

1                                    **Unstable Population Dynamics in Obligate Co-Operators**

2                                    Abdel Halloway<sup>1</sup>, Margaret A. Malone<sup>2</sup>, and Joel S. Brown<sup>2,3</sup>

3  
4  
5

6                                    <sup>1</sup>Department of Botany and Plant Pathology, Purdue University  
7                                    915 W. State St., West Lafayette, IN 47907

8

9                                    <sup>2</sup>Department of Biological Sciences, University of Illinois at Chicago  
10                                    845 W. Taylor St. (M/C 066) Chicago, IL 60607

11

12                                    <sup>3</sup>Integrated Mathematical Oncology, Moffitt Cancer Center  
13                                    SRB-4, 12902 USF Magnolia Drive Tampa, FL 33612

14

15

16                                    **Corresponding Author**

17                                    Abdel Halloway

18                                    Department of Botany and Plant Pathology, Purdue University  
19                                    915 W. State St., West Lafayette, IN 47907

20                                    [ahallowa@purdue.edu](mailto:ahallowa@purdue.edu)

21

22

23                                    **Key Words**

24                                    Game theory, cooperation, Allee effect, fusion-fission, population dynamics, conservation

25 **Abstract**

26 Cooperation significantly impacts a species' population dynamics as individuals choose  
27 others to associate with based upon fitness opportunities. Models of these dynamics typically  
28 assume that individuals can freely move between groups. Such an assumption works well for  
29 facultative co-operators (e.g. flocking birds, schooling fish, and swarming locusts) but less so for  
30 obligate co-operators (e.g. canids, cetaceans, and primates). With obligate co-operators, the  
31 fitness consequences from associations are stronger compared to facultative co-operators.  
32 Consequently, individuals within a group should be more discerning and selective over their  
33 associations, rejecting new members and even removing current members. Incorporating such  
34 aspects into population models may better reflect obligately cooperative species. In this paper,  
35 we create and analyze a model of the population dynamics of obligate co-operators. In our  
36 model, a behavioral game determines within-group population dynamics that then spill over into  
37 between-group dynamics. Our analysis shows that group number increases when population  
38 dynamics are stable, but additional groups lead to unstable population dynamics and an eventual  
39 collapse of group numbers. Using a more general analysis, we identify a fundamental mismatch  
40 between the stability of the behavioral dynamics and the stability of the population dynamics.  
41 When one is stable, the other is not. Our results suggest that group turnover may be inherent to  
42 the population dynamics of obligate co-operators. The instability arises from a non-chaotic  
43 deterministic process, and such dynamics should be predictable and testable.

## 44 **Introduction**

45 Cooperation – where the action of an individual benefits a recipient – is widely observed  
46 in nature, from the level of genes to organisms (West et al., 2007; Nowak, 2006). Individuals  
47 will choose to cooperate with others if fitness benefits, whether direct or indirect, outweigh the  
48 costs (Hamilton, 1964; Trivers, 1971; Taylor, 1992). Because cooperation leads to fitness  
49 benefits, it can have significant impacts on a species' population dynamics as individuals  
50 associate with others to form groups for greater fitness benefits. Linking the dynamics at the  
51 group level to the entire population will lend a greater understanding of the effects of  
52 cooperation on overall population dynamics (Bateman et al., 2018). We suggest that the type and  
53 context of cooperation must be considered when understanding the population dynamics of  
54 cooperative species. Cooperative societies can be categorized into two broad types: casual and  
55 demographic (Wilson, 1975). Casual societies (e.g. starling murmurations or fish schools) are  
56 characterized by a constant turnover of group membership with little to no lasting impact on a  
57 member's fitness. Demographic societies (e.g., most social primates, canids, cetaceans,  
58 elephants, lions, and eusocial insects), on the other hand, show limited exchange between groups,  
59 and dispersal between groups can have lasting fitness impacts on the group's members. This  
60 difference is due to whether cooperation is facultative and therefore helpful but not necessary for  
61 survival (casual societies) or obligate where individuals need others for survival and successful  
62 reproduction (demographic societies). The difference in cooperation means that obligate  
63 cooperators are more selective in their associations and helps explain their limited dispersal.  
64 Therefore, one would expect that the differences in cooperation would lead to distinct impacts on  
65 their population dynamics, particularly regarding stability.

66           Typically, swarm dynamics have been used to model the social and population dynamics  
67 of cooperative species (Couzin and Krause, 2003; Okubo, 1986; Gueron and Levin, 1995; Zemel  
68 and Lubin, 1995; Gueron et al., 1996; Bonabeau et al., 1999; Mirabet et al., 2007; Saffre and  
69 Deneubourg, 2002). This approach has worked well to model the population dynamics of  
70 facultatively cooperative species, however not as well for obligately cooperative species. While  
71 actors in a swarm model are selective regarding associations, dispersal is generally not limited  
72 with individuals moving freely between groups. On the other hand, some models with limited  
73 dispersal do not permit selectivity of any individual (Courchamp et al., 1999; Courchamp et al.,  
74 2000; Dennis, 2002). And more generally, not all individuals are selective in population models  
75 of cooperators. Whether models of swarm dynamics or of limited dispersal, the focus remains on  
76 an individual disperser and their choice of associations with non-dispersers lacking choice  
77 (Lehmann et al., 2006; Parvinen and Brannstrom, 2016). Including both limited dispersal and  
78 group-wide selectivity into a model of cooperative species' dynamics should better reflect the  
79 dynamics of obligate co-operators.

80           In this paper, we model the population dynamics of obligately cooperative species. First,  
81 we construct and analyze a specific model of population dynamics embedded with a behavioral  
82 game with group-wide selectivity. In this model, there is within-group cooperation, within-group  
83 competition, between-group competition, and limited dispersal between groups (specifically no  
84 movement). We analyze the model's population dynamics and behavioral dynamics separately  
85 before combining the two. From there, we relax our assumptions and generalize our analysis to a  
86 class of models that keeps all key features of the specific model. We show a mismatch in  
87 stability: a stable population size is not behaviorally stable and groups that are behaviorally  
88 stable are unstable in terms of population dynamics. In other words, a group can either have

89 behavioral stability or population size stability but never both. We go on to discuss the  
90 implications of our model including its relevance to real systems and future applications.

## 91 **Dynamics of the Specific Model**

### 92 *Population Dynamics*

93 To model the population dynamics of obligate cooperators, we first assume that  
94 individuals can cooperate with each other by forming associations, i.e. groups, to gain greater  
95 fitness. Here, we define fitness as an individual's expected per-capita growth rate. For the sake of  
96 simplicity, we assume all individuals are identical, distinguished only by whether they are within  
97 or outside a group. Each individual within a group can be described by the same fitness function.  
98 Only the number of individuals within the group directly determines fitness.

99 As individuals come together, an emergent group-level of cooperation appears as the  
100 aggregation of each individual's cooperative acts (Dugatkin, 1998). In terms of population  
101 dynamics, this is often modeled as an Allee effect, or the positive relationship between an  
102 individual's fitness and its associations within a group – typically measured as group size (Allee,  
103 1931; Allee, 1938; Trivers, 1971; Axelrod and Hamilton, 1981; Dugatkin, 1998; Nowak, 2006;  
104 Stephens et al., 1999; Angulo et al., 2018). We include this Allee effect to within-group  
105 dynamics but not between-group dynamics. We imagine that individuals benefit from group  
106 living via collective foraging, defense, or other positive social interactions yet suffer from  
107 resource sharing, disease transmission and other negative interactions. With group size, we  
108 assume that benefits to an individual increase linearly while fitness costs increase super-linearly  
109 leading to an overall humped-shaped relationship between group size and fitness (Terborgh,  
110 1983).

111 With these assumptions, we imagine  $n_g$  different groups, each with their own group size.

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

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

113 where  $x$  is the vector of group sizes  $x = (x_1, x_2, \dots, x_{n_g-1}, x_{n_g})$ . Here,  $x_i$  is the size of focal

114 group  $i$ ,  $x_R$  is the cumulative size of all other groups  $\sum_{j=1}^{n_g} x_j - x_i$ ,  $r$  is a growth rate scaling

115 factor,  $M$  is maximum potential group size, and  $\alpha$  is the strength of intergroup competition

116 (potentially determined by the depletion of shared resources). Since all individuals are identical,

117 all groups have the same fitness function allowing us to rescale per-capita growth rates by  $r$  to

118 give:

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

119 where  $\alpha_r = \frac{\alpha}{r}$  is the ratio of intergroup competition to the growth rate scaling factor. Let us

120 denote the equilibrium group size as  $x_F^*$  where growth rate equals zero. Solving for  $x_F^*$ , we obtain

121 two values where  $x_F^* = \frac{M}{2} (1 \pm \sqrt{1 - 4\alpha_r x_R})$ .

122 In this equation, fitness at first increases at low group sizes ( $x_i < \frac{M}{2}$ ) and then decreases

123 at high group sizes ( $x_i > \frac{M}{2}$ ) (Fig. 1a). Within-group interactions create an Allee effect and

124 fitness does not monotonically decline with more individuals (Fig. 1b) (Allee, 1931; Allee,

125 1938). The first two terms of equation (2) define these intra-group dynamics where the first term

126 represents the fitness benefits of group living and the second term represents the fitness costs of

127 group living. So long as  $x_i < M$ , the benefits from cooperation are greater than the costs of

128 competition and so fitness is positive; and if  $x_i < \frac{M}{2}$ , then the benefits of additional cooperation

129 are greater than the costs of additional competition, i.e. an individual's marginal contribution is  
130 positive, and the Allee effect holds. The third term of equation (2) represents the loss of fitness  
131 due to inter-group competition and is broadly assumed to be linear.

