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1 When to go with the crowd: Modelling synchronization of all-or-  
2 nothing activity transitions in grouped animals

3  
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13  
14 Abstract

15 For groups of animals to keep together, the group members have to perform switches between  
16 staying in one place and moving to another place in synchrony. However, synchronization  
17 imposes a cost on individual animals, because they have to switch from one to the other  
18 behaviour at a communal time rather than at their ideal times. Here we model this situation  
19 analytically for groups in which the ideal times vary quasi-normally and grouping benefit  
20 increases linearly with group size. Across the parameter space consisting of variation in the  
21 grouping benefit/cost ratio and variation in how costly it is to act too early and too late, the  
22 most common optimal solutions are full synchronization with the group staying together and  
23 zero synchronization with immediate dissolution of the group, if the group is too small for the  
24 given benefit/cost ratio. Partial synchronization, with animals at the tails of the distribution  
25 switching individually and the central core of the group in synchrony, occurs only at a narrow  
26 stripe of the space. Synchronization cost never causes splitting of the group into two as either  
27 zero, partial or full synchronization is always more advantageous. Stable solutions dictate  
28 lower degree of synchrony and lower net benefits than optimal solutions for a large range of  
29 the parameter values. If groups undergo repeated synchronization challenges, they stay  
30 together or quickly dissolve, unless the animals assort themselves into a smaller group with  
31 less variation in the ideal times. We conclude with arguing that synchronization cost is  
32 different from other types of grouping costs since it does not increase much with increasing

33 group size. As a result, larger groups may be more stable than smaller groups. This results in  
34 the paradoxical prediction that when the grouping benefit/grouping cost ratio increases, the  
35 average group sizes might decrease, since smaller groups will be able to withstand  
36 synchronization challenges.

37

38 Keywords: group behaviour; modelling of behaviour; synchronization; group cohesion; group  
39 size

40

41

## INTRODUCTION

42

43 Many animals live in stable or semi-permanent groups or at least spend shorter or  
44 longer periods of time in loose aggregations. In order to stay in proximity, group members  
45 need to coordinate when to stay in one place and when to travel. In other words, each animal  
46 has to strike a compromise between switching behavioural activities in close synchrony with  
47 others and switching the activities as close as possible to its individual ideal time (e.g.  
Ruckstuhl, 1999; Meldrum and Ruckstuhl, 2009).

48

49 One example of such situation is fleeing from a predator. In many instances, the  
50 predator is noted well ahead of possible attack (either directly by the animal itself or through  
51 the alert behaviour of other flock/herd members, Sirot and Touzalin, 2009) and then an  
52 “economics of fleeing” comes into effect (Ydenberg and Dill, 1986). Initially, the costs of  
53 staying are minute (because the risk of a successful attack from large distance is negligible)  
54 and therefore lower than the costs of fleeing (including energy for the flight and lost  
55 opportunity to continue with foraging or resting). As the predator approaches, costs of staying  
56 increase at an accelerating rate (because of the climbing probability of actual attack and risk  
57 of being caught) while the costs of fleeing remain stable or increase only slightly (e.g. the  
58 animal has to run faster or for longer). At the moment when the costs of staying overcome the  
59 costs of fleeing, the animal should depart. Because many factors affecting both types of costs  
60 (such as individual ability to evade attack, current position in the group, satiation/energy  
61 reserves) vary between individuals, the ideal departure time is different for each animal. If  
62 everybody sticks to its ideal timing, animals will depart individually, the group will  
63 disintegrate and the benefits of staying and behaving together will be lost. On the other hand,  
64 should the group stay fully together and enjoy the associated benefits, everybody has to make  
65 a smaller or larger concession from its ideal timing. This dilemma is present in every situation  
where grouped animals can draw a benefit from switching synchronously from one behaviour

66 to another such as departure from a resting place, stopping migration to rest, switching from  
67 monitoring a predator to fleeing. However, departure from a place is perhaps the most typical  
68 example and therefore the model will be described in terms of who leaves when.

69 Synchronization can be viewed as a consensus decision making (Conradt and Roper  
70 2005; Conradt and List, 2009). Several theoretical and empirical studies have documented  
71 that animals can “agree” on the common solution using simple behavioural rules (Couzin et al  
72 2005; Amé et al 2006; Martín et al 2006). If there are just two or a few disjunct possible  
73 solutions (e.g., a choice between distinct spatial goals or shelters) then simple local rules can  
74 be found that guide the group either to one of the goals, or lead to splitting of the group (Amé  
75 et al 2006, Couzin et al, 2005). Also, for groups of two animals and a continuous range of  
76 possible preferences (e.g., times of a behavioural switch), models have been developed that  
77 combine the mechanisms of coordination (e.g., communicating about inner state, simple  
78 reaction to the behaviour of the other animal) with their fitness outcomes (Rands et al., 2003;  
79 Dostálková and Špinka, 2007). Situations where there is a continuum of preferences in larger  
80 groups have been much less investigated. The only two previous studies to address these  
81 questions in terms of costs and benefits are those by Conradt and Roper. In the first paper,  
82 Conradt and Roper (2003) show that agreeing democratically on the time of the switch is  
83 usually more beneficial for the group than yielding to the time enforced by one leader animal,  
84 even if that animal has more experience or better judgement than the others. In their next  
85 study, Conradt and Roper (2007) document that for groups of three animals, agreeing on any  
86 of the three times preferred by the three group members is evolutionary stable. They then  
87 expand this analysis to larger groups and argue that also for those, any shared decision (e.g.,  
88 even departing when the first animal wants to depart) is evolutionary stable. This is due to the  
89 fact that if a small subset of the group chooses to depart at another time, it will acquire some  
90 benefit from more appropriate timing (i.e. it will decrease its consensus costs), but it loses the  
91 whole benefit of acting together with the original large group. This argument holds only if the  
92 costs are small relative to grouping benefits. Conradt and Roper (2007) state this verbally but  
93 stop short of analysing the balance between consensus costs and grouping benefits  
94 quantitatively and that is where our study carries on.

95 The trade-off can result in four types of situations: either all animals “agree” on a  
96 common departure time (full synchronization); or each animal leaves individually (no  
97 synchronization); or something in between occurs with some individuals departing on their  
98 own while the rest leaves at a common time (partial synchronization); and lastly, animals may

99 be also leaving in smaller subgroups (group splitting). Our model aims at answering three  
 100 questions. First, how probable are the cases of full, partial and zero synchronization, and of  
 101 group splitting? How do these probabilities depend on the benefit of being synchronized, and  
 102 the costs departing too early or too late? Second, are the animals in a group able to cooperate  
 103 on an optimal synchronization or are the evolutionary stable strategies for this  
 104 synchronization problem suboptimal in terms of resulting net benefits? Third, the  
 105 synchronisation of group departures may have an important influence on group stability and  
 106 therefore stable group size. Therefore we also asked: Will repeated synchronization  
 107 challenges lead to group stabilization or disintegration?

108

109 MODEL I DESCRIPTION: ONE COMMON DEPARTURE VERSUS INDIVIDUAL  
 110 DEPARTURES

111

112 The detailed elaboration of the model and derivation of its results is given in Appendix  
 113 A. We suppose that a group of  $N$  animals is about to switch from one behaviour to another  
 114 (e.g., to leave a resting place or to switch from monitoring a predator to fleeing). The animals  
 115 in the group have different ideal times for the switch. These individual ideal times  $t_i^*$  are  
 116 symmetrically distributed around zero and constrained to the interval  $(-t_{max}, t_{max})$ . For  
 117 simplicity we assume  $(-t_{max}, t_{max}) = (-1, 1)$  (Fig. 1). For most of the animals, the individual  
 118 ideal times are not far from  $t^* = 0$  while only a negligible proportion of animals prefer times  
 119 immediately after  $t^* = -1$  or just before  $t^* = 1$ . In other words, the probability of the position  
 120 of ideal time  $t^*$  for a randomly chosen animal is the highest for  $t^* \approx 0$  and it is close to zero  
 121 for  $t^*$  near  $-1, 1$ . We assume that concrete ideal times  $t^*$  are realizations of continuous random  
 122 variable "ideal time" defined by its density function  $f$ .

123

The model is setup in terms of grouping benefits and synchronization costs.

124

An animal that departs at a moment  $t_i$  when a fraction  $p(t_i)$  ( $0 \leq p(t_i) \leq 1$ ) of the  $N$ -sized group  
 125 depart gets a grouping benefit proportional to the number of animals in the departing group,  
 126  $p(t_i) NQ$ , where  $Q$  is a constant. If an animal departs too early, i.e. at a time  $t_i$  before its ideal  
 127 time  $t_i^*$ , it is penalised by  $-(1-\omega)L(t_i^* - t_i)$ ; if it leaves too late at  $t_i > t_i^*$ , it receives the penalty  
 128 of  $-\omega L(t_i - t_i^*)$ . The parameter  $\omega$  ( $0 \leq \omega \leq 1$ ) describes whether it is more costly to leave  
 129 prematurely ( $\omega < 0.5$ ) or rather with a delay ( $\omega > 0.5$ ). The product  $NR$  (where  $R = Q/L$  and

130  $NR \geq 0$ ) is the second parameter of the model. The ratio  $R = Q/L$  quantifies how important it  
 131 is to be in synchrony with others, relative to the importance of departing close to the  
 132 individual ideal time. The ratio  $R$  is multiplied by the group size  $N$  because the model  
 133 assumes that the larger the group, the higher the grouping benefit. Thus the product  $NR$   
 134 quantifies how much an animal can get from synchronization: the higher the parameter  $NR$ ,  
 135 the higher net potential benefit can the animals cash from being staying with the group.

136 The model examines how an animal should behave (i.e., when to leave) in order to  
 137 accrue the highest possible net benefit, given its specific ideal time  $t_i^*$  and the parameters  $NR$   
 138 and  $\omega$ . Parameters  $NR$  and  $\omega$  are equal for all animals in the group. Group size  $N$  is considered  
 139 fixed for this model. We consider two strategies: either to depart individually at its own ideal  
 140 time, or to leave together with other animals in one mass departure (Fig. 1). The solitary  
 141 departure avoids any penalization for improper timing but gets no benefit from  
 142 synchronization, hence its net benefit is zero. The animals participating in the mass departure  
 143 benefit from synchronization (in direct proportion to the percentage of animals that leave with  
 144 them), but pay for deviating from their ideal times. The cost of participating in the mass  
 145 departure are higher for animals at the tails of the distribution and therefore, animals at the  
 146 tails should be more inclined to use the solitary strategy while animals with their  $t_i^*$  closer to  
 147 the centre of the distribution should rather join the mass departure (Fig. 1). We suspect that  
 148 when  $\omega < > 0.5$ , the time of mass departure  $t_D$  will be different from zero and also the times  $t_1$   
 149 and  $t_2$  (breaking points where the solitary changes into the mass departure strategy and back)  
 150 will be asymmetrically positioned. In the solution of the model, we are searching for such  
 151 combination of times  $t_1$ ,  $t_D$  and  $t_2$  that brings the highest net benefit, depending on the  
 152 parameters  $NR$  and  $\omega$ . If  $t_1 = t_2$ , then each animal departs on its own and there is no  
 153 synchronization. If  $-1 < t_1 < t_2 < 1$ , then some animals depart solitary and some in the mass  
 154 departure, and we label this partial synchronization. And finally full synchronization occurs  
 155 when  $t_1 = -1$  and  $t_2 = 1$ .

