

1 **Energetic requirements of the transition from solitary to group living**

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3 **Authors:** Sumaiya Rahila I. K.¹, Momoka Nii¹, Takuya Okabe¹, Hiromu Ito^{2,3}, Muhammad
4 Almaududi Pulungan⁴, Satoru Morita¹, Kazuya Kobayashi⁵, Mitsutoshi Setou⁶, Kikuo
5 Iwabuchi⁷, Kenji Matsuura⁸, Jin Yoshimura^{2,9,10,11,12*}.

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7 **Affiliations:**

8 ¹Graduate School of Integrated Science and Technology, Shizuoka University, 3-5-1
9 Johoku, Naka-ku, Hamamatsu, 432-8561, Japan.

10 ²Department of International Health, Institute of Tropical Medicine, Nagasaki
11 University, Nagasaki 852-8523, Japan.

12 ³Department of Environmental Sciences, Zoology, University of Basel, Basel 4051,
13 Switzerland.

14 ⁴Graduate School of Science and Technology, Shizuoka University, 3-5-1 Johoku,
15 Naka-ku, Hamamatsu, 432-8561, Japan.

16 ⁵Hokkaido Forest Research Station, Field Science Education and Research Center,
17 Kyoto University, Hokkaido, 088-2339, Japan

18 ⁶Department of Cellular and Molecular Anatomy, Hamamatsu University School of
19 Medicine, Higashi-ku, Hamamatsu, 432-3192, Japan.

20 ⁷Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu,
21 Tokyo, 183-8509, Japan.

22 ⁸Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University,
23 Kyoto, 606-8502, Japan.

24 ⁹Department of Environmental and Forest Biology, State University of New York
25 College of Environmental Science and Forestry, Syracuse, NY 13210 USA.

26 ¹⁰Marine Biosystems Research Center, Chiba University, Uchiura, Kamogawa, Chiba
27 299-5502, Japan.

28 ¹¹Department of Biological Sciences, Tokyo Metropolitan University, Hachioji, Tokyo,
29 192-0397 Japan

30 ¹²The University Museum, University of Tokyo, Bunkyo-ku, Tokyo, 113-0033 Japan

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34 **Corresponding Author:**

35 Jin Yoshimura (yoshimura.jin@shizuoka.ac.jp)

36 **Highlights**

- 37 - The energetic requirement for group living is analyzed from the perspective of
38 Holling's functional responses.
- 39 - Type III functional response is the necessary condition for positive group benefits.
- 40 - Sufficient conditions require the constraints on the coefficient of a nonlinear term for
41 synergy.
- 42 - Functional response of the predator may act as the dilution effect on the prey, while
43 synergistic benefit of the prey contributes to its group living.

44

45 **Abstract**

46 Synergy is known to be vital for the group collaboration among non-kin individuals. In
47 order to evaluate the condition of synergy that initiates group living, we build a model
48 of food intake based on three types of functional response. We show that type III
49 functional response is prerequisite for synergy to allow group living. The optimal
50 number of gathering individuals can be also evaluated from Type III functional response
51 curve. Type III functional response consists of terms depending linearly and bilinearly
52 on the number of individuals and the bilinear term represents synergy. For a fixed value
53 of the linear coefficient, there are upper and lower boundaries of the bilinear coefficient
54 for synergistic collaboration. The dilution effect can be incorporated into the model
55 through the functional response of predator. Thus, the functional response of the
56 predator as well as that of the prey contribute to the group living of the prey. Our model
57 shows that group livings are categorized into three types, namely those due to (1)
58 synergy effect of the own group, (2) dilution effect against the predator, and (3) both
59 effects contributing together. The predator's functional response plays a decisive role in
60 the last two types, where the predator response should be of anti-Type III (i.e., Type II).

