The Population Dynamics of Obligately Cooperative Species Are Inherently Unstable

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Abstract

Cooperation, defined as the act of an individual which benefits a recipient, is widely observed to occur within many species. There are strong implications of the addition of cooperation on population dynamics as cooperation allows for actor choice with individuals choosing group associations based usually on differences in fitness. There are at least two types of cooperative acts: facultative and obligate. Facultative cooperation such as 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 social canids, cetaceans, primates, and eusocial insects only grant partial actor choice with the

consequences of non-cooperation being more severe. The population dynamics of facultative cooperative species are well-modeled, but not so for obligate co-operators. This is because models assume no actor choice where individuals are permanently fixed to their group. Doing so implicitly engenders stability into the system leading to false conclusions regarding the nature of the species' population dynamics. In this paper, we created a model to analyze the population dynamics of obligate cooperators; it works by embedding a behavioral game of association with partial actor choice into a fitness dynamic. This model reveals three states based on strength of competition. In the first state under extremely strong competition, all groups will go extinct. Under the second state of moderately strong competition, the groups will exist at an unstable equilibrium. In the third state of weaker competition, the groups will show localized extirpations and constant turnover. As well, we generalize our results to show that obligate cooperative species can never achieve full stability due to the mismatch between the game's equilibrium and the fitness equilibrium. Our results, general enough to apply to most systems, show that the constant extirpation dynamics seen in obligately cooperative species are not necessarily a function of external stochastic events but instead inherent to their dynamics. The extirpation and group turnover seen among obligately cooperative societies are inherent to their population dynamics. While other factors may exacerbate the instability, they can only be secondary explanations. Because the instability arises out of a non-chaotic discrete process, it means that the dynamics are predictable and can be tested against experiments and simulations. Furthermore, our results lead to strong implications of for the conservation of obligately cooperative species. Firstly, it shows the importance of intergroup dynamics and the creation and destruction of new groups. Secondly, to conserve such species requires large areas with multiple

groups due to intrinsic group extinction and the need for a bonding process to stabilize the

dynamics.

Introduction

Cooperation, defined as some action of an individual which directly benefits a recipient and is selected for, is widely observed in nature, from the level of genes to organisms, despite being seemingly mal-adaptive (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 due to an "orgy of mutual benefaction", especially when the cooperation is obligate (May, 1981; 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). Including processes such as negative density dependence, non-linear benefits and diminishing returns, predation, and frequency dependence can restore stability in mutualistic interactions (Vandermeer and Boucher, 1978; Boucher et al., 1982). Such effects though are only geared towards between population cooperation and not within population interactions. Whether the population dynamics of within population cooperators can achieve stability has yet been studied.

Cooperation can be thought of quite simply as a trade-off. An individual will associate with others if the benefits, generally measured in terms of fitness, outweigh the cost (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 the 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 the Allee effect leads to an (often-ignored) interplay between the associations of members within a group and their fitness.

As well, the nature of the individual cooperation can result in different types of cooperative groups, or societies. E. O. Wilson (1975) recognized two broad subtypes, casual and demographic, based upon time-dependent patterns. Casual societies, with their high immigration and emigration rates, exist over such short timescales such that belonging to a society has 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 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. Casual societies are temporary as 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 the other members of the group to be successful. This difference in cooperation is of immense consequence when modelling the population dynamics of cooperative species.

Game theory is a commonly used tool to explain cooperation mathematically. Coalition game theory in particular deals with how individuals will aggregate into groups or coalitions when given different rewards based upon their coalition. This makes it ideal to understand the dynamics of cooperative species. Scientists modelling swarm dynamics often use coalition 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 are free to join and leave any group as they please

(Gueron and Levin, 1994; Zemel and Lubin, 1995; Gueron et al., 1996; Bonabeau et al., 1999;

Mirabet et al., 2007; Saffre and Deneubourg, 2002). This though does not work well for obligate

cooperative species who are much more limited in their ability to unilaterally move from one

group to another. In addition, many models of swarm dynamics ignore the consequences of

choosing associations by not including fitness dynamics. Better models more reflective of the

biology of obligately cooperate species can lead to a solid understanding of their population

dynamics.

