Title: **“**Constructed Games”

Acknowledgements: I am grateful to Alexander Schaefer, Ryan Muldoon, Justin Bruner, Alexandra Oprea, Hannah Rubin, the graduate students and postdocs of the PPE program at the University at Buffalo, the audience of The Puzzle of Social Behavior: Game Theory and Beyond Workshop in Bielefeld, and one anonymous reviewer for helpful feedback that greatly strengthened and informed the direction and framing of the paper.

Word Count: 4,313

Abstract: To date, most analyses of evolutionary games have assumed that evolution is a unidirectional process: Natural selection is represented in the form of payoffs, and organisms must either adapt to the selective pressures in play, or die. Nevertheless, there is a growing consensus that organisms frequently engage in *niche-constructing* behaviors that alter the selective pressures they are subject to. Niche-constructing behaviors can be modeled game-theoretically, as behaviors that impact payoffs (and therefore relative fitness). I demonstrate that such behaviors enable cooperation to emerge from the prisoner’s dilemma and argue that niche construction likely impacts the evolutionary dynamics of other games.

Introduction

According to standard evolutionary theory, organisms’ adaptations are unilaterally shaped by natural selection. In the words of George C. Williams, “Adaptation is always asymmetrical, organisms adapt to their environment, never vice versa” (Williams, 1992, p. 484; Odling-Smee, Laland, and Feldman, 2003). There is nevertheless a growing consensus that many organisms engage in behaviors and that impact the selective pressures acting on them. Such selectionaltering behaviors are often termed ‘niche-constructing,’ with a population’s ‘niche’ defined as the sum of all the selection pressures acting on it. Researchers who believe that niche construction significantly impacts evolutionary dynamics argue that the standard theory should be abandoned in favor of an *extended evolutionary theory*, in which natural selection and niche construction act as parallel evolutionary processes (Odling-Smee, Laland, and Feldman, 2003).

Proponents of extended evolutionary theory argue that niche construction fundamentally alters the evolutionary process through the introduction of feedback loops (Lewontin, 1983; Odling-Smee, Laland, and Feldman, 2003; Odling-Smee, 1988). We cannot sidestep the role of niche construction in the evolutionary process by stating that niche-constructing behaviors are merely the product of natural selection. That would be to ignore the fact that niche construction itself influences the selection pressures under which niche-constructing behaviors, as well as other traits, evolve. It is not merely the case that successful niche construction alters selection pressures in ways that further incentivize the proliferation of the beneficial niche-constructing behaviors themselves; rather, alterations in selection pressures that are initially caused by niche construction may additionally affect the evolution of *other* organismal traits that may, at least at first glance, appear unrelated. For this reason, we may wonder whether niche-constructing behaviors may initiate feedback loops that influence the evolution of cooperation or other behavioral traits. I aim to show that such queries are not misplaced.

Despite the growing consensus that niche construction plays an important role in determining evolutionary trajectories, many researchers in biology and theoretical biology seem reluctant to fully embrace an extended theoretical framework (Odling-Smee, 1988). One possible reason for this hesitancy is that they may doubt the extent to which niche construction impacts the particular evolutionary phenomena under their study. Another possible reason is that the standard paradigm is theoretically simple, and researchers may be reluctant to abandon a simple theoretical framework in favor of a more complex one, if they are not yet thoroughly convinced of the latter's benefits. Nevertheless, if niche construction impacts evolutionary dynamics in at least *some* circumstances, then the practice of consistently omitting niche construction from theoretical biological models will lead researchers to misrepresent the evolutionary dynamics of at least *some* types of biological systems (Odling-Smee, Laland, and Feldman, 2003). In what follows, I argue that, by largely failing to consider the impacts of niche-constructing behaviors on relevant selection pressures, many modern evolutionary game theorists may be inadvertently mischaracterizing the evolutionary dynamics that emerge from particular types of games, including the prisoner's dilemma.