156 The net benefit function  $B(t_1, t_D, t_2)$  is the sum of the grouping benefit function  $B_G(t_1, t_D, t_2)$   
 157 and timing cost function  $B_C(t_1, t_D, t_2)$ .

158  $B(t_1, t_D, t_2) = B_G(t_1, t_D, t_2) + B_C(t_1, t_D, t_2)$ , where

$$159 \quad B_G(t_1, t_D, t_2) = NR \left( \int_{t_1}^{t_2} f(x) dx \right)^2$$

$$160 \quad B_C(t_1, t_D, t_2) = -\omega \int_{t_1}^{t_D} (t_D - x)f(x)dx - (1-\omega) \int_{t_D}^{t_2} (x - t_D)f(x)dx$$

161 Thus, the individually departing animals do not get any grouping benefits and do not pay any  
 162 timing (synchronization) costs, whereas for animals leaving in the mass departure, the net  
 163 benefit equals the grouping benefit minus the synchronization costs due to un-ideal timing of  
 164 the departure.

165 We look for two types of solutions: an optimal and a stable one. The optimal solution  
 166 is such that an animal acquires, on average, the highest summary net benefit, whereas the  
 167 stable solution is a solution whose net benefit cannot be improved by unilateral adoption of  
 168 another solution by a small subset of the animals.

169 Therefore optimization procedure means to find triplets  $[t_1, t_D, t_2]$  depending on  $NR$  and  $\omega$  so  
 170 that the value of net benefit function  $B$  is maximal. Using the classical method for maxima

171 finding we obtain the set of maxima ( $\frac{\partial B}{\partial t_1} = \frac{\partial B}{\partial t_2} = \frac{\partial B}{\partial t_D} = 0$ ) inside and on the borders of the

172 simplex  $\{-1 \leq t_1 \leq t_D \leq t_2 \leq 1\}$  that correspond to zero, partial and full behavioural

173 synchronization.. After comparison of all possible maximal points for given parameters  $NR$

174 and  $\omega$  we obtain the point of global maximum – the optimal strategy  $I=[t_1, t_D, t_2]$ .

175 The strategy  $I = [t_1, t_D, t_2]$  is then stable, if the mixed net benefit is locally maximal. We

176 consider an alternative strategy  $J$  "sufficiently" close to the strategy  $I$ , defined as  $J = [u_1, u_D,$

177  $u_2]$ . The mixed net benefit can be defined as  $B(I, J) = B_G(I, J) + B_C(J) = NR$

178  $(\int_{t_1}^{t_2} f(x)dx)(\int_{u_1}^{u_2} f(x)dx) + B_C(J)$ , where  $B_C(J) = B_C(u_1, u_D, u_2)$  as defined earlier. Then  $I$  is

179 stable if  $B(I, J) < B(I, I)$  for each  $I \neq J$ .

180

## 181 MODEL II DESCRIPTION: SPLITTING INTO SUBGROUPS

182 The model assumes the same situation with the same costs and benefits as Model I.

183 However, for each level of relative grouping benefit (i.e., for each  $NR$ ), it compares the net

184 benefit of two strategies: one mass departure versus departure in two subgroups. For

185 simplicity, time costs are kept symmetric (corresponding to  $\omega = 0.5$ ) and only the optimal

186 solution is sought. The full description and solution of Model II is given in Appendix B.

187

188

## RESULTS

189 *Model I: optimal solution*

190 Fig. 2 shows which of the three basic scenarios (full, partial and no synchronization)  
191 brings the highest net benefit for specific combinations of  $NR$  and  $\omega$ . Most of the parameter  
192 space is occupied by either no synchronization (the area below the lower full line) or full  
193 synchronization (the area above the upper full line) while partial synchronization is superior  
194 only within the narrow croissant-shaped area. As  $\omega$  deviates more and more from 0.5, full  
195 synchronization becomes the most prominent strategy. This is because for  $\omega$  near zero or one,  
196 departing after or before the individual ideal time, respectively, gets almost no penalty and  
197 thus animals can cheaply achieve a common departure by waiting very late or by acting very  
198 prematurely.

199 Fig. 2 also maps (in grades of gray shading) the net benefits achieved by the optimal  
200 strategies. Higher net benefits can be harvested (for the same value of parameter  $NR$ ) for  
201 extreme values of  $\omega$ , where either premature action or delay are cheap and full  
202 synchronization is therefore easily achieved by agreeing to a very early or very late common  
203 departure

204

205 *Model I: stable solution*

206 Fig. 3 illustrates the distribution of stable solutions across the parameter space.  
207 Similarly to the optimal solutions, there is a croissant-shaped area (delimited by dashed lines  
208 in Fig 3) within which partial synchronization is a stable strategy. Above the croissant, full  
209 synchronization is stable. The lower boundary for partial synchronization and the boundary  
210 between partial and full synchronization are both shifted upwards (specifically, to twice as  
211 high  $NR$ ) in comparison with the optimal solution. That is, the stable solution dictates a lower  
212 degree of synchronization than the optimal solution in a large area of the parameter space,  
213 including a place where the optimal solution prescribes full synchrony while the stable  
214 solution is no synchrony at all (Fig. 4). In this area, the stable strategy brings substantially  
215 lower net benefit than the optimal one (Fig. 4). Why this is so? An animal should participate  
216 in the mass departure only if the benefit outweighs the cost. The cost of improper timing is  
217 always paid solely by the specific individual, but there are two kinds of benefits: one goes to  
218 the animal itself (as it is part of the synchronized subgroup) and another goes to every  
219 synchronized animal because through the contribution of the focal animal, the synchronized

220 subgroup increases in size. In the optimal solution, where the costs and benefits are averaged  
221 over the group, both types of benefits enter the equation and they are able to pay for higher  
222 timing cost, thus drawing more of the animals from the tails into the synchronization. In the  
223 stable solution, only the first type of benefit counts and thus more animals will opt out the  
224 synchrony.

225         The second difference between the stable and the optimal solutions is that zero  
226 synchronization is a stable strategy across all the parameter space, and not only below the  
227 croissant. In the areas of higher and high  $NR$ , i.e. within and above the croissant, two stable  
228 strategies coexist: the partial/full synchronization and the zero synchronization, of which the  
229 former brings higher net benefit. Zero synchronization is stable because once it becomes  
230 established, each animal departs at a different time and therefore it is difficult for a small  
231 fraction of animals to set foot with an alternative strategy, as their attempts to synchronize get  
232 no support from the majority.

233

#### 234 *Splitting into subgroups*

235 Splitting into two subgroups is never an optimal strategy because for any given  $NR$ , the  
236 optimal strategy with one central departure always brings higher net benefit than the best two-  
237 departure option (Fig. 5).

238

#### 239 *Repeated synchronizations*

240         What happens when the synchronization challenge is repeated? If the grouping  
241 benefit/consensus cost ratio ( $NR$ ) is high, then no animals are shed and the group remains of  
242 the same size across a single or repeated challenges. Low  $NR$  leads to zero synchronization  
243 and therefore to immediate dispersal of the group on the first challenge. The interesting case  
244 occurs with partial synchronization during which the group size is trimmed (Fig. 6). What  
245 happens on the next encounter depends on what is the distribution of ideal times in the  
246 downsized group. To simplify the solution, we restrict the analysis of this problem to  
247 symmetric costs of time (corresponding to  $\omega = 0.5$  in the previous model) and to the optimal  
248 solution.

249         If each animal keeps its ideal time from one challenge to the next then during partial  
250 synchronization both the group size and the variability of the density distribution of ideal

251 times is also trimmed (Fig. 6b), but the latter more so because the costly tails of the  
252 distribution are shed. Therefore, the grouping benefit/consensus cost ratio increases and the  
253 group size stabilizes at a reduced size. The derivation of this result is given in Appendix C.  
254 We call this option the Assortment scenario as it results in a subgroup where members are  
255 more alike in terms of their time preferences than in the original group.

256 If partial synchronization leads to a smaller group in which the variation of ideal times  
257 remains as large as before the reduction (i.e. individuals do not keep their individual times  
258 from one challenge to another, Non-Assortment scenario), then the consensus costs remain  
259 unaltered while grouping benefits fall (Fig. 6c). Consequently, the group is reduced further  
260 during next challenge or challenges until it disintegrates (see Appendix C).

261

262 *Minimal group size*

263 It follows from the analysis of repeated synchronizations that in Fig. 2, that the upper  
264 border of the partial synchronization area delineates the minimal  $R$  value for which the group  
265 of size  $N$  remains cohesive in the Non-Assortment scenario, and the lower border demarcates  
266 group cohesion boundary for the Assortment scenario. In the analysis of Models I and II, we  
267 have assumed that the group size was fixed, and the relative “per animal” grouping benefit  $R$   
268 was varied. Conversely, the chart can be understood as illustrating how the stability of a  
269 group depends on its size  $N$ , for a given “per animal” grouping net benefit  $R$  (Fig. 7).

270

271 DISCUSSION

272 Our models yield three main insights into the links between the grouping-benefit-  
273 versus-consensus-costs trade-off, behavioural synchronization and group size and stability.

274 First, the results indicate that synchronization of departures will often be an all-or-  
275 nothing phenomenon. Model predicts that if the benefit of staying in a group of animals  
276 depends linearly on the size of the group (which is the assumption of the model) and the cost  
277 of staying in the group varies quasinormally among the group members, then the group will  
278 most of the time either switch behaviour synchronously and thus stay together, or all  
279 individuals will behave independently and the group will disintegrate. The cases when  
280 animals at the tails of the distribution will act solitarily and the rest of the group in synchrony  
281 are predicted to be rare. In other words, the overall grouping-benefit-to-consensus-costs ratio

282 is predicted to decide, in most cases, for all animals to either depart synchronously or  
283 individually, with individual differences such as boldness/fearfulness (Reale et al., 2007) or  
284 satiation (Rands et al., 2004) playing only a marginal role in this situation. Moreover, Model  
285 II shows that splitting into two subgroups brings lower net benefit than the central  
286 synchronization in one group, indicating that synchronization challenges will not lead to  
287 separation into smaller units. Finally, the analysis of repeated synchronization events with no  
288 assortment shows that even when partial synchronization occurs, the group will quickly  
289 diminish and disintegrate.

