

Evolution of cooperative strategies from first principles

Mikhail Burtsev¹ & Peter Turchin²

One of the greatest challenges in the modern biological and social sciences is to understand the evolution of cooperative behaviour. General outlines of the answer to this puzzle are currently emerging as a result of developments in the theories of kin selection^{1–7}, reciprocity^{8–10}, multilevel selection^{11–15} and cultural group selection^{16,17}. The main conceptual tool used in probing the logical coherence of proposed explanations has been game theory, including both analytical models and agent-based simulations^{6,7,9,18–24}. The game-theoretic approach yields clear-cut results but assumes, as a rule, a simple structure of payoffs and a small set of possible strategies. Here we propose a more stringent test of the theory by developing a computer model with a considerably extended spectrum of possible strategies. In our model, agents are endowed with a limited set of receptors, a set of elementary actions and a neural net in between. Behavioural strategies are not predetermined; instead, the process of evolution constructs and reconstructs them from elementary actions. Two new strategies of cooperative attack and defence emerge in simulations, as well as the well-known dove, hawk and bourgeois strategies. Our results indicate that cooperative strategies can evolve even under such minimalist assumptions, provided that agents are capable of perceiving heritable external markers of other agents.

The two-dimensional artificial world in our model is divided into cells, which either contain a resource bundle or are empty. An empty cell can acquire a resource bundle with a certain probability per time step and lose it when resource is consumed by an agent. Agents are characterized by a set of receptors, a set of effectors and a neural net connecting receptors to effectors. Each effector is responsible for a particular action. Agents can do nothing (rest), consume the resource bundle if it is present (eat), produce offspring (divide), go forward to a neighbour cell (move), make a turn to the left or right (turn), and attack another agent if present in the same cell (attack). All actions spend energy taken from the agent's internal store. If internal energy is completely depleted, the agent dies. The least energetically demanding action is rest, the most demanding is attack. Consumption of resource increases the internal store of energy subject to an upper limit (the maximum energy that can be stored). When an agent divides, one offspring is created and placed in the same cell as the parent. The parent then transfers half of its energy to the offspring. When one agent hits another, the victim loses an amount of energy, which is gained by the attacker (see Methods for energetic costs of actions).

Sensory inputs of agents include its internal store of energy, whether there are resources in the agent's field of vision (the cell it is in, the neighbour cell in front of the agent, and the cells on the right and left), and how many other agents are in the field of vision. Each agent has external phenotype that is coded by a vector of integer values (markers). The markers do not influence behaviour but function only as indicators of similarity. The euclidian distance

between an agent's markers and the markers of another agent in the cell (a potential subject for attack) is also a sensory input. Behaviour of an agent is controlled by a simple one-layer neural net. Both weights of the neural net and external markers are inherited by the offspring when an agent divides, subject to a set rate of mutation. Details of the implementation of the model are given in the Methods.

All of our simulations were started with an initial population of agents that were unaware of markers (the matrix coefficients connecting input from markers to actions were preset to zero). Thus, the use of markers in a population had to evolve from a blank slate. Because markers and behaviours are not linked (apart from both being inherited from the ancestors), agents can lose cooperative behaviours by mutation while retaining 'in-group' markers. Thus, the structure of the model allows free-riders to arise.

The number of potential behavioural strategies in our model is astronomical ($>10^{1,000}$; see Methods). Because of the vast number of potential strategies, it is difficult to understand exactly what are the behaviours that evolve in the simulation—each matrix of neural weights is a 'black box'. To make sense of our results, we confronted agents that evolved in our simulations with a discrete set of stimuli and noted the action taken. This approach enabled us to classify strategies into aggressive or not, and those discriminating in-group versus out-group members (see Methods).

Our study examined the spectrum of strategies evolving in the full model versus the simplified version in which agents could not detect external markers. We also determined how the carrying capacity of the environment (varied by increasing the size of resource bundles while keeping the rate of bundle appearance constant) affects the strategies evolved.

