$$

$$P_3 = B - (N-1)\beta(x_1 + x_2) \tag{7}$$

$$P_4 = B - c(1 - \frac{r}{N}) \tag{8}$$

Since $P_1 + P_3 = P_2 + P_4$, the quotient $\frac{x_1 x_3}{x_2 x_4}$ denotes an invariant of motion and hence the sets

$$W_K = \{\mathbf{x} \in S_n : x_1 x_3 = K x_2 x_4\} \tag{9}$$

(with $K > 0$) provide a foliation of the state space S_4 into invariant manifolds (see figure 1).

It is thus sufficient to study the dynamics on the two-dimensional manifolds, which are saddle-like surfaces spanned by the edges $G_1 - G_2 - G_3 - G_4 - G_1$. There is no rest point in the interior of these surfaces. The flow on the edge G_1G_2 points towards G_1, and on the edges G_2G_3 as well as G_4G_3 it points towards G_3. The edge G_1G_4 consists of fixed points.

To make things interesting we shall always assume

$$\beta > \frac{c}{N-1}(1 - \frac{r}{N}) \tag{10}$$

which states that the total fine imposed on a non-cooperative player by its punishing co-players is higher than the net costs of contributing to the public goods. Then the point

$$Q =: (\frac{(N-r)c}{\beta N(N-1)}, 0, 0, 1 - \frac{(N-r)c}{\beta N(N-1)}) \tag{11}$$

lies on G_1G_4. The transversal eigenvalues of the points on the segment G_1Q are negative, and hence are saturated, i.e. Nash equilibria. The points between Q and G_4 are not. This yields the phase portrait in figure 2. It follows that all initial conditions lead either to G_3 or to the segment G_1Q. If we assume that random shocks occasionally perturb the system, we see that in the long run, the asocial equilibrium G_3 gets always established – just the same prediction as with classical game theory, conflicting with empirical evidence.

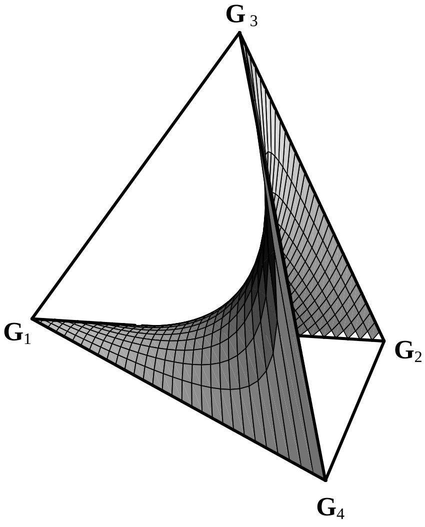

FIGURE 1. The Wright manifold: the invariant of motion $\frac{x_1x_3}{x_2x_4} = K$ foliates the state space S_4 into invariant manifolds W_K, shown here for $K = 1$.

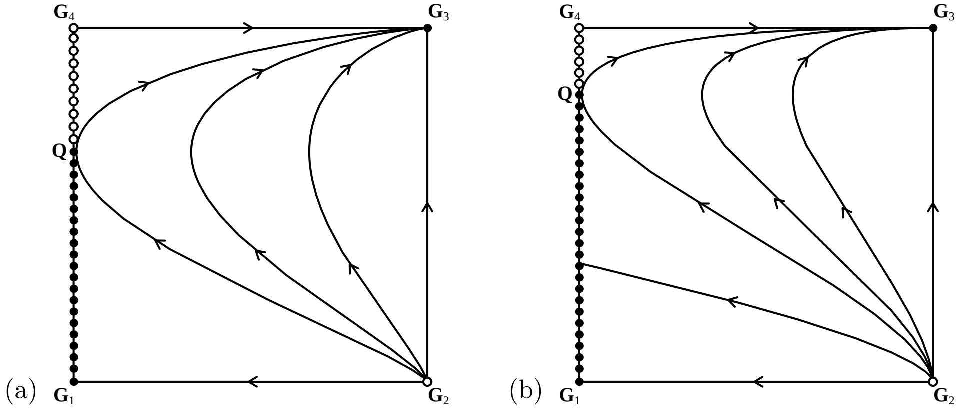

FIGURE 2. Replicator dynamics for public goods games with punishment on the invariant manifold W_K for $K = 1$: (a) for group sizes of $N = 5$ and (b) $N = 10$ players. The edge G_1G_4 is a line of fixed points. On G_1Q they are stable (closed circles) and on QG_4 unstable (open circles). Even though the social state G_1 and the asocial G_3 are both stable, random shocks eventually drive the system to the asocial equilibrium G_3. For larger group sizes Q approaches G_4 and consequently the system takes longer to reach G_1. Parameters: $r = 1.5, c = 4, \gamma = 1, \beta = 2, \mu = 0$.