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 (Courchamp et al., 1999; Courchamp et al., 2000; Dennis, 2002) in the

vein of the patch model framework where an individual's fitness is tied to its local environment

(Chesson, 1981; Durrett and Levin, 1994). These models correctly recognize the difficulty to

which unilateral immigration and emigration from a group happens but ignore the process

completely, implicitly assuming that individuals within a group will still associate even as their

fitness decreases with an increasing group size. This can lead to false conclusions by

engendering an assumed stability into the dynamics. Allowing individuals to choose their

associations can give a better understanding of the population dynamics of obligately cooperative

species.

In this paper, we model the population dynamics of obligately cooperative species two

ways. First we construct an explicit model by embedding a behavioral game inside a fitness

dynamics and analyze it to determine potential outcomes. In this model, each group is granted a fitness dynamics, the fitness of an individual follows in accordance with a simple Allee dynamic, and individuals cannot unilaterally move from one group to another. From there, we relax our assumptions and generalize our analysis to show that no cooperative species will be able to achieve stability in population dynamics. We give examples of our modeled dynamics seen in nature and suggest insights obtained from and future applications for this new model.

Possible Dynamics

Model

To first understand the population dynamics of obligately cooperative societies, we constructed and analyzed a simple mathematical model inspired by the biology of eusocial honey bees (genus *Apis*). We imagine a site filled with multiple groups each situated in a hive. Each group has its own population dynamic determined by the fitness of each individual. We refer here to fitness is synonymous with per-capita growth rate (measured as average individual reproduction) instead of the broader term of inclusive fitness.

Fitness Function

The fitness function for each group is given by the equation

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

where x_i is the size of the focal group, x_R is the total size of all other groups $\sum x_{-i}$, r is a growth rate scaling factor (e.g. the intrinsic reproductive rate of the queen), M is the maximum group size (potentially determined by the size of the hive), and α is the strength of intergroup competition (potentially determined by the nectar resources available to the hives). We assume that all individuals are identical – much like worker bees – distinguished only by whether they

are within or outside the group and that each hive adheres to the same fitness function with the same parameters. Since everything is identical, we can write our equation as

$$F(x_i, x_R) = \left(\frac{x_i}{M}\right)\left(1 - \frac{x_i}{M}\right) - \alpha_r x_R$$

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 get two roots of the model $\frac{M}{2}\left(1 \pm \sqrt{1 - 4\alpha_r x_R}\right)$.

This equation uses the weak Allee effect. The Allee effect is a standard phenomenon seen in cooperative societies (Allee, 1931; Allee, 1938). Unlike competitive models which assume that additional individuals always result in lower fitness, models with the Allee effect assume that additional individuals increase fitness at lower numbers, reaching maximum fitness at some intermediate value, before decreasing and hitting zero (Courchamp et al., 1999; Stephens et al., 1999). If one were to plot fitness $F(x_i)$ versus group size x_i, competitive models show a function with a monotonic decline from a positive fitness while functions with the Allee effect broadly have an inverted bowl shape (Fig. 1a,b). The Allee effect is classified into two strengths: strong and weak. At group size 0, the weak Allee effect has fitness positive or zero $F(0) \geq 0$ while with the strong Allee fitness is negative $F(0) < 0$ leading to a minimum viable group size. The hive of a eusocial honey bee species shows a definite Allee effect. Additional members eases detecting and gathering nectar, protecting against other hives as well as caring for young. If the members become too much though, then problems with crowding such as overheating, waste, and disease become greater. This leads to a hump-shaped fitness response for members within a hive.