61

62 **Keywords:** the origin of sociality, solitary individuals, Holling's functional response,
63 linear and bilinear coefficients, energetic requirement, dilution effect

64

65 **1. Introduction**

66 Society is found in several unrelated animals (Wilson, 1975). To establish society, the
67 benefit of group living is indispensable, that is, synergy, a total benefit greater than the
68 sum of the contributions of solitary individuals. Synergy is found in various organisms
69 from bacteria to humans. For example, we can look at eusociality, an extreme form of
70 sociality, where almost all individuals become non-breeding helpers to assist a few
71 reproductive individuals called kings and queens. We find it evolved widely in
72 phylogenetically independent diploid organisms, e.g., termites (Thorne, 1997), aphids
73 (Aoki, 1977, Stern, 1996, Aoki and Imai, 2005), gall thrips (Crespi et al., 1992), beetles

74 (Anderson, 1984), spongy-dwelling shrimps (Duffy et al., 2000) and naked mole rats
75 (Wilson, 1975, Burda et al., 2000).

76 We define synergy as a condition in which a total benefit of individuals is greater than
77 the sum of the individual contributions. Mathematically, synergy is represented by a
78 positive nonlinear dependence of total benefits on the number of individuals. There
79 should be many mechanisms to create such synergistic benefits in animal society. We
80 suspect a common principle behind these various mechanisms.

81 In ecology, a functional response originally refers to the number of preys eaten by a
82 predator as a function of prey density in predator-prey interactions (Holling,
83 1959a,1959b, Begon et. al., 1996). In this sense, a functional response generally means
84 the intake rate of a consumer as a function of food density (the amount of food available
85 in a given ecotope). We here apply this concept to social behavior of animals. A
86 functional response of a group of individuals corresponds to the total benefit created by
87 individuals as a function of the number of individuals.

88 Three types of functional response (Type I, II and III) are usually observed in foraging
89 and other behavioral activities (Holling, 1959a,1959b, Begon et. al., 1996). In Hollings'
90 seminal papers, functional response is originally considered the amount of prey caught
91 by a predator as a function of prey density (Holling, 1959a,1959b). According to
92 Holling, Type I is a linear response without saturation. Type II is an initial linear
93 response with saturation. Type III is a sigmoidal response. This original idea is
94 generalized widely in ecology as the rate of intake (e.g., energy gain and fitness) as a
95 function of environmental factors, such as food density (Begon et. al., 1996). Here, we
96 apply this concept to the food intake as a function of the number of individuals. We do
97 not consider a super-linear response without saturation (e.g., an exponential growth
98 without limit), because saturation is an unavoidable condition in natural response.

99 We illustrate the synergistic effect of group living on food (wood) digestion in a nest of
100 wood roaches as an example. The roaches are detritivores that consume energy from
101 dead plants (mostly wood) with the help of symbiotic bacteria residing in their midgut.
102 The symbiotic microorganisms produce enzymes to decompose cellulose and lignin.
103 Here, for instance, each individual roach cannot decompose dead wood effectively. It is
104 because each of them has an insufficient number of symbiotic microorganisms that
105 secrete digestive enzymes. Aggregation by many roaches enables to digest the wood
106 efficiently.

107 There should be many mechanisms to create such nonlinear contribution in animal
108 society. We assume that the three types of functional response consist of a linear term
109 and a bilinear term in the number of individuals. The former represents the contributions
110 proportional to the number of individuals, whereas the latter does the additional benefits
111 due to aggregation (group living).

112 We ignore the higher-order terms because we are interested in the origin of group living
113 from solitary individuals to a small group. Similar studies have been published for
114 investigating the evolution and the stability of cooperative groups (Kokko et al., 2001,

115 Haiert et al., 2002, Michor and Nowak, 2002, 16, Sumpter, 2010, Cornforth et al.,
 116 2012). These works assume the presence of a social group and analyze the evolutionary
 117 games among interacting individuals. In other words, they study the evolution of
 118 cooperative behavior in public goods games. In contrast, we focus on the origin of
 119 grouping behavior from one to two individuals. Here we investigate the necessary and
 120 sufficient conditions for linear and bilinear coefficients (terms) by assuming three types
 121 of functional response.