Let us now assume that players occasionally learn about the type of their co-players, and that players who normally are contributors may change their mind and decide, with a small probability μ, not to contribute if they know that this entails no risk, i.e. that all other players are of the non-punishing types G_3 or G_4. This alters the payoff values. Players with strategy G_i now have an expected payoff $P_i(\mu)$, with

$$P_1(\mu) = B - c(1-\frac{r}{N})[1-\mu(x_3+x_4)^{N-1}] - (N-1)\gamma(x_2+x_3) \tag{12}$$

$$P_2(\mu) = B - (N-1)\beta(x_1+x_2) - (N-1)\gamma(x_2+x_3) \tag{13}$$

$$P_3(\mu) = B - (N-1)\frac{rc}{N}\mu(x_1+x_4)(x_3+x_4)^{N-2} - (N-1)\beta(x_1+x_2) \tag{14}$$

$$\begin{aligned} P_4(\mu) = B &- (N-1)\frac{rc}{N}\mu(x_1+x_4)(x_3+x_4)^{N-2} \\ &- c(1-\frac{r}{N})[1-\mu(x_3+x_4)^{N-1}] \end{aligned} \tag{15}$$

where B remains unchanged (see eq. (4)). Indeed, the terms P_3 and P_4 for non-punishers are modified by the expected value of the loss due to contributors changing their mind: for each of the $N-1$ co-players, this happens if (a) the co-player is a contributor, and (b) all $N-2$ by-standers are non-punishers, which are independent events. The terms P_1 and P_4 for contributors are modified whenever all $N-1$ co-players are non-punishers. Note that one could also assume that players who ordinarily would not contribute change their mind if they notice that the co-players are punishers. But we shall not consider this possibility, because it has, somewhat surprisingly, less dramatic effects [15].

Again, $P_1(\mu)+P_3(\mu) = P_2(\mu)+P_4(\mu)$ and hence the W_K are invariant manifolds. For small $\mu > 0$, the orientation of the flow on the edges G_1G_2, G_2G_3 and G_3G_4 remains unchanged, but the edge G_1G_4 no longer consists of rest points: the flow on this edge now points towards G_1. The vertices G_1 and G_3 are sinks within each W_K, and G_2 and G_4 are sources, as can be seen by linearisation. Thus there exists at least one rest point in the interior of each W_K, for topological reasons. Moreover, there is only one such point (which accordingly must be a saddle point, see figure 3). Indeed, it must satisfy $P_1(\mu) = P_2(\mu)$, which yields

$$\begin{aligned} f(y) &:= P_1(\mu) - P_2(\mu) \\ f(y) &= \mu\frac{(N-r)c}{N}y^{N-1} - \beta(N-1)y + [\beta(N-1) - \frac{(N-r)c}{N}] = 0. \end{aligned} \tag{16}$$

with $y = x_3 + x_4$, i.e. the frequency of non-punishers. This equation has a unique solution $y = \hat{y}$ in $]0,1[$ because f is strictly convex, $f(1) < 0$, and $f(0) > 0$. In addition, the fixed point must satisfy $P_2(\mu) = P_3(\mu)$ and hence,

$$\gamma z = \frac{rc\mu}{N}(1-z)\hat{y}^{N-2} \tag{17}$$

with $z = x_2 + x_3$, i.e. the frequency of non-contributors. Eq. (17) uniquely specifies z. Note that for $\mu \to 0$ all interior fixed points converge to Q.

In the whole state space we therefore have a bistable situation: apart from a set of measure zero, all initial conditions lead to the social or to the asocial state. Numerical simulations show that even for very small μ the basin of attraction of the social equilibrium G_1 can be substantial.

