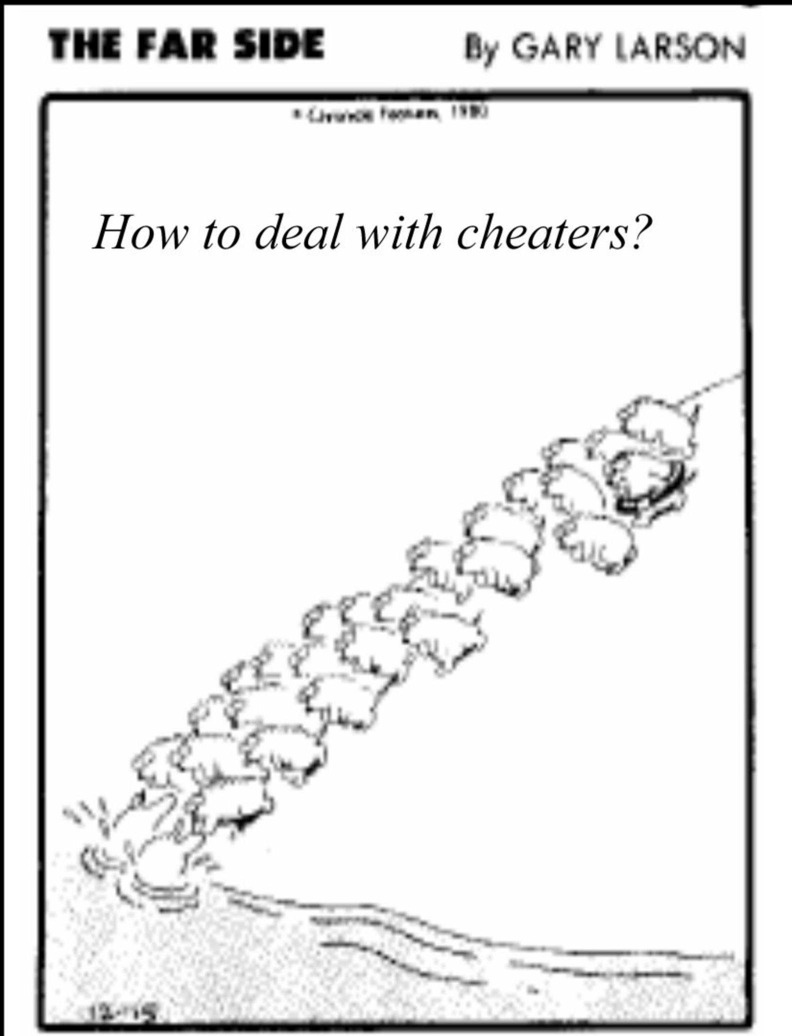
Cooperation between individuals of same species can appear to be 'altruistic' – i.e., costly to actor in terms of fitness (usually current reproductive output) while benefiting the recipient in similar terms. Such behavior towards offspring is not problematic since they ARE parental fitness. When directed towards other individuals it calls for expectation; how can a fitness-costly behavior persist in a population? Shouldn't selection act quickly to remove such behavioral tendencies.

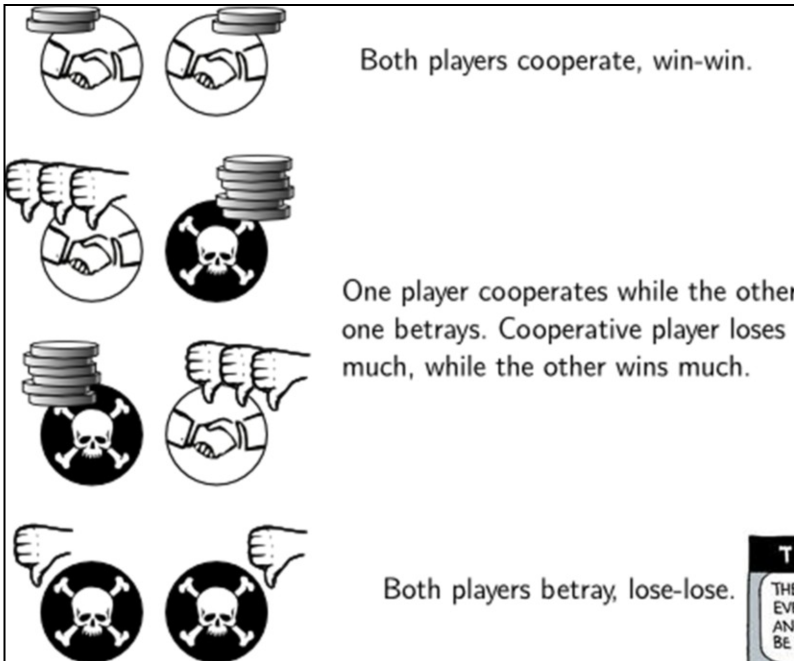
Florida scrub jays are an example of such behavior; they raise young cooperatively with up to several 'secondary' adults assisting one pair of breeding adults in raising their young. Why don't the secondaries simply go off and raise their own brood?