122

123 2. Models and Results

124 For the simplicity of the model, we assume here that there is no cost to join the group
 125 members. We illustrate three types of functional response with a simple expression as
 126 follows. Type I functional response assumes a linear increase in food intake with the
 127 number of individuals n ($=1, 2, 3, \dots$),

$$128 \quad f_I(n) = a_1 n. \quad (1)$$

129 Type II functional response has a decelerating intake for a small number of individuals,
 130 while saturation occurs for a large number,

$$131 \quad f_{II}(n) = \frac{a_2 n}{1 + a_2 n}. \quad (2)$$

132 Type III functional response is similar to type II in that saturation occurs for a large
 133 number, while it has an accelerating intake for a small number. The accelerating part is
 134 described as $f_{III}(n) = a_3 n + bn^2$ for a small value of n , while saturation for a large n
 135 may be described in many ways, among which we may adopt a hyperbolic tangent
 136 function,

$$137 \quad f_{III}(n) = \tanh(a_3 n + bn^2). \quad (3)$$

138 In the current models, the linear coefficients a_i (for $i = 1, 2$ and 3) represent the food
 139 intake by each solitary individual without synergy, while the bilinear coefficient b does
 140 the effect by synergistic collaboration. The latter effect is proportional to n^2 , the
 141 encounter probability of two individuals. Type III response means that b is positive.
 142 Figure 1 illustrates these three types of functional response.

143 Type 3 response is obtained as follows. Suppose that food source is sectioned into L
 144 patches (sites) of equal area. First, we consider the case in which the number of
 145 decomposer insects is so small ($n \ll L$) that a single patch is not visited by more than
 146 two individuals. If each individual visits any patch equally likely, the probability that a
 147 single patch contains two individuals while the other patches have just one is given by
 148 $p_2 = \frac{n(n-1)}{2} \times \left(\frac{1}{L}\right) \left(1 - \frac{1}{L}\right) \left(1 - \frac{2}{L}\right) \dots \left(1 - \frac{n-2}{L}\right) \cong \frac{n(n-1)}{2L}$. The first factor $n(n-1)/2$ is
 149 the number of ways of choosing two from n individuals, while the others are the
 150 probabilities of singly distributed individuals. Thus, the functional response of food
 151 decomposition is given by $p_2(D_2 + D_1(n-1))$, where D_1 and D_2 are food

152 decomposition by one and two individuals, respectively. To this, the case of each patch
 153 being not occupied by more than one individual is added, i.e., $(1 - p_2)nD_1 + p_2(D_2 +$
 154 $D_1(n - 1))$. Next, we consider that the functional response converges to a finite value
 155 D for a large value of n . If D is adopted as the unit of measure ($D = 1$), D_1 and D_2 are
 156 replaced by $d_1 = D_1/D$ and $d_2 = D_2/D$, respectively. Thus, we obtain $f_{III}(n) \cong a_3n +$
 157 bn^2 with $a_3 = d_1 + (d_1 - d_2)/(2L)$ and $b = (d_2 - d_1)/(2L)$. The saturation effect
 158 may be taken into account by the hyperbolic tangent function, i.e., $\tanh(x) \cong 1$ for
 159 $|x| \gg 1$. The relation $f_{III}(n) \cong a_3n + bn^2$ is ensured due to the absence of the second
 160 order term in $\tanh(x) \cong x - x^3/3$ for $|x| \ll 1$.

161 We now consider food intakes per individual, $f_\alpha(n)/n$ ($\alpha = I, II, III$) (Fig. 2). In order
 162 for synergy to occur, the food intake per individual should be larger than that of an
 163 individual for some $n > 1$. Therefore, type III is prerequisite, i.e., the only functional
 164 response that satisfies this condition (Fig. 2). The condition for synergy is given as
 165 follows. For some integer $n > 1$,