132 We can now analyze the overall population dynamics of the entire system of groups. This  
133 analysis replicates Wang et al. (1999), revealing the same qualitative results with minor  
134 differences. Therefore, we keep this section brief. With a single group, there are two equilibria:  
135  $x_F^* = 0, M$ . The first equilibrium is unstable, the second is stable. Therefore, any group of strictly  
136 positive size will grow or shrink to  $M$  (Fig. 3a,b,c). With a single group, we also note that the  
137 Allee effect is weak (fitness at  $x_F^* = 0$  is non-negative,  $F(0,0) \geq 0$ ) (Courchamp et al., 1999b;  
138 Stephens et al., 1999; Angulo et al., 2018). When another group is added, inter-group  
139 competition induces a strong Allee effect (fitness at  $x_F^* = 0$  is strictly negative,  $F(0,0) < 0$ ).  
140 Outcomes now depend upon the strength of inter-group competition  $\alpha_r$  (Fig. 2). If inter-group  
141 competition is strong  $\alpha_r \geq \frac{1}{M}$ , then either only one group survives or both groups go extinct (Fig.  
142 2a). The equilibrium where both go extinct is a saddle-point (unstable except for when the initial  
143 population sizes of the two groups are equal) while the equilibria where only one group survives  
144 is locally stable (the group with the larger size outcompetes the other). As inter-group  
145 competition weakens  $\frac{1}{3M} < \alpha_r < \frac{1}{M}$ , there arises an unstable (saddle point) interior equilibrium  
146 (Fig. 2b,c). The equilibrium where both groups go extinct is now fully unstable. The equilibria  
147 with just one surviving group remain locally stable.

148 If competition weakens even further  $0 < \alpha_r < \frac{1}{3M}$ , two new interior equilibria appear  
149 where both groups co-exist at positive but unequal sizes. These two new interior equilibria are  
150 unstable stable. The former interior equilibrium where both groups have the same population size  
151 now becomes locally stable (Fig. 2d). With weak competition, there is a strong Allee effect and

152 each group has an extinction threshold based on the number of individuals in the other group. If  
153 the initial sizes of both groups are above their extinction thresholds, competition is too weak to  
154 drive extinction, and the two groups will persist at the interior equilibrium of equal sizes. If one  
155 or both groups are below their extinction thresholds, then the smaller group will go extinct and  
156 the larger group will grow to size  $M$ . As intergroup competition disappears, the interior  
157 equilibrium with equal sizes becomes globally stable as both reach maximal carrying capacity,  
158 and the other interior equilibria merge with the two in which only one group survives. These two  
159 equilibria and the one in which both groups go extinct are all unstable.

160 As we add additional groups, the same fundamental dynamics remain (see SI). The only  
161 difference is that inter-group competition must be weaker – specifically, it must be scaled by  
162  $\frac{1}{n_g - 1}$  where  $n_g$  is the number of groups – for the interior equilibrium to be locally stable. More  
163 generally, we can say that for any system of  $n_g$  groups, the only stable interior equilibrium (all  
164 groups at strictly positive size) occurs when all groups, equal in size, are at a size  $\frac{2}{3}M$  or greater.  
165 For this to occur with an increasing number of groups, inter-group competition must decrease. If  
166 not, then the addition of more groups destabilizes the interior equilibrium and leads to a collapse  
167 of group numbers.

### 168 ***Behavioral Dynamics***

169 A behavioral game of association can be embedded into equation (2). In this game, we  
170 assume that individuals are “rational” and seek associations that maximize their fitness (per-  
171 capita growth rate). Since all individuals are identical, only group size determines the fitness of  
172 each member. We also assume that individuals are dealing with limited information, namely that  
173 they can only “see” their fitness in relation to the size of their current group and are blind to the  
174 influences of non-group members. In essence, individuals can only understand the marginal



175 contribution of an additional group member to average fitness. Under these assumptions, we can  
176 obtain the “association” function by taking the partial derivative of the fitness function with  
177 respect to  $x_i$ . This association function  $A(x_i)$  indicates the marginal contribution of an individual  
178 to the others’ fitness (equation 3).

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

179 We call the group size which maximizes fitness the optimal group size and denote it by  $x_A^*$ .  
180 Because  $A(x_i)$  starts at a positive point and declines linearly (and therefore monotonically) with  
181 increasing group size, we can say simply solve for  $A(x_i) = 0$  to obtain  $x_A^*$ , resulting in  $x_A^* = \frac{M}{2}$ .  
182 This value provides maximum fitness as confirmed by taking the second derivative.

183         Typically in models of cooperative species, only the dispersing individual is selective and  
184 given choice of association. However, all individuals in a group should be just as selective as the  
185 disperser. We can use coalitional (a.k.a. cooperative) game theory to analyze the behavior of all  
186 individuals en masse. Coalition game theory seeks to understand two things: how individuals  
187 select their associations and how the resulting payoff to that coalition is distributed in an  
188 equitable and efficient manner (von Neumann and Morgenstern, 1944; Peleg and Sudhölter,  
189 2007). In coalitional game theory, there are  $N$  players who can choose to associate with other  
190 players to form various coalitions  $C = \{C_1, C_2, \dots, C_{n_c}\}$ . Through their associations, they receive  
191 a payoff  $v(C_i)$ . If all players choose to form a single coalition  $C = \{N\}$ , this is known as the  
192 grand coalition. In our case, the players are the individuals within a group  $N = x_i$ , and the total  
193 payoff to the group is its growth rate  $v(C_i) = x_i \cdot F(x_i)$ . By assuming that all individuals are  
194 identical, payoffs are equally shared among all members and can be represented as fitness or per-

195 capita growth rate  $F(x_i)$ . Using this framework, we can analyze how individuals should choose  
196 their associations.

197 For illustrative purposes, we analyze the behavioral game in which there is a single group  
198 facing no inter-group competition ( $\alpha_r x_R = 0$ ). However, the general principles remain the same  
199 regardless of the presence or strength of inter-group competition. Based on the association  
200 function  $A(x_i)$ , the marginal contribution of an individual is positive  $A(x_i) > 0$  when group size  
201  $x_i < x_A^*$ . Under these conditions, the game is super-additive, i.e. all individuals receive greater  
202 fitness from being in one large coalition of  $x_i$  rather than separated into smaller coalitions. As  
203 such, there is no incentive for any individual to seek a group of a lower size. However, if the  
204 group is larger than its optimal size  $x_i > x_A^*$ , then the behavioral game is no longer super  
205 additive. Instead, the marginal cost of an individual is negative  $A(x_i) < 0$ . Therefore, individuals  
206 in a marginally smaller group will obtain greater fitness. As such, individuals in a group of size  
207  $x_i > x_A^*$  will prefer to be in a smaller coalition, specifically at the optimal group size  $x_A^*$ . The  
208 group is not behaviorally stable as individuals will leave or be forced out from the current group,  
209 creating new groups in the process (Fig. 3b). Summarily, through coalition game theory any  
210 group smaller than optimal group size is behaviorally stable while any group larger than optimal  
211 group size is behaviorally unstable.

212 Now with population and behavioral dynamics analyzed separately, we can combine  
213 them to derive a full picture of the population dynamics of cooperative species. We seek the  
214 possibility of a joint population and behavioral equilibrium and show it to be impossible.

### 215 ***Overall Population Dynamics***

216 In our specific model, any fully stable equilibrium must have all groups at a size  $\frac{2}{3}M$  or  
217 greater and that more groups in a system lead to greater instability. Analysis of behavioral

218 dynamics shows that current groups will split and new groups will be formed so long as the  
219 current group's size is beyond  $x_A^* = \frac{M}{2}$ . Combining the two results, we obtain the main result:  
220 over time, the behavioral dynamics of cooperative species will tend towards more groups when  
221 population dynamics are stable, and a stable behavioral equilibrium will lead to unstable  
222 population dynamics and an eventual collapse of group numbers. Through this, we see that there  
223 is a mismatch between the regions where population dynamics and behavioral dynamics are  
224 stable. Later, we show this to be a more general phenomenon. For now, we look in detail at the  
225 potential dynamics of our specific model.

226 We add to our model the limited dispersal behavior seen in obligate cooperators. To do  
227 so, we make additional assumptions. Groups can only split (i.e. members can leave or be forced  
228 out of a group but not join other groups), group size only increases through reproduction (a  
229 consequence of the former assumption), and splits only happen when the system is at a  
230 population equilibrium. In addition to limiting the dispersal of individuals, these assumptions  
231 render analyses more tractable which allow for clarity when describing the potential dynamics.

232 In our analysis, we begin by assuming a single group without competition. So long as  
233 initial population size is strictly positive, the group will either grow or shrink to the stable  
234 equilibrium  $x_F^* = M$ . Our behavioral analysis shows that a single group of size  $M$  is unstable.  
235 There is a strong incentive for the members to achieve a group of size  $x_A^*$ . Therefore, as the  
236 group's size reaches  $x_F^*$ , it splits into two groups, both of size  $x_A^* = \frac{M}{2}$  (Fig. 3d).

237 After the split, the addition of another group means both groups are facing competition  
238 with  $x_R$  equaling  $x_A^*$  for both groups. The fitness for both groups is  $F(x_A^*, x_A^*) = 0.25 - \alpha_r \frac{M}{2}$ .  
239 The size of inter-group competition  $\alpha_r$  will determine the long-term dynamics of our system.  
240 There are two thresholds of  $\alpha_r$ . There is the main threshold  $\alpha_r = T_1$  which divides competition

241 into strong and weak, and a secondary threshold  $\alpha_r = T_2 > T_1$  which divides strong competition  
242 further into moderately strong and extremely strong. These three strengths of competition –  
243 extremely strong, moderately strong, and weak – correspond to the dynamics of total extinction,  
244 unstable equilibria, and group turnover respectively, which we explore further.