One possibility is that they're 'learning' something that will be useful when they do go off on their own. That's an easy answer – how would you test it? What patterns does it predict in helpers and their behavior?

BUT if no such delayed but direct benefit accrues, then what?



In particular, it seems that any population of altruistic actors/cooperators would be extremely vulnerable to INVASION by a rare mutant that receives the altruistic behavior of others, but does not reciprocate – acts selfishly itself...



		Player B: Cooperate	Player B: Defect
Player A	Cooperate	A→3, B→3 Reward for mutual cooperation	A→0, B→5 Sucker's payoff and temptation to defect
	Defect	A→5, B→0 Temptation to defect and sucker's payoff	A→1, B→1 Punishment for mutual defection

One hypothesis for evolution of cooperative behavior depends on delayed reciprocity; or *delayed fitness benefits* to actor through reciprocal interactions with others, where the benefits end up greater than the costs of the cooperative behavior.

This notion can be approached through game theory. The classic game here is called 'Prisoner's Dilemma'; you can look up the reference of the name – but it is a two-player game with simple strategy options; when encountering another player, either act cooperatively in some way, or act selfishly (usually called 'defect'). As in the hawk-dove game, the 'best' strategy from a group perspective can often be to cooperate (as with this payoff matrix. But in a population of cooperators, a rare defector would have very high fitness, gaining the defection bonus in every interaction; cooperate is not ESS. An all defector population can't easily be invaded by cooperate (unless in large numbers simultaneously) so is an ESS in the simple game.

So, the usual problem with cooperation; how can it survive selfish defectors ('cheaters').

Some strategies

Here is a description of some of the basic strategies used in our simulations as well as in the literature:

all_c
: Always cooperates. [c]*

all_d
: Always defects. [d]*

tit_for_tat
: The tit_for_tat strategy was introduced by Anatole Rapoport. It begins to cooperate, and then play what its opponent played in the last move.

spiteful
: It cooperates until the opponent has defected, after that move it always defects.

soft_majo
: Plays opponent's majority move, if equal then cooperates. First move is considered to be equality.

per_ddc
: Plays periodically : [d,d,c]*

per_ccd
: Plays periodically : [c,c,d]*

mistrust
: Defects, then plays opponent's move.

per_cd
: Plays periodically [c,d].

pavlov
: The win-stay/lose-shift strategy was introduced by Martin Nowak and Karl Sigmund. It cooperates if and only if both players opted for the same choice in the previous move.

tf2t
: Cooperates except if opponent has defected two consecutive times.

hard_tft
: Cooperates except if opponent has defected at least one time in the two previous move.

slow_tft
: Plays [c,c], then if opponent plays two consecutive time the same move plays its move.

