The Population Dynamics of Obligately Cooperative Species Are Inherently Unstable

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Abstract

Cooperative acts is widely observed in nature. Because cooperation allows individuals to choose their associations based on differences in fitness opportunities, such behaviors directly influence population dynamics. Cooperative acts can be classified into two types: facultative and obligate. Facultative cooperation seen in starling murmurations, fish schools, and locust swarms grant the actors full choice over their associations since the consequences of non-cooperation are not severe. Obligate cooperation like that of canids, cetaceans, primates, and eusocial insects only grant partial actor choice as the consequences of non-cooperation are more severe. The population dynamics of facultative cooperative species are well-modeled, but not so for obligate co-operators. In this paper, we model and analyze the population dynamics of obligate cooperators by embedding a game theoretic behavioral dynamic into a within group population dynamic with additional between group dynamics. Our model confirms previous results showing within group cooperation leading to unstable population dynamics and go further by showing that more groups lead to greater population instability. Our behavioral analysis also shows that stable population equilibria will lead to behavioral instabilities. From there, we generalize our results to show that obligate cooperative species can never achieve full stability due to the fundamental mismatch between the stability of the behavioral equilibrium (ESS) and the stability of the population size equilibrium. Our results, general enough to apply to most systems, show that the constant group turnover seen in obligately cooperative species are not necessarily a function of external stochastic events but instead inherent to their dynamics.

Significance

Obligately cooperative species show population dynamics of constant group turnover. Through mathematical analysis, we show that these dynamics are intrinsic and unavoidable. Other factors may exacerbate the instability but can only be secondary. Processes like group fusion or costs to group splitting can help further stabilize dynamics though not sufficiently to overcome overall instability. Because the instability arises out of a non-chaotic deterministic process, the dynamics are predictable and can be tested against experiments and simulations. In addition, this instability means cooperative species are particularly vulnerable and require large protected areas compared to their non-cooperative counterparts. We feel this work can prove to be a starting point for further research into the population dynamics of obligately cooperative species.

Introduction

Cooperation – where an action of an individual benefits a recipient – is widely observed in nature, from the level of genes to organisms, despite being seemingly maladaptive (West et al., 2007; Nowak, 2006). The origination and persistence of cooperative behaviors has puzzled scientists in both evolution and ecology for decades (Darwin, 1871; Hamilton, 1964; Axelrod, 1981). Within ecology, the question is "how is cooperation maintained through time?" Whether studied mathematically or experimentally, between or within populations, ecologists have frequently noted that adding cooperation and mutual benefit to population dynamics destabilizes the population equilibrium (Briand and Yodzis, 1982; Aviles, 1997; Aviles, 1999; Wang et al., 1999; Lopez-Ruiz and Fournier-Prunaret, 2004; Graham et al., 2007; Yurtsev et al., 2016). May (1981) described this as an "orgy of mutual benefaction", especially when the cooperation is obligate. Including processes such as negative density dependence, non-linear benefits and diminishing returns, predation, and frequency dependence can restore stability to mutualistic interactions (Vandermeer and Boucher, 1978; Boucher et al., 1982). Such effects have been considered for cooperation between populations and not for within population interactions. Whether the population dynamics of within population cooperators can achieve stability has yet to be studied.

Cooperation can be thought of quite simply as a trade-off. An individual will associate with others if the benefits, measured in terms of fitness, outweigh the costs (Hamilton, 1964). If cooperating with other individuals leads to greater fitness, then cooperative individuals will do better than non-cooperative individuals. As more individuals cooperate, this leads to a larger group level of cooperation which is the aggregation of each individual's cooperative acts (Dugatkin, 1998). In terms of population dynamics, this is often modelled as an Allee effect, or

the positive relationship between an individual's fitness and its associations in that group, typically measured as group size (Allee, 1931; Allee, 1938; Trivers, 1971; Axelrod and Hamilton, 1981; reviewed in Dugatkin, 1998 and Nowak, 2006; Stephens et al., 1999). The addition of an Allee effect leads to an (often-ignored) interplay between the associations of members within a group and their fitness.

E. O. Wilson (1975) recognized two broad subtypes of cooperation within groups, casual and demographic. In casual societies, there are high immigration and emigration rates, short timescales of membership, and consequently little to no lasting impact on an individual's fitness. Examples may include murmurations of starlings or schools of fish. Demographic societies, on the other hand, have much less migration between groups thereby existing long enough to affect longer term fitness. These include most social primates, canids, cetaceans, elephants, lions, and eusocial insects. The reason for this temporal division is due to the nature of cooperation within each society. In casual societies, cooperation between individuals is merely facultative. Benefits are gained from cooperation but are not necessary for an individual or mating pair to succeed. In demographic societies, the cooperation is obligate and individuals are reliant on other members of the group. Facultative and obligate forms of cooperation should have different consequences for the population dynamics of cooperative species.

Game theory provides a common modelling tool for understanding cooperation as an adaptation. Coalition game theory, in particular, deals with how individuals will aggregate into groups or coalitions when given different rewards based upon their coalition and its size. Scientists studying swarm dynamics model coalitions using game theory to determine the distribution of group sizes (Couzin and Krause, 2003; Okubo, 1986). These models work well for facultatively cooperative species as they grant actors full choice over their associations with

individuals freely joining and leaving groups (Gueron and Levin, 1994; Zemel and Lubin, 1995; Gueron et al., 1996; Bonabeau et al., 1999; Mirabet et al., 2007; Saffre and Deneubourg, 2002). Such models may not apply to obligately cooperative species who may be more limited in their ability to unilaterally move from one group to another. In addition, many models of swarm dynamics ignore the consequences of behavioral choices on population dynamics. We suggest that models which are more reflective of the biology of obligately cooperate species and include behavioral and population dynamics will lead to quite different equilibrial and/or non-equilibrial states.

Attempts have been made to model the population dynamics of obligately cooperative species. When doing so, many scientists model the population dynamics of each group, viewing them as fixed entities (Aviles, 1999; Wang et al., 1999; Courchamp et al., 1999; Courchamp et al., 2000; Dennis, 2002). In the vein of the patch model framework, an individual's fitness is heavily dependent upon the group in which it lives (Chesson, 1981; Durrett and Levin, 1994). Switching between groups is costly, if impossible. While these models recognize the difficulty of disallowing unilateral immigration and emigration from a group happens, they ignore the process completely, implicitly assuming that individuals within a group will still associate even as an individual's fitness declines with increasing group size. This absence of individual choice creates an assumed stability in the population dynamics and decouples the different groups even when these groups may be well aware of each other. If individuals can choose their associations, the stability properties of the population dynamics may change for obligately cooperative species.