3. **Optional Public Goods.** We now exclude the possibility of punishing co-players, but assume instead that players have the option of not participating in

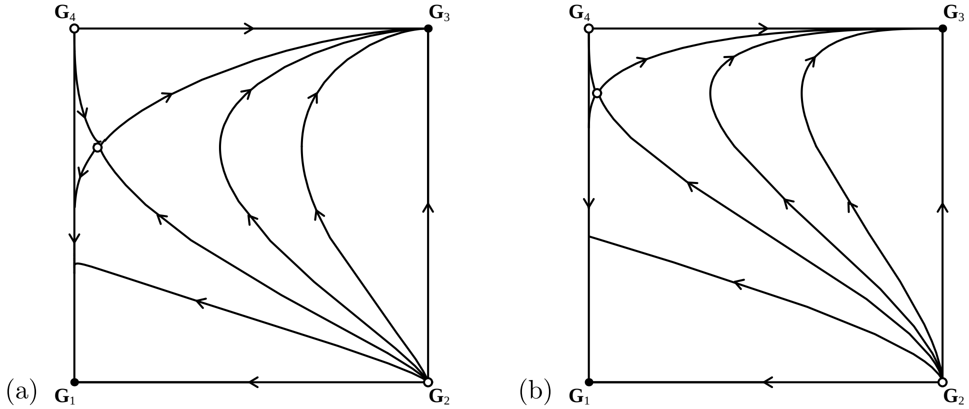

Figure 3. Replicator dynamics for public goods games with punishment and reputation: (a) for group sizes of $N = 5$ and (b) $N = 10$ players. Introducing reputation results in a bi-stable situation. Depending on the initial configuration, the systems ends either in the social equilibrium G_1 or the asocial G_3. Instead of Q and the line of fixed points along G_1G_4 there appears an interior fixed point which essentially determines the size of the two basins of attraction. For increasing group sizes N the fixed point approaches G_4 and thereby increases the basin of attraction of G_1. Parameters: $r = 1.5, c = 4, \gamma = 1, \beta = 2, \mu = 0.2$.

the public goods game, but can instead turn to some autark activity yielding an average payoff σ which is unaffected by the other players. To fix ideas, imagine that within the large population, random samples of N players are asked whether they wish to engage in a public goods game or prefer the autark activity. We shall consider only three strategies: the cooperators and the defectors, who opt for the public goods game, with the intention either to contribute or to exploit, and the loners, who prefer not to join the group of public goods players anyway. These three strategies are fixed in advance, and do not depend on the size or composition of the group playing the public goods game. But it can happen, of course, that in a sample only a single cooperator or defector is willing to engage in the public goods game. In this case, the game will not take place and the players must go for autarky.

We denote by x, y and z the frequencies of cooperators, defectors and loners, respectively, and by P_x, P_y and P_z their average payoff. Clearly

$$P_z = \sigma \tag{18}$$

where we shall always assume that

$$0 < \sigma < (r-1)c. \tag{19}$$

The frequency of cooperators among the players actually willing to join a public goods group is

$$f = \frac{x}{x+y}. \tag{20}$$

The payoff for a defector in a group of S players, of which m are cooperators, is mrc/S. Both m and S are random variables. For any given S the average payoff for a defector is specified by

$$\sum_{m=0}^{S-1} rc\frac{m}{S}\binom{S-1}{m} f^m(1-f)^{S-1-m} = frc\frac{S-1}{S} \tag{21}$$

and therefore the average payoff for a defector who is not the only member of the group is

$$\sum_{S=1}^{N} frc\frac{S-1}{S}\binom{N-1}{S-1} z^{N-S}(1-z)^{S-1} = frc(1-\frac{1-z^N}{N(1-z)}). \tag{22}$$

Altogether this yields an average payoff for a defector

$$P_y = \sigma z^{N-1} + frc(1-\frac{1-z^N}{N(1-z)}). \tag{23}$$

Given that there are $S-1$ co-players in the group, switching from being a defector to being a cooperator yields $c(1-\frac{r}{S})$. For the cooperator's average payoff P_x one therefore obtains

$$P_y - P_x = \sum_{S=2}^{N} c(1-\frac{r}{S})\binom{N-1}{S-1} z^{N-S}(1-z)^{S-1} \tag{24}$$

i.e.

$$P_x = P_y - cF(z) \tag{25}$$

where

$$F(z) = 1 + (r-1)z^{N-1} - \frac{r}{N}\frac{1-z^N}{1-z} \tag{26}$$

an expression which depends neither on f nor on σ. The average payoff in the population $\bar{P} = xP_x + yP_y + zP_z$ is given by

$$\bar{P} = \sigma - [(1-z)\sigma - c(r-1)x](1-z^{N-1}). \tag{27}$$

Due to assumption (19), the three strategies form a rock-scissors-paper cycle: if most players cooperate, it is best to defect; if most players defect, it is best to abstain from the public goods game; and if most players are loners, it is best to cooperate. It is only this third statement which is non-intuitive. But if the frequency of loners is high, then most groups are small, and among mostly small groups, cooperation can be a better option than defection. Indeed, in spite of the fact that within every group, defectors do better than cooperators (by economising their own contribution), it can happen that across all groups, cooperators do better, on average, than defectors. This is an instance of Simpson's paradox.