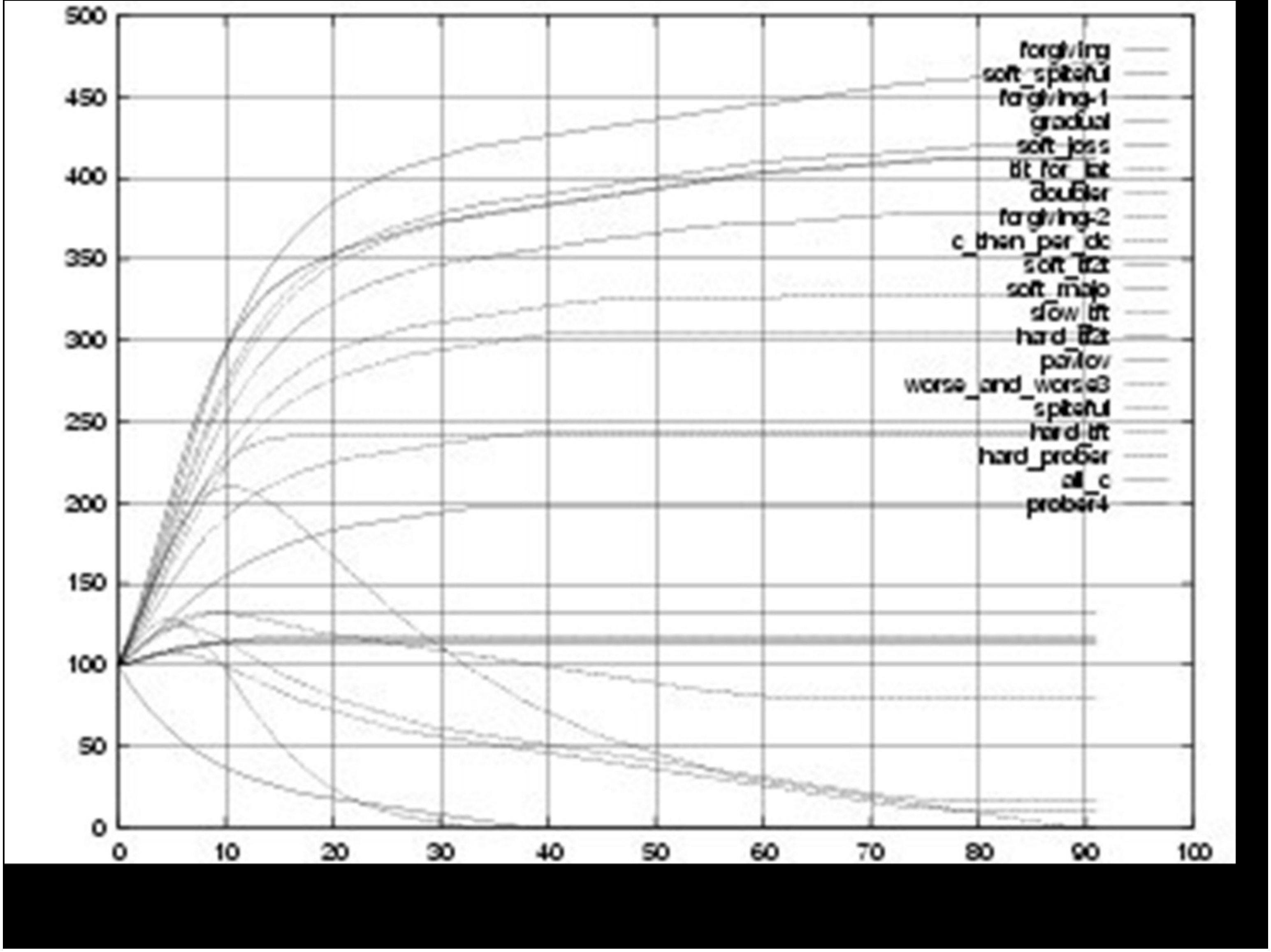
hard_majo
: Plays opponent's majority move, if equal then defects. First move is considered to be equality.

random
: Cooperates with probability 1/2.

One possibility is that, if interactions are frequent and repeated, so 'players' encounter each other multiple times, AND actors can remember previous encounters AND behave flexibly depending on the history of such encounters, it is possible that winning (maximum-fitness-accumulating) playing strategies may allow cooperation IF they also include ways to punish defectors/cheaters.