290         Second, Model I shows that when individuals in groups behave selfishly, a much  
291 weaker synchronization, higher probability of group disintegration and lower net benefits are  
292 predicted than in groups that behave optimally from the overall fitness point of view. This is  
293 due to the fact that the cost of staying with the group is carried individually by each animal,  
294 whereas benefits from the presence of the individual in the group are cashed both by the  
295 animal in question (it enjoys the company of others) and by all other group members (because  
296 the groups stays larger). Therefore, if the animal counts in only its own benefits (the stable  
297 solution), it is prepared to expend less costs to stay in the group than if everybody's benefits  
298 are taken into account. Moreover, Model I documents that zero synchronization is a stable  
299 solution all across the parameter space. Why zero synchronization is stable everywhere and  
300 full synchronization is not? Full synchronization is unstable with low  $NR$  since any individual  
301 can, independently of what others do, default from the synchrony, leave at its individual ideal  
302 time and cash in the benefit of not paying any penalty for improper timing. In the contrary,  
303 skipping individually from zero synchronization to a partial or full synchronization just by  
304 individual action is impossible, since in order to achieve synchrony, you need pals to go with  
305 you. The existence of zero synchronization as a solution for the entire parameter space in the  
306 stable, but not in the optimal solution further underscores the general implication of our  
307 models that evolutionary stable regime of synchronized departures will often bring  
308 substantially lower net benefit than the optimal one.

309         The optimal-stable solution dichotomy shows that there is a Prisoners Dilemma type  
310 of game underlying our models (Fletcher and Zwick, 2007). If an animal plays Stable against  
311 a group that plays Optimal, it gets a better pay-off than if it would play Optimal. However, as  
312 animals shift from the Optimal to the Stable strategy, the whole group gradually starts playing  
313 Stable, and everybody ends with a worse pay-off than it would get if the whole group kept  
314 playing Optimal. The combination of our two models thus predicts that sub-optimally low

315 degree of synchronization will be frequently observed in departures and other major cohesion  
316 influencing behavioural switches unless the optimal strategy could be maintained by altruism-  
317 supporting mechanisms such as relatedness, reciprocity or assortment (Fletcher and Zwick,  
318 2006, 2007; Frommen et al., 2007; Fischhoff et al., 2009).

319 Third, and perhaps most interestingly, the current study brings to light the  
320 phenomenon of minimal stable group size. To our knowledge, this is the first study pointing  
321 to this phenomenon and identifying synchronization of behaviour as its driving force. Our  
322 results indicate that the need to synchronize the starts and stops of movements will in many  
323 cases set a minimal threshold group size below which group cohesion will no longer be  
324 beneficial. The situation is especially clear in the non-assortment scenario, where groups  
325 above a size that makes full synchronization stable are predicted to stay together while  
326 smaller groups should disintegrate. Thus the model predicts that when per capita grouping  
327 benefits are high, the average group size should decrease because small groups will be able to  
328 withstand synchronization challenges.

329 How does this seemingly paradoxical prediction arise? The synchronization cost  
330 differs substantially from other types of grouping costs considered so far. In most of the  
331 models and reviews published to date, the costs to an individual of being in a group were  
332 thought in terms of foraging interference (Stillmann et al., 2000; Sansom et al., 2007),  
333 reproductive interference (Westneat and Sherman, 1997), proximity-transmitted pathogens  
334 (Côté and Pohlin, 1995) or similar factors. For instance, in their influential book, Krause and  
335 Ruxton (2002, page 41) list twelve different types of grouping costs, but do not mention  
336 synchronization cost. The costs listed by Krause and Ruxton were assumed to increase with  
337 increasing group size, often at an accelerating rate (Fig. 8a). In contrast, the synchronization  
338 cost in our model remains constant, irrespective of group size (Fig. 8b). This is because the  
339 synchronization cost to an individual is given by the time distance between its ideal time and  
340 the time of common departure and this distance neither shrinks nor expands if more or fewer  
341 other animals also pay their costs. Previous models assumed that even very small grouping is  
342 better than solitary life and sought to find the optimal and the maximal stable group size (Fig.  
343 8a). Our model shows that when the need to synchronize is the major cost of grouping, then  
344 net benefit may be lower in small groups than in solitary animals and a certain group size is  
345 needed for the grouping benefits to offset the synchronization costs (Fig. 8b). It remains to be  
346 investigated how important role the movement synchronization costs play in determining  
347 animal group sizes in nature. In some cases, it is possible that the synchronization and other

348 types of grouping costs will combine so that the resulting cost function, together with  
349 depreciating grouping benefits, will set both minimum and maximum profitable group size  
350 (Fig. 8c). Our results also show that smaller groups are stable if animals assort according to a  
351 feature that determines their preferred departure times such as boldness/shyness (Croft et al.,  
352 2009) or body size (Ruckstuhl, 1999; Hoare et al., 2000).

353         The predictions of our models are linked to two crucial assumptions, namely that the  
354 grouping benefit increases linearly with the group size, rather than according to a depreciating  
355 function, and that the heterogeneity in ideal departure times is unimodally distributed. If the  
356 first assumption is relaxed, regular group splitting might occur in the form of a fission-fusion  
357 dynamics (Conradt and Roper, 2000; Pays et al., 2007). If ideal times are not unimodally  
358 distributed, more permanent splitting will probably happen, such as in the case of sexual  
359 segregation (Ruckstuhl and Kokko, 2002). Also, the total constancy of synchronization cost  
360 over all group sizes is an idealization since in very small groups with quorum decision-  
361 making, individual animals will have some influence on the time of common departure and  
362 cost will be consequently somewhat lower. Further, our model only addresses possible  
363 decrease in size, splitting or dissolution of already existing groups, but not their formation or  
364 increase through individuals joining. Finally, the models only address major behavioural  
365 transitions in a world where being member of a group is an all-or-nothing state that has to be  
366 defended or abandoned during a challenge, rather than a state defined by a continuous  
367 proximity in space (Ruckstuhl and Kokko, 2002; Rands et al., 2004) or continuous degree of  
368 synchronization in time (Šárová et al., 2007; Michelena et al., 2008). Nevertheless, Models I  
369 and II apply not only to timing, but also to any situation where a group, in order to stay  
370 together, must reach a consensus along a continuous variable such as gradient in space,  
371 escalation of conflict with other group etc.

372         In conclusion, this study documents that synchronization of activity switches such as  
373 departures brings a specific type of grouping costs that has specific consequences. First, it  
374 may most often cause groups to either stay together or completely dissolve during  
375 synchronization challenges. Second, it implies that groups will often react to synchronization  
376 challenges with lower-than-optimal synchronization because of the Prisoners-Dilemma type  
377 of payoff inherent to the situation. And third, synchronization cost will often set a limit of a  
378 smallest group size below which grouping is no longer advantageous over the solitary  
379 condition.

380

381

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383

384

#### REFERENCES

385 Amé, J.M., Halloy, J., Rivault, C., Detrain, C., Deneubourg, J.L., 2006. Collegial decision  
386 making based on social amplification leads to optimal group formation. *PNAS* 103(15), 5835-  
387 5840., doi:10.1073/pnas.0507877103.

388 Conradt, L., List, C. 2009. Group decisions in humans and animals: a survey. *Phil. Trans. R.*  
389 *Soc. B* 364(1518), 719-742., doi: 10.1098/rstb.2008.0276.

390 Conradt, L., Roper, T.J., 2000. Activity synchrony and social cohesion: a fission-fusion  
391 model. *Proc. R. Soc. London B* 267(1458), 2213-2218.

392 Conradt, L., Roper, T.J., 2003. Group decision-making in animals. *Nature* 421(6919), 155-  
393 158., doi:10.1038/nature01294

394 Conradt, L., Roper, T.J., 2005. Consensus decision making in animals. *Trends Ecol. Evol.*  
395 20(8), 449-456., doi:10.1016/j.tree.2005.05.008.

396 Conradt, L., Roper, T.J., 2007. Democracy in animals: the evolution of shared group  
397 decisions. *Proc. R. Soc. London B* 274(1623), 2317-2326., doi:10.1098/rspb.2007.0186

398 Côté, I.M., Poulin, R., 1995. Parasitism and group size in social animals - a meta-analysis.  
399 *Behav. Ecol.* 6(2), 159-165.

400 Couzin, I.D., Krause, J., Franks, N.R., Levin, S.A., 2005. Effective leadership and decision-  
401 making in animal groups on the move. *Nature* 433(7025), 513-516., doi:10.1038/nature03236.

402 Croft, D.P., Krause, J., Darden, S.K., Ramnarine, I.W., Faria, J.J., James, R., 2009.  
403 Behavioural trait assortment in a social network: Patterns and implications. *Behav. Ecol.*  
404 *Sociobiol.*, 63(10), 1495-1503., doi: 10.1007/s00265-009-0802-x.

405 Dostálková, I., Špinka, M., 2007. Synchronization of behaviour in pairs: the role of  
406 communication and consequences in timing. *Anim. Behav.* 74(6), 1735-1742.,  
407 doi:10.1016/j.anbehav.2007.04.014.