In this paper, we model the population dynamics of obligately cooperative species in two ways. First, we construct and analyze a model of population dynamics that has a behavioral game embedded inside. In this model, each group has its own population dynamic with Allee

effects within groups. We assume that individuals cannot unilaterally move from one group to another but can move when a certain requirement is met. We separately analyze the population dynamics and the behavioral dynamics of the model before combining the two. From there, we relax our assumptions and generalize our analysis to include movement between groups based on individual choice. In this case, we show that a stable population size is not an evolutionarily stable strategy (ESS) for individual choice and that at the ESS for individual choice, population dynamics cannot be fully stable. The model can result in a stable equilibrium of choice dynamics or population dynamics but never both. We provide candidate examples from nature of our modeled dynamics and suggest future applications for this new model.

Model Dynamics

Population Dynamics

To first understand the population dynamics of obligately cooperative societies, we construct and analyze a simple mathematical model inspired by the biology of obligate cooperators, e.g. meerkats, naked mole rats, social weavers, social spiders, elephants, etc. We imagine a site filled with multiple herds or groups. Each group has its own population dynamics in which fitness is defined as per-capita growth rate (measured as average individual reproduction).

The fitness function (per capita growth rate) for each group is given by equation (1).

$$F(x_i, x_R) = r\left(\frac{x_i}{M} - \frac{x_i^2}{M^2}\right) - \alpha x_R \tag{1}$$

In this equation, x_i is the size of the focal group, x_R is the cumulative population size of all other groups $\sum x_{-i}$, r is a growth rate scaling factor, M measures the capacity of each group to support group members (if there is just one group, it is the group's carrying capacity), and α is the strength of intergroup competition (potentially determined by the depletion of resources or

shared space by all groups). For the sake of tractability, we imagine that all individuals are identical, distinguished only by whether they are within or outside the group and that each group possesses the same fitness function with the same parameters. This leads to two assumptions: that all individuals within a group are uniform in fitness and that it is only the number of individuals and not the properties of the individual that determines fitness within a group. Since all individuals are identical, all groups have the same fitness function allowing us to rescale per-capita growth rates by r to give:

$$F(x_i, x_R) = \frac{x_i}{M} - \frac{x_i^2}{M^2} - \alpha_r x_R \tag{2}$$

where $\alpha_r = \frac{\alpha}{r}$ is the ratio of the strength of intergroup competition to the growth rate scaling factor. Let us denote the equilibrium population size of the group as x_F^*. Solving for x_F^*, we obtain two roots of the model where $x_F^* = \frac{M}{2}\left(1 \pm \sqrt{1 - 4\alpha_r x_R}\right)$.

This equation has an Allee effect where fitness at first increases $\left(x_i < \frac{M}{2}\right)$ and then decreases $\left(x_i > \frac{M}{2}\right)$ with group size (Fig. 1a) unlike strict competition in which fitness monotonically declines with group size (Fig. 1b) (Allee, 1931; Allee, 1938). The first two terms of equation (2) define these intra-group dynamics where the first term represents the fitness benefits of group living and the second term represents the fitness costs. We imagine that individual benefits of group living and cooperation, such as foraging, defense, or other positive social interactions increases linearly while fitness costs, such as resource sharing and disease, increase super-linearly, specifically quadratically. This set-up is in keeping with the schematic illustrated by Terborgh (1983). So long as $x_i < M$, the benefits of cooperation are greater than the costs of competition and so fitness is positive; and if $x_i < \frac{M}{2}$, then the benefits of additional cooperation are greater than the costs of additional competition, an individual's marginal

contribution is positive, and the Allee effect holds. The third term of equation (2) represents loss

of fitness due to inter-group competition and is broadly assumed to be linear.

We now take a look at how groups might interact with each other via intra-group

population dynamics. This analysis replicates the same results from Wang et al. (1999), revealing

the same qualitative results with minor differences. Therefore, we go through this section fairly

briefly. With a single group, they dynamics are quite clear. There are two equilibria: $x_F^* = 0, M$.

The first equilibrium is unstable, the second is stable. Therefore, any group with positive size

will grow or shrink to M (Fig. 3a,b,c). With a single group, there is also a weak Allee effect

(fitness at $x_F^* = 0$ is 0 or positive), not the strong Allee effect (fitness at $x_F^* = 0$ is negative)

(Courchamp et al., 1999; Stephens et al., 1999).

Competition between two groups now induces a strong Allee effect with results

dependent upon the strength of inter-group competition α_r (Fig. 2). Let's denote the groups'

sizes as $x = (x_1, x_2)$ with x^* denoting an equilibrium. If $\alpha_r \geq \frac{1}{M}$, then there will be three

equilibria: $x^* = (0, M)$, $x^* = (M, 0)$, and $x^* = (0,0)$ (Fig. 2a). The first two equilibria are

locally stable; with whichever has the largest group size outcompeting the other. The third

equilibrium is saddle point stable – locally unstable except when group sizes are equal.

If $\frac{1}{3M} < \alpha_r < \frac{1}{M}$, then there is a new interior equilibrium where $x^* = (M - \alpha_r M^2, M - $

$\alpha_r M^2)$ in addition to the previous 3 (Fig. 2b,c). This new interior equilibrium now has saddle

point stability while the equilibrium of $x^* = (0,0)$ is fully unstable. $x^* = (0, M)$ and $x^* = $

$(M, 0)$ both remain locally stable.

Lastly, when $0 < \alpha_r < \frac{1}{3M}$, there are two new interior equilibria: $x^* = \left(\frac{M}{2}\left(1 + \right.\right.$

$\left.\left.\sqrt{1 - 4\alpha_r x_2}\right), \frac{M}{2}\left(1 - \sqrt{1 - 4\alpha_r x_1}\right)\right)$ and $x^* = \left(\frac{M}{2}\left(1 - \sqrt{1 - 4\alpha_r x_2}\right), \frac{M}{2}\left(1 + \sqrt{1 - 4\alpha_r x_1}\right)\right)$.

These two new interior equilibria are partially stable while $x^* = (M - \alpha_r M^2, M - \alpha_r M^2)$ now becomes locally stable (Fig. 2d). In the previous case when $\alpha_r > \frac{1}{3M}$, the instability of the equilibria were driven by inter-group competition. Because competition was stronger, any size advantage led the smaller group to be driven to extinction. In this case of weak competition though, the Allee effect and its associated extinction threshold determines the outcome of within and between group population dynamics. If initial population sizes have both above their extinction thresholds, then coexistence will result at the interior equilibrium. If initial population sizes has one group below its extinction threshold then it will go extinct and the other group's size will go to M. As intergroup competition goes to 0, the interior equilibrium of $x^* = (M, M)$ becomes globally stable and the three equilibria of $x^* = (0,0)$, $x^* = (M, 0)$ and $x^* = (0, M)$ become unstable.