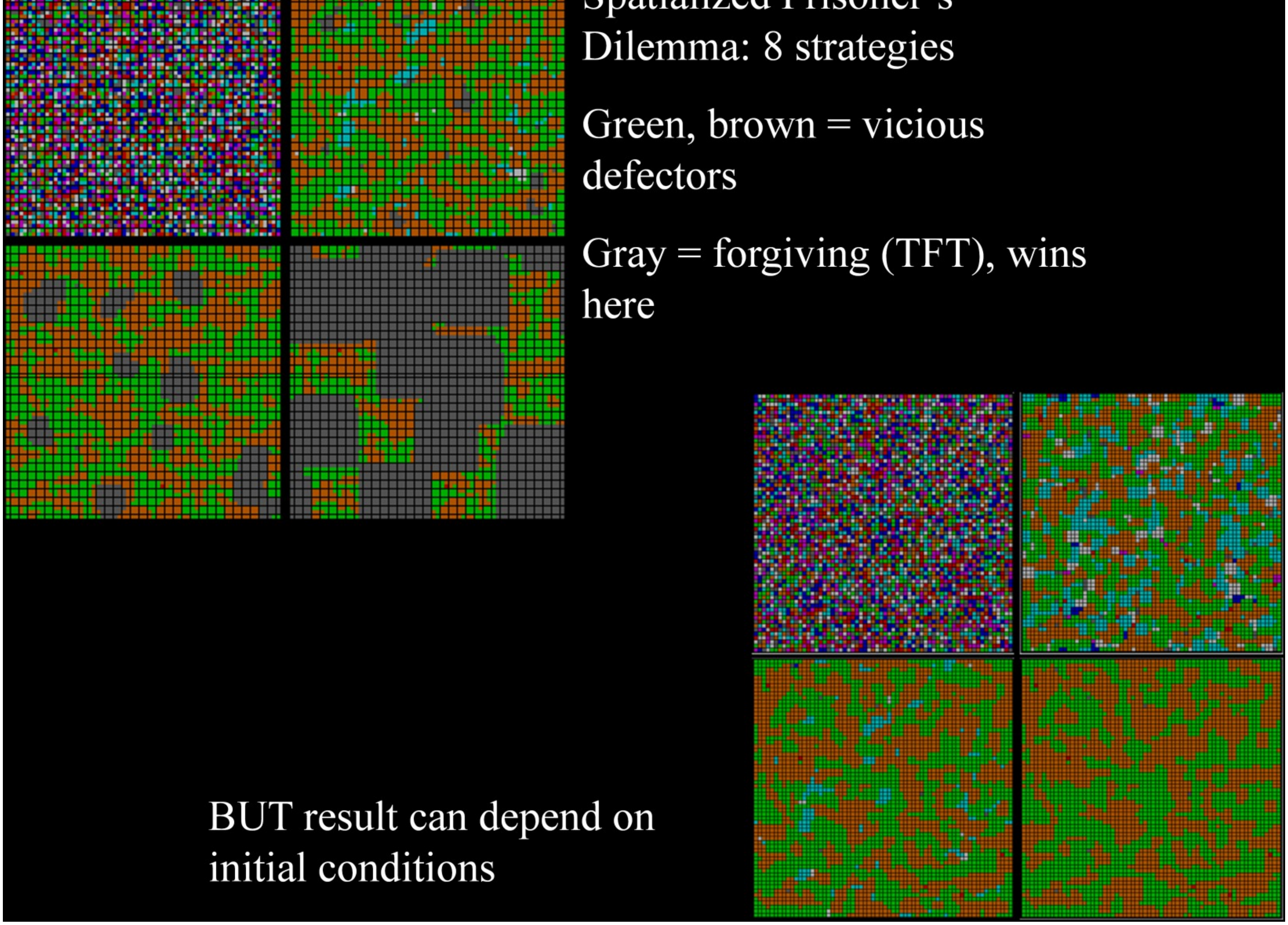
A simple one, for example: 'tit-for-tat', in which actor takes strategy that 'opponent' played in last encounter. Or 'grudging cooperator' where a previously defecting opponent must cooperate TWICE before player will cooperate on next encounter. And so on.

Rapoport initiated a series of computer simulations with agent-based models to assess the fitness/success of many such (over 60 in later simulations), using a variety of formats (round-robins, tournaments, free-for-alls...)