408 Fischhoff, I.R., Dushoff, J., Sundaesan, S.R., Cordingley, J.E., Rubenstein, D.I., 2009.  
409 Reproductive status influences group size and persistence of bonds in male plains zebra

- 410 (*Equus burchelli*). *Behav. Ecol. Sociobiol.*, 63(7), 1035-1043., doi: 10.1007/s00265-009-  
411 0723-8.
- 412 Fletcher, J. A. and Zwick, M., 2006. Unifying the theories of inclusive fitness and reciprocal  
413 altruism. *Am. Nat.* 168(2), 252-262.
- 414 Fletcher, J. A. and Zwick, M., 2007. The Evolution of Altruism: Game theory in multilevel  
415 selection and inclusive fitness. *J. Theor. Biol.* 245(1), 26-36., doi:10.1016/j.jtbi.2006.09.030.
- 416 Frommen, J.G., Mehli, M., Brendler, C., Bakker, T.C.M., 2007. shoaling decisions in three-  
417 spined sticklebacks (*gasterosteus aculeatus*) - familiarity, kinship and inbreeding. *Behav.*  
418 *Ecol. Sociobiol.*, 61(4), 533-539.
- 419 Hoare, D.J., Krause, J., Peuhkuri, N., Godin, J.G.J., 2000. Body size and shoaling in fish. *J.*  
420 *Fish Biol.*, 57(6), 1351-1366
- 421 Krause, J., Ruxton, G. (Eds), 2002. *Living in Groups*, Oxford University Press, Oxford.
- 422 Martín, J., Luque-Larena, J.J., Lopez, P., 2006. Collective detection in escape responses of  
423 temporary groups of Iberian green frogs. *Behav. Ecol.* 17(2), 222-226., doi:  
424 10.1093/beheco/arj024.
- 425 Michelena, P., Gautrais, J., Gérard, J. F., Bon, R., and Deneubourg, J. L., 2008. Social  
426 cohesion in groups of sheep: effect of activity level, sex composition and group size. *Appl.*  
427 *Anim. Behav. Sci.* 112(1-2), 81-93., doi:10.1016/j.applanim.2007.06.020.
- 428 Pays, O., Benhamou, S., Helder, R., Gérard, J.F., 2007. The dynamics of group formation in  
429 large mammalian herbivores: an analysis in the european roe deer. *Anim. Behav.* 74(5), 1429-  
430 1441., doi:10.1016/j.anbehav.2007.02.012.
- 431 Rands, S.A., Cowlshaw, G., Pettifor, R.A., Rowcliffe, J.M., Johnstone, R.A., 2003.  
432 Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423(6938), 432-  
433 434., doi: 10.1038/nature01630.
- 434 Rands, S. A., Pettifor, R. A., Rowcliffe, J. M., and Cowlshaw, G., 2004. State-dependent  
435 foraging rules for social animals in selfish herds. *Proc. R. Soc. London B* 271(1557), 2613-  
436 2620., doi:10.1098/rspb.2004.2906.

- 437 Reale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J., 2007. Integrating  
438 animal temperament within ecology and evolution. *Biol. Rev.* 82(2), 291-318., doi:  
439 10.1111/j.1469-185X.2007.00010.x.
- 440 Ruckstuhl, K.E., 1999. To synchronise or not to synchronise: a dilemma for young bighorn  
441 males? *Behaviour*, 136(), 805-818
- 442 Ruckstuhl, K.E., Kokko, H., 2002. Modelling sexual segregation in ungulates: effects of  
443 group size, activity budgets and synchrony. *Anim. Behav.* 64(6), 909-914.,  
444 doi:10.1006/anbe.2002.2015.
- 445 Sansom, A., Cresswell, W., Minderman, J., and Lind, J., 2008. Vigilance benefits and  
446 competition costs in groups: do individual redshanks gain an overall foraging benefit? *Anim.*  
447 *Behav.* 75(6), 1869-1875., doi:10.1016/j.anbehav.2007.11.005.
- 448 Šárová, R., Špinka, M., and Panamá, J. L. A., 2007. Synchronization and leadership in  
449 switches between resting and activity in a beef cattle herd a case study. *Appl. Anim. Behav.*  
450 *Sci.* 108(3-4), 327-331., doi:10.1016/j.applanim.2007.01.009.
- 451 Sirot, E., Touzalin, F., 2009. Coordination and synchronization of vigilance in groups of prey:  
452 the role of collective detection and predators' preference for stragglers. *Am. Nat.* 173(1), 47-  
453 59., doi: 10.1086/593358.
- 454 Stillman, R.A., Goss-Custard, J.D., Alexander, M.J., 2000. Predator search pattern and the  
455 strength of interference through prey depression. *Behav. Ecol.* 11(6), 597-605.
- 456 Westneat, D.F., Sherman, P.W., 1997. Density and extra-pair fertilizations in birds: a  
457 comparative analysis. *Behav. Ecol. Sociobiol.* 41(4), 205-215.
- 458 Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. *Adv. Study*  
459 *Behav.* 16, 229-249.
- 460

461

## FIGURE CAPTIONS

462 Fig. 1 An example of the density and distribution functions  $f(t)$  and  $F(t)$  in Model I. This  
 463 specific function was used for calculating results displayed in Figs. 2 to 6. The dotted line and  
 464 the left scaling on the  $y$ -axis displays the density function  $f(t)$  of the ideal individual times  $t$   
 465 within the group. The thin solid line and the right scaling on the  $y$ -axis displays the  
 466 distribution function  $F(t)$ , representing the number of animals that are beyond their ideal time  
 467  $t$ . The bold solid line illustrates an example of the two behavioural options available in the  
 468 model. Animals that have their ideal switch points before time  $t_1$  and after time  $t_2$  leave  
 469 individually at their respective ideal times, while all animals with  $t_1 \leq t \leq t_2$  depart together at  
 470  $t_D$ . The letters  $b, c, d$  denote intervals used for description of the model in Appendix A.

471

472 Fig. 2 Optimal strategies and their net benefits as dependent on the parameters  $\omega$  and  $NR$ . The  
 473 thick lines demarcate boundaries between the areas of zero synchronization, partial  
 474 synchronization and full synchronization. The net benefit increases with the darkness of the  
 475 shading. The curved lines are isolines of equal levels of net benefit. The net benefit level is  
 476 described by the number on the isolines.

477

478 Fig. 3 Stable strategies, and their net benefits, as dependent on the parameters  $\omega$  and  $NR$ . The  
 479 two dotted lines demarcate boundaries between the areas of zero synchronization, partial  
 480 synchronization and full synchronization. The shading and the isolines have the same  
 481 meaning as in Fig. 2.

482

483 Fig. 4 Differences between benefits of stable and optimal strategies in the parameter space  $\omega$ ,  
 484  $NR$ . The thick and dotted lines are those given in Figs. 2 and 3. The darker the shading, the

485 higher is the difference in benefit between the optimal and the stable strategy. The curved  
486 lines are isolines of equal levels of this difference.

487

488 Fig. 5 Net benefits of the one-departure (solid curve) and two-departure (dashed curve)  
489 strategies in Model II, as dependent on  $NR$ .

490

491 Fig. 6. Effect of repeated synchronizations in the case of a 50% partial synchronization. a)  
492 Original density function  $f(t)$  (dashed line, left scaling on the  $y$ -axis) and cumulative  
493 distribution function  $F(t)$  (full line, right scaling on the  $y$ -axis) before the partial  
494 synchronization. After the partial synchronization, only half of the animals are left in the  
495 group and therefore the functions change shape to b) in the case of Assortment scenario and to  
496 c) in the case of Non-Assortment scenario.  $N$  = number of animals in the group,  $\sigma$  =  
497 variability of the density distribution. See text for more explanation.

498

499 Fig. 7. Group stability as dependent on the group size. For this example, the  $R$  parameter was  
500 fixed at  $R = 0.02$ .

501

502 Fig. 8. Grouping benefits and costs as dependent on group size according to a) previous  
503 models published before this study, b) this study and c) possible combined scenario. Solid  
504 lines = grouping benefit, dashed lines = grouping cost.  $N_{min}$ ,  $N_{max}$  = minimal and maximal  
505 group size in which net benefit is higher than in solitary animals.  $N_{opt}$  = group size bringing  
506 the highest benefit.

507

508 APPENDIX A: DETAILS AND SOLUTION OF MODEL I

509

510 1. ASSUMPTIONS ABOUT IDEAL SWITCH TIMES

511 We suppose that:

512 1. We have the set of  $N$  animals.

513 2. There exist the ideal switch points denominated as  $t_i^*$  for the animal  $i$ ,  $1 \leq i \leq N$  that  
514 are the realizations of the random variable  $T^*$ , which is defined by its continuous  
515 density function  $f$ .

516 3. The function  $f$  has the following properties:

517 a.  $f$  is symmetric in 0.

518 b.  $f(t) > 0$  in the interval  $(-1, 1)$ ,  $f(t) = 0$  for  $t \notin (-1, 1)$ .

519 c.  $f'(t) \geq 0$  in the interval  $(-1, 0)$ ,  $f'(t) < 0$  in the interval  $(0, 1)$

520 d.  $\int_{-1}^1 f(t) dt = 1$ .

521

522 2. ASSUMPTIONS ABOUT STRATEGIES

523 A strategy  $I = [b, c, d]$  is defined by constants  $b, c, d$

524 
$$b = t_1 - (-1) = t_1 + 1$$

525 
$$c = t_D - t_1$$

526 
$$d = t_2 - t_D \text{ (see Fig. 1),}$$

527 Where  $b + c + d \leq 2$ ,  $b \geq 0$ ,  $c \geq 0$ ,  $d \geq 0$ . The behaviour of an individual  $i$  with the ideal switch

528 time  $t_i^*$  is determined by the position of  $t_i^*$  on the interval  $(-1, 1)$ , according to Table A.1

529

530 3. ASSUMPTIONS ABOUT THE NET BENEFIT FUNCTION

531

532 Let  $U(x, b, c, d)$  be the utility function for ideal switch point placed in position  $x$  on time axis.

533 Let it be continuous function to the exclusion of points  $-1+b$ ,  $-1+b+c$ ,  $-1+b+c+d$ . Let it be

534 defined by the following Table A1.

535

536 Table A1. Definitions of behaviours and of the utility function. For synchronized departures,

537 the first part of the utility function quantifies the grouping benefit, the second quantifies the

538 synchronization costs.  $R, \omega$  are parameters,  $R \geq 0, 1 \geq \omega \geq 0$

539

Intervals defining position of ideal switch time point	Behaviour	Utility function $U(x, b, c, d)$
$t_i^* \in (-1, -1 + b)$	non-synchronized departures, each at individual $t_i^*$	0
$t_i^* \in (-1 + b, -1 + b + c)$	synchronized departure at $-1 + b + c$	$NR \left( \int_{-1+b}^{-1+b+c+d} f(x) dx \right) - \omega ((-1 + b + c) - x)$
$t_i^* \in (-1 + b + c, -1 + b + c + d)$	synchronized departure at $-1 + b + c$	$NR \left( \int_{-1+b}^{-1+b+c+d} f(x) dx \right) - (1 - \omega)(x - (-1 + b + c))$
$t_i^* \in (-1 + b + c + d, 1)$	non-synchronized departures, each at individual $t_i^*$	0

540

541

542 • The net benefit  $B$  for given  $b, c, d$  and for given position of ideal switch point (e.g. for  
543 given  $x$  on time axis) is defined  $B(x, b, c, d) = f(x)U(x, b, c, d)$  where  $f(x)$  is the density  
544 function defined above.