#### 245 Total Extinction and Unstable Equilibria

246 Our main threshold of inter-group competition  $T_1$  determines the fitness of two groups  
247 just after splitting. In our model,  $T_1 = \frac{1}{2M}$ . If  $\alpha_r > T_1$ , then the fitness of each group is negative  
248  $F(x_A^*, x_A^*) < 0$ , and both groups will simultaneously decline in size. As both groups decline in  
249 size, individual fitness partially falls due to the Allee effect but also partially rises due to release  
250 from inter-group competition. The balance between these effects determine whether the groups  
251 will reach a positive equilibrium group size less than  $x_A^*$  or go extinct; this is determined by the  
252 second threshold  $T_2 = \frac{1}{M}$ .

253 If inter-group competition is moderately strong  $T_1 < \alpha_r < T_2$ , then the increasing fitness  
254 that comes from less inter-group competition eventually outweighs the decrease in fitness from a  
255 smaller group size. Both groups equilibrate at a size that is less than  $x_A^*$ . This equilibrium is  
256 behaviorally stable, but it is an unstable saddle-point with regard to population. With the slightest  
257 inequality in the two groups' sizes, the smaller one will go extinct while the larger grows to  
258  $x_F^* = M$ . If inter-group competition is extremely strong  $T_1 > \alpha_r$ , then the increasing fitness that  
259 comes from the decline of the other group is never enough to outweigh the decrease in fitness  
260 from a smaller group size; therefore, both groups will go extinct. Our analysis here accords with  
261 the analysis in the section on population dynamics.

#### 262 Group Turnover

263 If inter-group competition is weak  $0 < \alpha_r < T_1$ , then a more interesting dynamic occurs  
264 (Fig. 4). Here  $F(x_A^*, x_A^*) > 0$  meaning both groups will grow until reaching a new population  
265 equilibrium  $x_F^*$  where  $x_A^* < x_F^* < M$ . Let us denote the roots of the fitness function with  $x_R > 0$   
266 as  $X^*$  and  $Y^*$ ,  $0 < X^* < x_A^* < Y^* < M$ . Here,  $Y^*$  is the size of the groups at fitness equilibrium  
267  $x_F^* = Y^*$ , and  $X^*$  is the extinction threshold of each group. Since the groups are larger than  
268 optimal group size, they will split into two, creating four groups. However, since  $Y^* < M$ , the  
269 split will be unequal. One group will form a group of optimal group size  $x_A^*$ , while the other will  
270 be left in a group of size  $Y^* - x_A^*$ . As seen in the section on population dynamics, the eventual  
271 equilibrium of the system depends on whether any groups are below their extinction threshold.  
272 Therefore, in a multi-group population, it is the fitness of individuals in the smallest group that is  
273 key to understanding the dynamics.

274 Let  $x_{s,n}$  be the size of the smallest group, let  $X_{s,n}^*$  and  $Y_{s,n}^*$  be the roots of the fitness  
275 function for the smallest group, and let  $x_{R,n}$  be the size of the rest of the population from the  
276 perspective of the smallest group, all after the  $n$ -th split. After the first split, both groups grow  
277 from  $x_A^*$  to  $Y_{s,1}^*$ . As mentioned earlier, each group will split, giving us four groups: two larger  
278 groups of size  $x_A^*$  and two smaller groups of size  $x_{s,2} = Y_{s,1}^* - x_A^* = \frac{M}{2} \sqrt{1 - 4\alpha_r x_{R,1}}$ . Thus,  
279  $x_{R,2} = M + \frac{M}{2} \sqrt{1 - 4\alpha_r x_{R,1}}$  with the two new roots of  $X_{s,2}^*, Y_{s,2}^*$ . If the sizes of the smaller  
280 groups are much larger than the extinction threshold  $x_{s,2} \gg X_{s,2}^*$ , then the smaller groups persist.  
281 All four groups will grow to the new equilibrium and then split to give rise to eight groups, four  
282 large and four small. So long as  $x_{s,n} \gg X_{s,n}^*$ , the doubling of the group numbers will continue.

283 With each new group added,  $x_R$  gets bigger, and  $X^*$  and  $Y^*$  converge to  $x_A^*$  with  $X^*$   
284 getting bigger and  $Y^*$  getting smaller. Therefore, with each splitting of the groups ( $n$  increasing)

285  $x_{s,n}$  gets smaller and closer to the extinction threshold of  $X^*$  which it eventually reaches. There is  
286 still a division between the group with half of them at  $x_A^*$  and the rest at size  $x_{s,n} < x_A^*$ . These  
287 smaller groups will be extirpated which returns the system to the previous state. This leads to a  
288 cycling of the system in which there is a constant turnover of groups. For example, imagine there  
289 are 16 groups all at size  $Y_{s,4}^*$  after the fourth split. These groups will then split to create 32  
290 groups, 16 larger groups at size  $x_A^*$  and 16 smaller groups at size  $x_{s,5} = Y_{s,4}^* - x_A^*$ . If those 16  
291 smaller groups are at or below the extinction threshold, they will go extinct which returns the  
292 system to having 16 groups at  $x_A^*$  which then grow to the fitness equilibrium  $Y_{s,5}^* = Y_{s,4}^*$ . The  
293 process then repeats again, creating the turnover dynamic.

294 This turnover dynamic depends upon a threshold value of  $x_R$ . Determining the threshold  
295 is tricky as it can happen even when  $x_{s,n} > X_{s,n}^*$ ,  $F(x_{s,n}, x_{R,n}) > 0$ . However, we can find an  
296 upper bound to  $x_R$ . When  $x_{s,n} \leq X_{s,n}^*$ , individuals within the smaller groups are at or below the  
297 extinction threshold and have negative or zero fitness  $F(x_{s,n}, x_{R,n}) \leq 0$ . This guarantees  
298 turnover dynamics as the larger groups have positive fitness leading to their growth which then  
299 lowers the fitness of the smaller groups. As such, the  $x_R$  which makes  $x_s = X^*$  is the upper  
300 bound of the threshold value. 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).  
301 This population is of finite size (assuming  $\alpha_R \neq 0$ ) and will be reached after some time, meaning  
302 there will be eventual cycles with larger groups splitting and smaller groups being extirpated  
303 (Fig. 5).

### 304 **Argument for the General Instability of the Behavioral and Population Dynamics**

305 Now we present a more general demonstration of the fundamental mismatch between a stable  
306 population equilibrium and a stable behavioral equilibrium. We retain the majority of our earlier  
307 fundamental assumptions including 1) cooperation leading to fitness benefits, 2) all individuals

308 being identical and only distinguished by presence or absence in a group, 3) individuals seeking  
 309 to maximize their fitness but only know the size of their current group. We relax our previous  
 310 assumption relating to dispersal. Individuals can join existing groups, and behavioral dynamics  
 311 can occur concurrently with the population dynamics.

312 Let  $\frac{dx_i}{dt} = x_i \cdot F_i(x)$  be the population dynamics within group  $i$  where  $F_i(x)$  gives the  
 313 expected per capita growth rate and is assumed to be a continuously differentiable (at least  $C^2$ )  
 314 function of  $x = (x_1, x_2, \dots, x_{n_g})$  which is the vector of group sizes for all groups numbering 1 to  
 315  $n_g$ . We refer to  $F_i(x)$  as group  $i$ 's fitness function. Taking the partial derivative of  $F_i(\vec{x})$  with  
 316 respect to  $x_i$  and fixing all other variables to the  $x_{-i} = (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_{n_g})$  results in a  
 317 function of association  $A_i(x_i)|_{x_{-i}} = \frac{\partial F_i(x)}{\partial x_i}$  for focal group  $i$  which gives the change of the  
 318 group's per capita growth rate due to additional members, i.e. an individual's marginal fitness  
 319 contribution. When  $A_i(x_i)|_{x_{-i}}$  is positive (or negative), additional members increase (or  
 320 decrease) an individual's fitness. We call these states cooperative and competitive respectively.  
 321  $A_i(x_i)|_{x_{-i}}$  also determines the preference of individual group members for more or fewer  
 322 members. In a cooperative state, individuals at best do not want the group size to decrease and  
 323 will resist splitting and behaviorally favor an increase, and vice-versa for group sizes in a  
 324 competitive state.

325 Let  $x^* = (x_1^*, x_2^*, \dots, x_{n_g}^*) \geq 0$  be a solution to the equation  $F_i(x^*) = 0$  for all  $i \in$   
 326  $\{1, \dots, n_g\}$ . Let  $i^+ \subseteq \{1, \dots, n_g\}$  be the subset of all groups with positive population size. We can  
 327 analyze the stability of this point through the Jacobian  $J$ . The diagonals of the Jacobian are

328  $\frac{\partial(dx_i/dt)}{\partial x_i} |_{x^*} = \frac{\partial(x_i \cdot F_i(x))}{\partial x_i} |_{x^*} = F_i(x^*) + x_i^* \cdot A_i(x_i^*) |_{x_{-i}^*} = x_i^* \cdot A_i(x_i^*) |_{x_{-i}^*}$  for all  $i \in$

329  $\{1, 2, \dots, n_g\}$ . As  $x_i^* \geq 0$ , the diagonals are either 0 or reflect the sign of the behavioral game at  
330 that point. If the equilibrium is cooperative for all groups in the set  $i^+$  ( $A_i(x_i^*)|_{x^*} > 0$  for all  $i \in$   
331  $i^+$ ), then the trace of the Jacobian is positive,  $\text{Tr}(J) > 0$ . Since the sum of all eigenvalues is  
332 positive, at least one eigenvalue is positive, and this vector of equilibrium population sizes is  
333 unstable.

334 If at least one of the groups in  $i^+$  is at a competitive state, then all eigenvalues could be  
335 negative, meaning the population dynamics could be at a stable equilibrium. Those competitive  
336 groups though are at a behaviorally unstable equilibrium. Since  $F_i(x)$  is  $C^2$  smooth for all  $i$ , then  
337 there exists a point of lower population size  $x_i < x_i^*$  that gives higher fitness  $F_i(\{x_i, x_{-i}^*\}) >$   
338  $F_i(x^*)$ . If this is the case, coalition game theory tells us that a coalition of  $x_i^*$  in group  $i$  will not  
339 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  
340 that maximizes the group's per capita growth rate.