Association Function

Due to the Allee effect, there is a behavioral game of association. Individuals wish to maximize fitness and therefore will prefer to be within a group that maximizes its fitness. Since

each individual is identical, it is only group size that determines the fitness of each member. 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 would reside entirely below zero; each extra individual has a negative effect on 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

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

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 $A(x_A^*) = 0$ and is negatively sloped; in our case, $x_A^* = \frac{M}{2}$ always. More broadly, as long as $A(x_i) > 0$, the group has no incentive to split and will be stable in association.

With the model in hand, we can now illuminate some possible dynamics.

Short Term Intragroup Dynamics

In order to characterize the dynamics, we must understand that there are two processes at work: short term intragroup dynamics and long term intergroup dynamics. We can understand the short term intragroup dynamics using coalition game theory. We begin by assuming a single group facing no competition $\alpha_r x_R = 0$. Under this condition, the group will grow until it reaches $x_F^* = M$ (Figure 2a,b,c). As well, we assume only splitting dynamics initially; group size can only be increased through reproduction.

According to coalition game theory, members of the group will prefer to be at the optimal group size x_A^*. However, $F(x_A^*, 0) > 0$ meaning members of the group will continue to reproduce

until fitness is 0 at the final group size $x_F^* > x_A^*$ with $A(x_F^*) < 0$. This creates a mismatch between the optimal group size and the final group size. Since $F(x_F^*, 0) = 0 < F(x_A^*, 0)$, there is a strong incentive for the members to form separate groups of size x_A^* than in stay in one group of size x_F^*. Therefore, as the group's size reaches x_F^*, it will split into multiple groups of size x_A^*. In the absence of competition, $x_A^* = \frac{x_F^*}{2}$ leading to the creation of two groups both of size x_A^* (Figure 2d). The splitting process is assumed to be permanent with each new group is granted its own fitness dynamic.

This process is quite similar to the swarming behavior seen in *Apis* bees. When a hive has reached capacity or there are too many bees, a new queen will emerge and the old queen with approximately half the workers will leave the original hive to find a new one.

Now with multiple groups, intergroup competition begins and we can determine longer term dynamics.

Long Term Intergroup Dynamics

With the addition competition, we still assume that splitting proceeds according to the principles laid out in short term intragroup dynamics, namely that a group at x_F^* will split into two groups at x_A^*. At this point, $x_R = x_i = x_A^*$ meaning $F(x_A^*, x_A^*) = 0.25 - \alpha_r \frac{M}{2}$. The size of α_r will determine the long term dynamics of our system. There are two thresholds of α_r: the main threshold T_1 which divides competition strength 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 constant extirpation respectively.

Total Extinction and Unstable Equilibria

Our main threshold T_1 determines the fitness of groups just after splitting; in our case,

$T_1 = \frac{1}{2M}$. If $\alpha_r > T_1$, then $F(x_A^*, x_A^*) < 0$ meaning both groups will decline in size and decline

simultaneously due to symmetry between the groups. 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 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 ($T_2 = \frac{1}{M}$).

If $\alpha_r \geq T_2$, we call this extremely strong competition and $F(x_i, x_i) < 0 \ \forall \ x_i \in (0, x_A^*]$.

When this occurs, both groups will continue to go shrink in size until they go extinct. This is

because competition is so strong that even small populations of other groups can significantly

negatively impact the fitness of focal group members. With moderately strong competition

$T_1 < \alpha_r < T_2$, then after splitting $F(x_A^*, x_A^*)$ will still be negative, leading to both groups shrinking.