The literature that currently exists at the nexus of game theory and niche construction theory is rather limited. Past approaches to modeling niche construction in the context of evolutionary games have been somewhat localized and narrow in scope, focusing specifically on the role of niche construction in the evolution of cancer cells (Bergman and Gligorijevic, 2015), costs to future generations that result from current consumption of abiotic resources (Lehmann, 2008), and the coevolution of cooperation and population structure (Powers, 2010). In contrast, I here aim to produce rather generalizable results that are derived using only the simplest of modeling tools: continuous replicator dynamics and expanded payoff matrices. My goal is to demonstrate that niche-constructing behaviors can coevolve with, and thereby affect the evolutionary trajectories of, other, social behaviors that are of interest to evolutionary game theorists. In the following section, I utilize a toy model to illustrate how a defection-thwarting niche-constructing behavior may coevolve with cooperation in a transforming prisoner's dilemma. I then derive general conditions under which niche construction can be expected to alter game dynamics. Insofar as it utilizes replicator dynamics to analyze the effects of feedback loops, my analysis shares certain similarities with the "eco-evolutionary" game framework put forward by Tilman, Plotkin, and Akçay (2020); however, while their analysis focuses specifically on how feedback from niche construction influences resource extraction strategies, I analyze how such feedback loops alter the evolutionary trajectories of strictly social behaviors, e.g. cooperation.

An objection, originally attributed to Godfrey-Smith (1996), may be raised here. The fitness functions utilized by evolutionary game theorists are always frequency-dependent. In other words, the fitness of any particular type of individual is generally taken to be a function of the proportions of other types of individuals in the same population. Strategies adopted by each type of individual affect the fitness of other types of individuals in the population, thereby also affecting whether the proportions of those types of individuals in the population subsequently increase (or decrease). Insofar as *any* action that an individual takes within the context of an evolutionary game creates a feedback loop that affects the fitness of other individuals, can't we argue that such models already incorporate some form of niche construction?

My response to this objection is rather straightforward. Even if most existing evolutionary game-theoretic models already incorporate this one oddly specific and extremely limited form of niche construction – allowing the proportion(s) of type(s) that exist in a population at some time t_1 to influence the proportion(s) of those same type(s) that exist in the same population at some later time t_2 – such models nonetheless fail to accommodate the fuller and richer spectrum of niche-constructing behaviors common throughout the natural world, many of which are capable of impacting the dynamics of common evolutionary games and hence the evolutionary trajectories of focal behavioral traits analyzed within the context of those games. My goal in this paper is to argue that evolutionary game theorists should consider the impacts of other sorts of niche-constructing behaviors that alter the fitness of individuals via changes made to crucial aspects of a game environment (i.e., those aspects affecting payoffs), and not artificially narrow their focus to only those "niche-constructing" behaviors that merely modify the *players*.

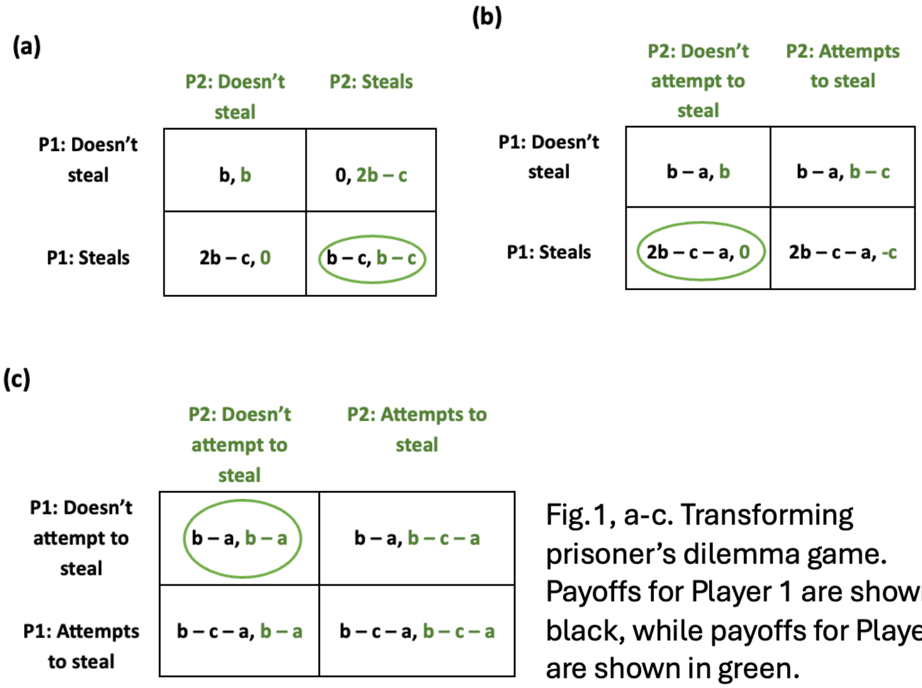
I am well aware of the fact that my analysis in the following section breaks what is often regarded as one of the "unwritten rules" of classical game theory, i.e., that the payoffs of a game are generally taken to be unalterable by its players. In my decision to model niche-constructing behaviors as payoff-modifying, I am assuming that evolutionary games are "open" to transformation by the organisms that play them. It is only in this way that the bidirectional evolutionary process posited by niche construction theorists can be fully realized within the context of a game-theoretic model: Natural selection is represented in the form of payoffs, and niche construction enables organisms to modify selective pressures by modifying those payoffs. While this assumption is unconventional, I see no reason why it ought to be controversial.