545 • The net benefit  $B$  for the whole group is defined as

$$546 \quad B(b, c, d) = \int_{-1+b}^{-1+b+c} B(x, b, c, d) dx + \int_{-1+b+c}^{-1+b+c+d} B(x, b, c, d) dx = \int_{-1+b}^{-1+b+c} f(x)U(x, b, c, d) dx +$$

$$547 \quad \int_{-1+b+c}^{-1+b+c+d} f(x)U(x, b, c, d) dx$$

548

## 549 4. CALCULATION OF OPTIMAL STRATEGIES

550 4.1. Derivation of the net benefit function

$$551 \quad B(b, c, d) = -\omega(-1+b+c) \int_{-1+b}^{-1+b+c} f(x)dx + \omega \int_{-1+b}^{-1+b+c} xf(x)dx + (1-\omega)(-1+b+c) \int_{-1+b+c}^{-1+b+c+d} f(x)dx -$$

$$552 \quad (1-\omega) \int_{-1+b+c}^{-1+b+c+d} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right)^2$$

553

554

555

556 4.2. Conditions for the local maxima of net benefit.557 To obtain internal maxima we have the following conditions inside of the simplex  $b + c + d \leq$ 558  $2, b \geq 0, c \geq 0, d \geq 0 : dB/db = dB/dc = dB/dd = 0.$ 

559 Therefore the following relations must be valid:

$$560 \quad dB/dd = f(-1+b+c+d) \left( 2NR \int_{-1+b}^{-1+b+c+d} f(x)dx - (1-\omega)d \right) = 0 \quad (\text{A.1})$$

561

$$562 \quad dB/dc = dB/dd - \omega \int_{-1+b}^{-1+b+c+d} f(x)dx + \int_{-1+b+c}^{-1+b+c+d} f(x)dx = 0 \quad (\text{A.2})$$

563

$$564 \quad dB/db = dB/dc + f(-1+b) \left( \omega c - 2NR \int_{-1+b}^{-1+b+c+d} f(x)dx \right) = 0 \quad (\text{A.3})$$

565

566 As  $f(-1+b+c+d) > 0$  inside the simplex, we can derive the following relations

$$567 \quad \int_{-1+b}^{-1+b+c} f(x)dx = \frac{\omega(1-\omega)}{2NR} c. \quad (\text{A.4})$$

568

$$569 \quad \int_{-1+b+c}^{-1+b+c+d} f(x)dx = \frac{\omega(1-\omega)}{2NR} d, \quad (\text{A.5})$$

$$570 \quad \int_{-1+b}^{-1+b+c+d} f(x)dx = \frac{\omega(1-\omega)}{2NR} (c+d), \quad (\text{A.6})$$

571

572

$$573 \quad c = \frac{(1-\omega)d}{\omega} \quad (\text{A.7})$$

574 According to the conditions for the function  $f$  and according to the mean value theorem we

575 can see that  $1/2 \leq \frac{\omega(1-\omega)}{2NR} \leq f(0)$ .

576 As slopes of the lines in the right sides of relations (A.4) - (A.6) are the same, the solution of

577 this system is unique. That means there exists unique triplet  $[b, c, d]$  inside of the simplex

578  $b + c + d \leq 2$ ,  $b \geq 0$ ,  $c \geq 0$ ,  $d \geq 0$  that can be maximum of  $B$ . This fact is valid for each

579  $[\omega, NR]$ ,  $\omega(1-\omega) \geq NR \geq \frac{\omega(1-\omega)}{2f(0)}$ .

580

### 581 4.3. Other maxima.

582 Other maxima are placed on the border of the simplex. The possible points of maxima are

583  $b \geq 0$ ,  $c = d = 0$ , and  $b = 0$ ,  $c + d = 2$ . The first case describes the set of non-synchronized

584 switches, the second case describes the set of totally synchronized switches.

585

### 586 4.4. Conclusion – the points of maxima of optimal strategies

587 • ZERO SYNCHRONIZATION. If  $NR \leq \frac{\omega(1-\omega)}{2f(0)}$ , then zero synchronization strategy

588  $[b, 0, 0]$ , is the optimal strategy and brings the net benefit.

589  $B(b, 0, 0) = 0$ .

590

591 • PARTIAL SYNCHRONIZATION. If  $\frac{\omega(1-\omega)}{2f(0)} < NR < \omega(1-\omega)$ , then partial

592 synchronization strategy  $[b, c, d]$ ,  $b + c + d < 2$ ,  $b > 0$ ,  $c > 0$ ,  $d > 0$ ,  $c = \frac{(1-\omega)d}{\omega}$ ,

593 such that relations (A.4) - (A.7) are valid, is the optimal strategy and brings the net

594 benefit

$$595 \quad B(b, c, d) = \omega \int_{-1+b}^{-1+b+c} xf(x)dx - (1-\omega) \int_{-1+b+c}^{-1+b+c+d} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right)^2$$

596

597 • FULL SYNCHRONIZATION. If  $NR \geq \omega(1-\omega)$ , then the full synchronization  
598 strategy

599 •  $[0, c, d]$ ,  $c + d = 2$ , such that  $c = \frac{(1-\omega)d}{\omega}$ , is the optimal strategy and brings

600 the net benefit

601

$$602 \quad B(0, c, 2-c) = NR - \int_{-1+c}^1 xf(x)dx,$$

603

## 604 5. CALCULATION OF STABLE STRATEGIES

605 5.1. Derivation of the benefit functions.606 Let  $I = [b, c, d]$  and  $J = [p, q, r]$  are two strategies. Benefit of the strategy  $I$ , in the group,607 where strategy  $J$  is present can be expressed by

$$608 \quad B(I, J) = -\omega(-1+p+q) \int_{-1+p}^{-1+p+q} f(x)dx + \omega \int_{-1+p}^{-1+p+q} xf(x)dx + (1-\omega)(-1+p+q) \int_{-1+p+q}^{-1+p+q+r} f(x)dx - (1-$$

$$609 \quad \omega) \int_{-1+p+q}^{-1+p+q+r} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right) \left( \int_{-1+p}^{-1+p+q+r} f(x)dx \right)$$

610 If  $I$  is replaced by  $J$ , then

$$611 \quad B(I, I) = -\omega(-1+b+c) \int_{-1+b}^{-1+b+c} f(x)dx + \omega \int_{-1+b}^{-1+b+c} xf(x)dx + (1-\omega)(-1+b+c) \int_{-1+b+c}^{-1+b+c+d} f(x)dx - (1-$$

$$612 \quad \omega) \int_{-1+b+c}^{-1+b+c+d} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right)^2$$

613

614 We define a function

$$\begin{aligned}
615 \quad G(p, q, r) &= B(I, J) - B(I, I) = -\omega(-1+p+q) \int_{-1+p}^{-1+p+q} f(x)dx + \omega \int_{-1+p}^{-1+p+q} xf(x)dx + (1-\omega)(-1+p+ \\
616 \quad q) &\int_{-1+p+q}^{-1+p+q+r} f(x)dx - (1-\omega) \int_{-1+p+q}^{-1+p+q+r} xf(x)dx + \omega(-1+b+c) \int_{-1+b}^{-1+b+c} f(x)dx - \omega \int_{-1+b}^{-1+b+c} xf(x)dx - (1-\omega)(-1 \\
617 \quad + b+c) &\int_{-1+b+c}^{-1+b+c+d} f(x)dx + (1-\omega) \int_{-1+b+c}^{-1+b+c+d} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right) \left( \int_{-1+p}^{-1+p+q+r} f(x)dx \right) - NR \\
618 \quad &\left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right)^2 \\
619 \quad G(b, c, d) &= 0. \\
620
\end{aligned}$$

621 Strategy  $I$  is stable if and only if  $G(p, q, r) < 0$  for  $p \neq b, q \neq c, r \neq d$  and  $J = I$  is local  
622 maximum of  $G, G(b, c, d) = 0$ .  
623

624

## 625 5.2. Conditions for the local stability

626 By the same procedure as in point 2 we will try to find maxima of  $G$  inside of simplex  $p+q+$

627  $r \leq 2, p \geq 0, q \geq 0, r \geq 0$ , where in addition  $b+c+d \leq 2, b \geq 0, c \geq 0, d \geq 0$ .

628 Conditions similar to (A.1) - (A.3) are

$$629 \quad dG/dr = f(-1+p+q+r) \left( NR \int_{-1+b}^{-1+b+c+d} f(x)dx - (1-\omega)r \right) \quad (A.8)$$

$$630 \quad dG/dq = dG/dr - \omega \int_{-1+p}^{-1+p+q+r} f(x)dx + \int_{-1+p+q}^{-1+p+q+r} f(x)dx \quad (A.9)$$

$$631 \quad dG/dp = dG/dq + f(-1+p) \left( \omega q - NR \int_{-1+b}^{-1+b+c+d} f(x)dx \right) \quad (A.10)$$

632 At the point of maxima the function  $G$  must be concave, that means in our case  $\frac{\partial^2 G}{\partial p^2}(b, c, d)$

633  $= (1-\omega)f(-1+b+c+d) - f(-1+b+c) + \omega f(-1+b) < 0$ . That means  $0 < b < 1, 2 > b+c+d$

634  $> 1$ .

635 Here strategy  $I$  is stable, if, in agreement with procedure in point 2,

$$636 \quad 2\omega(1-\omega) \geq NR \geq \frac{\omega(1-\omega)}{f(0)}, \quad c = \frac{(1-\omega)d}{\omega}, \quad \omega \int_{-1+b}^{-1+b+c+d} f(x)dx = \int_{-1+b+c}^{-1+b+c+d} f(x)dx,$$

$$637 \quad NR \quad \int_{-1+b}^{-1+b+c+d} f(x) dx = (1-\omega)d, \quad b < 1 \quad \text{and} \quad b + c + d > 1$$

638

### 639 5.3. Other stable strategies

640 On the border of the simplex  $p + q + r \leq 2, p \geq 0, q \geq 0, r \geq 0$  other stable strategies are  
 641 placed. Here in addition  $b + c + d \leq 2, b \geq 0, c \geq 0, d \geq 0$ .

642 If the point  $[b, c, d]$  is point of local maximum of the function  $G$  and if we have normal vector  
 643  $n = (n_1, n_2, n_3)$  to the border of the simplex  $p + q + r \leq 2, p \geq 0, q \geq 0, r \geq 0$  at that point  $[b,$   
 644  $c, d]$ , then there exist positive numbers  $\lambda_1, \lambda_2, \lambda_3$  so that

$$645 \quad dG/dr - \lambda_1 n_1 = 0$$

$$646 \quad dG/dq - \lambda_2 n_2 = 0$$

$$647 \quad dG/dp - \lambda_3 n_3 = 0$$

648

649 Therefore we can conclude results about all maxima of  $G$ .

650

651

### 652 5.4. Conclusion – stable strategies

653 The following three strategies (and no other strategy) are locally stable:

654

- 655 • ZERO SYNCHRONIZATION. The zero synchronization strategy  $[b, 0, 0]$ , is stable  
 656 for any combination of values  $R, \omega$  and brings the net benefit  
 657  $B(b, 0, 0) = 0$ .