With two groups, instability occurs first from the inherent advantage accruing to the group with the larger population size (inter-group competition) and later the within group dynamic associated with the Allee effect and extinction threshold. As we add additional groups, the same fundamental dynamics remain. The only difference is that inter-group competition must be ever weaker for the interior equilibrium to be locally stable. Specifically, inter-group competition must be scaled by a multiple of $\frac{1}{k-1}$ where k is the number of groups to achieve the same dynamics. Inter-group competition must be lower and lower if an interior equilibrium is to maintain its stability as groups are added. If not, then *the addition of more groups destabilizes the interior equilibrium and ensures the extinction of some groups*.

With population dynamics in hand, we now turn to behavioral dynamics.

Behavioral Dynamics

A behavioral game of association can be embedded into equation (2). Individuals may want leave their present group and join another so as to increase their fitness. Since each individual is identical, only group size determines the fitness of each member. Coalition game theory can tell us how associations will form or disband based upon the payoff to the individuals. We make the key assumption that individuals have limited information. Specifically, we assume that individuals only know how fitness changes with the size of the individual's group, i.e. the marginal contribution of an additional memberto average fitness.

Taking partial derivative of the fitness function with respect to x_i, hereafter known as the association function $A(x_i)$, indicates the marginal contribution of an individual to the others' fitness. In the case of strictly competitive models, the association function will always be negative as each extra individual decreases the fitness of others (Fig. 1d). With the addition of the Allee effect, the association function now has domains where it is positive (Fig 1c). In our model, the association function is:

$$A(x_i) = \frac{\partial F(x_i)}{\partial x_i} = \frac{1}{M}\left(1 - \frac{2x_i}{M}\right) \tag{3}$$

It starts at a positive point $\frac{1}{M}$ and declines linearly with group size. According to coalition game theory, each individual prefers to be in a group whose size maximizes its fitness. This corresponds to the optimal group size x_A^* where $A(x_A^*) = 0$. Solving for this optimal group size, we get $x_A^* = \frac{M}{2}$. At this group size, no member of the group can do better by unilaterally leaving its present group. Such a group size is a Nash equilibrium for the behavioral game of selecting groups. But, will behavioral dynamics result in the Nash equilibrium?

To initially characterize the behavioral dynamics, we start with a single group that therefore faces no inter-group competition $(\alpha_r x_R = 0)$. For this specific behavioral game, we also assume that groups can only split (i.e. members can only leave a group and not join other

groups), group size only increases through reproduction, splits only happen when fitness across all groups is 0, and the splitting process is permanent with each new group is granted its own population dynamic.

A single group by itself will grow so long as its size is positive and less than $x_F^* = M$ (Fig 3a,b,c). According to coalition game theory, group members will prefer to be at the optimal group size $x_A^* = \frac{M}{2}$ (Fig 3b). However, fitness at optimal group size is positive ($F(x_A^*, 0) > 0$) meaning members of the group will continue to reproduce until fitness is 0 at the final group size $x_F^* > x_A^*$. Because $A(x_F^*) < 0$ (Fig. 3c), this creates a mismatch between the optimal group size and the final group size. Since fitness at the final group size is lower than fitness at optimal group size ($F(x_F^*, 0) < F(x_A^*, 0)$), there is a strong incentive for the members to form separate groups of size x_A^* than to stay in one group of size x_F^*. Therefore, as the group's size reaches x_F^*, it will split into two groups, both of size $x_A^* = \frac{M}{2}$ (Fig. 3d).

When a group is facing competition, there are two options. Firstly, if x_F^* is equal the smaller root, then it is smaller than x_A^*. In this case, there is no incentive for the group members to split as it will lead to a decrease in fitness. If x_F^* is equal to the larger root, then it is still larger than x_A^*, leading to similar dynamics. The only difference is that the sizes of each group after splitting will be unequal. The two groups will have the size $\frac{M}{2}$ and $\frac{M}{2}\sqrt{1 - 4\alpha_r x_R}$ (Note: in this case, it is the members of the larger group that leave the original group to maximize their fitness). With or without inter-group competition, the basic outcome is still the same. If a group is of a size larger than x_A^*, *then it will split into two and new groups will be created.*

Now with population and behavioral dynamics analyzed separately, we can combine them to derive a full picture of the population dynamics of cooperative species. We do this by investigating the possibility of a joint equilibrium and show that there is no such possibility.

Total Population Dynamics

Analysis of within group population dynamics shows that any fully stable equilibrium must have all groups at a size greater than x_A^* and that more groups in a system leads to greater instability. Analysis of behavioral dynamics shows that new groups will be formed so long as a group's size is beyond x_A^*. Combining the two results, we get the main result: *over time, the behavioral dynamics of cooperative species will tend towards more groups when population dynamics are stable, and a stable behavioral equilibrium will lead to unstable population dynamics and an eventual collapse of group numbers.* We now show this analytically.

Starting with one group, that group will grow to a final group size x_F^*. From there, it will split into two groups of optimal group size x_A^*. At this point, the size of the rest of the population x_R is equal to x_A^*. Solving for fitness at this point, we get $F(x_A^*, x_A^*) = 0.25 - \alpha_r \frac{M}{2}$. The size of inter-group competition α_r will determine the long term dynamics of our system. There are two thresholds of α_r. There is the main threshold T_1 which divides competition into strong and weak, and a secondary threshold $T_2 > T_1$ which divides strong competition further into moderately strong and extremely strong. These three strengths of competition – extremely strong, moderately strong, and weak – correspond to the dynamics of total extinction, unstable equilibria, and group turnover respectively.

Total Extinction and Unstable Equilibria

Starting with a single group, it will grow to size M and then split into two groups of size $\frac{M}{2}$. Our main threshold of inter-group competition T_1 determines the fitness of two groups just after splitting. In our model, $T_1 = \frac{1}{2M}$. If $\alpha_r > T_1$, then the fitness of the groups is negative $F(x_A^*, x_A^*) < 0$ meaning both groups will decline in size and decline simultaneously due to the groups' equal sizes. The decline in size of the focal group will cause individual fitness to lower

for that group, but the decline of the other group will also cause the fitness of individuals of the focal group to rise due to release from inter-group competition. Since both groups shrink at the same time, the balance between the rise and fall of fitness governs whether the groups will reach a positive equilibrium group size less than x_A^* or go extinct; this is determined by the second threshold $T_2 = \frac{1}{M}$. This threshold maps neatly onto the α_r noted in section on population dynamics.