Toy Model: Deceptive Digging in Eastern Gray Squirrels

Below, I develop a toy model to illustrate how payoff changes introduced by niche construction enable cooperative dynamics to emerge from the prisoner's dilemma. While the toy model is constructed around a singular, real-world example, the same cooperative, coevolutionary dynamics emerge from any prisoner's dilemma in which a niche-constructing behavior successfully thwarts defection with some threshold probability *p*.

The Model: Steele et al. (2008) studied a deceptive digging behavior in Eastern gray squirrels. Ordinarily, a squirrel caching (i.e., burying) a nut will dig a single hole, place the nut inside the hole, and cover it with dirt. However, Easten gray squirrels have been observed to frequently perform an alternative behavior that involves digging and covering multiple holes throughout the process of caching a single nut, typically placing the nut in the final hole dug. Steele et al. suggest that this deceptive digging behavior is a learned technique to combat the effects of pilfering (i.e., the theft of nuts by other squirrels). They observed that individual squirrels in an experimental scenario became more likely to perform the deceptive digging behavior after their nuts were stolen. Moreover, while in the field, they observed cases in which other squirrels attempted to steal nuts from the empty, deceptively dug holes – only to discover that the holes were, in fact, empty. Steele et al. note that tree squirrels are highly motivated by visual cues, and that squirrels who want to steal nuts often search in locations where they have seen conspecifics digging. Deceptive digging thwarts would-be nut thieves by leading them to search in the wrong location. This niche-constructing behavior not only impacts the game environment in a regular and observable manner across time – namely, by creating an increasing number of empty holes – but also reduces the benefits that can be obtained by pilfering.

We may be interested in knowing how the feedback loop initiated by this particular niche-constructing behavior, deceptive digging, impacts the selection pressures acting on another behavioral trait, nut stealing. Steele et al. (2008) note that Eastern gray squirrels do not defend territories, and that reciprocal nut stealing between squirrels is reasonably common. We can therefore model nut stealing behavior in the context of a one-shot, two-player game, where both players are randomly drawn from the same population (Fig.1, below).



(a)

	P2: Doesn't steal	P2: Steals
P1: Doesn't steal	b, b	0, 2b – c
P1: Steals	2b – c, 0	b – c, b – c

(b)

	P2: Doesn't attempt to steal	P2: Attempts to steal
P1: Doesn't steal	b – a, b	b – a, b – c
P1: Steals	2b – c – a, 0	2b – c – a, -c

(c)

	P2: Doesn't attempt to steal	P2: Attempts to steal
P1: Doesn't attempt to steal	b – a, b – a	b – a, b – c – a
P1: Attempts to steal	b – c – a, b – a	b – c – a, b – c – a

Fig.1, a-c. Transforming prisoner's dilemma game. Payoffs for Player 1 are shown in black, while payoffs for Player 2 are shown in green.