341 An individual's preferred state is one that maximizes its fitness. A necessary condition is  
342 that  $A_i(x_i^*)|_{x_{-i}^*} = 0$  and  $\frac{\partial A_i(x_i^*)|_{x_{-i}^*}}{\partial x_i} < 0$ . If there is an  $x^*$  satisfying these conditions for all groups,  
343 then diagonals of the Jacobian matrix  $J$  are all 0; therefore, the sum of all eigenvalues are 0. If  
344 this is the case, then there is either a mix of positive and negative eigenvalues (meaning unstable  
345 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  
346 partially stable state and not a neutrally stable state. This means there are clear domains of  
347 instability on whose boundary the point  $x^*$  resides.

348 According to this analysis, there will be a fundamental mismatch between stable  
349 behavioral dynamics and stable population dynamics in obligate cooperative species, and their  
350 overall population dynamics will always be unstable.



351 **Discussion**

352           We have analyzed the population dynamics of obligately cooperative species with limited  
353 dispersal. We embedded a behavioral game with these properties into a model of population  
354 dynamics. There were three potential outcomes: 1) extinction of all groups, 2) unstable equilibria  
355 of population sizes within groups, and 3) group turnover. The cooperative species fails to achieve  
356 stable population dynamics due to a mismatch between the stability of the behavioral equilibrium  
357 and that of the population dynamics. While we are not the first to note that local extinctions and  
358 extirpations occur in population dynamics due to Allee effects, our model shows them to be  
359 intrinsic and unavoidable. Our findings join other mathematical analyses in generalizing the  
360 phenomenon to factors intrinsic of obligately cooperative species.

361           Empirically, many obligately cooperative species including mole-rats, social spiders, and  
362 banded mongooses do not show stable population dynamics and instead show constant group  
363 turnover (Jarvis et al., 1994; Aviles, 1997; Clutton-Brock et al., 1999). Hypotheses with  
364 mathematical support have been developed to explain the phenomenon. Aviles (1999) noted that  
365 cooperation can magnify reproductive output, leading to oscillations and chaotic behavior, and  
366 ultimately extinction of a group. Chourchamp et al. (1999a) and Wang et al. (1999) both showed  
367 the importance of a within-group extinction threshold. Our results align further indicate the  
368 importance of extinction thresholds. However, whereas groups by assumption had extinction  
369 thresholds in prior models, we show that this extinction threshold necessarily emerges due to  
370 intergroup competition regardless of whether the Allee effect is strong or weak. Furthermore,  
371 more groups lead to greater instability. The models of Chourchamp et al. (1999a) and Wang et  
372 al. (1999) relied on external factors to drive the instability. With the addition of a behavioral  
373 game of group splitting and formation, we show that new groups will constantly be created,

374 leading to unstable population dynamics and an eventual collapse of group numbers. Among all  
375 the hypotheses for the instability of obligately cooperative systems, our model with an embedded  
376 behavioral game shows how these dynamics are not only intrinsic but unavoidable.

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

### 383 *Short-Term Intragroup Dynamics*

384         In our model, each group has its own population dynamic with an Allee effect. With the  
385 Allee effect, there is a non-zero optimal group size which maximizes fitness for the group  
386 members. We assume that individuals in a group whose size is beyond the behavioral optimum  
387 will split off to form their own smaller groups. This enhances overall fitness of the group. We are  
388 not the first to understand that group splitting can occur due to an Allee effect. For example,  
389 Crema (2014) incorporated the Allee effect into a simulation model to understand human  
390 settlement dynamics. Fission-fusion group dynamics, permanent or otherwise, are a well-studied  
391 aspect of cooperative societies with examples ranging from ants to cetaceans to humans.

392         In our model, we made some simplifying assumptions at the expense of realism. For both  
393 models, we assumed: 1) cooperation leads to fitness benefits, 2) individuals are identical and  
394 only distinguished by their present group size, 3) individuals seek to maximize fitness, 4) the  
395 overall number of players within a group changes according to the average fitness of group  
396 members, and 5) individuals have limited information, specifically they only know about the

397 fitness function of their present group. For the specific model, we added the assumptions that 6)  
398 individuals cannot leave a group and join another established group, i.e. groups form by the  
399 fission of existing ones, and 7) behavioral dynamics occur when the system has reached the  
400 population equilibrium. Some may have more relevance (1, 3, 4) to biological systems than  
401 others (2, 6, 7), but these assumptions allow for conclusions to be derived analytically. In most  
402 eusocial insects for example, individuals within a caste are largely identical (though not between  
403 castes), and in honey bees, creation of a new colony happens when the hive has reached its  
404 maximum capacity and splits into roughly equal sizes (a process known as swarming) (Fell et al.,  
405 1977). Many obligate cooperators may not be able to join their group of choice, though perhaps not  
406 as restrictive as modeled. Assumption 5 is particularly interesting. Individuals are necessarily  
407 limited in information about other groups, but how and to what extent is quite variable.  
408 Furthermore, many behaviors evolve such that they appear as if they have more information than  
409 possible, i.e. instinct. Overall, we feel the assumptions mimic key features of natural systems  
410 while maintaining analytical tractability.

### 411 *Long-Term Intergroup Dynamics*

412 Over time, the process of groups growing and splitting results in the long-term population  
413 dynamics of that species. Under conditions of strong inter-group competition, our model  
414 illustrates an initial split followed by both groups simultaneously shrinking to extinction or some  
415 non-equilibrium state. This likely manifests as a spatial dynamic. If inter-group competition is  
416 spatially dependent, then a group that splits into two, only to remain close, might compete  
417 strongly with each, leading to one or both of their extinctions. Rather, on a larger scale, we are  
418 likely to see group turnover under conditions of weak inter-group competition. Over longer time

419 scales, our model shows oscillations of the total population size with repeated instances of group  
420 extirpations and splitting events (Fig. 5).

421         Despite unstable population dynamics, the overall population size and the number of  
422 groups can persist indefinitely within a bounded state. With moderately strong competition, if the  
423 groups become unequal in size, then the largest one will grow to maximum size while the  
424 smallest goes extinct. At this point, the remaining group splits into two and returns to the same  
425 original condition. In such a case, though one of the original groups is gone, a new group has  
426 taken its place akin to the way a lizard may regrow its tail. With weak competition and group  
427 turnover, the overall population exhibits a stable limit cycle. Smaller groups are constantly going  
428 extinct, resetting the system to a previous state. This bounds the range of size over which the  
429 overall population will cycle. Old groups go extinct and new groups are created which function  
430 identically to the old groups. In addition, while the population dynamics may be unstable, the  
431 distribution of group sizes can be relatively stable.

432         Studies of long-term population dynamics which focus on the overall population but do  
433 not assess the fates of individual groups can attribute fluctuations in population dynamics to  
434 external factors. For example, recent population decline to near extirpation of the Isle Royale  
435 wolves is attributed to genetic inbreeding or predator-prey dynamics, and a call for human-  
436 mediated immigration of new wolves into the Isle Royale population (Hedrik et al. 2014). While  
437 there are many environmental factors that may contribute to extirpations, especially those  
438 anthropogenic in nature, our model provides support that extirpations and group turnover may  
439 simply be an intrinsic property of social animals, a base upon which other factors may be added.

440 *The Limits of Our Model*

441           Altering the assumptions of our model results in different system dynamics, some of  
442 them being quite trivial. For example, little happens when we alter the function (eq. 1) for group  
443 dynamics, mostly resulting in the ability to split into multiple groups and a budding dynamic (see  
444 SI). Other alterations have larger impacts. Removing assumption 6 (individuals cannot join  
445 groups) allows for the fusion of smaller groups which can engender some stability (but not full  
446 stability) into the system. If these groups can fuse into larger groups, then they can escape  
447 extinction by being in groups larger than the extinction threshold as well as reducing intergroup  
448 competition. The inclusion of fusion reduces the upper and lower bounds of the non-equilibrium  
449 dynamics associated with total population size and group number (see SI for a specific example).  
450 It must be noted though that even with fusion, population dynamics are not truly stable and still  
451 result in limit cycles.

452           If we alter assumption 5 and let individuals have perfect information, they may not  
453 choose to split a group if inter-group competition is strong. At the core of the splitting process  
454 are individuals seeking a group size that maximizes fitness. If competition is strong ( $\alpha_r \geq T_1$ ),  
455 then it is always better for individuals to be in one group of size  $M$  than two groups of size  $x_i$   
456 and  $M - x_i$  ( $0 < x_i < M$ ) since the fitness cost of intergroup competition always outweighs the  
457 fitness benefits of being inside a group. Group splitting becomes a kind of “mutually assured  
458 destruction. If competition is weak ( $\alpha_r < T_1$ ), then eventually intra-group competition will  
459 exceed inter-group competition. Even with perfect information, splitting will still occur, the only  
460 difference being that optimal group size is greater than previously  $x_A^* > \frac{M}{2}$ .

461           We can even relax the central tenant of obligate cooperation (assumption 1). Instead,  
462 what if there are no fitness benefits to association, only a difference in fitness costs  $F_i(x_i, x_R) =$   
463  $1 - \frac{x_i^2}{M^2} - \alpha_r x_R$ . In such a case, individuals seek a group size which minimizes their cost. In such

464 a case, there can be a splitting dynamic and unstable population dynamics similar to what we  
465 have analyzed. The addition of cooperation guarantees an optimal group size of greater than 1.  
466 Under perfect information, there will only be an optimal group size if intergroup competition is  
467 not so strong as to create mutually assured destruction, yet not so weak as to have individuals  
468 choosing to be by themselves. Under limited information, then no matter the strength of inter-  
469 group competition, individuals will choose not to associate with others.