Group Turnover

If $0 < \alpha_r < T_1$, then inter-group competition is weak and a more interesting dynamic occurs. Because T_1 does not map neatly onto the domain of α_r in the fitness dynamics, we analyze these dynamics separately. Here $F(x_A^*, x_A^*) > 0$ meaning both groups will grow until reaching a new x_F^*. With $x_R > 0$, the roots of the fitness function are no longer 0 and M but X^* and Y^*, $0 < X^* < x_A^* < Y^* < M$. Here Y^* is the size of the groups at fitness equilibrium, and X^* is the extinction threshold of each group. As stated before, a group at a fitness equilibrium smaller than M will split into unequal group sizes, and the extinction threshold acts as a basin of attraction for various stable states. Therefore, in a multigroup population, it is the fitness of individuals in the smallest group that drives the dynamics. Let $x_{s,n}$ be the size of the smallest group, $X_{s,n}^*$ and $Y_{s,n}^*$ the roots of the fitness function for the smallest group and $x_{R,n}$ the size of the rest of the population from the perspective of the smallest group, all after the n-th split. After the first split, both groups grow from x_A^* to $Y_{s,1}^*$. Members will be behaviorally unstable at this point and each group will split, giving us four groups: two larger groups of size x_A^* and two smaller groups of size $x_{s,2} = Y_{s,1}^* - x_A^* = \frac{M}{2}\left(\sqrt{1 - 4\alpha_r x_{R,1}}\right)$. As well, $x_{R,2} = M + \frac{M}{2}\sqrt{1 - 4\alpha_r x_{R,1}}$ with the two new roots $X_{s,2}^*, Y_{s,2}^*$. If $x_{s,2} \gg X_{s,2}^*$, then the process repeats with all four groups growing and

then splitting to give rise to eight groups, four large and four small. As long as $x_{s,n} \gg X_n^*$, the doubling of the groups (half of them large and half of them small) will continue.

After a certain split $ℏ$, the smaller groups will eventually go extinct and be extirpated, resetting the system to the previous state and leading to a cycle of groups splitting unevenly with smaller groups being extirpated and large groups growing back to previous size i.e. group turnover. The turnover dynamic depends upon a threshold value of x_R. Determining when this occurs is tricky though as it can happen even when $x_{s,ℏ} > X_{s,ℏ}^*$, $F(x_{s,ℏ}, x_{R,ℏ}) > 0$. We can find an upper bound to x_R. When $x_{s,n} \leq X_{s,n}^*$, individuals within the smaller group will have negative or zero fitness $F(x_{s,n}, x_{R,n}) \leq 0$ which guarantees turnover dynamics as the larger groups have positive fitness leading to their growth which then lowers the fitness of the smaller group. The x_R which makes $x_s = X^*$ is the upper bound. Solving for this, we get $x_R = \frac{1}{4\alpha_r} - \frac{1}{16\alpha_r}(1 - 2\alpha_r M)^2$ (see SI for full work). This population is of a finite size and will be reached after some period of time, meaning that there will be eventual cycles with groups forming and being extirpated (Fig. 4).

Additional Dynamics

Using a more general version of the model (see SI), we can reveal two new dynamics: budding and multiple splitting. In our model, the fitness function was symmetrical on the interval $[0, M]$. If the fitness function is asymmetrical, then we could get an optimal group size x_A^* greater than or less than $\frac{M}{2}$.

If $x_A^* > \frac{M}{2}$, then there is still splitting into two groups where one is larger than the other, $x_1 = x_A^* > x_2$. In this case, the first group will always exert a stronger competitive effect on the other group and so $F(x_1, x_2) > F(x_2, x_1)$. If in addition at least $F(x_2, x_1) \leq 0$, then the second group will be extirpated while the other persists. This leads to a continual budding process in

which a smaller group is split off from a larger group only to summarily be extirpated. If $F(x_2, x_1) > 0$, then we can get additional outcomes.

If $x_A^* < \frac{M}{2}$, then there will be splitting into multiple groups. In the absence of inter-group competition, a group of size M will break off into n_g groups where n_g is $\frac{M}{x_A^*}$ rounded up $\left(n_g = \left\lceil \frac{M}{x_A^*} \right\rceil \right)$. If $\frac{M}{x_A^*}$ is not an integer, then there will be a straggler group of size of $M - kx_A^*, k = \left\lfloor \frac{M}{x_A^*} \right\rfloor$. Because not all groups are necessarily of the same size, the dynamics are generally harder to analyze but should follow the same basic format of total extinction, unstable equilibria, and group turnover. We refer the readers to the supplementary information for full analysis of this section.

General Argument of Instability

Here, we present the general argument that no cooperative society can achieve a fully stable population equilibrium through the embedding of a behavioral game within fitness dynamics. We keep the majority of our earlier assumptions but now allow individuals to join groups and behavioral dynamics to occur regardless of whether or not a group is at a population equilibrium. We present this argument two ways: first verbally, then mathematically.

Verbal Presentation

Within the population dynamics of obligately cooperative species, there is a behavioral game of association in play where the number of individuals in a group determines each individual's fitness. We can analyze the behavioral game by determining an individual's marginal contribution to the fitness of the other members of the group. If the marginal contribution is positive, then we say the group is in a cooperative state; if negative, competitive. Each individual's most preferred state is at a local fitness maximum. If the group is in a cooperative state, then the group will not wish to reduce members and instead will willingly

accept members if available. If the group is in a competitive state though, a reduced group size gives the members greater fitness which they will seek by removing members. Therefore, the stable behavioral equilibrium for a group happens when the individuals are at a local fitness maximum or barring that the group is in a cooperative state; if not, then the size of the group will change and the group will not be at a behavioral equilibrium.

A stable population equilibrium for a single group occurs when fitness is 0 and the marginal contribution to fitness is negative, i.e. a competitive state. In a multi-group system, this has to happen for at least one group for the entire system to be stable with regards to population dynamics. Therefore, a stable population size cannot also be a stable behavioral equilibrium for at least one of the groups. We can also say that if all groups are cooperative or at local maxima i.e. at a stable behavioral equilibirum, then the system will not be at a stable population size. *Therefore, there is always a mismatch between a stable behavioral equilibrium and a stable population size.*

We now present this formally in a mathematical framework.

Mathematical Presentation

Let $\frac{dx_i}{dt} = x_i * F_i(\vec{x})$ be the population dynamics of a group i where $F_i(\vec{x})$ is a smooth function describing per-capita growth rate of the group and $\vec{x} = \left\{x_1, x_2, \dots, x_{n_g}\right\}$ is the vector of group sizes for all groups numbering 1 to n_g. We refer to $F_i(\vec{x})$ as the fitness function.

Taking the partial derivative of $F_i(\vec{x})$ with respect to x_i and fixing all other variables to the point $\hat{x}_{-i} = \left\{\hat{x}_1, \hat{x}_2, \dots, \hat{x}_{i-1}, \hat{x}_{i+1}, \dots, \hat{x}_{n_g}\right\}$ gives us a function of association $A_i(x_i)|_{\hat{x}_{-i}} = \frac{\partial F_i(\vec{x})}{\partial x_i}$ for focal group i which states the contribution of additional members to group i. If $A_i(x_i)|_{\hat{x}_{-i}}$ is positive, then additional members increase an individual's fitness; if negative,

decrease. As previously, we say call these respective states cooperative and competitive.