Analysis of the model without markers showed that the strategies evolving in the simulation corresponded to those in the well-known game of dove–hawk–bourgeois²⁵. Doves never attack other agents and attempt to escape when attacked, whereas hawks make a living by predation on other agents. The bourgeois strategy in our model is to stay in the same cell and immediately attack any invader, while ignoring agents in neighbouring cells (unlike the hawks). In the model without markers the dominant strategy is bourgeois, provided that the carrying capacity of a single cell is sufficient for supporting a sedentary agent (amount of resource in a bundle is sufficient for survival until the next bundle appears). Below this threshold, C_1 , the bourgeois strategy is impossible, because agents are forced to keep moving to get enough food to survive, and the population is divided between doves and hawks. The long-term population density increases linearly with carrying capacity until it reaches C_1 and then becomes flat (Fig. 1). This is because once the bourgeois strategy takes over, each cell can be occupied by only a single agent. Even when resources are sufficient to support more than one agent per cell, they fight until only one remains.

¹Department of Non-linear Dynamics, Keldysh Institute of Applied Mathematics of RAS, Moscow 125047, Russia. ²Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3042, USA.

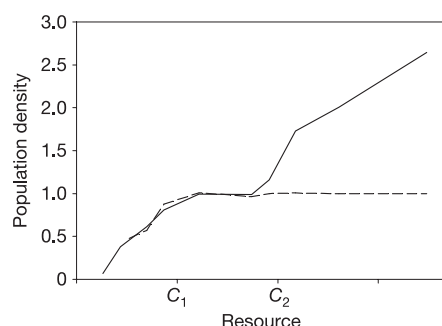


Figure 1 | The effect of resource abundance on population density.

Population density (average number of agents per cell) as a function of the abundance of resources (the size of resource bundle randomly appearing in a cell with a fixed probability). Broken curve, model version without external markers; solid curve, model with markers.

In the full model, in which agents can evolve the ability to detect phenotypic similarity, three kinds of cooperative strategies emerged. The first one was simply the cooperative version of the dove. Cooperative doves ignored out-group (phenotypic distance large) members, but left cells with in-group (phenotypic distance is small) members to avoid competing with them. In the second strategy, agents also left cells with in-group members, but when they detected out-group members they attacked them. We term this strategy 'raven', because, according to the Russian proverb, 'a raven will not peck out the eye of another raven'. The third cooperative strategy was to stay in the same cell with in-group members and collectively fight with any out-group invader. Having to share limited resources of the cell meant that agents using this cooperative defence strategy were small (had small stores of internal resource), but they still had a good chance of defeating a large invader because of their advantage in numbers. This strategy resembles the 'mobbing' behaviour that many species of small birds, such as starlings, use to drive away large predators. For this reason, we call it the 'starling' strategy.

The emergence of the starling strategy has a marked effect on the relationship between carrying capacity and long-term population density. For lower values of carrying capacity, the curve in the full model follows that of the model without markers. But once it exceeds the threshold $C_2 = 2C_1$, the density curve again begins to rise (Fig. 1). Analysis of the effect of carrying capacity on the prevalent strategies, evolved by agents, indicates the mechanism of this rise. If carrying capacity is insufficient to support at least two agents in a cell ($C < C_2$), the starling strategy cannot invade the population. Instead, the dominant strategy is raven, whose frequency increases linearly with C for $C < C_1$, and saturates at a high level for $C_1 < C < C_2$ (Fig. 2). So far, the only difference resulting from

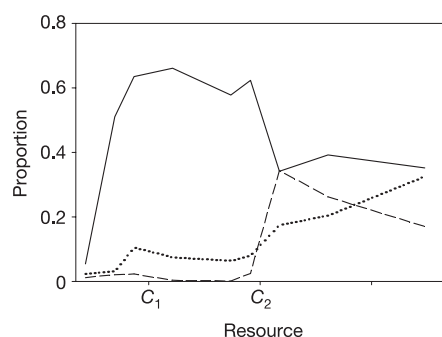


Figure 2 | The effect of resource abundance on the long-term proportions of agents using various strategies. Average proportion of agents using the raven (unbroken line), the cooperative dove (dashed line) and the starling (dotted line) strategies in the full model with markers as a function of the abundance of resources. Proportions do not add up to one because there are other strategies, including the non-cooperative ones.