We might first consider a scenario in which there is no deceptive digging (Fig.1a). Each of our two squirrels is in possession of a nut, and has the opportunity to attempt to steal its partner's nut. For simplicity, let us assume that, when there is no deceptive digging, every attempt to steal a nut is successful. Moreover, let us assume that there are just two types of individuals: those who steal nuts, and those who don't. We can define the benefit of a single nut as b, and the energetic cost of each nut-stealing expedition as c. Let us assume that b and c are both small, positive numbers, with $b > c$. Furthermore, let us assume that the energetic cost of stealing a nut, *c*, is smaller than the energetic cost incurred while foraging for one's own nut, so that stealing others' nuts is profitable. Assume that each player begins the game with a single nut. If neither player steals the other's nut, each receives the benefit *b*, because both are still in possession of their original nuts. If both players steal, they each receive the benefit of *the other's* nut, *b*, minus the energetic cost *c* required to steal. If one player steals and the other doesn't, the stealing player receives the benefit of two nuts, *2b*, minus the energetic cost of stealing a nut, *c* – and the player who doesn't steal gets nothing. Note that, as long as $b > c > 0$, this symmetrical payoff matrix meets the definition of a prisoner's dilemma given by Axelrod and Hamilton (1981). In this particular scenario, stealing one's partner's nut is considered an act of defection, while refraining from stealing is a cooperative act. Under these circumstances, selection should favor nut stealing, given that the unique pure-strategy equilibrium of the game is [Steal, Steal]. If both players are randomly drawn from a well-mixed population, and each randomly drawn pair of individuals only plays the game once, we would expect the population to quickly – and irreversibly – become dominated by nut thieves.

However, consider how the situation changes if some of the squirrels in the population acquire the ability to perform the deceptive digging behavior. Now, if we randomly draw two individuals from the population, and make them play our nut stealing game, it is possible that one of the players (say, Player 1) will be a deceptive digger, and the other player (Player 2) won't be. Just for now, let us assume that squirrels who perform the deceptive digging behavior are always successful at preventing others from stealing their nuts. It would then appear that the ability to perform this behavior gives Player 1 an advantage. Player 1's deceptive digging behavior introduces asymmetry into the payoff matrix (Fig.1b). Just as before, when neither player attempts to steal, they both receive the benefit b, because they are both still in possession of their original nuts. However, if Player 2 attempts to steal Player 1's nut, Player 2 will simply waste time and energy (c) searching in empty holes for a nut that it can't find. The result is that if Player 2 attempts to steal, and Player 1 doesn't, Player 1 will still have the benefit, b, of its own nut, while Player 2 will have the benefit of its own nut, b, minus the energetic cost of its unsuccessful nut-stealing expedition, c. On the other hand, if Player 1 attempts to steal Player 2's nut, it does so successfully. (Recall that, above, we made the simplifying assumption that every attempt to steal a nut is successful.) The result is that, when Player 1 steals and Player 2 does not attempt to steal, Player 1 receives the benefit of two nuts, $2b$, minus the cost of stealing a nut, c, and Player 2 receives nothing. Meanwhile, if both players attempt to steal, Player 1's attempt is successful, and Player 2's isn't. The result is that Player 1 receives the benefit of two nuts, $2b$, minus the cost, c, of stealing a nut, while Player 2 just expends energy (c) searching for a nut that it can't find. Assuming that Player 1 incurs a small energetic cost, a, as a consequence of performing the deceptive digging behavior, we see that it pays Player 1 to steal if $2b – c – a > b – a$, or if $b > c$; because we assumed at the outset that $b > c$, this means that it always pays Player 1 to steal. Meanwhile, it only pays Player 2 to steal if $-c > 0$; because we assumed that the energetic cost, c, of stealing another's nut is always positive, this means that it never pays Player 2 to steal. The result is that the unique pure-strategy equilibrium of the asymmetrical game shown in Fig.1b occurs at [Steal, Don't steal].

Because the deceptive digging behavior confers a fitness advantage on the individuals who possess it (i.e., it enables squirrels in our nut stealing game to steal others' nuts, while simultaneously preventing their nuts from being stolen by others), we would expect the vast majority of individuals in the population to eventually adopt the behavior. Then, when two individuals who possess the deceptive digging trait are randomly drawn from the population to play the game (Fig.1c), neither will be able to benefit from stealing, with the result that the unique pure-strategy equilibrium of the game will be [Don't steal, Don't steal]. In other words, the proliferation of the deceptive digging behavior causes the prisoner's dilemma game of Fig.1a to be transformed into the mutually cooperative game shown Fig. 1c. (Such a game in which mutual cooperation is incentivized is sometimes referred to as a "prisoner's delight.")