### 470 *Conservation Implications*

471 While much has been learned from the social structure of species of high conservation  
472 concern (Pusey et al. 2007), our findings suggest future research and conservation efforts should  
473 add inter-group dynamics as a major driver for maintaining species population. Our modelling  
474 results invite more attention to measuring the size of intra-group Allee effects and the strengths  
475 of inter-group competition. Stephens and Sutherland (1999) and Courchamp et al. (2008) focus  
476 on the conservation implications of Allee effects in the context of species exploitation, habitat  
477 loss, and habitat fragmentation. Long-range dispersal is an important mechanism of species'  
478 range expansions, and dispersal due to group splitting may provide further insights into Allee  
479 effects and biological invasions (Lodge, 1993; Taylor and Hastings, 2005).

480 Our results point to four main effects relevant for the conservation of cooperative species.  
481 Firstly, these dynamics are intrinsic and will happen regardless of the environmental conditions.  
482 Simply managing for greater environmental stability will not prevent group extinction or  
483 collapse. Persistent, and not necessarily stable, populations should be the goal. Secondly, the  
484 average overall population size over time will be smaller than the potential carrying capacity,  
485 and the overall population more prone to total extinction due to the constant fluctuations.  
486 Therefore, maximizing overall population is critical. Thirdly, there must be a sufficiently large

487 population to allow smaller groups to fuse. The smaller the group, the more likely it is below its  
488 internal extinction threshold. By fusing, these smaller groups can avoid the extinction threshold  
489 which also has the benefit of boosting average overall population size. And lastly, stronger inter-  
490 group competition is more likely to lead to unstable dynamics. Diminished resources and lack of  
491 territory between groups can enhance competition and lead to greater instability.

492 All four of the reasons point to the disproportionate impact that habitat fragmentation and  
493 loss should have on obligate cooperative species. Often conservation practices are implemented  
494 over smaller scales, with protection for species being implemented in a distinct area of land or  
495 for a specific group of that species. For such species, single large conservation areas may be  
496 preferable over several small ones (SLOSS) (MacArthur and Wilson 1967, Diamond 1975,  
497 Simberloff and Abele 1982). A single large conservation area not only mitigates issues such as  
498 inbreeding depression but also may stabilize the population dynamics of obligately cooperative  
499 species. Conservation areas should be large enough to harbor multiple groups ensuring minimal  
500 inter-group competition. Numerous widely dispersed groups can also withstand environmental  
501 stochasticity and may permit a robust fusion process that stabilizes overall population dynamics.

## 502 *Prospectus*

503 In this paper, we provide a simple model to derive the population dynamics of obligately  
504 cooperative species. Our work offers a starting point for further analysis of cooperative species  
505 population dynamics. Firstly, we can more realistic models by further exploring the assumptions  
506 of our model or adding features. Such examples would include movement between groups before  
507 equilibria, hierarchy and dominance within the group, meta-population and spatial dynamics,  
508 source-sink dynamics, evolution, explicit consumer-resource dynamics, and variations on  
509 intergroup competition including non-linear competition, asymmetric competition, exploitative

510 vs. interference competition, and fixed and variable intergroup costs. Demographic stochasticity  
511 and kin structure are features of smaller obligate cooperative groups not included in this model.  
512 Evolution in particular may yet prove fruitful; one way a group may escape the effects of  
513 competition in this model is by increasing its growth rate. While the term  $\alpha_r$  was used as inter-  
514 group competition in this manuscript, it also includes growth rate. Higher intra-group growth  
515 rates concomitantly reduce  $\alpha_r$ . We can see this in Figure 5. After the second splitting event, the  
516 dark red group that goes extinct has a larger maximal group size and larger initial size (and  
517 therefore exerts greater competitive force) but a smaller growth rate than either the purple or  
518 gold group which both persist. This suggests that a higher growth rate within a group alleviates  
519 inter-group competition more so than a larger group size. This lines up with the hypothesis that  
520 the evolution of eusociality and division of reproductive work is due to group competition  
521 (Reeve and Hölldobler, 2007).

522         With more complex models, we can compare the mathematical results against real-world  
523 data. We see many examples of group splitting and turnover in nature. Group splitting occurs  
524 among rhesus monkeys, lions, sponges, male hyenas, and invasive Argentine ants (Chepko-Sade  
525 and Sade, 1979; Dittus, 1988; Pusey and Packer, 1987; Blanquer et al., 2009; Holekamp et al.,  
526 1993; Suarez et al. 2000). We see group turnover among Isle Royale wolves, large primates, wild  
527 dogs, elephants, mole-rats, mongooses, spiders, and chimpanzees (Peterson and Page, 1988;  
528 Ripple and Beschta 2012; Kalpers et al., 2003; Burrows, 1991; Armbruster and Lande, 1993;  
529 Parker and Graham 1989; Jarvis et al., 1994; Aviles, 1997; Clutton-Brock et al., 1999; Goodall  
530 1986). In particular, the Damaraland mole-rats display a process much like the model. Smaller,  
531 newly founded groups are more likely to die out due to competition from larger, more  
532 established groups (Jarvis et al., 1994). Intergroup competition seems to be a factor in group



533 extirpations of chimpanzees (Goodall 1986). By comparing simulated data from our models to  
534 real-world data such as bee swarming or the colonization of wolves in new areas (Oldroyd et al.,  
535 1997; Peterson and Page, 1988), we may be able to test how the mismatch between behavioral  
536 and population dynamics govern the loss and formation of groups. Because obligately  
537 cooperative species often have a significant impact on the ecosystem, whether through  
538 ecosystem engineering, their status as keystone species, or accounting for a significant  
539 percentage of the biomass of the ecosystem (in some species, all three), it is imperative that  
540 ecologists understand the population dynamics of these species (Jones et al., 1994; Ripple and  
541 Beschta, 2012; Hoelldolber and Wilson, 1990). Better knowledge will help ecologists and  
542 wildlife conservations better manage and save their populations and the ecosystems in which  
543 they live (Stephens and Sutherland, 1999).

544 **Acknowledgements**

545           The authors wish to thank C.J. Whelan, K. Staňková, and G.G. McNickle for their  
546 discussion, review, and comments on the paper. AH wishes to thank the NSF for funding his  
547 graduate studies. This material is based upon work supported by the National Science  
548 Foundation Graduate Research Fellowship under Grant Nos. DGE-0907994 and DGE-1444315.  
549 Any opinion, findings, and conclusions or recommendations expressed in this material are those  
550 of the author(s) and do not necessarily reflect the views of the National Science Foundation.

551 **References**

- 552 Allee, W.C. 1931. *Animal Aggregations: A Study in General Sociology*, University of Chicago,  
553 Chicago, IL, United States of America
- 554 Allee, W.C. 1938. *The Social Life of Animals*, Heinemann, London, United Kingdom
- 555 Angulo, E., G.M. Luque, S.D. Gregory, J.W. Wenzel, C. Bessa-Gomes, L. Berec, and F.  
556 Courchamp. 2018. Allee effects in social species. *Journal of Animal Ecology* **87**:47-58
- 557 Armbruster, P. and R. Lande. 1993. A population viability analysis for African elephant  
558 (*Loxodonta africana*): how big should reserves be?. *Conservation Biology* **7**:602-610
- 559 Aviles, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders.  
560 Pages 476-498 in J.C. Choe and B.J. Crespi, editors. *The evolution of social behaviour in*  
561 *insects and arachnids*. Cambridge University Press, Cambridge, United Kingdom
- 562 Aviles, L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the  
563 evolution of sociality. *Evolutionary Ecology Research* **1**:459-477
- 564 Axelrod, R. and W.D. Hamilton. 1981. The evolution of cooperation. *Science* **211**:1390-1396
- 565 Bateman, A.W., A. Ozgul, M. Krkošek, and T.H. Clutton-Brock. 2018. Matrix models of  
566 hierarchical demography: linking group- and population-level dynamics in cooperative  
567 breeders. *The American Naturalist* **192**:188-203
- 568 Blanquer, A., M.J. Uriz, and J. Caujapé-Castells. 2009. Small-scale spatial genetic structure in  
569 *Scopalina lophyropoda*, an encrusting sponge with philopatric larval dispersal and  
570 frequent fission and fusion events. *Marine Ecology Progress Series* **380**:95-102
- 571 Bonebeau, E., L. Dagorn, and P. Fréon. 1999. Scaling in animal group-size distributions.  
572 *Proceedings of the National Academy of Sciences* **96**:4472-4477

- 573 Chepko-Sade, B.D. and D.S. Sade. 1979. Patterns of group splitting within matrilineal kinship  
574 groups. *Behavioral Ecology and Sociobiology* **5**:67-86
- 575 Clutton-Brock, T.H., D. Gaynor, G.M. McIlrath, A.D.C MacColl, R. Kansky, P.Chadwick, M.  
576 Manser, J.D. Skinner, and P.N.M. Brotherton. 1999. Predation, group size and mortality  
577 in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology*. **68**:672-683
- 578 Courchamp, F., B. Grenfell, and T. Clutton-Brock. 1999. Population dynamics of obligate co-  
579 operators. *Proceedings of the Royal Society of London B* **266**:557-563
- 580 Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the  
581 Allee effect. *Trends in Ecology and Evolution* **14**:405-410
- 582 Courchamp, F., T. Clutton-Brock, and B. Grenfell. 2000. Multipack dynamics and the Allee  
583 effect in the African wild dog, *Lycaon pictus*. *Animal Conservation* **3**:277-285
- 584 Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee effects in ecology and conservation.  
585 Oxford University Press, Oxford, United Kingdom
- 586 Couzin, I.D. and J. Krause. 2003. Self-organization and collective behavior in vertebrates.  
587 *Advances in the Study of Behavior* **32**:1-75
- 588 Crema, E.R. 2014. A simulation model of fission-fusion dynamics and long-term settlement  
589 change. *Journal of Archeological Method and Theory* **21**:385-404
- 590 Diamond, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the  
591 design of natural reserves. *Biological conservation* **7**: 129-146.
- 592 Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* **96**:389-401
- 593 Dittus, W.P. 1988. Group fission among wild toque macaques as a consequence of female  
594 resource competition and environmental stress. *Animal Behaviour* **36**: 1626-1645.