$$166 \quad \frac{f_{III}(n)}{n} > \frac{f_{III}(1)}{1}. \quad (4)$$

167 The following values/numbers are just an example of numerical calculations for the
 168 given function to illustrate the consequences of the current model. The synergistic
 169 benefit of synergy $(f_{III}(n)/n - f_{III}(1)/1)$ is plotted as a function of the bilinear (non-
 170 linear) coefficient b for $n = 2$ and $a_3 = 0.15$ (Fig. 3a), indicating that there are a lower
 171 and upper bound for b to satisfy the condition (Eq. (4)), i.e., $0.004 < b < 0.36$. For $n = 2, 3$
 172 and 4, the region for synergy is plotted in Figure 3b. The upper bound varies
 173 significantly depending on a_3 and n (Fig. 3b). The smaller a_3 , the larger the region for b
 174 to cause synergy. As n increases, the region for synergy shrinks. Figure 3b also
 175 indicates that a_3 has the upper bound, e.g., $a_3 < 0.184$ for $n = 4$. Figure 3c indicates
 176 that the lower bound for b is so small that, in so far as b is positive, this condition is
 177 always satisfied in practice. The conditions for $n = 3$ and 4 are not necessarily satisfied
 178 even if $n = 2$ is satisfied. However, the condition for $n = 2$ is satisfied if that for $n = 3$ is.
 179 Thus, the condition for $n = 2$ is least stringent (the sufficient condition for synergy).
 180 Under these conditions, the optimal number n^* of cooperating individuals is the integer
 181 n^* that maximizes $f_{III}(n)/n$, i.e., $\frac{f_{III}(n^*)}{n^*} = \max \left\{ \frac{f_{III}(n)}{n} \right\}$, e.g., $n^* = 2$ in Figure 2.

182 In the above, we have not taken account of the dilution effect to avoid becoming the
 183 target of predation by other animals. In the presence of the dilution effect, the overall
 184 fitness of a surviving individual is given by $w(n) = v(n)e^{-\frac{\lambda(n)k(n)}{n}T}$, where $v(n) =$
 185 $f_\alpha(n)/n$, $\lambda(n)$ is the average attack rate directed at a group of n individuals per time
 186 unit, $k(n)$ is the average number of prey a predator is able to kill from a group of n
 187 individuals, and T is the time to the next reproductive event (Equation (6) in Lehtonen
 188 and Jaatinen, 2016). The function $k(n)$ describes the predator's functional response to
 189 prey density. Thus, the potential benefits of grouping depend not only on the type of
 190 functional response of the prey but also on that of the predator. In place of Eq. (4), the
 191 condition for grouping is now given by $w(n) > w(1)$, which is equivalent to

192 multiplying the right-hand side of Eq. (4) with the factor $e^{\left(\frac{\lambda(n)k(n)}{n} - \frac{\lambda(1)k(1)}{1}\right)T}$.
 193 Accordingly, the advantage of grouping is decreased (or increased) if this factor is
 194 larger (or smaller) than 1, i.e., if $\frac{\lambda(n)k(n)}{n} - \frac{\lambda(1)k(1)}{1} > 0$ (or < 0). Consequently, grouping
 195 of the prey is suppressed if the predator's functional response is Type III, i.e., $k(n)/n >$
 196 $k(1)/1$, while it is promoted if the prey's functional response is Type III. Conversely,
 197 grouping of the prey is promoted if the predator's functional response is Type I and
 198 Type II. This is the dilution effect (Lehtonen and Jaatinen, 2016).

199 To illustrate the condition of group living, let us assume $f(n) = an + bn^2$ and $k(n) =$
 200 $An + Bn^2$ for the functional response of the prey and the predators, respectively. As
 201 shown above, the parameters b of the prey (and B of the predator) can be evaluated from
 202 the food capture efficiencies of one and two prey (and predator) individuals, in
 203 principle. Here we neglect saturation effect because we are interested in the inception of
 204 group living (a small number of prey individuals). Type I, II, and III responses
 205 correspond to $b=0$ ($B=0$), $b<0$ ($B<0$), and $b>0$ ($B>0$), respectively. The condition
 206 $w(2) > w(1)$ leads to an inequality for the ratio b/a , which is shown in Fig. 4. Group
 207 living is promoted unconditionally when the functional response of the predator is of
 208 Type II (i.e., $B<0$) and that of the prey is of Type III (i.e., $b>0$). Even if the prey's
 209 functional response is Type II ($b<0$), group living is possible if the predator's functional
 210 response is Type II ($B<0$). As denoted in Fig.4, this grouping is not due to improved
 211 foraging ($b>0$) but due to the dilution effect ($B<0$). Note that the above condition in Eq.
 212 (4) holds as it is if the predator's functional response is type 1, i.e., $k(n)/n = k(1)/1$,
 213 and if the attack rate $\lambda(n)$ is independent of n .