In order to study the dynamics, it is convenient to effectuate a change in variables, and consider, instead of $(x, y, z) \in S_3$, the two variables $(f, z) \in [0,1] \times [0,1]$. This yields

$$\dot{f} = -f(1-f)cF(z) \tag{28}$$

and by (27)

$$\dot{z} = [\sigma - c(r-1)f]z(1-z)(1-z^{N-1}) \tag{29}$$

Dividing the right hand sides of the previous two equations by the positive factor $f(1-f)z(1-z)(1-z^{N-1})$, which corresponds to a change in velocity and does not affect the orbits, one obtains

$$\dot{f} = \frac{-cF(z)}{z(1-z)(1-z^{N-1})} \tag{30}$$

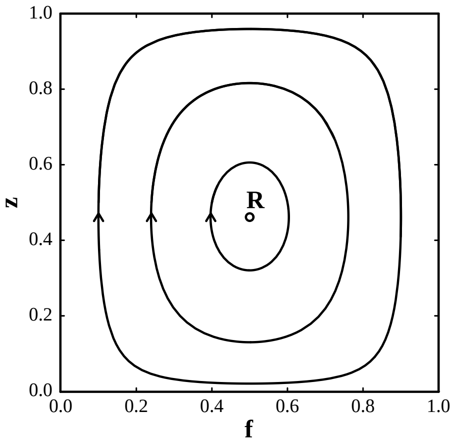

FIGURE 4. Replicator dynamics for optional public goods games: in order to prove that for $r > 2$ all orbits are closed (see figure 5b), the replicator equation is rewritten as a Hamiltonian system on $]0,1[\times]0,1[$ through an appropriate change of variables $f = \frac{x}{x+y}$.

and

$$\dot{z} = \frac{\sigma - c(r-1)f}{f(1-f)} \tag{31}$$

which is a Hamiltonian system for (f, z) in $[0,1] \times [0,1]$. For $r \leq 2$ one has always $f \to 0$ because $F(z)$ is positive on $[0,1[$. For $r > 2$ there exists a unique zero $\hat{z}$ of $F(z)$ in $]0,1[$. This follows from the fact that $G(z) := (1-z)F(z)$ (which has the same zeros as $F(z)$ in $]0,1[$) satisfies $G(0) > 0$, is negative for $z \neq 1$ close to 1 and has a second derivative

$$G''(z) = z^{N-3}(N-1)[(N-2)(r-1) - z(Nr - N - r)] \tag{32}$$

which changes sign only once in $]0,1[$. In this case all orbits in $]0,1[\times]0,1[$ are closed orbits surrounding $(\frac{\sigma}{c(r-1)}, \hat{z})$, see figure 4.

Translating this into the replicator dynamics on S_3, one sees that for $r \leq 2$ the point $(0,0,1)$ (loners only) is a homoclinic rest point (see figure 5a), whereas for $r > 2$, all orbits in $\operatorname{int} S_3$ are closed orbits surrounding $(\hat{x}, \hat{y}, \hat{z})$ where

$$\hat{x} = \frac{\sigma}{c(r-1)}(1-\hat{z}) \tag{33}$$

$$\hat{y} = (1 - \frac{\sigma}{c(r-1)})(1-\hat{z}) \tag{34}$$

(see figure 5b). We note that by increasing the sample size N, the equilibrium value $\hat{z}$ increases: there will be less and less willingness to participate in the public goods, but f and hence the ratio between cooperators and defectors remains unchanged. Increasing the loner's payoff σ leaves the loner's frequency unchanged, and increases the equilibrium value $\hat{x}$ of cooperators. Increasing the multiplication factor r (the 'interest rate' of the public good) results in a larger equilibrium value $\hat{y}$ of defectors. It is easy to see that the time-averages for the payoff values P_x, P_y and P_z must all be equal, and hence equal to σ. Thus, in spite of endless oscillations in the population, no type does better, on average, than the loners. The public goods is a