- 595 Dugatkin, L.A. 1998. *Game Theory and Cooperation*. *Game Theory and Animal Behavior* ed.  
596 L.E. Dugatkin & H.K. Reeve. Oxford University Press, Oxford, United Kingdom
- 597 Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge University  
598 Press, Cambridge, United Kingdom
- 599 Gueron, S. and S.A. Levin. 1995. The dynamics of group formation. *Mathematical Biosciences*  
600 **128**:243-264
- 601 Gueron, S., S.A. Levin, and D.I. Rubenstein. 1996. The dynamics of herds: from individuals to  
602 aggregates. *Journal of Theoretical Biology* **182**:85-98
- 603 Hamilton, W.D. 1964. The genetical evolution of social behavior. I and II *Journal of Theoretical*  
604 *Biology* **7**:1-52
- 605 Hedrick, P.W., R.O. Peterson, L.M. Vucetich, J.R. Adams, and J.A. Vucetich, 2014. Genetic  
606 rescue in Isle Royale wolves: genetic analysis and the collapse of the  
607 population. *Conservation genetics* **15**: 1111-1121.
- 608 Hoelldobler, B. and E.O. Wilson. 1990. *The Ants*. Harvard University Press, Harvard, MA,  
609 United States
- 610 Holekamp, K.E., J.O. Ogutu, H.T. Dublin, L.G. Frank, and L. Smale. 1993. Fission in a spotted  
611 hyena clan: consequences of prolonged female absenteeism and causes of female  
612 emigration. *Ethology* **93**:285-299
- 613 Jarvis, J.U.M., M.J. O’Riain, N.C. Bennet, and P.W. Sherman. 1994. Mammal eusociality: a  
614 family affair. *Trends in Ecology and Evolution* **9**:47-51
- 615 Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*  
616 **69**:373-386

- 617 Kalpers, J., E.A. Williamson, M.M. Robbins, A. McNeilage, A. Nzamurambaho, N. Lola, and G.  
618 Mugiri. 2003. Gorillas in the crossfire: population dynamics of the Virunga mountain  
619 gorillas over the past three decades. *Oryx* **37**:326-337.
- 620 Lehmann, L., N. Perrin, and F. Rousset. 2006. Population demography and the evolution of  
621 helping behaviors. *Evolution* **60**:1137-1151
- 622 Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*  
623 **8**:133-137
- 624 MacArthur, R. H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton, NJ,  
625 United States of America
- 626 Mirabet, V., P. Auger, and C. Lett. 2007. Spatial structures in simulations of animal grouping.  
627 *Ecological Modelling* **201**:468-476
- 628 Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science* **314**:1560-1563
- 629 Okubo, A. 1986. Dynamical aspects of animal grouping: swarms, schools, flocks, and herds.  
630 *Advances in Biophysics* **22**:1-94
- 631 Oldroyd, B.P., E.G. Thexton, S.H. Lawler, and R.H. Crozier. 1997. Population demography of  
632 Australian feral bees (*Apis mellifera*). *Oecologia* **111**:381-387
- 633 Parker, I.S., and A.D. Graham. 1989. Elephant decline (Part I) downward trends in African  
634 elephant distribution and numbers. *International Journal of Environmental*  
635 *Studies* **34**:287-305.
- 636 Parvinen, K. and Å Brännstrom. 2016. Evolution of site-selection stabilizes population  
637 dynamics, promotes even distribution of individuals, and occasionally causes  
638 evolutionary suicide. *Bulletin of Mathematical Biology* **78**:1749-1772

- 639 Peleg, B. and P. Sudhölter. 2007. Introduction to the Theory of Cooperative Games. Springer-  
640 Verlag Berlin Heidelberg
- 641 Peterson, R.O. and R.E. Page. 1988. The rise and fall of Isle Royale wolves, 1975–1986. Journal  
642 of Mammalogy **69**:89-99
- 643 Pusey, A.E. and C. Packer. 1987. The evolution of sex-biased dispersal in lions. Behaviour  
644 **101**:275-310
- 645 Pusey, A.E., L. Pintea, M.L. Wilson, S. Kamenya, and J. Goodall. 2007. The contribution of  
646 long-term research at Gombe National Park to chimpanzee conservation. Conservation  
647 Biology **21**:623–634
- 648 Reeve, H.K and B. Hölldolber. 2007. The emergence of a superorganism through intergroup  
649 competition. Proceedings of the National Academy of Sciences **104**:9736-9740
- 650 Ripple, W.J. and R.L. Beschta. 2012. Trophic cascades in Yellowstone: The first 15 years after  
651 wolf reintroduction. Biological Conservation **145**:205-213
- 652 Saffre, F. and J.L. Deneubourg. 2002. Swarming strategies for cooperative species. Journal of  
653 Theoretical Biology **214**:441-451
- 654 Simberloff, D., and L.G. Abele. 1982. Refuge design and island biogeographic theory: effects of  
655 fragmentation. The American Naturalist **120**:41-50.
- 656 Stephens, P.A. and W.J. Sutherland. 1999. Consequences of Allee effect for behaviour, ecology  
657 and conservation. Trends in Ecology and Evolution **14**:401-405
- 658 Stephens, P.A., W.J. Sutherland, and R.P. Freckleton. 1999. What is the Allee effect? Oikos  
659 **87**:185-190

- 660 Suarez, A.V., D.A. Holway, and T.J. Case. 2000. Patterns of spread in biological invasions  
661 dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of*  
662 *the National Academy of Sciences* **98**:1095-1100
- 663 Taylor, P.D. 1992. Inclusive fitness in a homogenous environment. *Proceedings of the Royal*  
664 *Society of London B* **249**:299-302
- 665 Taylor, C.M. and A. Hastings. 2005. Allee effects in biological invasions. *Ecology Letters* **8**:895-  
666 908
- 667 Terborgh, J. 1983. *Five new world primates: a study in comparative ecology*. Princeton, NJ,  
668 United States of America
- 669 Trivers, R.L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*  
670 **46**:35-57
- 671 von Neumann, J. and O. Morgenstern. 1944. *Theory of Games and Economic Behavior*,  
672 Princeton University Press, Princeton, New Jersey, United States of America
- 673 Wang, G., XG. Liang, and FZ. Wang. 1999. The competitive dynamics of populations subject to  
674 an Allee effect. *Ecological Modelling* **124**:183-192
- 675 West, S.A., A.S. Griffin, and A. Gardner. 2007. Social semantics: altruism, cooperation,  
676 mutualism, strong reciprocity, and group selection. *Journal of Evolutionary Biology*.  
677 **20**:415-432
- 678 Wilson, E.O. 1975. *Sociobiology: The New Synthesis*. The Belknap Press of Harvard University  
679 Press, Cambridge, Massachusettes
- 680 Zemel, A. and Y. Lubin. 1995. Inter-group competition and stable group sizes. *Animal*  
681 *Behaviour* **50**:485-488
- 682



683 Table 1: A reference table of all the parameters used in this paper.

<b>Symbol</b>	<b>Definition</b>
$n_g$	The number of groups in a population
$x$	The vector of all group sizes
$x_i$	The size of group $i$
$x_{-i}$	The vector of all group sizes except for group $i$
$x_R$	The size of the rest of the population
$M$	Maximum potential group size
$r$	A growth rate scaling factor
$\alpha$	The strength of intergroup competition
$\alpha_r$	The ratio between the strength of intergroup competition and the growth rate scaling factor
$F(\cdot)$	The fitness function of a group in our specific model
$A(\cdot)$	The association function of a group in our specific model
$x_F^*$	Equilibrium group size
$x_A^*$	Optimal group size
$T_1$	The main threshold of $\alpha_r$ that divides competition into weak and strong
$T_2$	The secondary threshold of $\alpha_r$ that divides strong competition into moderately strong and extremely strong
$X^*$	The smaller root of the fitness function when $x_r > 0$
$Y^*$	The larger root of the fitness function when $x_r > 0$
$x_{s,n}$	The size of the smallest group in a population after the $n$ -th split
$X_{s,n}^*$	The smaller root of the smallest group's fitness function after the $n$ -th split
$Y_{s,n}^*$	The larger root of the smallest group's fitness function after the $n$ -th split
$x_{R,n}$	The size of the rest of the population from the perspective of the smallest group after the $n$ -th split
$F_i(\cdot)$	The fitness function of group $i$
$A_i(\cdot)$	The association function of group $i$
$x^*$	A solution to the equation $F_i(x^*) = 0$
$\tilde{x}_i$	The optimal group size of group $i$ such that $\tilde{x}_i < x_i^*$
$i^+$	The set of all groups with positive population size

685 Fig. 1 A figure of the fitness (a, b) and association (c, d) functions of our model (a, c) and strictly  
686 competitive model  $\left(F(x_i) = r \left(1 - \frac{x_i}{M}\right)\right)$  (b, d). (a) Our model's fitness function (b) The  
687 competitive model's fitness function (c) Our model's association function (d) The competitive  
688 model's association function. Open circles indicate the group size that gives the maximum  
689 fitness, i.e. optimal group size, while closed circles indicate the stable fitness equilibrium. One  
690 can see that in both systems, the optimal group size and stable fitness equilibrium do not match;  
691 however, there is greater implication on the population dynamics in our model as the association  
692 function has both positive and negative elements, lending itself to behavioral game.  $r = 1, M =$   
693 100