Fig.2

Player 2

Player 1	Don't dig, Don't steal (x_1)	Don't dig, Steal (x_2)	Dig, Don't Steal (x_3)	Dig, Steal (x_4)
Don't dig, Don't steal (x_1)	b, b	0, 2b – c	b, b – a	0, 2b – c – a
Don't dig, Steal (x_2)	2b – c, 0	b – c, b – c	b – c, b – a	-c, 2b – c – a
Dig, Don't steal (x_3)	b – a, b	b – a, b – c	b – a, b – a	b – a, b – c – a
Dig, Steal (x_4)	2b – c – a, 0	2b – c – a, -c	b – c – a, b – a	b – c – a, b – c – a

We can reformat the transforming prisoner's dilemma game of Fig. 1 as a single simultaneous-move game (Fig.2) in which there are four "strategies," each of which represents a combination of a social-behavioral type (i.e., stealing/defecting or non-stealing/cooperative) and a niche-constructing type (i.e., deceptive digging or no deceptive digging): "Doesn't steal, doesn't dig" (x_1), "Steals, doesn't dig" (x_2), "Doesn't steal, digs" (x_3), and "Steals, digs" (x_4). This enables us to then derive the following fitness functions, one for each of the four "types":

Fitness of x_1 *("Doesn't dig, doesn't steal")* $= bx_1 + bx_3$ **Eq. 1**

Fitness of x_2 *("Doesn't dig, steals")* $= (2b - c)x_1 + (b - c)x_2 + (b - c)x_3 - cx_4$ **Eq. 2**

Fitness of x_3 *("Digs, doesn't steal")* = $(b-a)x_1 + (b-a)x_2 + (b-a)x_3 + (b-a)x_4$ **Eq.3**

Fitness of x_4 *("Digs, steals")* = $(2b-c-a)x_1 + (2b-c-a)x_2 + (b-c-a)x_3 + (b-c-a)x_4$ **Eq.4**

Assuming that the average fitness of the population is simply the sum of the proportion of each type, multiplied by that type's fitness, or

Average fitness = $x_1[\,Fitness\ \ x_1] + x_2[Fitness\ \ x_2] + x_3[Fitness\ \ x_3] + x_4[Fitness\ \ x_4]$ **Eq.5**

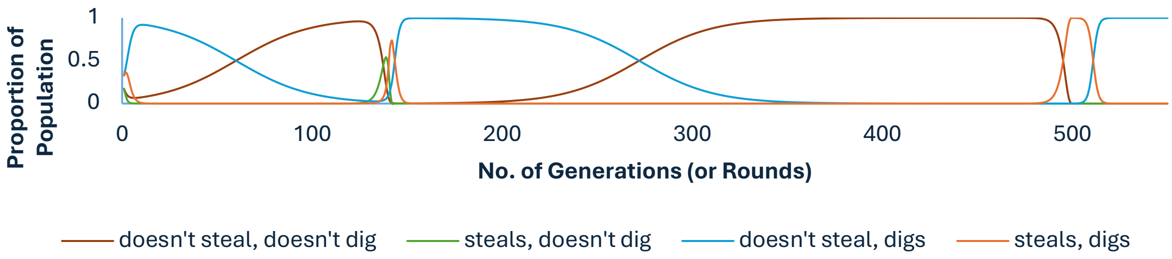
and that the proportion of each type *i* in a particular generation x_i' is related to the proportion of that type in the previous generation x_i in the following way,

$$(x_i)' = (x_i)\left(\frac{Fitness(x_i)}{Average\ fitness}\right)$$ **Eq.6**

we can utilize the continuous replicator dynamics to analyze the evolutionary trajectories of the four behavioral types. Setting $b = 2$, $c = 1$, and $a = 0.1$ yields the graph shown in Fig.3. As expected on the basis of our preliminary analysis above, the population is quickly taken over by niche-constructing cooperators (blue line) who play at the cooperative equilibrium of the "prisoner's delight" game shown in Fig.1c. However, because the performance of the niche-constructing behavior always entails a small energetic cost (*a*), a monomorphic (i.e., single-strategy) population of niche-constructing cooperators is vulnerable to invasion by non-niche-constructing cooperators (red line). Because, in the absence of nut thieves, the ability to perform the deceptive digging behavior doesn't provide a squirrel with fitness benefits that outweigh the energetic cost (*a*) of performing the behavior, niche-constructing cooperators (blue line) are eventually replaced by non-niche-constructing cooperators (red line). Eventually, the population consists solely of non-niche-constructing cooperators, who cooperate with each other in the prisoner's dilemma game shown in Fig.1a. This situation is not stable, and leaves the population vulnerable to invasion by either stealing type (green and orange lines).