When a bunch of strategies are placed in initial population, greedy ones (defectors) expand AT FIRST, but, as they increase in frequency, 'punishing but generous' strategies (like tit for tat) do progressively better (because they 'punish' defectors but cooperate with others – this doesn't help in a population with few defectors, but makes a big difference when defectors are commmon). In nearly all simulations, some sort of 'generous tit-for-tat' variant wins.

But there's a tricky thing here: it's NOT ESS: an all tit-for-tat population can be invaded by pure cooperators (everybody will cooperate all the time, so equal fitness), who will 'drift' to increased abundance eventually. But then, a selfish/defector can invade. Which sets the stage for a punishing generous strategy... So frequencies can oscillate!



A (possibly) more realistic simulation has interactions between players not random, but gives each player spatial coordinates, and allows interaction with neighbors only (you can modify to allow limited movement and so forth).

The 'spatialized iterated prisoner's dilemma' game tends to be won by generous or forgiving punishers as well – but results CAN depend on initial configuration. Initial conditions may matter; cooperators or forgiving tit for tat may go extinct before gaining a fitness edge...

Conrad Power (2009)
A Spatial Agent-Based Model of N-Person Prisoner's Dilemma Cooperation in a Socio-Geographic Community
Journal of Artificial Societies and Social Simulation vol. 12, no. 1 8
<http://jasss.soc.surrey.ac.uk/12/1/8.html>

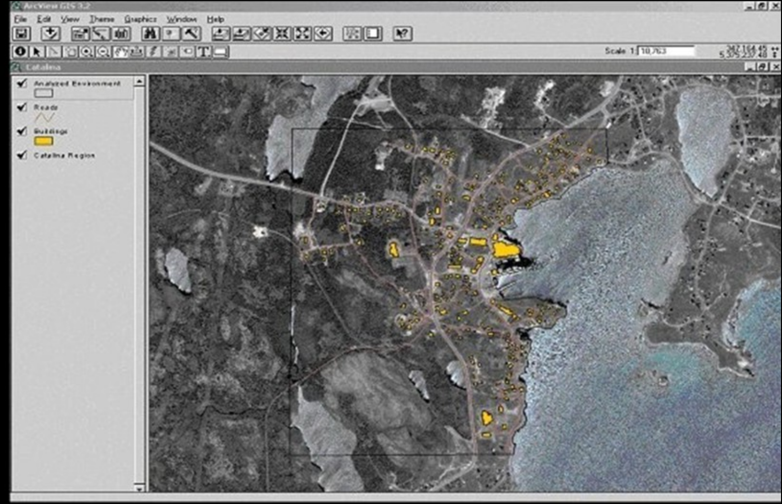
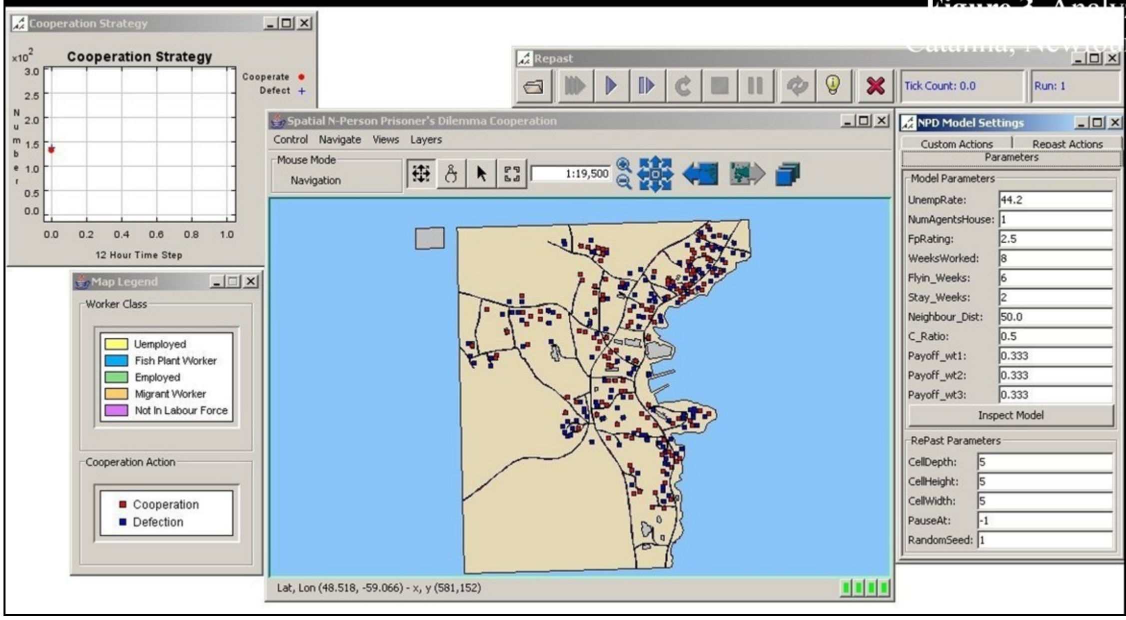