$A_i(x_i)|_{\hat{x}_{-i}}$ also determines preference of individual group members under the assumption of limited information. In a cooperative state, individuals do not want the group size to decrease and will resist splitting (and in fact prefer group size to increase) while individuals in a competitive state want the group size to decrease and will seek splitting or removing individuals.

Let $x^* = \left\{ x_1^*, x_2^*, \ldots, x_{n_g}^* \right\} \geq 0$ be a solution of the equation $F_i(x^*) = 0$ of at least C^2 smoothness around x^* for all $i \in \{1, 2, \ldots, n_g\}$. Let $i^+ \in i$ be the set of all groups with positive population size. We can analyze the stability of this point through the Jacobian J. The diagonals of the Jacobian are $\dfrac{\partial \left(dx_i/dt \right)}{\partial x_i} \Big|_{x^*} = \dfrac{\partial \, (x_i * F_i(\vec{x}))}{\partial x_i} \Big|_{x^*} = F_i(x^*) + x_i^* * A_i(x_i^*) \Big|_{x_{-i}^*} = x_i^* *$ $A_i(x_i^*) \Big|_{x_{-i}^*} \ \forall \, i \in \{1, 2, \ldots, n_g\}$. As $x_i^* \geq 0$, the diagonals are either 0 or reflect the sign of the behavioral game at that point. If the equilibrium is cooperative for all groups in the set i^+ $(A_i(x_i^*)|_{\vec{x}^*} > 0 \ \forall \, i \in i^+)$, then the trace of the Jacobian is positive, $Tr(J) > 0$. Therefore as the sum of all eigenvalues is positive, at least one eigenvalue is positive. This means that population dynamics are at an asymptotically unstable equilibrium.

If at least one of the groups in i^+ is at a competitive state, then all eigenvalues could be negative, meaning the population dynamics could be at an asymptotically stable equilibrium. Those competitive groups though are at a behaviorally unstable equilibrium. Since $F_i(\vec{x})$ is C^2 smooth for all i, then there exists a point of lower population size $x_i < x_i^*$ that gives higher fitness $F_i(\{x_i, x_{-i}^*\}) > F_i(x^*)$. If this is the case, coalition game theory tells us that a coalition of x_i^* in group i will not form; instead, individuals will break off to form a group of size $\tilde{x}_i < x_i^*$ where $\tilde{x}_i$ is a group size at a maximum of the fitness function less than x_i^*.

An individual's preferred state is one that maximizes its fitness. This occurs when

$A_i(x_i^*)|_{x_{-i}^*} = 0$ and $\dfrac{\partial A_i(x_i^*)|_{x_{-i}^*}}{\partial x_i} < 0$. If there is a x^* which satisfies these conditions for all groups,

then diagonals of the Jacobian matrix J are all 0; therefore, the sum of all eigenvalues are 0. If

this is the case, then there is either a mix of positive and negative eigenvalues (meaning unstable

population dynamics) or all eigenvalues are 0. Because $\dfrac{\partial A_i(x_i^*)|_{x_{-i}^*}}{\partial x_i} < 0$, the latter corresponds to a

partially stable state and not a neutrally stable state. This means there are clear domains of

instability on whose boundary the point x^* resides.

Through a verbal and mathematical argument, we have shown that the population

dynamics of obligately cooperative species will exist in constant flux and instability.

Discussion

While we are not the first to note that local extinctions and extirpations occur in

population dynamics due to the Allee effect, we have shown them to be intrinsic and unavoidable

to the dynamics of obligately cooperative species. In ecological systems, it has been well-

documented that obligately cooperative species do not show stable population dynamics and

instead show constant group turnover (Jarvis et al., 1994; Aviles, 1997; Clutton-Brock et al.,

1999) with external factors often raised as the reasons for these dynamics. Our findings join

other mathematical analysis in generalizing the phenomenon to an intrinsic factor of obligately

cooperative species.

Many mathematical hypotheses have been developed to explain why the population

dynamics of cooperators are intrinsically unstable. Aviles (1999) noted that cooperation can

magnify reproductive output, leading to oscillations and chaotic behavior – and ultimately

extinction – of a group while Chourchamp et al. (1999) and Wang et al. (1999) both show the

importance of a within group extinction threshold. Our results align more so with the hypotheses

of Wang et al. (1999) and Courchamp et al. (1999). We extend upon their work to show that this extinction threshold will always appear due to intergroup competition regardless of whether the Allee effect is deemed strong or weak in its absence and that more groups leads to greater instability. With the addition of a behavioral game of association, we show that new groups will always be created, leading to instabilities and a collapse of group numbers. Among all these mathematical hypotheses, our results goes a step further by saying that these dynamics are not only intrinsic but unavoidable.

In addition, our results show that constant group turnover arise from a non-chaotic deterministic interactions. This means the localized group extinctions are a general, repeatable, and predictable pattern against which field studies and data can be tested. Using simulations and controlled experiments, we can now tease how attributes and traits of species along with environmental variables can affect the cooperative species' population dynamics (see Future Directions).

Short-Term Intergroup Dynamics

According to coalition game theory, individuals of a larger group will split off to form their own smaller groups if they can gain greater rewards. This exact dynamic is seen when the Allee effect is incorporated into a population model. With the Allee effect, there is now a non-zero optimal group size. Once the group size is beyond that point, there is a strong incentive for the group to split. We are not the first to understand that group splitting can occur due to an Allee effect. Crema (2014) used this exact process to understand human settlement dynamics in a simulation model. As well, fission-fusion group dynamics, permanent or otherwise, are a well-studied aspect of cooperative societies with examples ranging from ants, to cetaceans, to humans.

It must be noted that our assumptions for splitting are different from standard coalition game theory. In standard coalition game theory, players are rational (they wish to maximize their fitness), have perfect information (knowledge of the state of all groups and the environment as a whole), and the number of players is fixed. Under standard assumptions, groups will not split if competition is strong enough to force fitness at optimal group size negative, i.e. Mutually Assured Destruction. These assumptions are not biologically realistic. While players may be rational (evolution assures it), players do not have perfect information especially about the future. If players only have information about their own group, Mutually Assured Destruction cannot prevent group splitting. As well, in biological systems, the number of players is not fixed; reducing the numbers of individuals within a coalition may be one way to raise individual fitness. Infanticide is common in many species, and chimpanzees, spider monkeys, and southern muriquis can participate in lethal intragroup aggression (Kaburu et al., 2013; Valero et al., 2006; Campbell, 2006; Talebi et al., 2009). Using our more biologically reasonable assumptions, coalitions are more likely to split when the group is in a competitive state.