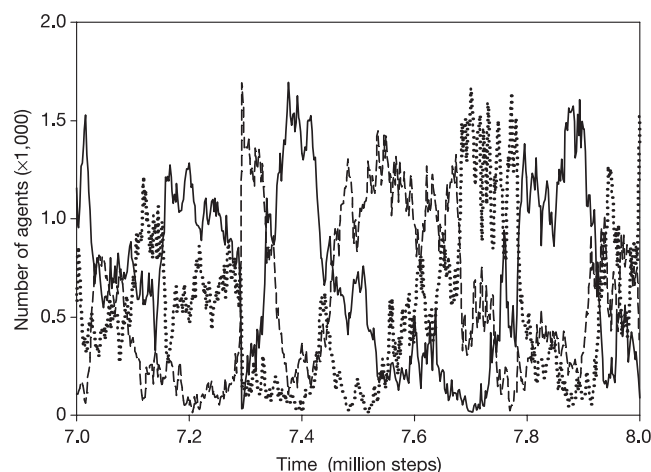


Figure 3 | Dynamic coexistence of the raven, the cooperative dove and the starling strategies. Numbers of agents using the raven (dashed line), the cooperative dove (dotted line) and the starling (unbroken line) strategies as a function of time in one realization of the model.

the agents' ability to use markers is the switch from the hawk and bourgeois to the raven strategy (predators recognize and do not attack in-group members). Once carrying capacity goes beyond C_2 , the starling strategy becomes viable. Starlings, however, do not drive ravens to extinction. Instead, we observe sustained oscillations in the numbers of starlings, ravens and doves (Fig. 3). As a result, all three strategies manage to coexist in the long term (Fig. 2).

For low carrying capacity ($C < C_1$), we observed the emergence of another new strategy, which was to leave the cell whenever any other agent (related or not) appeared in it. This strategy differs from that of the doves, who ignore unrelated agents and escape only if attacked. In fact, it is the exact opposite of the bourgeois and resembles strategies predicted to evolve at the 'anti-private-property equilibrium' (H. Gintis, personal communication). Another interesting behaviour was observed in starlings, which apparently show the previously predicted 'desperado effect'²⁶. If an internal resource of one of starlings in a cell falls below a certain level, this agent leaves the cell—apparently preferring to face an almost certain death in a fight for resources with out-group members, rather than continuing to deplete a possibly inadequate resource in its native cell.

Our results have important implications for the evolution of territoriality in animals (and private property in humans). With a few exceptions²⁷, theorists have paid little attention to the role that cooperation may have in the evolution of territoriality²⁸. Our study suggests that cooperative defence of territory can radically change the

Table 1 | List of input variables and their definitions

Input variable*	Value
I_1	Bias constant, k
I_2, I_3, I_4, I_5	k if there is resource bundle in the field of agent's vision; 0 in the opposite case
I_6, I_7, I_8, I_9	cN_c , where c is a constant, N_c is the number of agents in the given cell of the field of agent's vision
I_{10}	Value of internal resource, r
I_{11}	$r_{\max} - r$
I_{12}	$\sqrt{\sum_i (\bar{m}_i - \bar{m})^2}$, where \bar{m} is a centroid of markers of all agents at the current cell
I_{13}	$k \cdot \sqrt{\sum_i (m_i^p - m_i)^2} / 2M_{\max}$, where m^p is a marker of partner to interact

* Note that I_1 is a constant and that I_2 to I_5 are binary variables (k is a functional analogue of unity and was set equal to r_{\max} , where r_{\max} is the maximal possible value of stored internal resource).

Table 2 | The energetic costs of an agent's actions*

Output vector	Action	Change of internal resource r_i^\dagger
O_0	Rest	$-0.001r_{\max}$
O_1	Turn left	$-0.002r_{\max}$
O_2	Turn right	$-0.002r_{\max}$
O_3	Consume the resource bundle	$+[(0.06r_{\max}, 0.4r_{\max})^\ddagger]$
O_4	Move	$-0.004r_{\max}$
O_5	Divide	$-0.004r_{\max}\S$
O_6	Fight (randomly chosen agent in the cell)	The cost of attack is $0.1r_{\max}$; the gain is $+0.2r_{\max}$ if internal resource of the victim is $r_n \geq 0.2r_{\max}$ and $+r_n$ otherwise; the victim loses $-0.2r_{\max}$

*Note that r_{\max} is the energy storage capacity.

† This scheme of setting parameter values reflects our assumption that the energetic cost of movement (move, turn left, and so on) is greater than the cost of resting, whereas the cost of attack is much greater than the cost of movement. Note that energetic losses are indicated with a minus sign and gains with a plus sign.

‡ The energy intake was a parameter in the series of simulations in which food appears in the cell with the constant probability of 0.01 and the amount of resource in the bundle was varied between $0.06r_{\max}$ and $0.4r_{\max}$.