658

- 659 • PARTIAL SYNCHRONIZATION. If  $\frac{\omega(1-\omega)}{f(0)} \leq NR \leq 2\omega(1-\omega)$ , then partial  
 660 synchronization strategy  $[b, c, d]$ ,  $b + c + d < 2$ ,  $b > 0$ ,  $c > 0$ ,  $d > 0$ ,  $c = \frac{(1-\omega)d}{\omega}$ , is  
 661 stable and brings the net benefit

$$662 \quad B(b, c, d) = \omega \int_{-1+b}^{-1+b+c} xf(x)dx - (1-\omega) \int_{-1+b+c}^{-1+b+c+d} xf(x)dx + NR \left( \int_{-1+b}^{-1+b+c+d} f(x)dx \right)^2$$

663

664

- 665 • FULL SYNCHRONIZATION. If  $NR \geq 2\omega(1-\omega)$ , then the full synchronization

666 strategy  $[0, c, d]$ ,  $c + d = 2$ , such that  $c = \frac{(1-\omega)d}{\omega}$ , is stable and brings the net benefit

$$667 \quad B(0, c, 2-c) = NR - \int_{-1+c}^1 xf(x)dx,$$

668

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## APPENDIX B: DETAILS AND SOLUTION OF THE MODEL II

669  
670  
671  
672

1. ASSUMPTIONS ABOUT IDEAL SWITCH TIMES

673 The assumptions are the same as in Model I in Appendix A.  
674  
675

2. ASSUMPTIONS ABOUT STRATEGIES

677 A strategy  $I = [r, s]$  is defined by constants  $r, s$  where  $r \geq 0, s \geq 0, r + s \leq 1$ . The behaviour of an  
678 individual  $i$  with the ideal switch time  $t_i^*$  is determined by the position of  $t_i^*$  on the interval  $(-1,$   
679  $1)$ , according to Table B.1

680  
681

3. ASSUMPTIONS ABOUT THE NET BENEFIT FUNCTION

683 Let  $U(x, r, s)$  be the utility function for ideal switch point placed in position  $x$  on time axis.  
684 Let it be continuous function to the exclusion of points  $-r-s, -s, 0, s, r+s$ . Let it be defined by  
685 the following Table B.1.

686

687 Table B.1. Definitions of behaviours and of the utility function. For synchronized departures,  
688 the first part of the utility function quantifies the grouping benefit, the second quantifies the  
689 synchronization costs.  $R$  is a parameter,  $R \geq 0$ .

690

intervals defining position of ideal switch time point	Behaviour	benefit - cost function $U(x, b, c, d)$
$t_i^* \in (-1, -r-s)$	non-synchronized departures, each at individual $t_i^*$	0
$t_i^* \in (-r-s, -s)$	synchronized departure at $-s$	$2NR \int_{-1+b}^{-1+b+c+d} f(x)dx + (x+s)$
$t_i^* \in (-s, 0)$	synchronized departure at $-s$	$2NR \int_{-1+b}^{-1+b+c+d} f(x)dx - (x+s)$

$t_i^* \in (0, s)$	synchronized departure at $s$	$2 NR \int_0^{r+s} f(x) dx - (s-x)$
$t_i^* \in (s, r+s)$	synchronized departure at $s$	$2 NR \int_0^{r+s} f(x) dx - (x-s)$
$t_i^* \in (r+s, 1)$	non-synchronized departures, each at individual $t_i^*$	0

691

## 692 4. CALCULATION OF OPTIMAL STRATEGIES

693 4.1. Derivation of the benefit function

$$694 \quad B(r, s) = -2 \int_s^{r+s} x f(x) dx + 2s \int_s^{r+s} f(x) dx + 2 \int_0^s x f(x) dx - 2s \int_0^s f(x) dx + 2 NR \left( \int_0^{r+s} f(x) dx \right)^2$$

695

696 4.2. Conditions for the local maxima of benefit.

697 To obtain internal maxima we have the following conditions inside of the simplex

698  $r + s \leq 1, r \geq 0, s \geq 0: dB/dr = dB/ds = 0.$

699 Therefore the following relations must be valid:

700 
$$\frac{\partial B}{\partial r} = f(r+s) 4 NR \left( \frac{-r}{2NR} + \int_0^{r+s} f(x) dx \right) = 0 \quad (B.1)$$

701 
$$\frac{\partial B}{\partial s} = f(r+s) 4 NR \left( \frac{-r}{2R} + \int_0^{r+s} f(x) dx \right) + 2 \int_s^{r+s} f(x) dx - 2 \int_0^s f(x) dx = 0 \quad (B.2)$$

702 Conditions (C.1), (C.2) are true if and only if

703

704 
$$\frac{r}{2R} = \int_0^{r+s} f(x) dx = 2 \int_s^{r+s} f(x) dx = 2 \int_0^s f(x) dx.$$

705 From that  $\frac{1}{4f(0)} \leq NR \leq 1$

706

707 4.3. Other maxima.

708 Other maxima are placed on the border of the simplex. The possible points of maxima are

709  $r = s = 0$ , and  $r + s = 1$ . The first case describes the set of non-synchronized switches, the

710 second case describes the set of totally synchronized switches.

711 2.4. Conclusion – the points of maxima of optimal strategies

712 There exists interval  $(\alpha, \beta) \subset (\frac{1}{4f(0)}, 1)$  so that the following points are valid:

713 • ZERO SYNCHRONIZATION. For each  $NR$ ,  $NR \leq \alpha$   $B(0, 0)$  is maximum of  $B$ .

714  $B(0, 0) = 0$ .

715 • PARTIAL SYNCHRONIZATION. For each  $NR$ ,  $\alpha < NR < \beta$ , there exists  $[r, s]$ ,  $r +$   
716  $s < 1$ ,  $r > 0$ ,  $s > 0$  so that relations (1) - (2) are valid and  $B(r, s)$  is maximum of  $B$ .

$$717 \quad B(r, s) = -2 \int_s^{r+s} xf(x)dx + 2 \int_0^s xf(x)dx + 2NR \left( \int_0^{r+s} f(x)dx \right)^2$$

718

719 • FULL SYNCHRONIZATION. For each  $NR$ ,  $NR \geq \beta$ , there exists

720  $[r, s]$ ,  $r + s = 1$ ,  $\int_s^1 f(x)dx = \int_0^s f(x)dx$  so that  $B(1-s, s)$  is maximum of  $B$ .

$$721 \quad B(1-s, s) = -2 \int_s^1 xf(x)dx + 2s \int_s^1 f(x)dx + 2 \int_0^s xf(x)dx - 2s \int_0^s f(x)dx + NR/2$$

722

723

## 724 5. MODELS I AND II COMPARISON.

### 725 5.1. Reduced model I.

726 The model described in Appendix A can be reduced to symmetric case, if  $\omega = 1/2$ .

727 We defined the following transformations of variables in the model I:

728  $-1 + b = -e$ ,  $-1 + b + c = 0$ ,  $-1 + b + c + d = e$ . Then benefit function is function of one variable

729  $e$ :

$$730 \quad B(e) = -2 \int_0^e xf(x)dx + 4NR \left( \int_0^e f(x)dx \right)^2$$

731

732 The conditions for maxima of  $B$  are similar to general model I:

733

734 • ZERO SYNCHRONIZATION. For each  $NR$ ,  $NR \leq \frac{1}{4f(0)}$ ,  $B(0)$  is maximal.

735  $B(0) = 0$ .

736 • PARTIAL SYNCHRONIZATION. For each  $NR$ ,  $\frac{1}{4f(0)} < NR < 0.5$ , there exists  $0 <$

737  $e < 1$ , so that  $\frac{eL}{4NQ} = \int_0^e f(x)dx$  and function  $B$  is maximal.

738 
$$B(e) = -2 \int_0^e xf(x)dx + 4NR \left( \int_0^e f(x)dx \right)^2$$

739

740 • FULL SYNCHRONIZATION. For each  $NR$ ,  $NR \geq 1/2$ ,  $B(1)$  is maximal.

741 
$$B(1) = -2 \int_0^1 xf(x)dx + NR$$

742

743 5.2. Models I and II comparison

744 We denoted

745 
$$B1(e) \equiv -2 \int_0^e xf(x)dx + 4NR \left( \int_0^e f(x)dx \right)^2$$
 and

746 
$$B2(r, s) \equiv -2 \int_s^{r+s} xf(x)dx + 2s \int_s^{r+s} f(x)dx + 2 \int_0^s xf(x)dx - 2s \int_0^s f(x)dx + 2NR \left( \int_0^{r+s} f(x)dx \right)^2$$

747 Let  $(NR)_1$  is that value of parameter that  $\frac{1}{4} \left( \frac{1}{NR} \right)_1 = \int_0^1 f(x)dx = 1/2$ . That means  $(R)_1$  is limit

748 point common for full and partial synchronization in reduced model I.

749 Let  $(R)_2$  is that value of parameter that  $(NR)_2 = \beta$  in model II. Therefore the definition of

750  $(NR)_2$  in Model II is the same as definition  $(NR)_1$  in reduced model I.

751 Then  $B1(1) - B2(s, 1-s) = -2 \int_0^1 xf(x)dx + 1/2 + 2 - 2 \int_0^s xf(x)dx - \frac{1-s}{2} =$

752  $-4 \int_0^s xf(x)dx + s/2 \geq 0$ . This fact follows from  $\int_s^{r+s} f(x)dx = \int_0^s f(x)dx$  and  $\frac{r}{2} \left( \frac{1}{NR} \right)_2 = \frac{1}{2}$

753 But that means  $B1(e) \geq B2(r, s)$ , where  $e$  is maximal point for  $B1$  and  $[r, s]$  is maximal point

754 for  $B2$ .

755

756

757

5.3. Conclusion - models I and II comparison.

758 APPENDIX C: GROUP STABILIZATION OR DISSOLUTION AFTER REPEATED  
 759 SYNCHRONIZATION CHALLENGES

760 1. Assortment scenario

761 During the first challenge, the benefit function is, according to Appendix B, part 5.1

$$762 \quad B(e) = -2 \int_0^e xf(x)dx + 4NR \left( \int_0^e f(x)dx \right)^2 \quad (\text{C.1})$$

763 and the optimal degree of partial synchronization is defined by

764

$$765 \quad \frac{e^*}{4NR} = \int_0^{e^*} f(x)dx \quad (\text{C.2})$$

766 where  $e^*$  is the value of  $e$  bringing the optimal benefit during the first challenge.