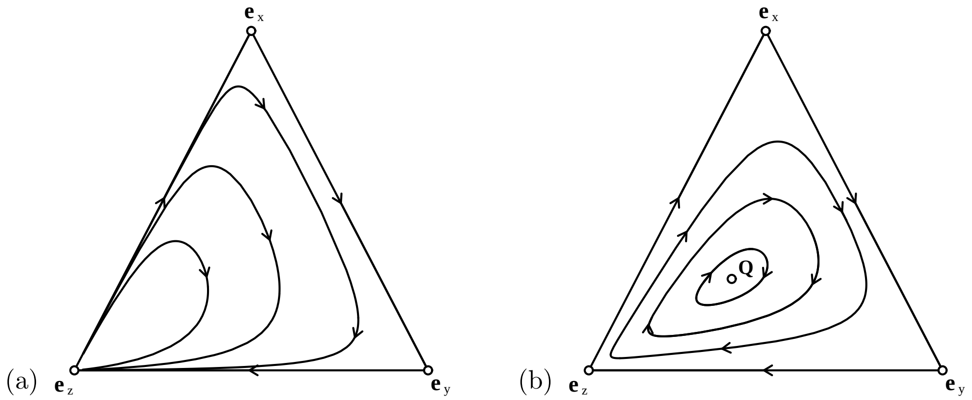

FIGURE 5. Replicator dynamics for optional public goods games in S_3: (a) for $r < 2$ and (b) for $r > 2$. The cyclic dominance of the three strategies is reflected in the heteroclinic cycle along the boundary of the simplex S_3. (a) For low multiplication factors, $\operatorname{int} S_3$ consists of homoclinic orbits only. Except for brief intermittent bursts of cooperation due to random shocks, the system always remains in $\mathbf{e}_z$. (b) In contrast, for higher r an interior fixed point Q appears surrounded by closed orbits. This results in periodic oscillations of cooperators, defectors and loners. Parameters: (a) $N = 5, r = 1.8, c = 1, \sigma = 0.5$, (b) $N = 5, r = 3, c = 1, \sigma = 1$.

tempting option, but it always gets undermined by defection. On the other hand, the option of dropping out of the game leads to ever recurrent bursts of cooperation.

4. **Discussion.** In this paper we have postulated that the frequencies of strategies change according to the replicator equation (1). What is the rationale behind this assumption? Let us consider a large population consisting of players who, occasionally, update their strategy in the following way: they randomly choose a model player and compare their own payoff with that of the model. If that payoff is higher than their own, they adopt it with a probability proportional to the payoff difference; if the model's payoff is lower, they stick to their strategy. It can be shown that this 'proportional imitation rule' induces the replicator dynamics [11, 12].

It should be stressed, however, that other updating rules lead to other dynamics. For instance, if the player adopts the model's strategy whenever it yields a higher payoff (i.e. with certainty instead of a certain propensity only) then the resulting dynamics is a differential equation with a discontinuous right hand side. This has been termed the 'imitate the better' rule [12]. Another conceivable scenario would be that occasionally, players update their strategy by switching to whichever strategy is optimal, given the current state in the population. The orbits of this 'best-reply' dynamics are piecewise linear, always pointing towards one of the corners of the simplex [10, 1].

In figures 6-8 we give examples of the 'imitate the better' rule and the 'best reply' dynamics, for the public goods game with punishment, with punishment and reputation as well as the optional public goods game. In each case, the state space is subdivided into regions differing by the rank ordering of the payoff values, and the vector fields (given by analytic expressions involving the payoffs in each