Figure 3. Analyzed Environment of Central Catalina, Newfoundland and Labrador, Canada



An even more complex (and realistic) spatialized version: this one uses a real map of a community to place 'players' and has rules for distances to which players may range in their interactions, and allows them to be mobile or not. Depending on the set-up results can differ.

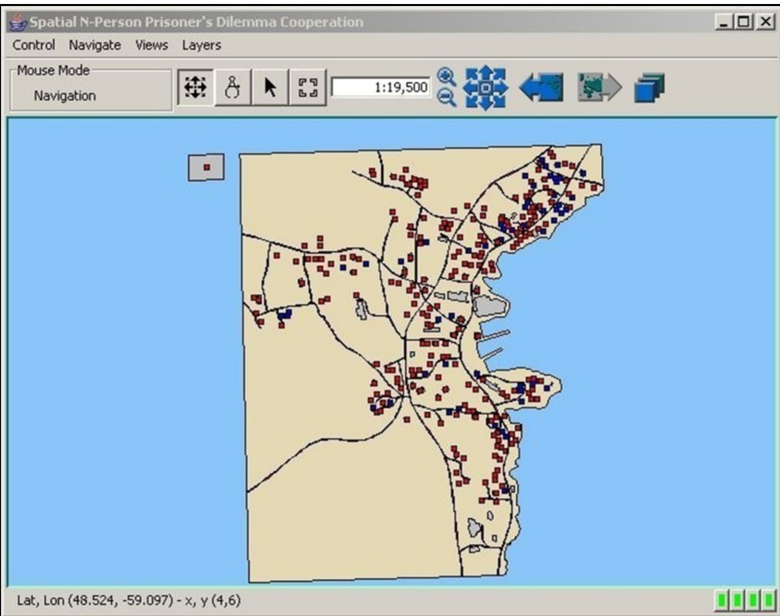


Figure 6. Map of Cooperation Pattern for Mobile Agents in a 50 Meter Neighbourhood

