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By-product mutualism with evolving common enemies

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HIGHLIGHTS

- We consider the common-enemy hypothesis of by-product mutualism.
- We provide micro-foundations for this hypothesis, using evolutionary game theory.
- We consider an asymmetric game where the common enemy is a strategic player.
- The common enemy may or may not be able to avoid the common-enemy effect.

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ABSTRACT

The common-enemy hypothesis of by-product mutualism states that organisms cooperate when it is in their individual interests to do so, with benefits for other organisms arising as a by-product; in particular, such cooperation is hypothesized to arise when organisms face the common enemy of a sufficiently adverse environment. In an evolutionary game where two defenders can cooperate to defend a common resource, this paper analyzes the common-enemy hypothesis when adversity is endogenous, in that an attacker sets the number of attacks. As a benchmark, we first consider exogenous adversity, where adversity is not subject to evolution. In this case, the common-enemy hypothesis is predicted when the degree of complementarity between defenders' defensive efforts is sufficiently low. When the degree of complementarity is high, the hypothesis is predicted only when cooperation costs are high; when cooperation costs are instead low, a competing hypothesis is predicted, where adversity discourages cooperation. Second, we consider the case of endogenous adversity. In this case, we continue to predict the competing hypothesis for a high degree of complementarity and low cooperation costs. The common-enemy hypothesis, however, only continues to be predicted for the lowest degrees of complementarity.

1. Introduction

Among several explanations for cooperation among organisms (for overviews, see Dugatkin, 1997, 2002a; Sachs et al., 2004; Lehman and Keller 2006; Nowak, 2006), by-product mutualism (West Eberhard, 1975; Brown, 1983) provides a particularly straightforward rationale: organisms cooperate when it is in their individual interests to do so, and the benefits that cooperation generates for other organisms merely arise as a by-product. The common-enemy hypothesis of by-product mutualism argues that by-product mutualism particularly applies when organisms face the "common enemy of a sufficiently adverse environment" (Mesterton-Gibbons and Dugatkin, 1992, p.273), where the literature gives diverse examples of adverse environments. Increased predation risk could induce prey to jointly defend against predators (Mesterton-Gibbons and Dugatkin, 1992, p.274; Spieler, 2003; Krams et al., 2010). Predators may engage in collective hunting when facing the adverse environment of a large and difficult-to-catch prey (Scheel and Packer, 1991; Mesterton-Gibbons and Dugatkin, 1992; Dugatkin, 2002b). Further suggested examples of adverse environments that induce cooperation include scarcity in the availability of resources (Strassman et al., 2000; Callaway et al., 2002), and harsh weather conditions (Dugatkin, 1997, p. 84). Finally Roberts (2005) links adverse environments to a higher degree of interdependence between cooperating organisms.

In examples where the common enemy takes the form of the physical environment, such as bad weather conditions, the level of adversity is exogenously given, in that it does not itself respond to the level of cooperation among the cooperating organisms (*exogenous adversity*). Yet, when the level of adversity is determined by the behavior or characteristics of another organism, such as the intensity with which a predator hunts in case of cooperatively defending prey, or the size of a prey in case of cooperatively hunting predators, the level of adversity may itself be subject to

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evolution, and may adapt to the level of cooperation among the cooperating organisms (*endogenous adversity*). Our paper shares the purpose of making adversity endogenous with Arenas et al. (2011). These authors extend the standard multi-player public goods game, by introducing a third strategy in the form of a "joker strategy", on top of the standard strategies of cooperating and of defecting. Jokers are assumed to always have the same payoff, and reduce the value of the public good by a fixed amount. Whereas in the absence of jokers only joint defection can evolve, the presence of jokers can lead to rock-scissors-papers dynamics, where a fraction of the population cooperates at any given point of time.

Our analysis differs from Arenas et al. (2011), in that we instead turn a variant of the standard public goods game into an asymmetric game, by adding a population of adversaries who are matched to the population of players playing the public goods game, who are worse off the higher the value of the public good produced by the players to whom they are matched, and who can either make few or many attempts to reduce the value of this public good. This alternative approach allows us to investigate the following question: if increased adversity, through the common-enemy effect, makes a first group of organisms (e.g. prey) cooperate more often, should a second group of organisms (e.g., predators) that determines the level of adversity and that has lower fitness the higher the level of cooperation, then not evolve to keep adversity limited, thus preventing the common-enemy effect from coming into force?