767

768 After the first challenge and partial synchronization group size is thus reduced from  $N$  to  $pN$

769 where  $p$  is the proportion of animals that have departed together on the first challenge and

770 therefore remain in the group

$$771 \quad p = \int_{-e^*}^{e^*} f(x)dx = 2 \int_0^{e^*} f(x)dx < 1.$$

772 All animals with their optimal times  $t^*_i$  within the interval  $(-1, -e^*)$  or the interval  $(e^*, 1)$

773 disappear from the group. The new density function  $f_{assort}(x)$  is defined as

774

$$775 \quad f_{assort}(x) = 0 \text{ for } x \in (-1, -e^*) \cup (e^*, 1),$$

$$776 \quad f_{assort}(x) = \frac{1}{p} f(x) \text{ for } x \in (-e^*, e^*).$$

777 The new optimal degree of partial synchronization is defined by

778

$$779 \quad \frac{e_{assort}^*}{4pNR} = \frac{1}{p} \int_0^{e_{assort}^*} f(x) dx$$

780 This equation is identical to (D.2) and therefore

781  $e_{assort}^* = e^*$ , which means that all animals will depart together during the second challenge  
782 and the group size will be stabilized.

783

## 784 2. Non-Assortment scenario

785 The density distribution of ideal times after the first challenge and partial synchronization  
786 under the non-assortment scenario  $f_{nonassort}$  remains the same as before the challenge as  
787 follows

788

$$789 \quad f_{nonassort}(x) = f(x) \text{ for } x \in (-1, 1).$$

790

791 From Appendix B we have for the partial synchronization during the first challenge

792

$$793 \quad \frac{e^*}{4NR} = \int_0^{e^*} f(x) dx \quad (C.3)$$

794

795 and similarly for second challenge

$$796 \quad \frac{e_{nonassort}^*}{4pNR} = \int_0^{e_{nonassort}^*} f_{nonassort}(x) dx = \int_0^{e_{nonassort}^*} f(x) dx \quad (C.4)$$

797

798 The function  $\alpha(e) = \int_0^e f(x) dx / \frac{e}{4NR}$  is decreasing and from (D.3) and (D.4) we have

$$799 \quad \alpha(e^*) = 1 > \alpha(e_{nonassort}^*) = 1/p.$$

800

801

802 Therefore  $e_{nonassort}^* < e^*$

803

804 and consequently a lower proportion of  $p_{nonassort} < p$  will depart together on the second

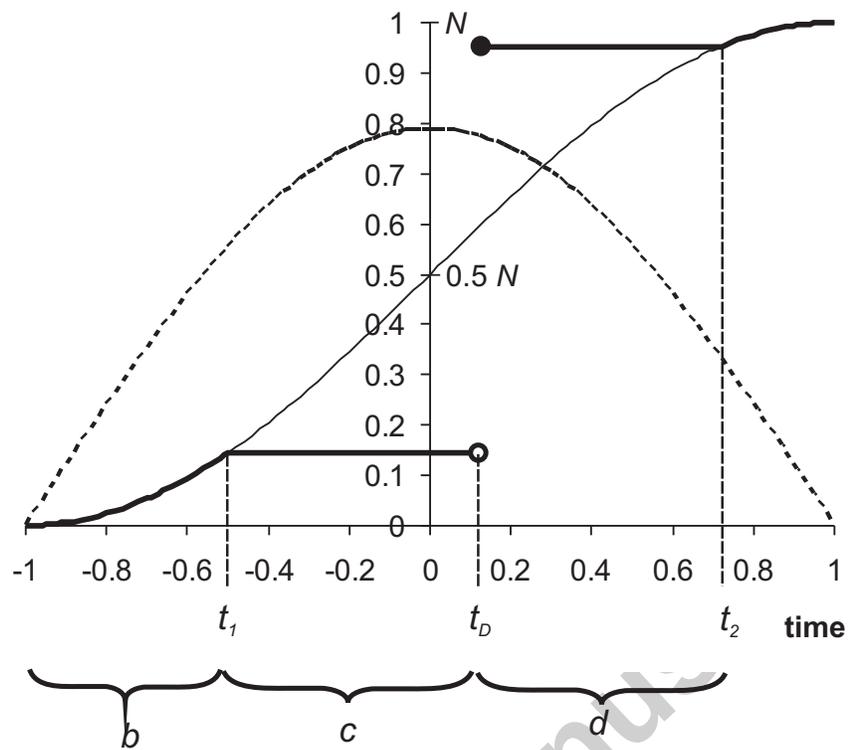
805 challenge, until eventually  $e_{nonassort}^* = p_{nonassort} = 0$  and the group will dissolve.

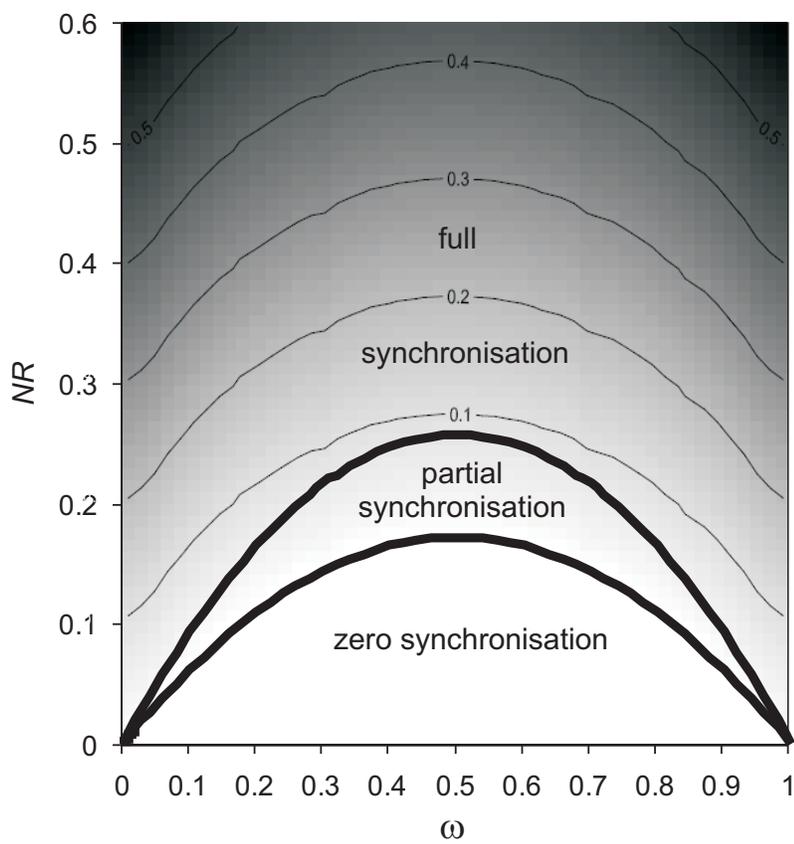
806

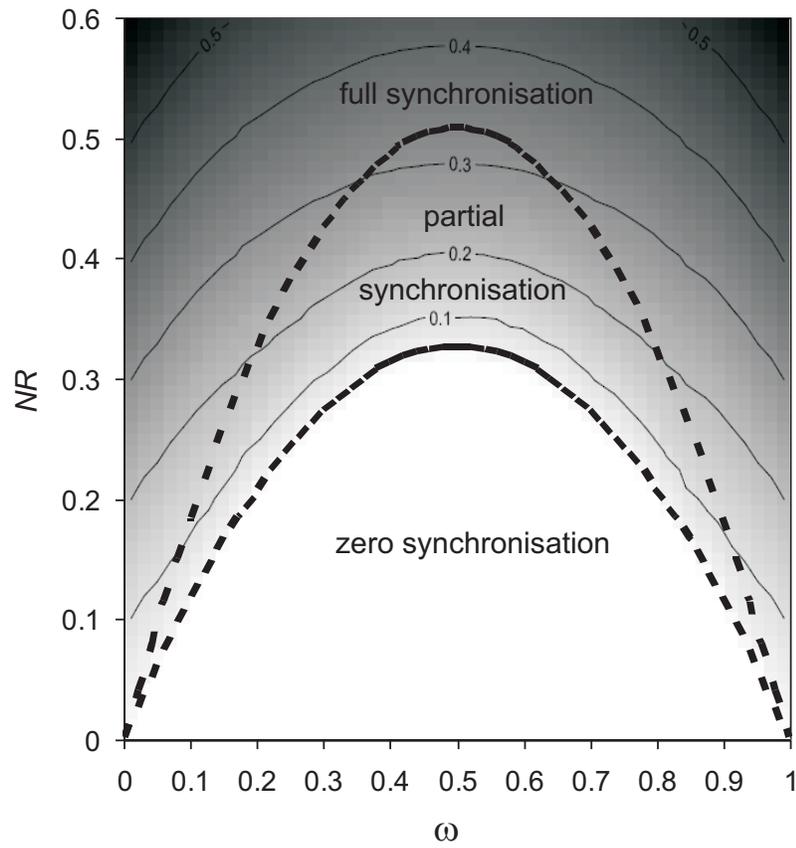
807 For any given value of parameter  $R$ , the optimal strategy of the reduced one-departure model

808 brings higher net benefit than the optimal strategy for the two-departure model II.