Nevertheless, as soon as the nut thieves re-emerge, the ability to perform the deceptive digging behavior once again becomes beneficial, and so niche-constructing cooperators (blue line) quickly take over the population once again. The population therefore remains largely cooperative over the long run, but cycles between states in which either (1) large numbers of niche-constructing individuals play at the cooperative equilibrium of the "prisoner's delight" game shown in Fig.1c (blue line) or (2) large numbers of non-niche-constructing individuals cooperate in the prisoner's dilemma shown in Fig.1a (red line).

Fig. 3:



In the absence of niche construction, the population would be consistently dominated by nut thieves. However, because the deceptive digging behavior effectively removes the temptation to defect, cooperation coevolves with this niche-constructing behavior, as the latter transforms the original prisoner's dilemma into a "prisoner's delight." While this game transformation is never permanent – as long as niche construction entails a positive energetic cost, no matter how small, the population will at times be dominated by non-niche-constructing cooperators who play the prisoner's dilemma, rather than the transformed game – the existence of at least a few niche-constructing individuals in the population effectively inoculates the population against successful invasions by large numbers of defectors.

While we initially set $b = 2$, $c = 1$, and $a = 0.1$, the cyclic, cooperative dynamics observed in Fig.3 always emerge when $b > c > a > 0$.[1] Slightly adjusting the parameter values within these constraints affects the speed of the dynamics but not their predominantly cooperative character. When $a > c$, the same general cyclic pattern still emerges, but the population also spends a significant amount of time in a third state in which niche-constructing defectors dominate. Nevertheless, such a population still spends a significant amount of time in both cooperative states, thereby maintaining a far greater degree of cooperation over the long run than could be maintained in the absence of the niche-constructing trait.

The Revised Model

Up until this point, we have assumed that the niche-constructing trait *always* effectively thwarts defectors. Given that this is a rather strong assumption, we may wonder what happens to the results described above when this assumption is relaxed. Assuming instead that the niche-

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[1] Observe that the game shown in Fig. 3 only remains a prisoner's dilemma so long as $2b - c > 0$, or $b > c$.

constructing behavior is effective only p percent of the time, and ineffective $1 - p$ percent of the time, we can use the payoffs in Fig.2 to revise the fitness equations (Eqs.1-4) given earlier in this section as follows:

Fitness of x_1 ("Doesn't dig, doesn't steal") $= bx_1 + bx_3$ **Eq. 1**

Fitness of x_2 ("Doesn't dig, steals") $= (2b - c)x_1 + (b - c)x_2 + [p(b - c) + (1 - p)(2b - c)]x_3 + [-pc + (1 - p)(b - c)]x_4$ **Eq.7**

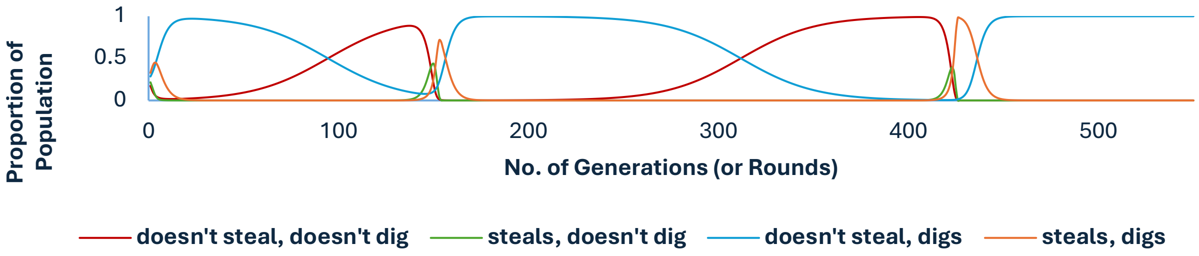
Fitness of x_3 ("Digs, doesn't steal") $= p\{(b - a)x_1 + (b - a)x_2 + (b - a)x_3 + (b - a)x_4\} + (1 - p)\{(b - a)x_1 - ax_2 + (b - a)x_3 - ax_4\}$ **Eq.8**