214

215 3. Discussion

216 We here show the necessary and sufficient conditions for synergy to work. The
 217 necessary condition is type III functional response (Fig. 2). The sufficient condition
 218 requires that the coefficient a_3 is less than an upper bound, and that the non-linear
 219 coefficient b is in a certain range for a given value of a_3 (Fig. 3). In the current model,
 220 a_3 represents the food intake rate by each single individual (without synergy), while b
 221 does the additional benefit due to grouping. Type III response means that b is positive;
 222 if $b = 0$, the response becomes Type II. As in termite colonies, animals living (thriving)
 223 in harsh environments have a great difficulty in finding and collecting food without
 224 synergy. This means that non-synergy parameter a_3 is exceptionally small in such
 225 animals. They are unable to survive without group living. Once grouping takes places
 226 (lower bound $<b<$ upper bound), it becomes possible for the animals to survive as a
 227 group. In case of Figure 2, groups of $n = 2, 3$ and 4 do better than the sum of
 228 independent individuals (sufficient condition). In the current model, $n = 2$ outperforms n
 229 $= 3$ and 4 , while $n = 5$ does not satisfy the condition for synergy (Fig. 2). This does not
 230 necessarily mean that grouping begins with optimal size $n^* = 2$, i.e., groups can be of
 231 greater than optimal size (Sibly, 1983). In the first place, the optimal group size may

232 depend on the saturation value of functional response, which is assumed unity in the
233 current model. Since the saturation value was just set as unity in this manuscript, the
234 evolution of group size is an issue outside the scope of the current model.

235 We here show the energetic requirement of synergy based on functional response.
236 Synergy thus explains transition from solitary to group living (Anderson, 1984, Nowak,
237 2006, Ohkubo et al., 2018). Grouping behavior (aggregation) should have been formed
238 because of benefits, e.g., bird flocks, animal herds with alarm calls, and larval and
239 hibernating aggregation in insects (Bonabeau et al., 1999). We may call this primitive
240 sociality, in which grouping may be ephemeral (temporal); it does not necessarily mean
241 to sustain.

242 An interesting case of group living is known in a halictid bee, where a nest hole on the
243 ground is shared by a group of individuals (Yagi et al., 2012, Ohkubo et al., 2018). A
244 non-breeding helper guards the entrance of a nest against ant predators, indicating
245 eusociality. However, in this species, two to several unrelated bees also share the nest
246 hole, where each bee digs their own reproductive chambers (cells). The hole entrance is
247 guarded by a single bee at a time and all individuals share the time of entrance guard.
248 Entrance guard will be the reason for synergy in this bee.

249 More generally, food collections of social hymenopterans (bees and wasp) may be
250 considered as a case of synergy. The cooperative foraging behavior of honey bees is
251 another good example. In this case, food (nectar and pollen) collection of bees is
252 enhanced by dance language. This synergy benefit may become crucial especially when
253 the resource is so scarce that an individual bee has difficulty in locating flowers with
254 nectar and pollen. Synergy contributions of honey bees under seasonal variations of
255 flowers (food resources) may be modeled by sequential dynamic programming (Mangel
256 and Clark, 1988).