We see many examples of group splitting in nature. For example, in primates, rhesus monkeys (*Macaca mulatta*) groups will divide along genealogies, and subordinate male and female macaques will form subgroups that eventually permanently leave to establish their own group (Chepko-Sade and Sade, 1979; Dittus, 1988). In other social mammals, such as lions, individuals will leave natal groups to create new smaller groups (Pusey and Packer, 1987). Honey bees, having reached maximum capacity in a hive, will split through the swarming process into two or more groups as one leaves to find a new hive. Splitting of social groups may also lead to long-range dispersal of animals; such is seen in the dispersal of sponges, male hyenas, and invasive Argentine Ants (Blanquer et al., 2009; Holekamp et al., 1993; Suarez et al.

2000). Long-range dispersal is an important mechanism of biological invasions and dispersal due to splitting may provide further insight to the implications of Allee effects in biological invasions (Lodge, 1993; Taylor and Hastings, 2005). Researchers often explain group splitting by external environmental factors and increases to an individual's reproductive success. Our model corroborates with the latter, suggesting that group splitting will occur regardless of external environmental factors.

Long-Term Intergroup Dynamics

Over time, the process of groups growing and splitting results in the long-term population dynamics of that species. Under conditions of strong inter-group competition, our model illustrates an initial split followed by both groups simultaneously shrinking to extinction or some unstable equilibrial state. To see these two phenomena on a global scale is extremely unlikely. Instead, these dynamics are likely to be seen quite locally. If inter-group competition is spatially dependent, then a group that splits into two, only to remain close, might compete strongly with each, leading to one or both of their extinctions. Rather, on a larger scale, we are much more likely to see the group turnover our model exhibits under conditions of weak inter-group competition. Over longer time scales, our model shows oscillation of total population over time with repeated instances extirpations and splitting events (Fig. 4).

With weak inter-group competition, our model shows oscillatory patterns at the scale of the total population, a feature commonly seen in social animals. Such oscillations are well documented for Isle Royale National Park wolves over nearly 3 decades and similar dynamics are occurring since the re-introduction of wolves into Yellowstone National Park (Peterson and Page, 1988; Ripple and Beschta 2012). Others include large primates, wild dogs, elephants, mole-rats, mongooses, and spiders (Kalpers et al., 2003; Burrows, 1991; Armbruster and Lande,

1993; Parker and Graham 1989; Jarvis et al., 1994; Aviles, 1997; Clutton-Brock et al., 1999). It is important to distinguish that the oscillations observed here occur at the scale of the total population and are not due simply fluctuations in the groups' size. These oscillations come about through the growth-splitting-extinction process of individual groups. The Damaraland mole-rats in particular display a process much like ours with smaller, newly-founded groups more likely to die out due to competition from larger, more established groups (Jarvis et al., 1994). Jane Goodall recorded the extirpation of the Kahama chimpanzee group due to inter-group competition in 1977, supporting our results that inter-group competition is the driving factor of group extinction and extirpation (Goodall 1986).

Many long term population studies focus on the overall population and do not account for group extirpations leading researchers to seek external environmental causes as reasons. For example, recent population decline to near extirpation of the Isle Royale Wolves is attributed to genetic inbreeding or predator-prey dynamics and a call for human mediated immigration of new wolves into the Isle Royale population (Hedrik et al. 2014). While there are many environmental factors that may contribute to extirpations, especially those anthropogenic in nature, our model provides support that extirpations and group turnover are an intrinsic property of social animals, a base upon which other factors may be added.

Stabilizing Influences

Our analysis shows that population dynamics of cooperative societies are inherently unstable. That said, there are stabilizing factors that can prevent excessive group splitting and turnover. The first and most important is a fusion process. The main reason for group turnover is that groups smaller than the extinction threshold will go extinct. If these groups can fuse into larger groups, then they can escape extinction by being greater than the extinction threshold as

well as reducing intergroup competition. By including the ability for groups to fuse, the system should generally move from a state of group turnover to a partially stable equilibrium (see SI for a specific example). It must be noted though that even with fusion, population dynamics are still not fully stable.

There also may be costs associated with splitting. These costs may be in the future, such as Mutually Assured Destruction as previously discussed, or present costs, like intragroup conflict which temporarily delays and/or suppresses the fitness of the individuals. Individuals with a very high discount rate may see the splitting process as too costly compared to potential future rewards. This may delay or prevent splitting in groups, engendering stability to the system.

Additional phenomena can stabilize the population dynamics of cooperative species but only exist in theoretical realms (see SI for these examples). Overall, with our assumptions, only few biologically relevant processes can partially stabilize these dynamics, and it seems no process can fully stabilize the system.

Conservation Implications

The conservation implications of inherent instability due to the Allee effect are great for the conservation of obligately cooperative species. Stephens & Sutherland (1999) and Courchamp et al. (2008) both draw attention to conservation and the Allee effect, especially focusing on Allee effects in context of species exploitation, habitat loss, and habitat fragmentation. While the Allee effect is often thought of occurring at small population sizes, pushing them to extinction, negative density dependence can occur at both large and small population sizes (Courchamp et al. 2008) resulting in important short and long term population dynamics which should be considered for conservation efforts. Courchamp et al. (2008)

investigated consequences of fragmentation and isolation on populations experiencing Allee effects and concluded risk for extinction was high for small and very small populations regardless of isolation.

Our results point to four main effects that have significant implications for the conservation of cooperative species. Firstly, these dynamics will happen regardless of the environmental conditions, and as such, greater environmental stability will not ultimately prevent group extinction or collapse. Robust, and not stable, populations should be the goal. Secondly, the average overall population size over time will be smaller than the potential carrying capacity, and the overall population more prone to total extinction due to the constant fluctuations. Therefore, maximizing overall population is critical. Thirdly, there must be a sufficiently large population to allow smaller groups to fuse. The smaller the group, the more likely it is to be below their internal extinction threshold. By fusing, these smaller groups can avoid the extinction threshold which also has the benefit of boosting average overall population size. And lastly, stronger inter-group competition is more likely to lead to unstable dynamics. Diminished resources and lack of territory between groups can enhance competition and lead to greater instability.

All four of the reasons point to the disproportionate impact that habitat fragmentation and loss has on obligate cooperative species. Often conservation practices are implemented over smaller scales, with protection for species being implemented in a distinct area of land or for a specific group of that species. Instead, protections must be implemented over as single large conservation areas over several small ones (SLOSS) (MacArthur and Wilson 1967, Diamond 1975, Simberloff and Abele 1982). A single large conservation area will not only help mitigate issues such as inbreeding depression, but also help stabilize population dynamics. Large

conservation areas which cover multiple groups will ensure there is minimal inter-group competition, a population large and spread out enough to withstand any negative environmental stochasticity, and a robust fusion process to stabilize population dynamics.

In addition, while much has been learned from the social structure of species of high conservation concern (Pusey et al. 2007), our findings suggest future research and conservation efforts should add inter-group dynamics as a major driver for maintaining species population.