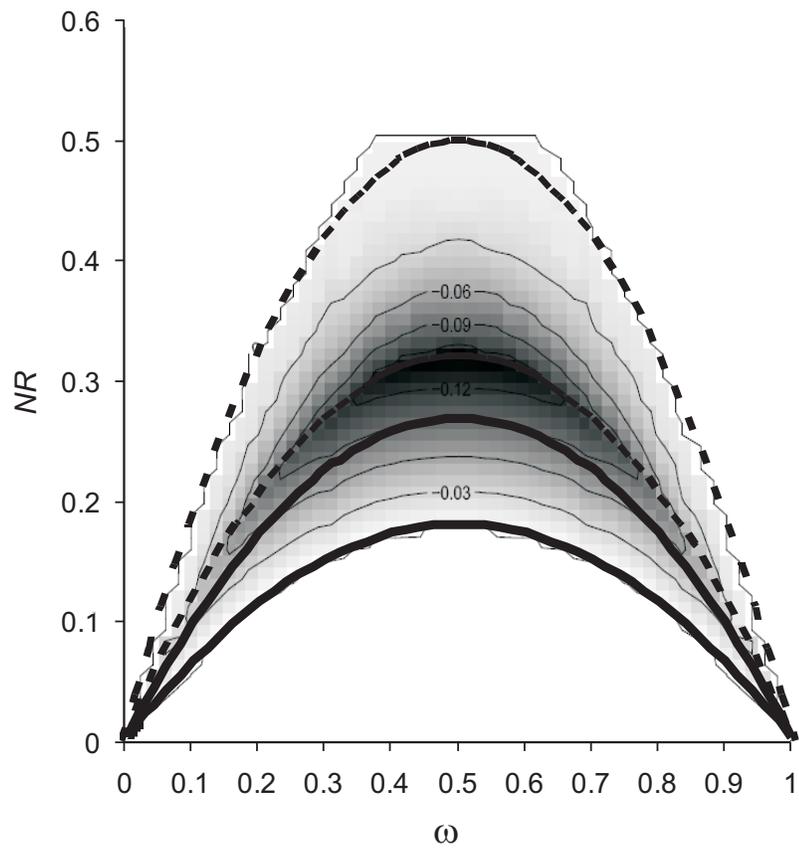
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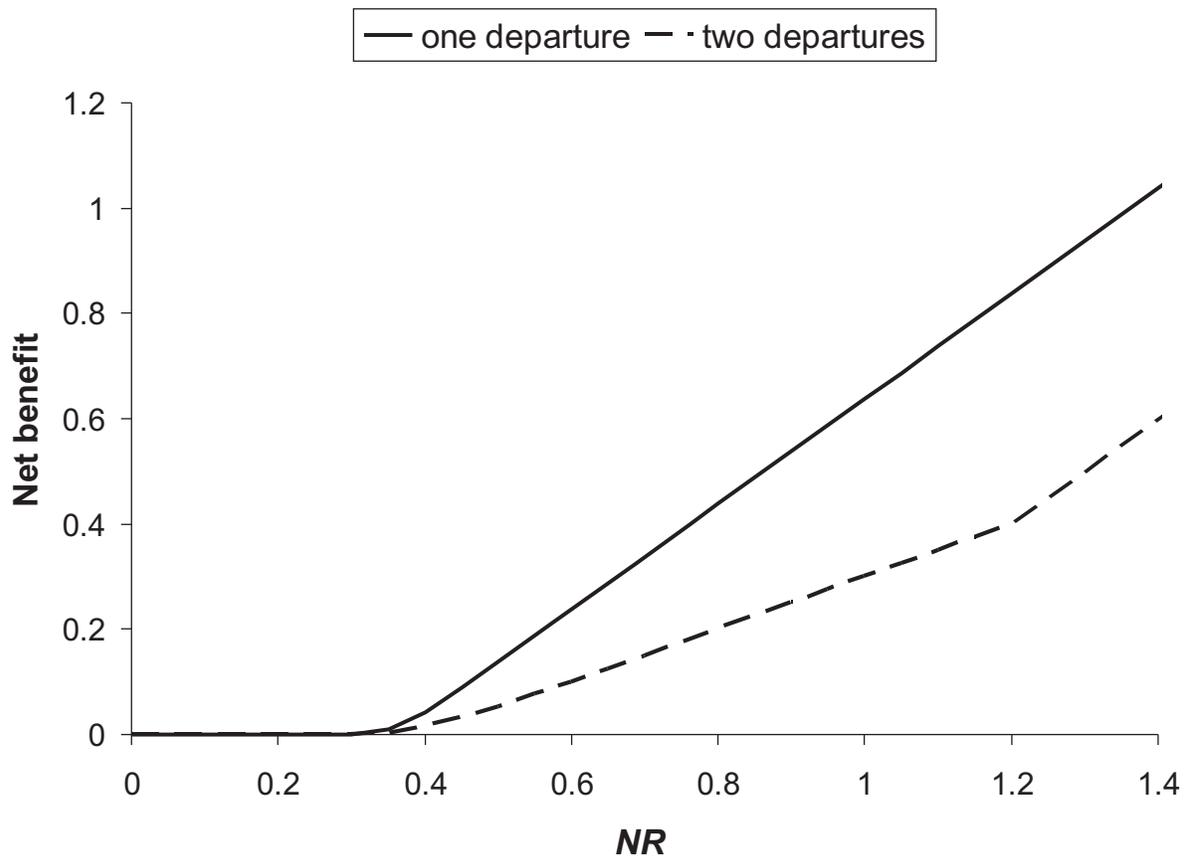




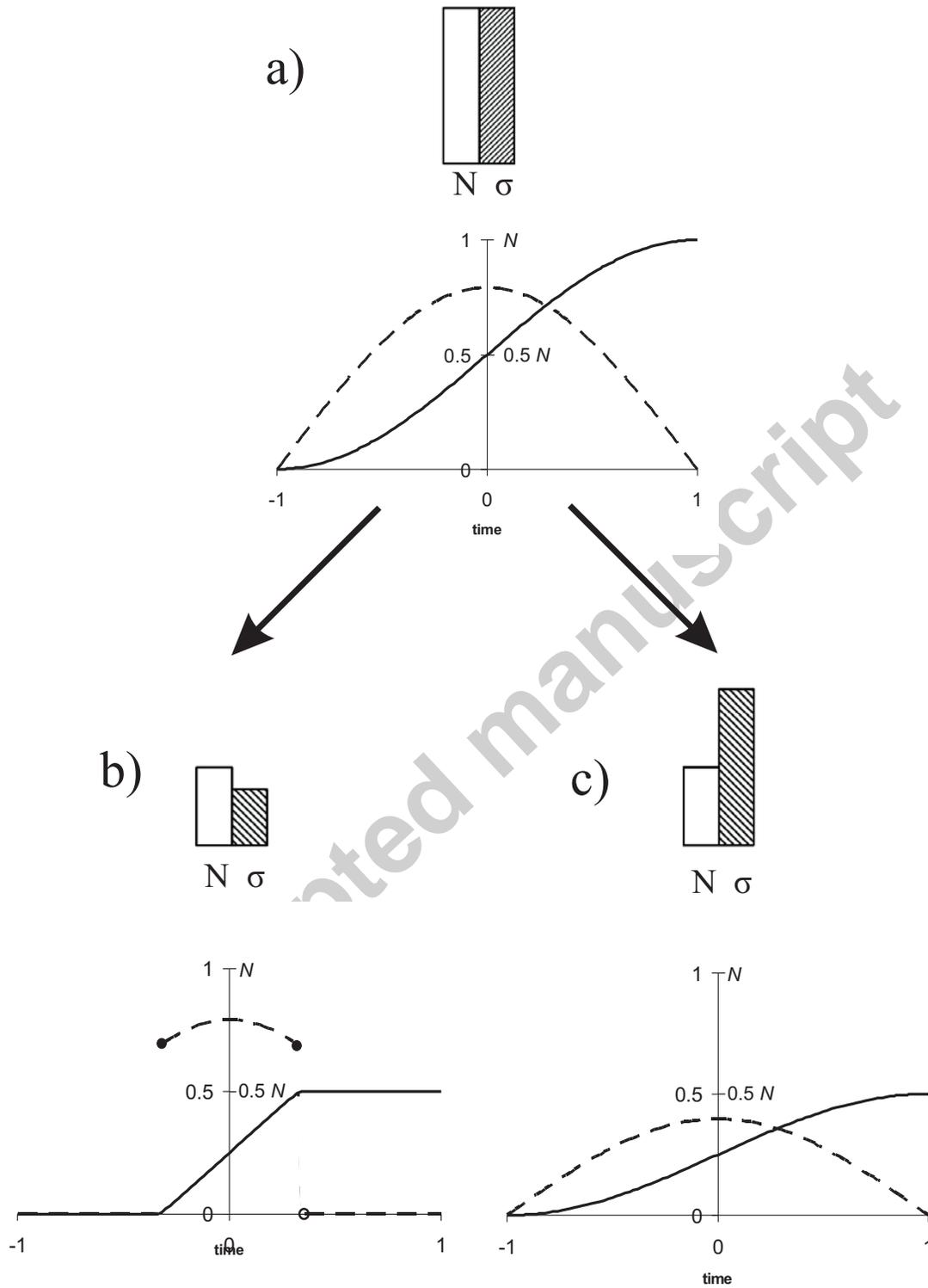


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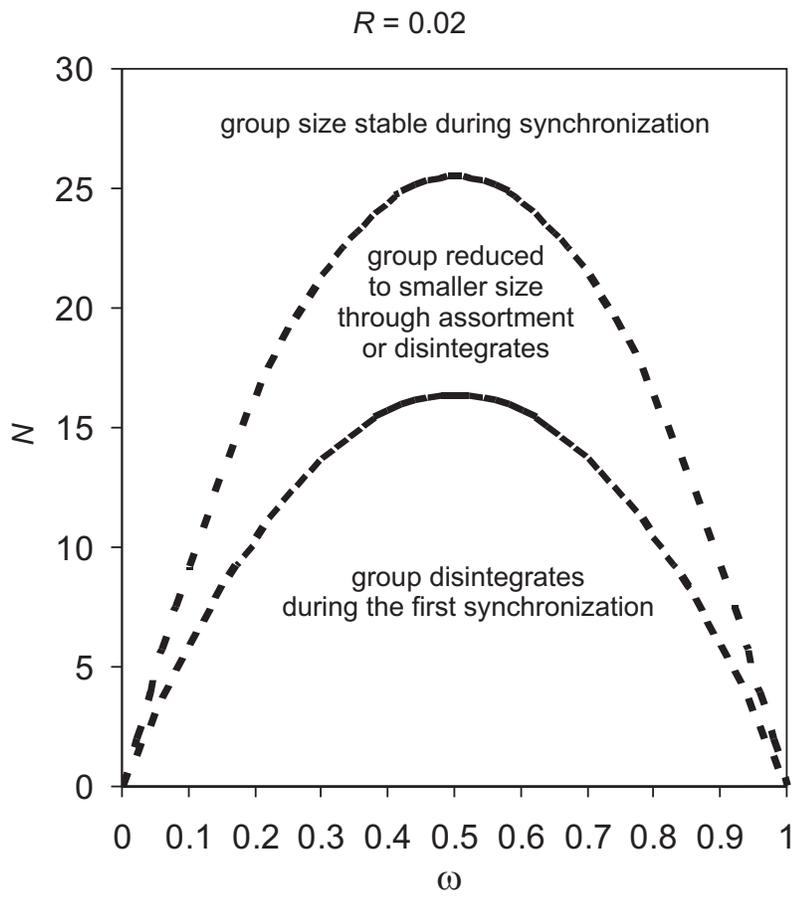


Figure 8