257 The dilution effect is another type of group benefits that is caused by the avoidance of
258 the predator (Lehtonen and Jaatinen, 2016). It is commonly observed that animal
259 aggregation is beneficial to reduce or avoid predation. In other words, this effect is due
260 to the functional response of the predator being of Type II, that is, the predation
261 efficiency decreases as the prey number increases. In contrast, the synergy effect of the
262 present model is due to the functional response of the prey being of Type III.
263 Accordingly, we have to consider the functional responses of the prey and predator
264 simultaneously (Fig. 4). Generally, we can categorise the grouping effects into three
265 types: (1) synergy only, (2) both synergy and dilution, and (3) dilution only. In Table 1,
266 we list possible animal candidates and their characteristics for each category. We hope
267 to see the empirical demonstrations of all three categories in future.

268 The advantage of grouping in aphids comes from synergistic benefits and the dilution
269 effect to avoid predation (Watanabe et al., 2016). The total number and the ratio of the
270 green and red morphs are both important for attracting cooperative ants that protect an
271 aphid colony. In this case, synergistic benefits are obvious, while the dilution effect is
272 also relevant against predation by flying predators attacking a colony from the air.

273 This concept may be applicable to the evolution of multicellular organisms from single-
274 cell organisms, e.g., the Ediacaran biota (Shen et al., 2008). It is also applicable to
275 symbiosis between different species (Pound, 1893), e.g., lichen (Nash, 2008), symbiotic
276 bacteria (Sachs et al., 2011) and deep-sea ecosystems (Gage and Tyler, 1991). As in
277 animals in harsh environments, these symbiotic organisms cannot survive without
278 symbiotic collaboration. We do not know the origin of these symbiosis. However, we
279 find them in extremely harsh environments where non-symbiotic organisms cannot
280 survive. We suspect that these symbiotic organisms invade into a vacant niche that
281 cannot be exploited by others, as in the lichen in the air (Pound, 1893, Gage and Tyler,
282 1991, Nash, 2008, Sachs et al., 2011).

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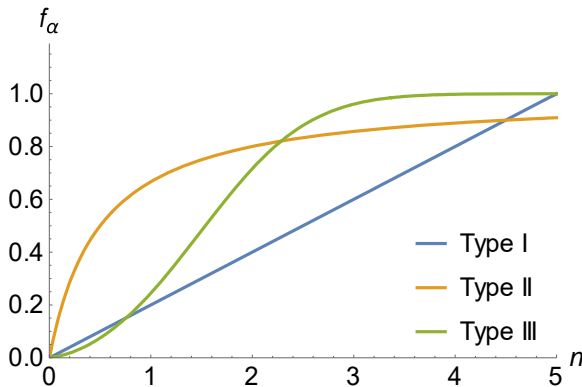
354 Table 1. Three types of grouping mechanisms and their possible animal candidates

Mechanism	Possible animal candidates
Synergy (top-right region in Fig. 4)	top predators (wolves, dorphins, killer whales, lions), social subterranean (underground) inhabitants (naked mole-rat, some termite species, some ant species, ground squirrels), social wood inhabitants (bark beetles, some termite species, wood roaches (genus <i>Cryptocercus</i>))
Synergy + Dilution (top-left region in Fig. 4)	some colony-forming animals (aphids, scale insects, birds), some social insects with bare/open nests (bees, wasps)
Dilution (bottom-left region in Fig. 4)	temporal animal aggregations (bird flocks, fish schools, animal herds, periorical cicadas)

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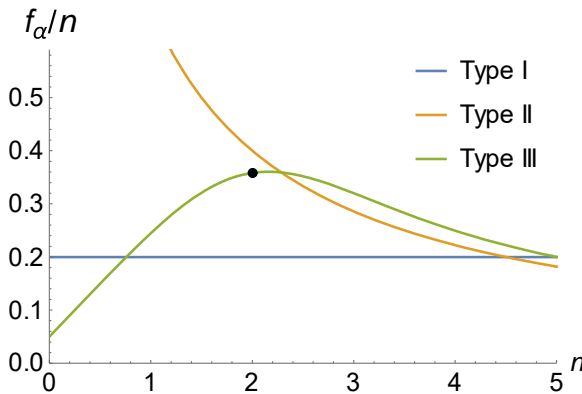


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359 Fig. 1. Total benefit of all individuals is plotted against the number of individuals for
 360 three types of functional response: Type I ($f_I(n)$), Type II ($f_{II}(n)$) and Type III (f_{III} -
 361 (n)). Type I is a linear response; Type II, a decelerating response; and Type III, a
 362 sigmoidal response. ($a_1 = 0.2, a_2 = 2, a_3 = 0.05$ and $b = 0.2$: these numbers are just
 363 an example for illustration.)