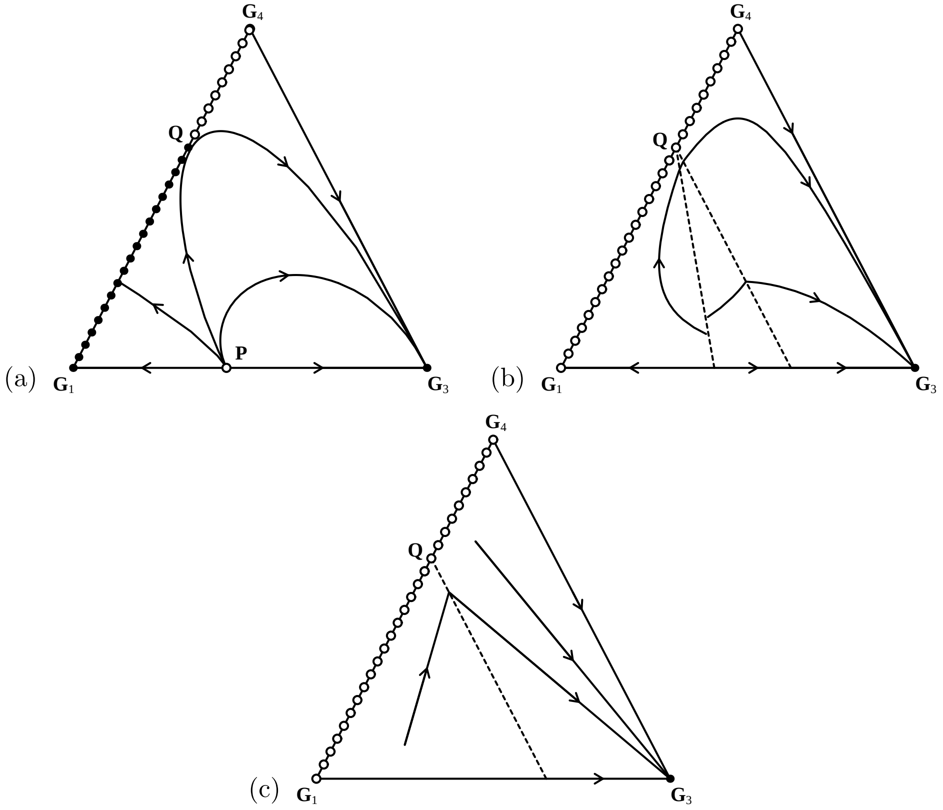

FIGURE 6. Sample trajectories in public goods games with punishment for different dynamics (in the absence of the paradoxical strategy G_2): (a) replicator dynamics, (b) imitate the better and (c) best-reply dynamics. The dashed lines indicate relevant isoclines for which the payoff of two strategies becomes equal. In the long run, the asocial G_3 state is eventually reached in all three scenarios. Only in (a) the system may remain close to social G_1 state for some time because the line of fixed points G_1Q is stable (closed circles). Nevertheless, random shocks will inevitably drive the system to G_3. In (b) and (c), all trajectories in $\operatorname{int} S_3$ lead directly to G_3. Parameters: $N = 5, r = 1.5, c = 4, \gamma = 1, \beta = 2, \mu = 0$.

region) present discontinuities along the boundaries. A full study of these dynamics is forthcoming.

We note that public goods games with more general payoff terms than those assumed in (2) and (3) can also be of interest, although a complete analysis of the dynamics seems presently out of reach. Preliminary numerical explorations suggest that while the details can be considerably different, the main outcomes are robust:

1. in the public goods with punishment, reputation effects may lead to a bistable situation. Depending on the initial condition, either the social or the asocial equilibrium prevails.