We investigate this question by adapting the game-theoretic model of collective defense by De Jaegher and Hoyer (2016a). In this model, two defenders face a number of random attacks, and individually decide either to cooperate (= defend) or to defect (= not defend). The authors investigate the effect of an increase in the number of attacks. Results depend on the degree of complementarity between defenders' defensive efforts, i.e. the degree to which each defender's defensive effort is critical in ensuring collective defense. When the degree of complementarity is high, for high cooperation costs, the size of the basin of attraction of an evolutionary stable strategy (or ESS; Maynard Smith and Price, 1973) where both defenders cooperate is larger the higher the number of attacks (common-enemy effect). This is because the dominant effect of an increase in the number of attacks is that it becomes less attractive for defenders to deviate from joint cooperation. When the degree of complementarity is high but cooperation costs are instead low, the size of the basin of attraction of an ESS where both defenders cooperate is smaller the higher the number of attacks (competing effect). This time, the dominant effect of an increase in the number of attacks is that it becomes less attractive for defenders to deviate from joint defection. For lower degrees of complementarity, a higher number of attacks makes it more attractive to defend independently of the other defender's behavior, and the common-enemy effect is always obtained.

As shown in the current paper, when the number of attacks is endogenous in being set by an attacker, the competing effect continues to be predicted for high complementarity and low cooperation costs. The common-enemy effect, however, is only fully maintained for the lowest degrees of complementarity. Intuitively, let attacking costs initially be high, so that attackers attack few times. If cooperation costs are high, defenders will still always defect. If attacking costs now decrease, leading attackers to attack more often, by the reasoning above, when complementarity is high it becomes less attractive for defenders to deviate from joint cooperation, and the common-enemy effect may apply, in that joint cooperation is achieved. Yet, once defenders have achieved joint cooperation, it is no longer worthwhile for attackers to attack more often, and the common-enemy effect is undone. The common-enemy effect becomes self-defeating, in the sense that once a high number of attacks have lead to joint cooperation, attackers no longer have an incentive to launch many attacks. When complementarity is low, an increase in the number of attacks after a decrease in attacking costs, does not lead defenders to achieve joint cooperation, but only makes a higher fraction of defenders cooperate. For this reason, attackers continue to attack when the common-enemy effect applies, and the common-enemy effect is no longer self-defeating.

The paper is structured as follows. Section 2 presents the model. As a benchmark, Section 3 shortly treats the case of exogenous adversity. Section 4 contains the central results of this paper. We end with a discussion in Section 5.

2. The model

We consider the following evolutionary game played by two infinitely large populations of defenders and attackers (for convenience, an attacker is referred to as "she" and a defender as "he"). At each point of time, two defenders are randomly matched to each other, and at the same time to one randomly-chosen attacker. Each attack by an attacker is targeted at a single, randomly chosen defender among the two defenders to whom she is matched. An attacker can launch either one ($A = 1$) or two ($A = 2$) random attacks on the two defenders to whom she is matched. When $A = 2$, the two attacks (interpreted as a process of statistical sampling of the two defenders) take place in a process of sampling with replacement, so that by coincidence the same defender may be attacked twice.

Any two defenders who are matched to each other hold a common resource, from which they always obtain the same fitness. Each defender either plays C (cooperates) or plays D (defects). Playing C means exerting effort to defend the common resource, and comes at a cost c; playing D means not exerting any effort, and incurring zero costs. If only one defender is attacked (which occurs either when $A = 1$, or when $A = 2$ but the same defender is by chance attacked twice), then what the other defender plays does not matter for the fitness both defenders obtain from their common resource. If the solely-attacked defender plays C, both defenders obtain the maximal fitness V from the common resource; if the solely-attacked defender plays D, both defenders obtain fitness $(1 - k)V$ net of cooperation costs, with $0 < k \leq 1$, where k is the *degree of complementarity* (see below). If both defenders are attacked (which occurs when $A = 2$, and by chance a different attacker is each time attacked), when they both play C, both obtain maximal fitness V from the common resource; when one plays C and the other D, they again both obtain fitness $(1 - k)V$ from the common resource; when they both play D, they both obtain zero fitness.

Restating the model, each defender may be seen as either contributing to the preservation of the fitness V obtained from the common resource, or not contributing. A defender may contribute in two ways: either by being attacked but playing C, or by not being attacked (in which case it does not matter whether he plays C or D). A defender does not contribute when playing D and being attacked. With this restatement of the model, the parameter k is more easily interpreted as the degree of complementarity (Ray et al., 2007) between the defenders' contributions, where $k = 1$ means perfect complementarity (= only when both defenders contribute can nonzero fitness be obtained); k=½ means that the defenders' contributions are perfect substitutes (= a second contributing defender adds as much to fitness as a first contributing