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

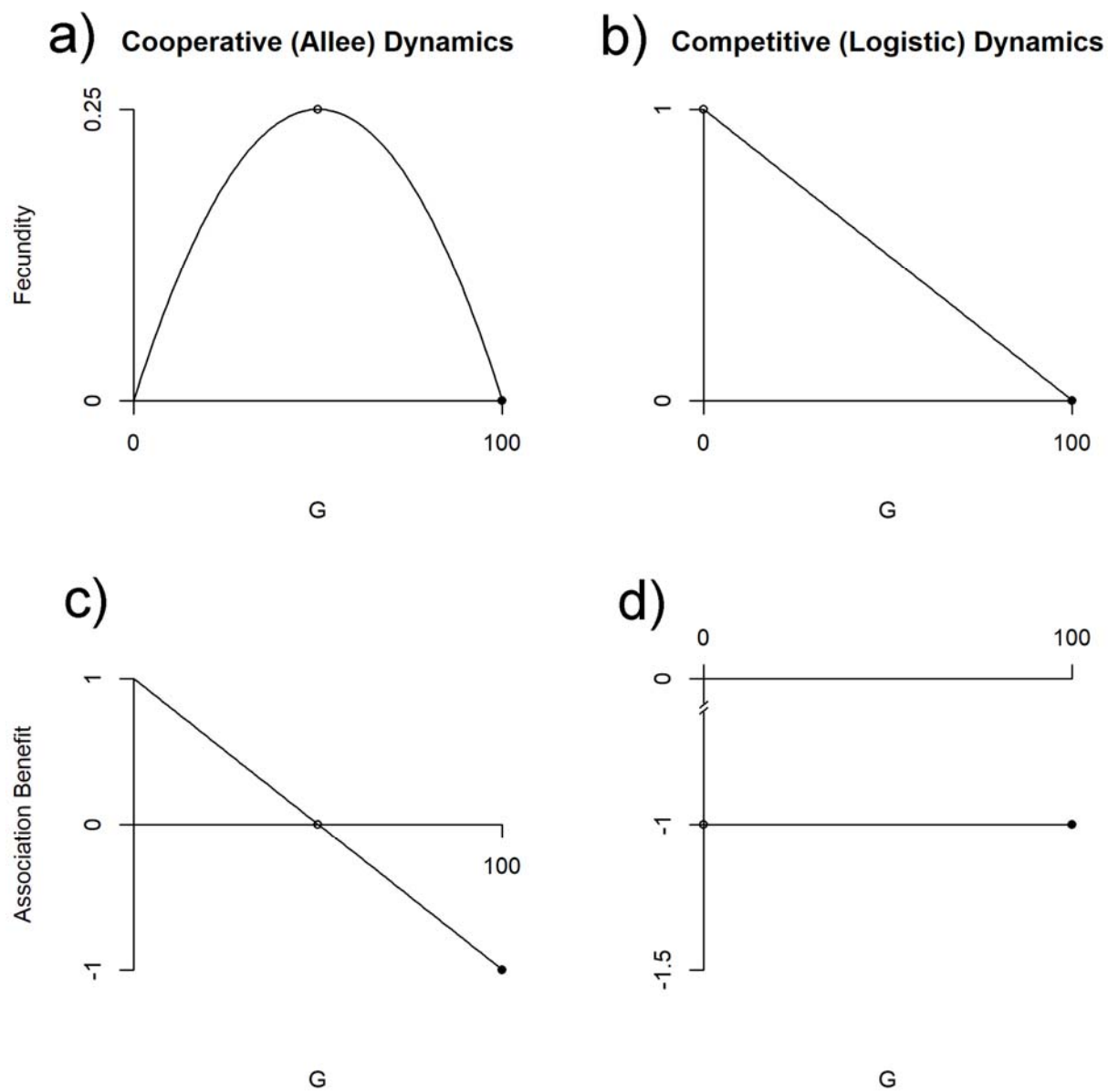
697 Fig. 3 A schematic of the process of group growth and splitting. On the left, a circle represents a  
698 group. On the right is said group's fitness function on top and association on the bottom. Our  
699 parameters for this model are  $r = 1, M = 100, \alpha = \frac{1}{150}$ . (a) The fitness function of a single group  
700 at extremely small population size  $x_1 = 0.5$  (b) The fitness function of the group when it is at its  
701 optimal size  $x_1 = x_A^* = \frac{M}{2}$ . In this case, all members of the group are at maximum fitness and  
702 satisfied with group size, but fitness is positive causing the group to continue growing. (c) At this  
703 point, the group is at maximum size  $x_1 = M$  so fitness is 0 and it will stop growing, but  $A(x_1) < 0$   
704 so the group members are unhappy. (d) The group just after splitting into two groups  $(x_1, x_2) =$   
705  $(x_A^*, x_A^*)$ . The new group (dotted line) leads to a lowering of fitness due to intergroup competition,

706 which in this case is below 0. Here,  $T_1 < \alpha_r < T_2$ , so both groups will go to an unstable  
707 equilibrium.

708 Fig. 4 A flowchart for how our model evolves starting with a single, cooperative group. Red-  
709 filled squares represent initial conditions, green-filled rounded rectangles represent transition  
710 states, yellow-filled circles represent “decision” points, and blue-filled hexagons represent end  
711 points. As seen here, there are either no endpoints (weak competition) or the endpoints are  
712 unstable (strong competition).

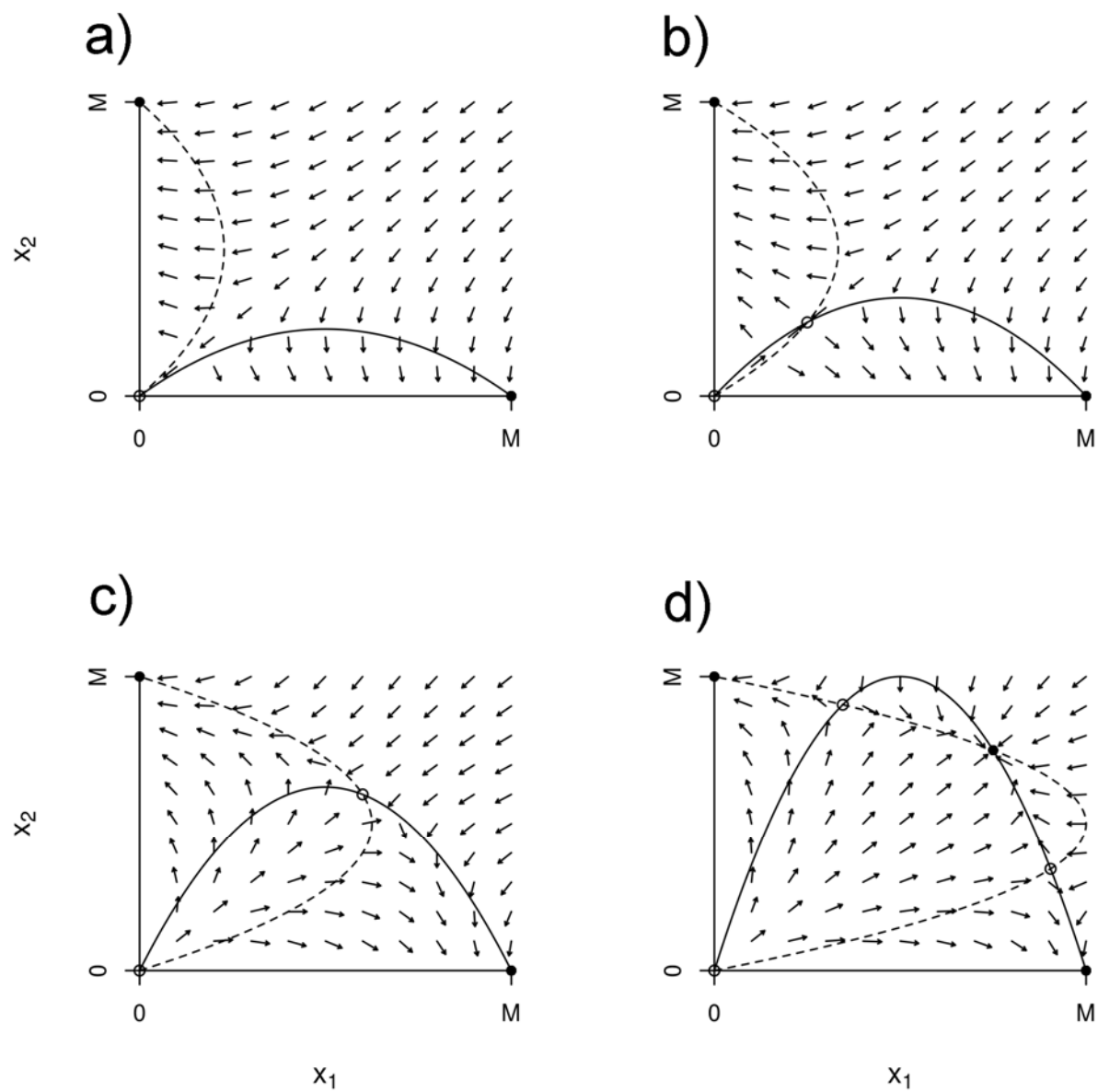
713 Fig. 5 A time series of the populations when  $0 < \alpha_r < T_1$ . One can see an initial buildup of  
714 groups and overall population before transitioning to group turnover and “oscillations”. Each  
715 group is represented by a color with groups constantly appearing, shrinking, and going extinct.  
716 Each new group was given a new  $r$  and  $M$  based on the logit normal distribution. The large,  
717 solid, vertical, black lines represent a time when the existing groups split. The dashed line  
718 represents the total population size.