Future directions

We provide a basic model to derive and understand the population dynamics of obligately cooperative species, but like any model, it does not fully address many of these species attributes. Many of the assumptions we make are simple, especially that all individuals are uniform and identical. Fitness is not identical among all members of a group, with breeding often reserved for specific members, and not all types of members are equally valuable. As well, we do not explicitly have a hierarchical organization among members of a group. We also make the assumption that the group members only leave when all fitness is at zero. Many times group members leave or are ejected before then, now faced with joining an established group or banding together with other ejected members to create a new group. How adding these attributes affects the population dynamics remains to be seen but should not affect the general argument of instability as it is a statement on the state of the population structure at a single point in time and not the dynamics.

As well as more realistic assumptions, we can also add more interesting features to the model to understand other aspects of obligately group dynamics. Such features would include meta-population dynamics, source-sink dynamics, evolution, spatial effects, limited resources, and manipulations of intergroup competition including non-linear competition, asymmetric

competition, exploitative vs. interference competition, and fixed and variable intergroup costs.

Evolution in particular may yet prove fruitful. One way a group may escape the effects of

competition in this model is by increasing its growth rate. α_r, though often noted as inter-group

competition, took into account growth rate. A larger growth rate works to minimize α_r. We can

see this in Figure 4. After the second splitting event, the light blue group that goes extinct has a

larger maximal group size and larger initial size (and therefore exerts greater competitive force)

but a smaller growth rate than either the purple or gold group which persist. This suggests that a

higher growth rate is more important against competition than a larger group size. This lines up

with the hypothesis that the evolution of eusociality and division of reproductive work is due

group competition (Reeve and Hölldobler, 2007).

Conclusion

In summary, our analysis shows that the population dynamics of cooperative species are

inherently unstable. In the case most likely to be seen in nature, population dynamics result in the

constant turnover of smaller groups splitting off from established ones. While this model is

simple, its applications are great. It can be used towards modelling swarming in bees or the

colonization of wolves in Isle Royale and Yellowstone National Park (Oldroyd et al., 1997;

Peterson and Page, 1988). More importantly, this work is the starting point for further analysis of

cooperative species population dynamics. Additional modifications could be added on to the

model to get at a truer picture of how these dynamics occur including asymmetric competition,

spatial effects, and evolutionary dynamics which will help to enrich our knowledge of population

dynamics of cooperative species. Practically, this is important because a significant number of

species from cetaceans, canids, and primates to lions, elephants, eusocial insects, and even

sponges show cooperative societies in which groups are tight-knit and discrete. Because these

species often have a significant impact on the ecosystem, whether through ecosystem engineering, their status as keystone species, or accounting for a significant percentage of the biomass of the ecosystem (in some species, all three), it is imperative that ecologists understand the population dynamics of these species (Jones et al., 1994; Ripple and Beschta, 2012; Hoelldolber and Wilson, 1990). Better knowledge will help ecologists and wildlife conservations better manage and save their populations and the ecosystems in which they live (Stephens and Sutherland, 1999).

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Fig. 1 A 2x2 panel figure of fitness and association functions vs. Allee-modified logistic and pure logistic $\left(F(G_i) = r \left(1 - \frac{G_i}{M} \right) \right)$. (a) The Allee fitness function (b) The logistic fitness function (c) The Allee association function (d) The logistic association function. Open circles indicate the maximum fitness, i.e. therefore the optimal group size from an individual's perspective (association equilibrium), while closed circles indicate the fitness equilibrium. One can see that in both systems, the association and fitness equilibriums do not match; however, there is greater implication in the Allee system as the association function has both positive and negative elements, lending itself to associative dynamics. $r = 1, M = 100$

Fig. 2 The isoclines, equilibria, and directional field of a two group system under different strength of competition α_r. (a) $\alpha_r = {1.1}/{M}$ (b) $\alpha_r = {0.75}/{M}$ (c) $\alpha_r = {0.4}/{M}$ (d) $\alpha_r = {0.25}/{M}$. Solid dots represent stable equilibria while open dots represent unstable equilibria.

Fig. 3 A schematic of the process of group growth and splitting. On the left, a circle represents a group. On the right is said group's fitness function on top and association on the bottom. Our parameters for this model are $r = 1, M = 100, \alpha = \frac{1}{150}$. (a) The fitness function of group 1 when G_1 is extremely small, 0.5 (b) The fitness function of group 1 when $G_1 = G_A^* = \frac{M}{2}$. In this case, all members of the group are at maximum fitness and satisfied with group size but fitness is positive and the group will continue to grow. (c) At this point, the group is at maximum size $G_1 = M$ so fitness is 0 and it will stop growing, but $A(G_1) < 0$ so the group members are unhappy. (d) The group has just split into two $(G_1, G_2) = (G_A^*)$. The creation of another group (dotted line) leads to the depression of the fitness function due to intergroup competition; in this case the entire fitness below 0. Here $T_1 < \alpha_r < T_2$ so both groups will go to an unstable equilibrium.