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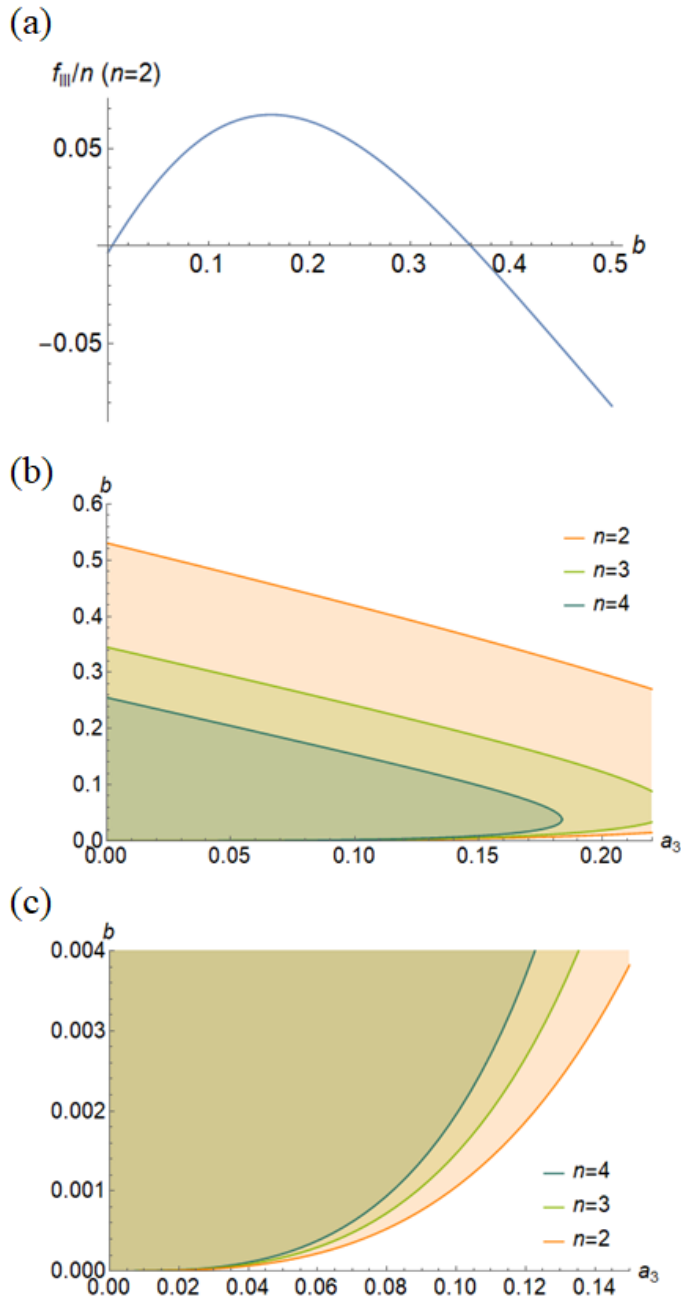


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368 Fig. 2. Per-individual benefit is plotted against the number of individuals for three types
 369 of functional response: Type I ($f_I(n)/n$), Type II ($f_{II}(n)/n$) and Type III ($f_{III}(n)/n$).
 370 The benefit per individual is constant in Type I; decreasing in Type II; first increasing
 371 and then decreasing in Type III. Group living has no benefit in Type I, while it is
 372 detrimental in Type II. Group living is optimal only under Type III functional response.
 373 The optimal number (dot) is $n^* = 2$ in Type III, while no optimal number in Type I and
 374 Type II. ($a_1 = 0.2, a_2 = 2, a_3 = 0.05$ and $b = 0.2$: these numbers are just an example
 375 for illustration.)