In this case though, competition is not strong enough to cause extinction and the groups will

reach a positive equilibrium size. With $x_F^* < x_A^*$, $A(x_F^*) > 0$ meaning the groups are at a

population equilibrium with neither wishing to split. Through calculations, we can show that

$\alpha_r = \frac{1-c}{M}$ achieves an equilibrium $x_F^* = cM, 0 \leq c \leq \frac{1}{2}$ (see SI). At such a point though, both groups

are at unstable population equilibria confirmed by Jacobian analysis (see SI). In this case,

disturbance leads to one of the groups going extinct while the other grows to M repeating the

process. When $\alpha_r = T_1$, this results in a unique case where population equilibrium is reached

immediately after splitting and individuals are at a fitness maximum. (Note: With regards to the

dynamics when $T_1 \leq \alpha_r < T_2$, one could claim that the system ends up in a near-identical state

from which the system was disturbed, therefore being a form of stability. We reject this

argument on technical terms. The groups themselves do not return to the equilibrium; instead a new group is born from the old ones. As an analogy, this process after disturbance is more akin to a tail being regrown after falling off a lizard rather than the tail returning to the lizard.)

Constant Extirpation

If $0 < \alpha_r < T_1$, then competition is weak and a more interesting dynamic occurs. 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^*, $0 < X^* < x_A^* < Y^* < M$. This introduces a minimum viable group size. If there exists a group of size $x_i < X^*$, then individuals will have negative fitness and the group shrink to extinction. Therefore, in a multigroup population, it is the fitness of individuals of the smallest group that drives the extirpation dynamics. Let $x_{s,n}$ be the group size of the smallest group, X_n^* and Y_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 to grow from x_A^* to Y_1^*. Members will be unhappy 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 $x_{s,2} = Y_1^* - x_A^* = \frac{M}{2}\left(\sqrt{1 - 4\alpha_r x_{R,1}}\right)$. As well, $x_{R,2} = M + \frac{M}{2}\sqrt{1 - 4\alpha_r x_{R,1}}$ with the two new roots X_2^*, Y_2^*. If $x_{s,2} \gg X_2^*$, then the process repeats with all four groups growing 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 $\hat{n}$, the smaller group will eventually go extinct, resetting the system to the previous state and leading to a cycle of groups splitting unevenly with smaller groups going extinct and large groups growing back to previous size i.e. constant extirpation. The extirpation dynamic depends upon a threshold value of x_R. Determining when this occurs is tricky though as it can happen even when $x_{s,\hat{n}} > X_{\hat{n}}^*$, $F(x_{s,\hat{n}}, x_{R,\hat{n}}) > 0$. We can though get an upper bound to x_R.

When $x_{s,n} \leq X_n^*$, individuals within the smaller group will have negative or zero fitness

$F(x_{s,n}, x_{R,n}) \leq 0$ which guarantees extirpation dynamics. The x_R which makes $x_s = X^*$ is the

upper bound. Solving for this, we get $x_R = \frac{1}{4\alpha_r} - \frac{1}{16\alpha_r}(1 - 2\alpha_r M)^2$.

Additional Dynamics

Extra analysis also yields potentially 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 $x_A^* >, < \frac{M}{2}$.

If $x_A^* > \frac{M}{2}$, then there is still splitting into two groups with 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 go extinct while the other one persists. This leads to a continual budding process in

which a smaller group is split off from a larger group only to summarily go extinct. If the second

criterion is not met, then we can get additional outcomes

If $x_A^* < \frac{M}{2}$, then there will be splitting into multiple groups. In the absence of competition,

a group of size M will break off into n_g groups, $n_g = \lceil \frac{M}{x_A^*} \rceil$. If $\frac{M}{x_A^*}$ is not an integer, then there will

be a straggler group of size of $M - kx_A^*, k = \lfloor \frac{M}{x_A^*} \rfloor$. Because not all groups are necessarily of the

same size, the dynamics are harder to analyze (although can be in some instances) but should

follow the same basic format of total extinction, unstable equilibria, and constant extirpation (see

SI).

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 present this argument two ways: first verbally, then mathematically.

Verbal Presentation

Essentially within the fitness 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 competitive state, then the group will not wish to reduce members and therefore be stable. If the group is in a competitive state though, the members realize a reduced group size gives them greater fitness and will seek to reduce the size of their group, perhaps by splitting it. Therefore, the stable behavioral equilibrium for a group happens when the individuals are at a local fitness maximum or barring that the group 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 fitness 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 fitness dynamics. Therefore, a stable fitness equilibrium cannot also be a stable behavioral equilibrium. 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 fitness equilibrium. Therefore, there is always a mismatch between a stable behavioral equilibrium and stable fitness equilibrium.