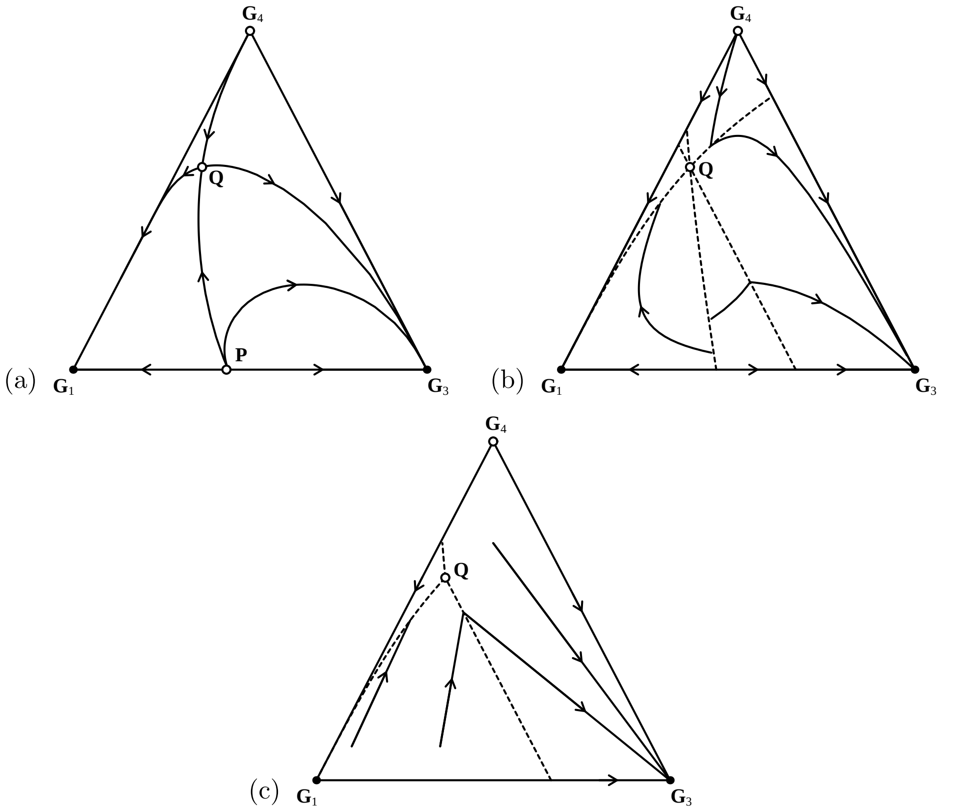

FIGURE 7. Sample trajectories in public goods games with punishment and reputation for different dynamics (in absence of the paradoxical strategy G_2): (a) replicator dynamics, (b) imitate the better and (c) best-reply dynamics. The dashed lines again indicate relevant isoclines for pairwise equal payoffs. The saddle point Q now lies in $\operatorname{int} S_3$ separating the basins of attraction of the social G_1 and the asocial G_3 states. The size of these basins varies considerably for the different dynamics with (a) having the largest and (c) the smallest. In (b) and (c) the approach of G_1 deserves some special attention: once the trajectory hits the isocline G_1Q, it remains there until random shocks eventually drive it along the isocline to the G_1 corner. Parameters: $N = 5, r = 1.5, c = 4, \gamma = 1, \beta = 2, \mu = 0.2$.

2. in the optional public goods game, a rock-scissors-paper dynamics can lead to the (often dynamic) co-existence of all three strategies. In particular, cooperation subsists, but does not achieve fixation.

During the last decades, many aspects of the social dilemma for public goods have been studied (see, e.g., [9, 2, 14, 5, 6]. In particular, relatedness between the players, assortative interactions (for instance, with nearest neighbors only) and repeated interactions turned out to be important factors for persistent cooperation. In this paper we have concentrated on the evolutionary dynamics in well-mixed