719 Fig. 1



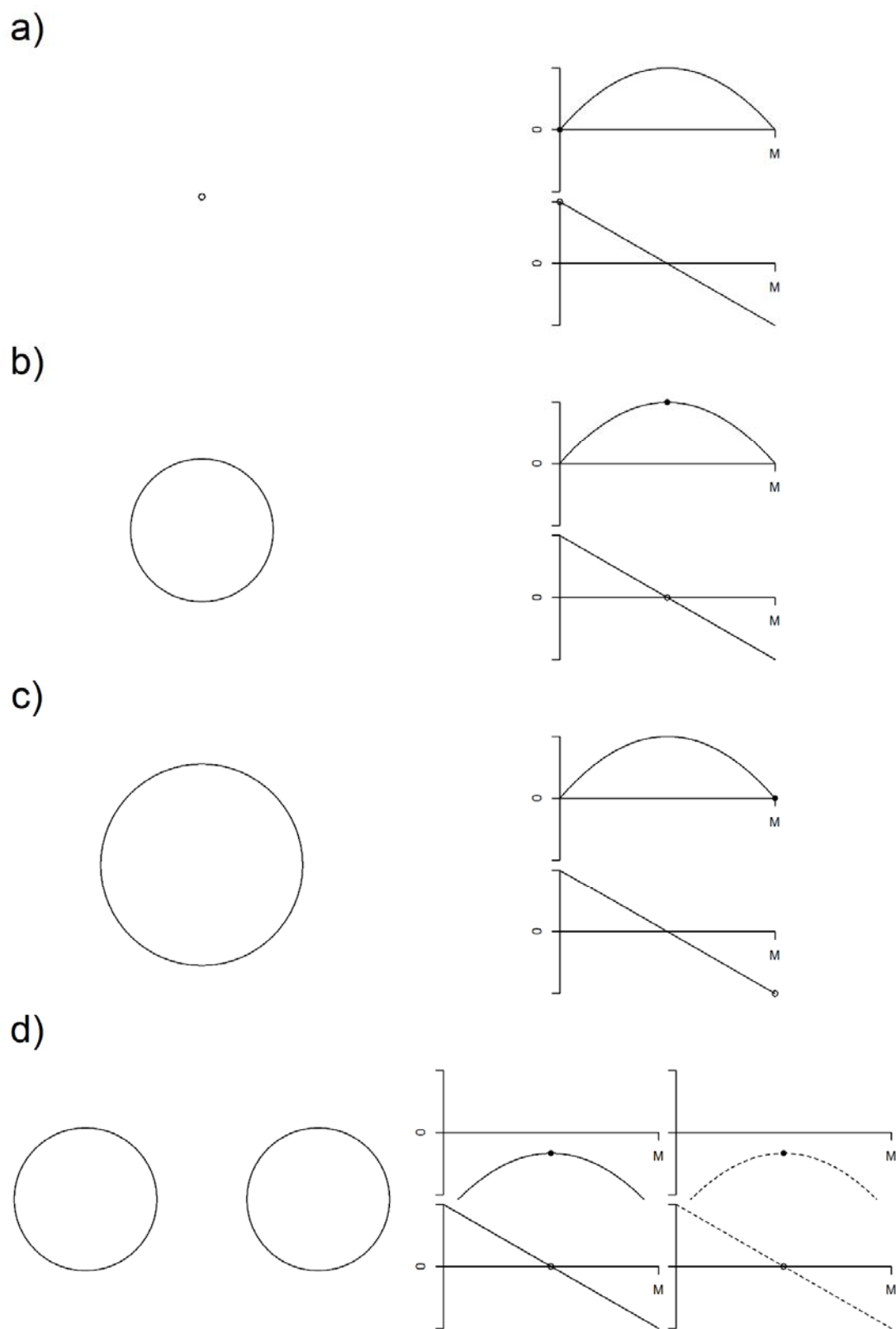
720

721 Fig. 2



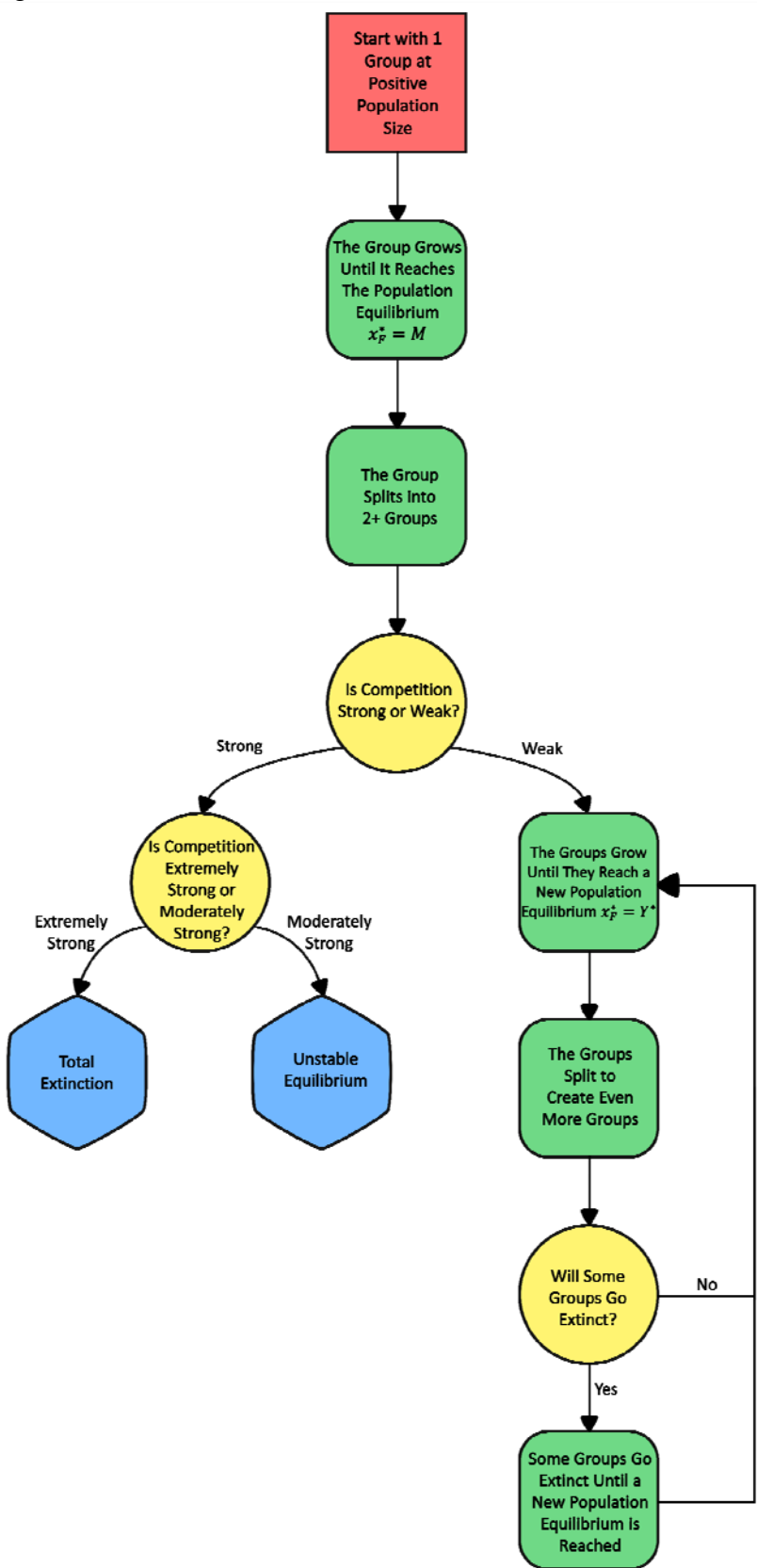
722

723 Fig. 3

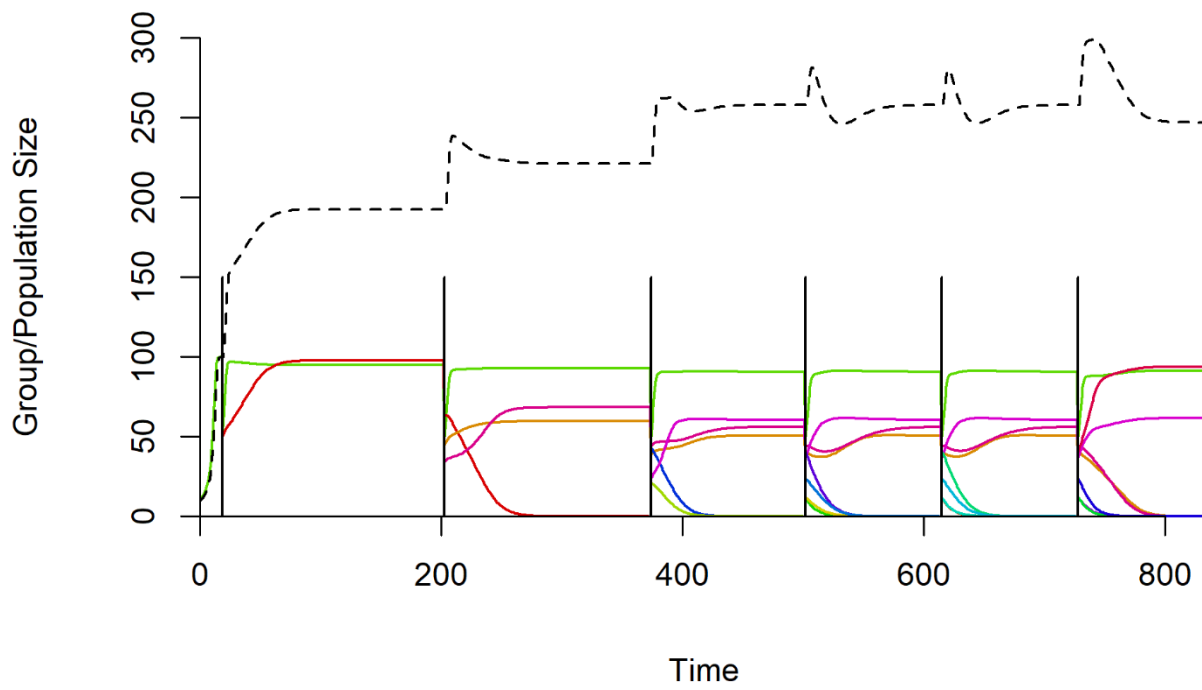


724

725 Fig. 4



727 Fig. 5



728