Fig. 4 A time series of the populations when $0 < \alpha_r < T_1$. One can see the initial disequilibrium dynamics before transitioning to extirpations. Each group is represented by a color with groups constantly appearing, shrinking, and going extinct. Each new group was given a new r and M based on the logit normal distribution. The large, solid, vertical, black lines represent a time when the existing groups split. The dashed line represents the total population size.
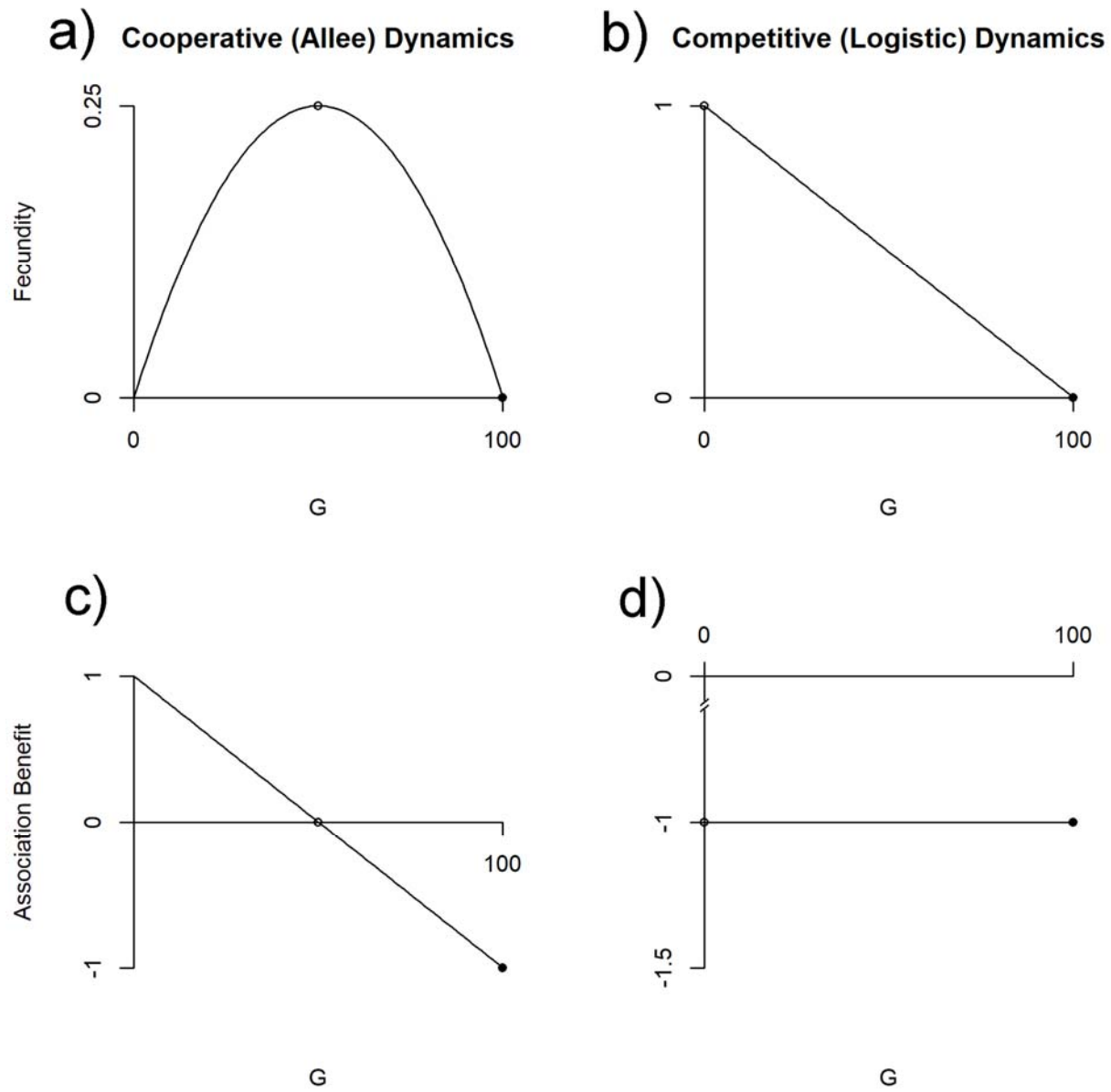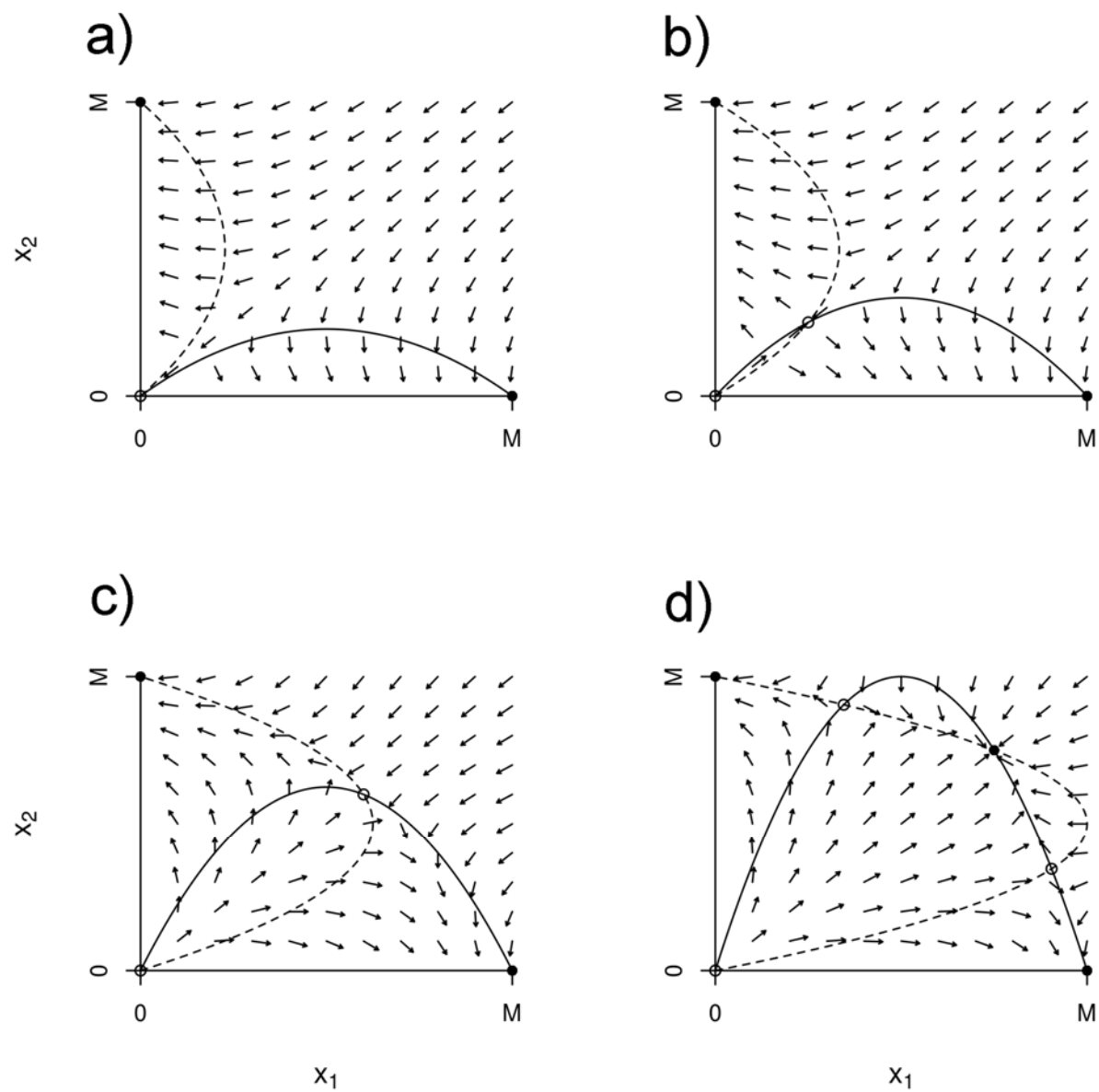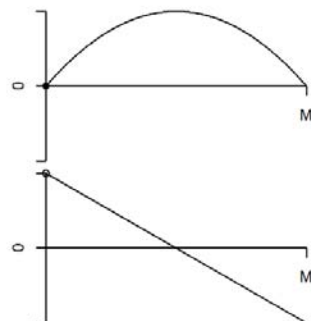
Fig. 1

Fig. 2

Fig. 3

a)

b)

c)

d)

Fig. 4