\S When the agent divides it spends $0.004r_{\max}$; half of the remaining energy is then transferred to the offspring.

course of evolution in resource-rich ($C > C_2$) environments. When the amount of resource becomes large enough to support more than one agent, and too large for a single agent to monopolize, solitary bourgeois are replaced by cooperative starlings, provided that agents can recognize in-group members. The starling strategy does not take over completely, however, but coexists with other strategies in a complex dynamical way (Fig. 3).

One potential strategy that did not evolve in our simulations was cooperative attack (the 'wolf' strategy), probably because agents lacked the appropriate effectors for travelling in groups in search of prey. In future work we plan to investigate whether adding such actions as 'follow another agent' could allow evolution of cooperative predation. Another limitation of our study was that agents could transmit traits (including phenotypic ones) only vertically from parent to offspring. This means that our 'in-group members' were also relatives. But one of the greatest puzzles about human ultrasociality is how cooperation between unrelated individuals can arise in the process of evolution. This issue can be addressed (and we plan to do so) by allowing cultural transmission of traits between group members.

In conclusion, our study shows that within the artificial evolution framework it is possible to model not only how one strategy displaces another (or not), but the very process by which new strategies emerge out of a very large space of possibilities. Our model did not endow agents with a set of preconceived strategies—all that we assumed was that agents have a set of elementary sensory inputs and a set of actions. The selection of appropriate connections between inputs and actions was moulded by the process of evolution. It is notable that the agents in our simulations evolved many of the strategies that were postulated by previous researchers. Thus, in the absence of phenotypic markers, three distinct strategies emerged corresponding to the dove, the hawk and the bourgeois. This shows that our results are not in opposition to game theory, but represent an extension of previous approaches. In the presence of markers, the evolution resulted in some predictable modifications of these basic strategies, but also in the emergence of a new one. Cooperative doves avoided competition with in-group members, whereas cooperative hawks—'ravens'—avoided attack on phenotypically similar agents. The new strategy was the starlings, who lived in groups and defended territory cooperatively against predation.

METHODS

Agents' behaviour and evolution. Behaviour of agents is governed by a simple control system in which each output associated with a specific action is connected to sensory inputs from the environment or the internal state of the

agent. The control system is linear and functions similarly to a feed-forward neural network with no hidden layer. To calculate the output vector \mathbf{O} of values, the input vector \mathbf{I} is multiplied by a matrix of weights \mathbf{W} , which are constrained to lie in the range $[-W_{\max}, W_{\max}]$:

$$O_j = \sum_i w_{ij} I_i \quad (1)$$

At each time step, the agent performs the action associated with the maximum output value (note that the order in which agents act is randomly shuffled every step). The input vector \mathbf{I} is populated with information about the presence of resource and other agents in the field of vision (the cell where the agent is, the neighbour cell in front of the agent, and the cells on the right and left), the level of internal resource and the euclidean distance between marker vectors of the agent and its partner for potential interaction. A full list of input variables and their definitions are given in Table 1. At the start of simulation, an initial population was formed from the agents with the same matrix of weights \mathbf{W} . All the weights in this matrix were set to zero except for three that defined the following simple strategy: move if a resource bundle is in the forward cell; eat if a resource is in the current cell; divide otherwise. Correspondence between outputs and actions, and how changes of the internal resource r depend on actions, are summarized in Table 2.

To speed up simulations, all variables were integers. For all simulations, the size of the world was 900 cells, W_{\max} was 1,000, r_{\max} was 5,000, the dimension of the marker vector was 10, and its values were bounded by $[-W_{\max}, W_{\max}]$.

If the agent executes the action 'divide', its offspring is placed in the same cell. The genome of the offspring is constructed in the following way: first, for every weight of the control system, a random value uniformly distributed on the interval $[-0.03W_{\max}, 0.03W_{\max}]$ is added; second, for every component of the marker, a random value uniformly distributed on the interval $[-0.15W_{\max}, 0.15W_{\max}]$ is added. A preliminary version of the model has been investigated in ref. 29.