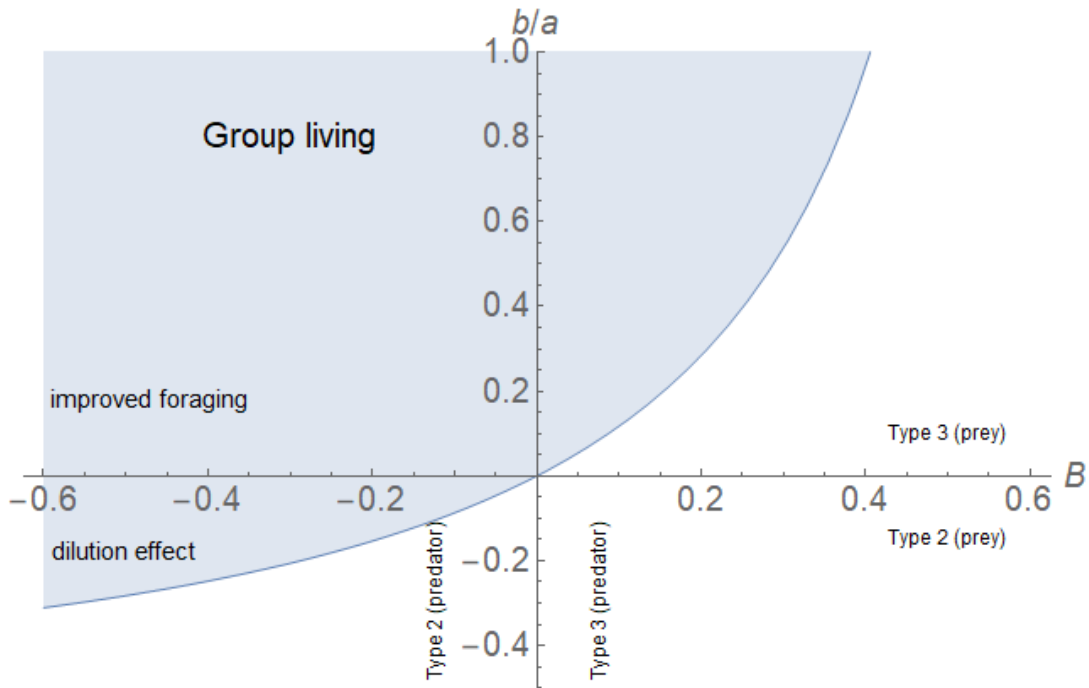
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379 Fig. 3. The parameter region in which the collaboration of n individuals is advantageous
 380 in Type III functional response. (a) The synergistic contribution $(f_{III}(n)/n - f_{III}(1)/1)$
 381 is plotted against parameter b for $n = 2$ and $a_3 = 0.15$. The parameter b should be
 382 larger than 0.004 and smaller than 0.36 for a positive effect. (b) The parameter regions
 383 for positive synergy ($n = 2, 3$ and 4). (c) Enlargement of (b): the lower boundary for
 384 the non-linear parameter b ($n = 2, 3$ and 4). The smaller a_3 , the larger the region for b
 385 to cause synergy. As n increases, the region for synergy shrinks. The numbers are just
 386 an example for illustration.

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390 Fig. 4. The parameter region in which group living is advantageous in Type III
391 functional response in the presence of predator-prey interactions with the dilution effect.
392 The x -axis signifies whether the predator's functional response is Type II ($B < 0$) or type
393 III ($B > 0$), while the y -axis signifies whether the prey's functional response is Type II
394 ($b < 0$) or Type III ($b > 0$). Group living in the bottom-left region ($B < 0$ and $b < 0$) is not
395 due to synergy but to dilution effect. In the right half region ($B > 0$), where the predator
396 has Type III response, group living is suppressed because grouping is advantageous
397 (disadvantageous) to the predator (prey) ($\lambda T = 1$).

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