In summary, any group size stable with regard to fitness dynamics is unstable with regard to behavioral dynamics, and any that is stable with regard to behavioral dynamics is unstable with regard to fitness dynamics. Even in the optimal scenario where every group is of a size that maximizes fitness and at a fitness equilibrium, the system is at best partially stable. We now present this formally in a mathematical framework.

Mathematical Presentation

Let $\frac{dx_i}{dt} = x_i * F_i(\vec{x})$ be the growth dynamics of a single group i where $F_i(\vec{x})$ is a smooth function describing per-capita growth rate of the group and $x = \{x_1, x_2, \ldots, x_{n_g}\}$ 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. We make the assumptions of uniformity and identity: that all individuals within a group have the same fitness (uniformity) and that it is only the number of individuals and not the properties of the individual that determines fitness within a group (identity).

Taking the partial derivative of $F_i(\vec{x})$ with respect to x_i and fixing all other variables to the point $\hat{x}^{-i} = \{\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_{i-1}, \hat{x}_{i+1}, \ldots, \hat{x}_{n_g}\}$ gives us a function of association $A_i(x_i)|_{\hat{x}^{-i}} = \frac{\partial F_i(\vec{x})}{\partial G_i}$ 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, additional members decrease individual fitness. We take these two states to represent cooperation and competition respectively. Using the assumption that individuals have limited information – specifically only the fitness dynamics within their current group – then $A_i(x_i)|_{\hat{x}^{-i}}$ also determines preference of individual group members. 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.

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 $i \in \{1, 2, \ldots, n_g\}$ with $x^+ \in x^*$ being 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 $\dfrac{\partial \left(dx_i / dt \right)}{\partial x_i} \Big|_{x^*} = \dfrac{\partial \left(x_i * F_i(\vec{x}) \right)}{\partial x_i} \Big|_{x^*} = F_i(x^*) + x_i^* * A_i(x_i^*) \Big|_{x^{*-i}} = x_i^* * A_i(x_i^*) \Big|_{x^{*-i}} \forall i \in \{1, 2, \ldots, n_g\}$. As $x_i^* \geq 0$, the diagonals are either 0 or reflect the sign of the association game at that point. If the equilibrium is cooperative for all groups in the set x^+, $A_i(x_i^*)|_{\vec{x}^*} > 0 \ \forall \ i \in x^+$, 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 x^+ is at a competitive state, then all eigenvalues could be negative, meaning the population dynamics could be at an asymptotically stable equilibrium. At such a point though, the individuals of the competitive groups are unhappy. 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 $\frac{\partial A_i(x_i^*)|_{x^{*-i}}}{\partial x_i} < 0$, 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 extinctions occur in population dynamics due to the Allee effect, we have shown them to be intrinsic and unaviodable to the dynamics of obligately cooperative species. In ecological systems, it has been well-documented that obligately cooperative species do not show stable equilibrial dynamics and instead show constant extirpation (Jarvis et al., 1994; Aviles, 1997; Clutton-Brock et al., 1999) with external factors are 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 – within a group while Wang et al. (1999) observed Allee effect in competing populations results in multiple stable states, majority of them which result in extinction especially when compounded with demographic and environmental stochasticity. Our results align the hypothesis of Chourchamp et al. (1999) who noted the existence of a minimum viable group size with the strong Allee effect. In our model, the existence of a minimum viable group size is what leads to instability. We extend upon the work to show this minimum viable group size will always be created regardless of the strength of the Allee effect with the simple addition

of a behavioral game of association and group competition. Among all these mathematical hypotheses, our results goes a step further to say that these dynamics are not only intrinsic but unavoidable.