Fitness of x_4 ("Digs, steals") $= p\{(2b - c - a)x_1 + (2b - c - a)x_2 + [p(b - c - a) + (1 - p)(2b - c - a)]x_3 + [p(b - c - a) + (1 - p)(2b - c - a)]x_4\} + (1 - p)\{(2b - c - a)x_1 + (b - c - a)x_2 + [p(b - c - a) + (1 - p)(2b - c - a)]x_3 + [p(-c - a) + (1 - p)(b - c - a)]x_4\}$

Eq.9

Utilizing Eqs.5 and 6 as before, we can now observe the evolutionary dynamics of the population when the niche-constructing behavior is effective only p percent of the time. Setting $p = 0.75$, $b = 2$, $a = 0.1$, and $c = 1$ produces the graph shown in Fig.4, which is not too dissimilar from our original results shown in Fig.3. In fact, the cooperative dynamics are maintained so long as $p > 0.5$. Niche-constructing behaviors that thwart defectors may enable the maintenance of cooperation even when they are not 100% effective – what is important is that the niche-constructing behaviors in question are effective a *sufficient* percentage of the time.

Fig.4:



A simple inequality defining the threshold value of p can be derived as follows. For any social-behavioral type x_i in the well-mixed population, let F_2 equal the average fitness of the type when it engages in niche-constructing behavior and F_1 equal the average fitness of the type when it does not. If we denote the average cost of engaging in the niche-constructing behavior as C, it is advantageous for the type x_i to perform the behavior at any given point in time iff

$$p(F_2) + (1 - p)(F_1) - C > F_1$$ **Eq.10**

or

$$p > \frac{C}{F_2 - F_1}$$ **Eq.11.**

If we allow B to represent the average fitness benefit gained from niche construction, thereby substituting B for $F_2 - F_1$ in Eq.11, we obtain

$$p > \frac{C}{B}$$ **Eq. 12**

which is structurally analogous to Hamilton's rule. Hamilton's (1964) rule, in its classical form, asserts that altruistic behavior evolves in the event that the coefficient of relatedness, r, exceeds the ratio of the cost of altruism for the giver to the fitness benefit for the recipient:

$$r > \frac{c}{b} \qquad \textbf{Eq.13.}$$

Such structural similarities appear consistent with the recent work of van Veelen (2025), who asserts that the classical form of Hamilton's rule is but one of many specific interrelated rules, some of which apply to non-social traits, that proceed from a general version of Hamilton's rule. Moreover, Eq.12 is applicable not only to defection-thwarting niche-constructing behaviors that arise within the context of the prisoner's dilemma, but to *any* niche-constructing behavior that enhances the fitness of at least one social-behavioral type within the context of *any* game. While I have here demonstrated that such fitness-enhancing niche-constructing behaviors have a tendency to transform the prisoner's dilemma in a way that facilitates the evolution of cooperation, it is possible for other types of unexpected coevolutionary dynamics involving niche-constructing behaviors to arise in other types of evolutionary games in which Eq.12 applies. (For example, in the context of a "chicken" or hawk-dove game, any niche-constructing behavior that increases the average cost incurred by players who "drive straight" can, at least temporarily, create a nearly monomorphic population of players who "swerve.")

I derived Eq.12 under the assumption that the niche-constructing behavior successfully increases the average fitness of the type x_i only p percent of the time. If, however, we revert to our earlier assumption that performing the niche-constructing behavior *always* increases the average fitness of type x_i, Eq.12 becomes

$$1 > \frac{C}{B} \qquad \textbf{Eq.14}$$

or $B > C$. Therefore, when the niche-constructing behavior is assumed to always enhance the fitness of type x_i, it will acquire the behavior so long as the fitness benefit exceeds the cost.

Conclusion

In this paper, I have done two things. First, I have demonstrated that stable, long-run patterns of cooperative behavior can emerge from the prisoner's dilemma with the assistance of a coevolving niche-constructing trait that successfully thwarts defectors (or reduces the temptation to defect) with some threshold probability p. Some recent work has explored the possibility that defection-thwarting behaviors may enable the evolution of cooperation in the presence of *other* cooperation-promoting mechanisms, including recognition mechanisms and conditional strategies (Zhang and Hu, 2026; Gao, Pan, and He, 2022). However, this paper is, to my knowledge, the first to suggest that defection-thwarting niche-constructing behaviors, taken on their own, are *sufficient* to promote the emergence of cooperation in one-shot games, in the absence of any other mechanism(s). Secondly, I have argued that such counterintuitive evolutionary dynamics may emerge not only from the prisoner's dilemma, but across a variety of game-theoretic contexts in which niche-constructing behaviors coevolve with other traits.