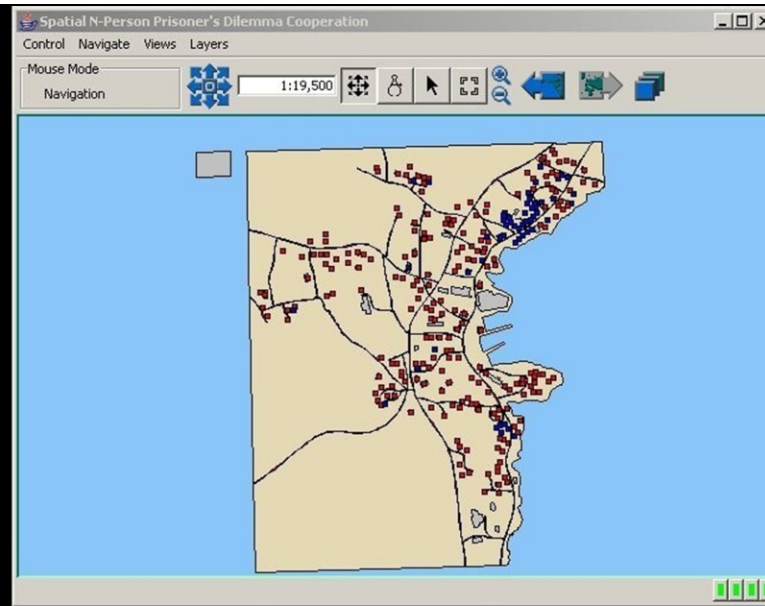
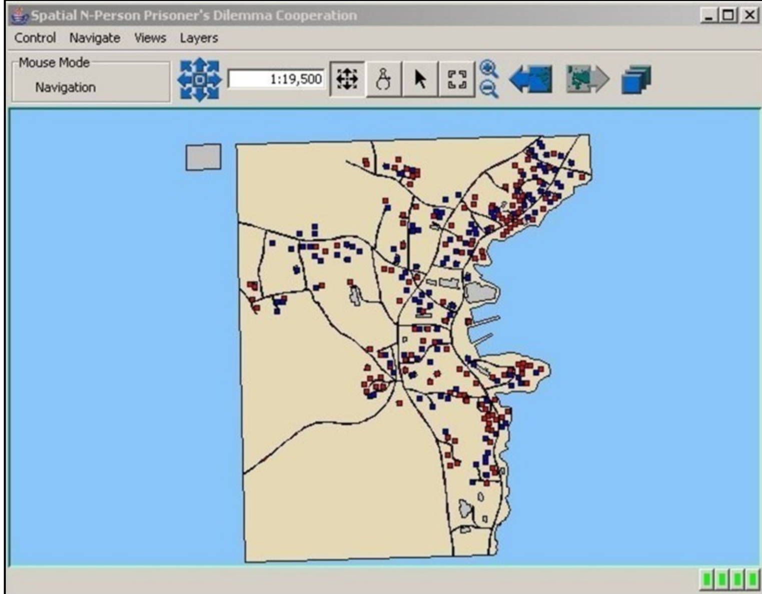
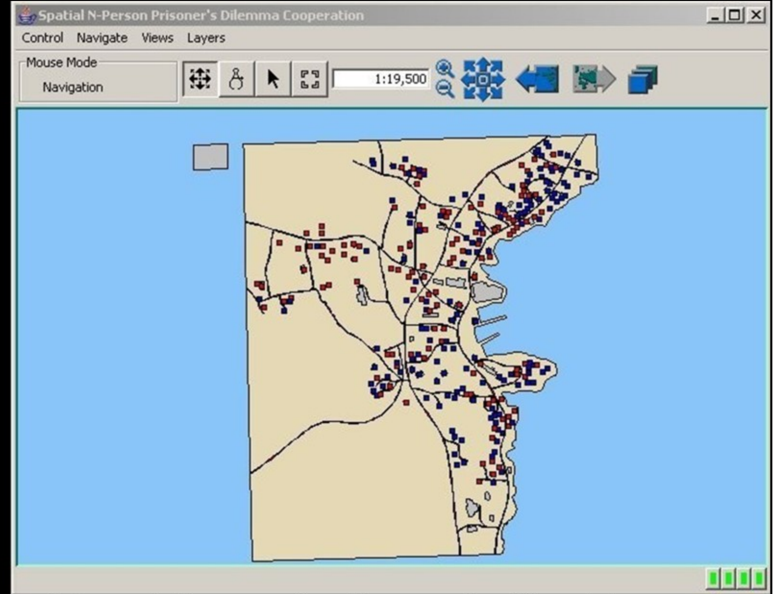


Figure 8. Map of Cooperation Pattern for Fixed Agents in a 50 Meter Neighbourhood

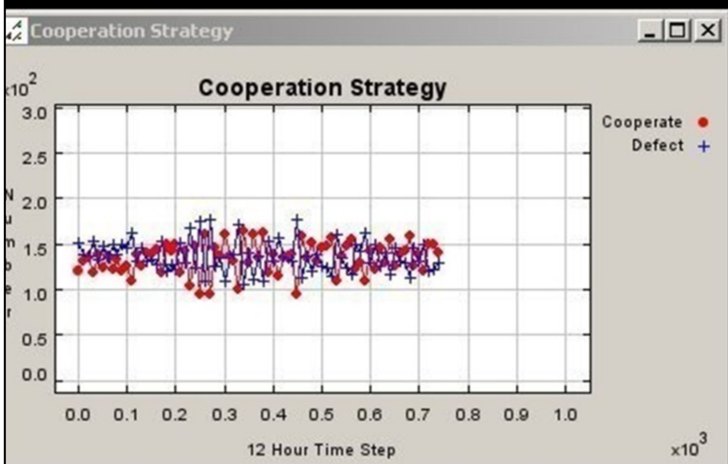
Where interactions are over relatively short distances only – i.e. among only close neightbors, cooperators tend to win – but some kinds of neighborhoods permit persistence of defectors (densely populated neighborhoods – so MORE players within the range)