Definition of strategies. In our model, every agent has 11 independent inputs from 13 available (I_1 is constant and $I_{11} = r_{\max} - I_{10}$) and seven actions. Assuming that we take into consideration only two possible values per input (this procedure gives us a lower bound on the estimate), the overall number of strategies can be estimated as $2^{7 \times 11}$, which approximately equals $10^{1.730}$. To reduce such a large space of strategies, we consider only six situations in which the agent was allowed to interact with an in-group or out-group member for three levels of internal resource ($0.02r_{\max}$, $0.5r_{\max}$ and $0.98r_{\max}$). We also group 'rest', 'eat' and 'turn' actions together because they correspond to the absence of direct interaction between agents. As a result, the strategy space was reduced to $4^6 = 4,096$ possible strategies. Frequencies of strategies in the population at a given point in time were calculated by picking every agent and calculating its actions for every situation.

Our classification of strategies, which evolved in the simulation, was based on this subset of strategy space. We treated an agent as a 'raven' if for any value of its internal resource it fights an out-group agent but leaves the cell with an in-group agent. A 'starling' was defined as an agent that does not leave the cell in the presence of in-group individuals and fights out-group agents for any value of internal resource $r \leq 0.5r_{\max}$.

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- Hamilton, W. D. The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**, 1–52 (1964).
- Maynard Smith, J. Kin selection and group selection. *Nature* **201**, 1145–1147 (1964).
- Michod, R. E. & Abugov, R. Adaptive topography in family-structured models of kin selection. *Science* **210**, 667–669 (1980).
- Lacy, R. C. & Sherman, P. W. Kin recognition by phenotype matching. *Am. Nat.* **121**, 489–512 (1983).
- Queller, D. C. A general model for kin selection. *Evolution* **46**, 376–380 (1992).
- Riolo, R. L., Cohen, M. D. & Axelrod, R. Evolution of cooperation without reciprocity. *Nature* **414**, 441–443 (2001).
- Axelrod, R., Hammond, R. A. & Grafen, A. Altruism via kin-selection strategies that rely on arbitrary tags with which they coevolve. *Evolution* **58**, 1833–1838 (2004).
- Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).
- Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577 (1998).
- Bowles, S. & Gintis, H. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theor. Popul. Biol.* **65**, 17–28 (2004).
- Sober, E. & Wilson, D. S. *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard Univ. Press, Cambridge, Massachusetts, 1998).
- Wilson, D. S. Altruism and organism: disentangling the themes of multilevel selection theory. *Am. Nat.* **150** (suppl.), 122–134 (1997).

13. Gintis, H. Strong reciprocity and human sociality. *J. Theor. Biol.* **206**, 169–179 (2000).
14. Bowles, S. in *Social Dynamics* (eds Durlauf, S. N. & Young, H. P.) 155–190 (MIT Press, Cambridge, Massachusetts, 2001).
15. Turchin, P. *Historical Dynamics: Why States Rise and Fall* (Princeton Univ. Press, Princeton, New Jersey, 2003).
16. Boyd, R. & Richerson, P. J. *Culture and the Evolutionary Process* (Univ. Chicago Press, Chicago, Illinois, 1985).
17. Richerson, P. J. & Boyd, R. in *Indoctrinability, Ideology, and Warfare* (eds Eibl-Eibesfeldt, I. & Salter, F. K.) 71–95 (Berghahn, New York, 1998).
18. Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390–1396 (1981).
19. Axelrod, R. *The Complexity of Cooperation: Agent-based Models of Competition and Collaboration* (Princeton Univ. Press, Princeton, New Jersey, 1997).
20. Epstein, J. M. & Axtell, R. *Growing Artificial Societies: Social Science from the Bottom Up* (Brookings Institution Press, Washington DC, 1996).
21. Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359**, 826–829 (1992).
22. McNamara, J. M., Barta, Z. & Houston, A. I. Variation in behavior promotes cooperation in the Prisoner's Dilemma game. *Nature* **428**, 745–748 (2004).
23. Nowak, M., Sasaki, A., Taylor, C. & Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650 (2004).
24. Hauert, C. & Doebeli, M. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* **428**, 643–646 (2004).
25. Maynard Smith, J. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–222 (1974).
26. Grafen, A. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.* **35**, 462–467 (1987).
27. Matthiopoulos, J., Moss, R. & Lambin, X. The kin facilitation hypothesis for red grouse population cycles: territorial dynamics of the family cluster. *Ecol. Model.* **147**, 291–307 (2002).
28. Maher, C. R. & Lott, D. F. A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.* **143**, 1–29 (2000).
29. Burtsev, M. S. Tracking the trajectories of evolution. *Artif. Life* **10**, 397–411 (2004).

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