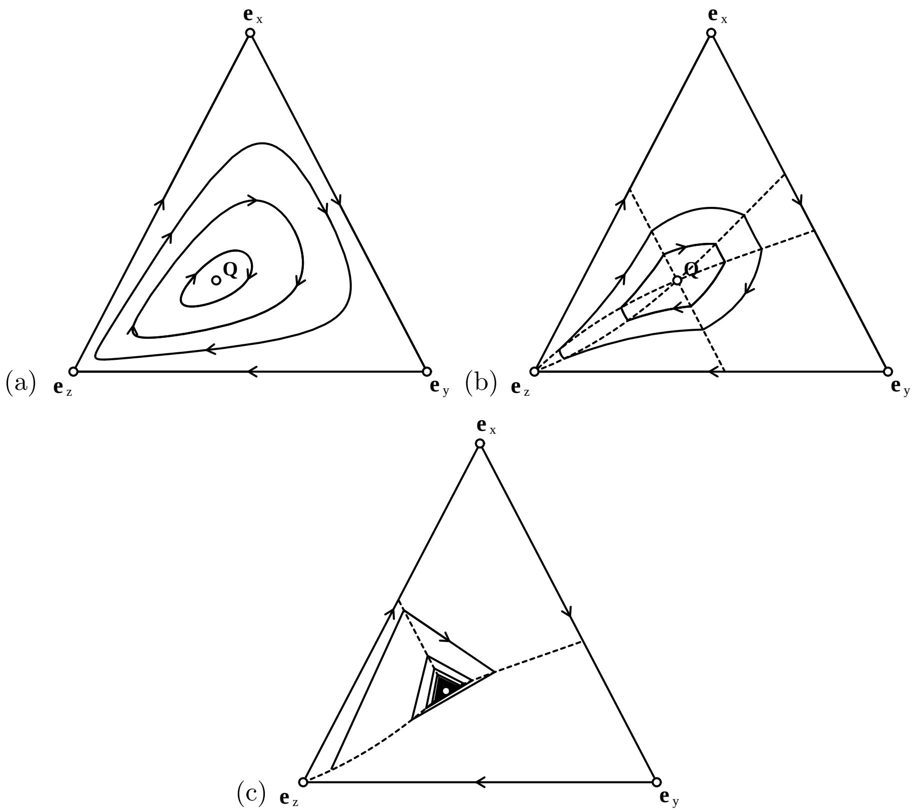

FIGURE 8. Sample trajectories in voluntary public goods games for different dynamics and with $r > 2$: (a) replicator dynamics (c.f. figure 5), (b) imitate the better and (c) best-reply dynamics. For all dynamics the cyclic dominance of the three strategies is reflected by the heteroclinic cycle along $\operatorname{bd} S_3$. The dashed lines indicate relevant isoclines for pairwise equal payoffs. In (a) and (b) the interior fixed point Q is a center surrounded by closed orbits but in (b) Q can turn into a source or sink depending on the parameter values. For the best-reply dynamics (c) Q becomes stable and all trajectories converge to Q in an oscillating manner. But note, when starting near the defectors corner e_y the system first evolves to e_z until random shocks eventually initiate convergence to Q. Parameters: $N = 5, r = 3, c = 1, \sigma = 1$.

populations of unrelated individuals meeting just once, and have studied the effect of two possible factors sustaining cooperation:

1. punishment (which requires individual discrimination of co-players, and a certain reputation effect); and
2. optional participation (which requires the possibility to withdraw from the public enterprise in favour of an autarkic strategy).

The replicator dynamics can be fully analysed in both cases, despite the fact that the payoff terms are non-linear. The results highlight an unexpected relatedness between the two models: In the optional public goods game, the possibility to withdraw from the game sustains cooperation. In the public goods game with punishment, it is the possibility to opportunistically withold the contribution which gives cooperators a chance to get established. In both cases, by asking less from cooperators, more cooperation can be achieved.

Acknowledgments. Ch.H. acknowledges support of the Swiss National Science Foundation 8220-64682; N.H. acknowledges a doctoral stipend from the Austrian Academy of Science; K.S. acknowledges support of the Wissenschaftskolleg WK W008 *Differential Equation Models in Science and Engineering.*

REFERENCES

[1] U. Berger, Best Response Dynamics for Role Games, International Journal of Game Theory 30 (2002), 527–538.
[2] K. G. Binmore, Playing fair: game theory and the social contract, Cambridge: MIT Press, 1994.
[3] A. M. Colman, Game Theory and its Applications in the Social and Biological Sciences, Oxford: Butterworth-Heinemann, 1995.
[4] R. M. Dawes, Social Dilemmas, Ann. Rev. Psychol. 31 (1980), 169–193.
[5] E. Fehr & S. Gächter, Cooperation and punishment in public goods experiments, Am. Econ. Rev. 90 (2000), 980–994.
[6] E. Fehr & S. Gächter, Altruistic punishment in humans, Nature 415 (2002), 137–140.
[7] C. Hauert, S. De Monte, J. Hofbauer, & K. Sigmund, Replicator dynamics in optional public goods games, J. theor. Biol. 218 (2002), 187–194.
[8] C. Hauert, S. De Monte, J. Hofbauer, & K. Sigmund, Volunteering as red queen mechanism for cooperation in public goods games, Science 296 (2002), 1129–1132.
[9] J. Henrich, R. Boyd, S. Bowles, C. Camerer, E. Fehr, H. Gintis, & R. McElreath, Cooperation, reciprocity and punishment in fifteen small scale societies, Am. Econ. Rev. 91 (2001), 73–78.
[10] J. Hofbauer & A. Gaunersdorfer Fictitious play, Shapley polygons, and the replicator equation, Games and Economic Behaviour 11 (1995), 279–303.
[11] J. Hofbauer & K. Sigmund, Evolutionary Games and Population Dynamics, Cambridge: Cambridge University Press, 1998.
[12] J. Hofbauer & K. Schlag, Sophisticated imitation in cyclic games, J. Evolutionary Economics 10 (2000), 523–543.
[13] J. H. Kagel & A. E. Roth, eds. The handbook of experimental economics, Princeton: Princeton University Press, 1995.
[14] M. Milinski, D. Semmann, & H.-J. Krambeck, Reputation helps solve the 'tragedy of the commons', Nature 415 (2002), 424–426.
[15] K. Sigmund, C. Hauert, & M. A. Nowak, Reward and punishment, Proc. Natl. Acad. Sci. USA 98 (2001), 10757–10762.

Received December 2002.

E-mail address: `Christoph Hauert <hauert@zoology.ubc.ca>`
E-mail address: `Nina Haiden <e9525868@fbma.tuwien.ac.at>`
E-mail address: `Karl Sigmund <karl.sigmund@univie.ac.at>`