In addition, our results show that local extirpations and constant group turnover can arise from a non-chaotic deterministic interactions. This means that the localized extinctions are a general, repeatable, and predictable pattern against which field studies and data can be tested. This predictability is the greatest value of our results. Using simulations and controlled experiments, we can now tease how attributes and traits of species along with environmental variables can affect local extirpation (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 cooperative dynamics of the Allee effect are 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 are all known to 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 strong competitive conditions, 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 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 extirpation dynamics our model exhibits under weak competitive conditions. Over longer time scales, our model shows oscillation of total population over time with repeated instances extirpations and splitting events (Fig. 3). In our spatially dependent context, a uniform distribution of groups with large home ranges will show, on average, weak competition.

With weak competition, our model shows oscillatory patterns at the population scale, 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 population scale and are not due simply fluctuations in the groups' size. These oscillations come about through a 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 intergroup competition in 1977, supporting our results that intergroup competition is the driving factor of group extinction (Goodall, 1986).

Many long-term population studies focus on population scales and do not account for group extirpations leading researchers to seek external environmental causes to explain the extirpations of social animals. 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 bonding process. When it comes to constant extirpation, smaller groups less than minimum viable population size will go extinct. If these groups can bond into larger groups, then they can escape extinction by being greater than the minimum viable group size (and in fact, at x_A^*) as well as reducing intergroup competition. By including the ability for groups to bond, the system should generally move from a state of constant extirpation to an unstable equilibrium (see SI for a specific example). It must be noted though that even with bonding, 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 that we discussed earlier, 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.

Though different phenomena can stabilize the dynamics of cooperative societies, they cannot fully stabilize the system and may only exist in theoretical realms (see SI).

Conservation Implications

The 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.

For species with the Allee effect also facing habitat loss or exploitation, difficulty in group bonding and reduced immigration are even more likely to drive extirpations. Courchamp et al. (2008) investigated consequences of fragmentation and isolation on populations experiencing Allee effects and concluded risk to extinction was high for small and very small populations regardless of isolation. 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 larger scales and cover multiple groups to ensure there is minimal intergroup competition and support enough groups for a robust bonding process to stabilize population dynamics and prevent total extinction, thus providing further support for large conservation areas in the single large or several small (SLOSS) debate in conservation (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 due to Allee effects via increasing group sizes and facilitating bonding. 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 be focused on intergroup 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 unrealistic, especially uniformity and identity. 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. For example, a group imbalanced towards one sex may favor an individual of the less frequent sex more than an individual of the group's dominant sex. 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 the fitness goes down to zero. Many times group members leave or are ejected before then, with them now either faced with joining an established group or banding together with ejected members from other groups to create a new one. How adding these attributes affects the

population dynamics remains to be seen but should not affect the general argument 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. In Figure 3 after the second bonding event, the light blue group that goes extinct has a larger maximal group size but a smaller growth rate than either the purple or gold group which persist despite the light blue having an initial higher group size and therefore exerting a stronger competitive effect. 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. Many more changes 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).