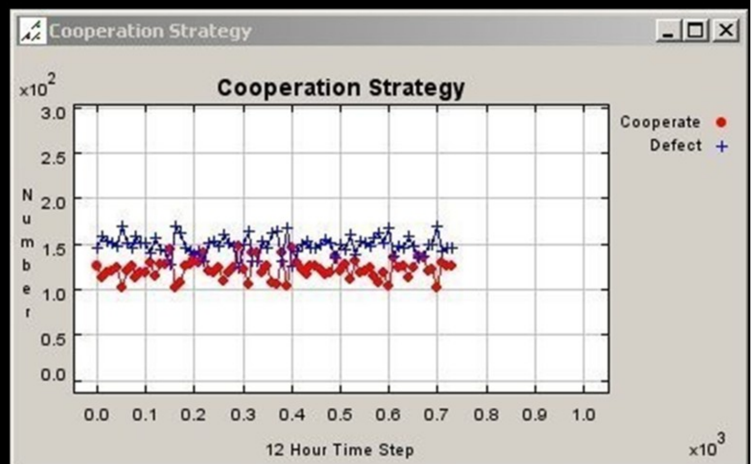


Map of Cooperation Pattern for Mobile Agents in a 150 Meter Neighbourhood



Map of Cooperation Pattern for Fixed Agents in a 150 Meter Neighbourhood





Where players interact over longer distances – especially if mobile – defectors do progressively better. Is this equivalent to saying that, in packed or populous envrionments , cooperation is less favored (perhaps because 'selfish' players are less likely to encounter 'punishment' from tit for tat-like strategies}?

In any case, these models suggest that cooperation can be supported, selectively, through fitness benefits gained through reciprocity IF conditions are right. The critical element may be whether selfish individuals – cheaters or defectors – are likely to be 'punished' by repeated encounters with strategies that penalize defection

J Theor Biol. 2007 Jun 7;246(3):420-9. Epub 2007 Jan 30.
Evolutionary stability of egg trading and parceling in simultaneous hermaphrodites: the chalk bass revisited.
Crowley PH, Hart MK.

Several species of simultaneously hermaphroditic seabasses living on coral reefs mate by alternating male and female roles with a partner. This is known as egg trading, one of the classic and most widely cited examples of social reciprocity among animals. Some of the egg-trading seabass species, including the chalk bass, Serranus tortugarum, switch mating roles repeatedly, having subdivided their clutch of eggs into parcels offered to the partner for fertilization. Here we attempt to understand these dynamics as a pair of evolutionary games, modifying some previous approaches to better reflect the biological system. We find that the trading of egg clutches is evolutionarily stable via byproduct mutualism and resistant to invasion by rare individuals that take the male role exclusively. We note why and how parceling may reflect sexual conflict between individuals in the mating pair. We estimate evolutionarily stable parcel numbers and show how they depend on parameter values. Typically, two or more sequential parcel numbers are evolutionarily stable, though the lowest of these yields the highest fitness. Assuming that parcel numbers are adjusted to local conditions, we predict that parcel numbers in nature are inversely related both to mating group density (except at low density) and predation risk.

A popular study system: simultaneous hermaphrodites – where a 'selfish' strategy might involve one individual fertilizing eggs of another and then not offereing eggs for fertilization (remember that sperm is cheap) if partner isn't 'optimal contributor of sperm for selfish players eggs.

How might players avoid being exploited by pure-selfish strategies? It appears that they do so by offering eggs in small parcels and only offering more parcels when other player offers their own parcel...

l starvation. The
the donor loses.

[redacted]

[redacted]

[redacted]