One final note. Observe that theoretical biologists often assert two mutually inconsistent claims about niche construction: (a) that a population's 'niche' consists of the sum of all selective pressures acting on the population and (b) that niche construction modifies selective pressures only via processes of physical environmental change. The style of model presented in this paper is consistent with claim (a), insofar as it can accommodate alterations in selection pressures (payoffs) that proceed from organism-induced changes in the physical environment in which a game is played (e.g., the additional holes dug by our squirrels) as well as similar types of alterations in selection pressures (payoffs) that proceed from organism-induced changes in other aspects of game environments that are less physical or tangible. Within the context of the model, niche-constructing behaviors just *are* those behaviors that create feedback loops by modifying payoffs. The advantage of such a model is that it possesses greater generalizability and wider applicability than previous game-theoretic models that have narrowly focused on player-induced modifications to entirely nonphysical “interaction environments” (e.g., Gao, Pan, and He, 2021) or evolutionary feedback loops within specific types of physical ecosystems (e.g., Tilman, Plotkin, and Akçay, 2020).

References

Axelrod, Robert, and William D. Hamilton. 1981. “The Evolution of Cooperation.” *Science* 211 (4489):1390-1396.

Bergman, Aviv, and Bojana Gligorijevic. 2015. “Niche Construction Game Cancer Cells Play.” *Eur. Phys. J. Plus* 130:203.

Gao, Liyan, Qiuhui Pan, and Mingfeng He. 2022. “Advanced Defensive Cooperators Promote Cooperation in the Prisoner’s Dilemma Game.” *Chaos, Solitons, & Fractals* 155 (111663).

Gao, Liyan, Qiuhui Pan, and Mingfeng He. 2021. “Environmental-Based Defensive Promotes Cooperation in the Prisoner’s Dilemma Game.” *Applied Mathematics and Computation* 401 (5821):126074.

Godfrey-Smith, Peter. 1996. *Complexity and the Function of Mind in Nature.* Cambridge: Cambridge University Press.

Hamilton, William D. 1964. “The Genetical Evolution of Social Behavior I & II.” *Journal of Theoretical Biology* 7:1-32.

Lehmann, Laurent. 2008. “The Adaptive Dynamics of Niche Constructing Traits in Spatially Subdivided Populations: Evolving Posthumous Extended Phenotypes.” *Evolution* 62 (3):549-566.

Lewontin, Richard C. 1983. “Gene, Organism, and Environment.” In *Evolution from Molecules to Men*, ed. D.S. Bendall, 273-285. Cambridge: Cambridge University Press.

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. 2003. *Niche Construction: The Neglected Process in Evolution.* Princeton: Princeton University Press.

Odling-Smee, F. John. 1988. “Niche-Constructing Phenotypes.” In *The Role of Behavior in Evolution*, ed. H.C. Plotkin, 73-132. Cambridge: The MIT Press.

Powers, Simon T. 2010. “Social Niche Construction: Evolutionary Explanations for Cooperative Group Formation.” *University of Southampton, School of Electronics and Computer Science, Doctoral Thesis*, 186pp.

Steele, Michael A., Sylvia L. Halkin, Peter D. Smallwood, Thomas J. McKenna, Katerina Mitsopoulos, and Matthew Beam. 2008. “Cache Protection Strategies of a Scatter-Hoarding Rodent: Do Tree Squirrels Engage in Behavioral Deception?” *Animal Behavior* 75 (2):705-714.

Tilman, Andrew R., Joshua B. Plotkin, and Erol Akçay. 2020. “Evolutionary Games with Environmental Feedbacks.” *Nature Communications* 11:915.

van Veelen, Matthijs. 2025. “The General Version of Hamilton’s Rule.” *eLife* 14:RP105065.

Williams, George C. 1992. “Gaia, Nature Worship, and Biocentric Fallacies.” *Quarterly Review of Biology* 67 (4):479-486.

Zhang, Yidong, and Yuhan Hu. 2026. “The Influence of Self-Protection Ability on the Evolution of Cooperation.” *Physics Letters A* 578 (131475).