Acknowledgements

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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 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. 3 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.
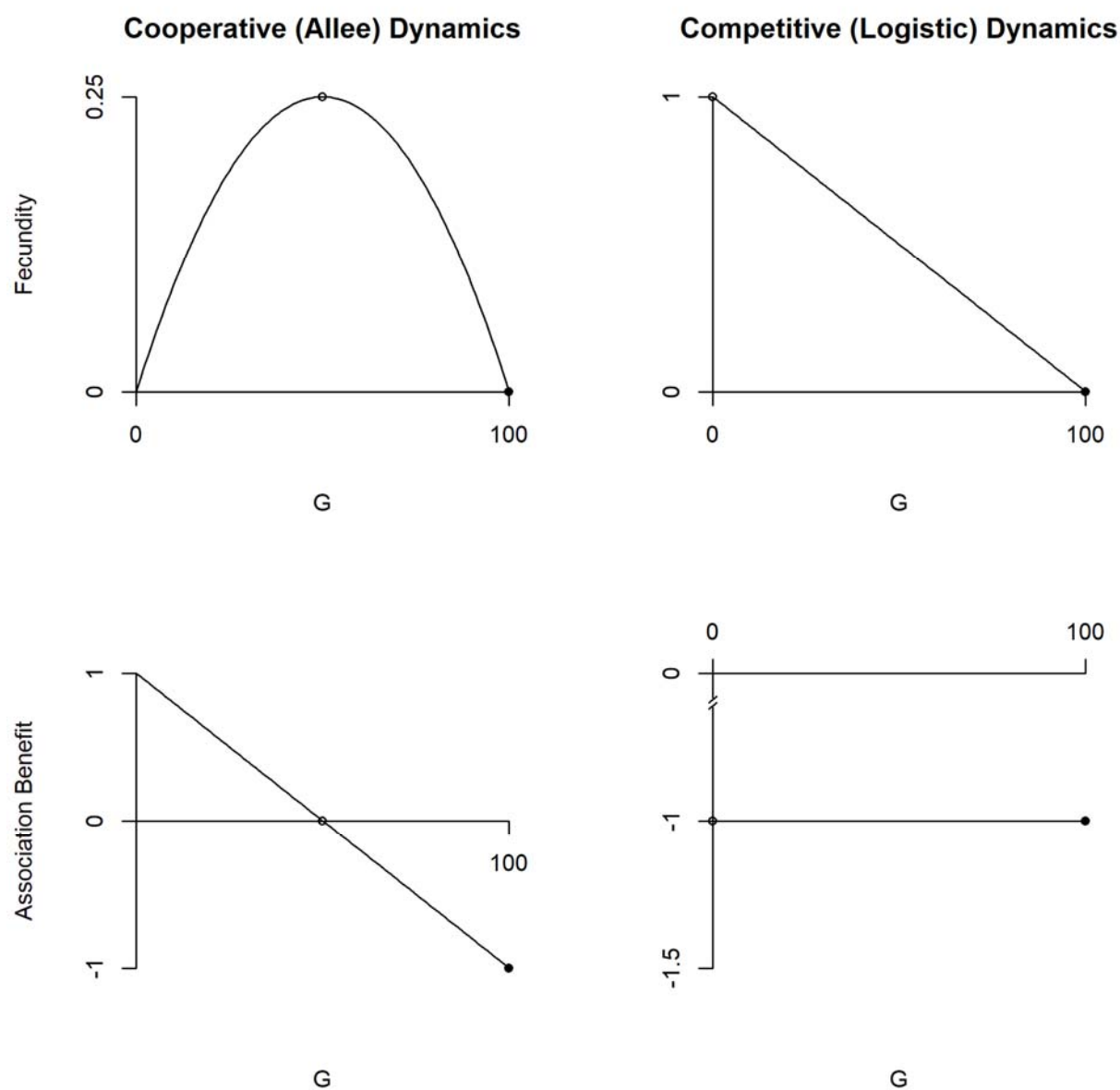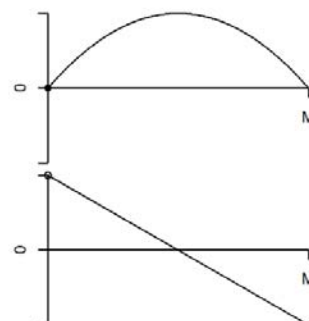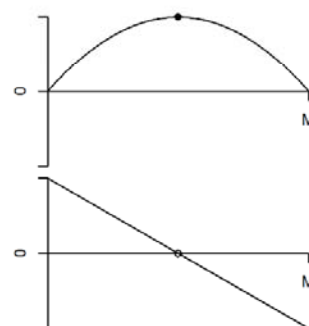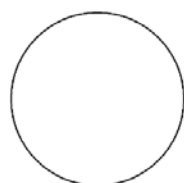
Fig. 1

Fig. 2

Fig. 3