



Title	Evolution of the optimal reproductive schedule in the ant <i>Camponotus (Colobopsis) nipponicus</i> (wheeler): a demographic approach
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3 Title: Evolution of the optimal reproductive schedule in the ant *Camponotus*  
4 (*Colobopsis*) *nipponicus* (Wheeler): A demographic approach.

5

6 Running title: Reproductive schedule in an ant.

7

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33

34 **Abstract**

35 1. Traits are hypothesized to optimize via natural selection. The schedule of  
36 reproduction is an important adaptive trait, but its evolution is difficult to study as  
37 measuring parameters is usually difficult. However, the sufficient amounts of  
38 demographic data enable us to estimate these parameters.

39 2. Here, we show that the reproductive schedule of the ant *Camponotus (Colobopsis)*  
40 *nipponicus* is tuned to maximize for life-time production of alates.

41 3. A colony started its reproduction 4 years after the colony founding, at which time  
42 they were far smaller than well-developed colonies. This contradicts the prediction of  
43 the Bang-bang strategy theory. The size distribution of colonies in the study area  
44 showed that the mortality of small colonies is much higher than that of large colonies.

45 4. A simulation analysis suggests that the colonies that are smaller than the threshold  
46 can still achieve significant improvement in colony survival to the next year by  
47 investing all resources in colony growth instead of reproduction. A sensitivity analysis  
48 for the starting year of reproduction showed that the observed schedule maximizes  
49 life-time alate production. The demographic data suggests a stable population, which is  
50 required for optimization through this maximization.

51 5. The observed reproductive schedule must be optimized, and the breakdown of the  
52 bang-bang theory is due to higher mortalities during the incipient stage of colonies. This  
53 study demonstrates that having enough demographic data creates a useful tool for  
54 studying the evolution of life-history characteristics.

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56 Keywords: Life history, Evolution, Reproductive schedule, Ant, Reproduction

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## 67 **Introduction**

68           The optimization theory predicts that traits of an organism must be optimized  
69 to maximize life-time reproductive success (Stephens & Krebs 1986; Parker & Maynard  
70 Smith 1990; Williams, 1992). Life history, itself, is a trait that seriously affects the  
71 outcome of life-time reproductive success (Stearns, 1992). Thus, several features of the  
72 life history of a species (growth patterns, timing of reproduction, longevity, etc.) would  
73 be optimized via natural selection in its environments.

74           The evolution of life history is an interesting issue in evolutionary biology  
75 (Stearns, 1992), but it is hard to approach because the required life-history parameters  
76 are not usually obtained without a great deal of effort and time. However, when there is  
77 enough demographic data, these parameters can be estimated (Rees & Woods, 1986;  
78 Preston *et al.*, 2000; Kéry *et al.*, 2004), giving us an easy way to approach this attractive  
79 issue.

80           The colonial life-cycle of social hymenopterans has been divided into three  
81 phases, i.e., founding, ergonomic, and reproductive stages (Wilson, 1971). The founding  
82 stage refers to a period during which a single or several queen(s) found a nest and rear  
83 the first brood without workers. After eclosions of the first workers, the life-cycle shifts  
84 to the ergonomic stage. In this stage, workers collect food and rear further workers, and  
85 the colony grows rapidly. At some colony size, they begin to produce alates, and the  
86 colonial life-cycle shifts to the reproductive stage. The colony allocates its resources to  
87 both workers (colony maintenance) and alates (reproduction).

88           Many social wasps and bees complete the above-described three colonial  
89 stages annually. Whereas a part of the colonies of wasps and bees and all ants survive  
90 for more than one year, they produce alates perennially (Wilson, 1971; Ross & Mathews,  
91 1991). In this condition, natural selection leads a colony to maximize for life-time  
92 reproductive success. Thus, because the reproductive schedule has such major effects on  
93 life-time reproductive success, several life history characteristics must evolve to  
94 maximize life-time fitness. For example, the following issues are typical life history  
95 traits that must be examined; when is the appropriate time to start reproduction, and  
96 how many resources should be allocated between growth and reproduction?

97           What is the best way to maximize alate reproduction in a colony as a whole?  
98 Oster and Wilson (1978) theoretically analyzed the reproductive schedules of social  
99 insects from the viewpoint of life history strategies, and they proposed a "bang-bang

100 model." This model predicts that a colony can maximize its reproductive output through  
101 investing all its resources in workers by the end of the ergonomic stage, but all of this  
102 investment should then be switched to alate production in the reproductive stage. This  
103 type of life cycle has been observed in annual paper wasps (reviewed in Ross &  
104 Matthews, 1991).

105           Oster and Wilson (1978) extended this model to perennial species and  
106 suggested that a colony should rear the maximum worker force as soon as possible.  
107 Then, it should invest a constant resource in colony maintenance and the rest to alate  
108 production in following life period. They called this type of strategy the "bang-bang  
109 strategy". However, for nonsocial organisms, Steans (1992) summarized that the body  
110 size and age at maturity are affected by several life history parameters, such as juvenile  
111 mortality, initial fecundity, and population dynamics. These factors also affect the  
112 reproductive schedule of social insect colonies. Thus, it is important that the  
113 reproductive schedule of colonies in social insects is studied in detail.

114           In perennial social insects, the relationship between colony growth and  
115 reproduction is not well known (but see Brian, 1957; Tschinkel, 1993). We hypothesize  
116 that if the life history (=reproductive schedule) has been optimized, a colony should  
117 allocate its resources to colony growth and alate production in order to maximize the  
118 life-time production of alates (the expected life-time numbers of reproductive females  
119 and males under the living environment). In this study, we examined this hypothesis in  
120 the ant *Camponotus (Colobopsis) nipponicus*. Based on the observed demographic data  
121 in the study population, the reproductive schedule of this species is interpreted from the  
122 perspective of optimization of life-history strategies.

123

## 124 **Materials and Methods**

### 125 *Biology of C. (C.) nipponicus*

126           *Camponotus (Colobopsis) nipponicus* is an arboreal, nocturnal ant that nests  
127 in the hollows of dead twigs in warm regions of Japan (Imai *et al.*, 2003). *C. (C.)*  
128 *nipponicus* is a monogynous species and has completely dimorphic worker subcastes  
129 (major and minor), both of which can store food as fat bodies in their gaster (Hasegawa,  
130 1992; 1993a). Adult workers overwinter with larvae that pupate by the next late June.  
131 The overwintered larvae rapidly grow after late March, and the sex of sexual's larvae  
132 can be discriminated after May (Hasegawa, 1992). Although several size classes of

133 larvae are found during hibernation, most of them do not attain queen-destined size until  
134 early June. All eggs in a queen-right colony are laid by the colony queen between May  
135 and October, and the male-destined eggs are laid predominately in July and August  
136 (Hasegawa, 1992; 1994). Thus, small larvae found in the nests at early summer should  
137 be developed from eggs laid after hibernation. *C. (C.) nipponicus* has a polydomous  
138 nest system, but behavioral interactions between different nest members allow us to  
139 identify clear boundaries among colonies (Hasegawa, 1992). Nuptial flights are  
140 conducted after early August (Hasegawa, 1992).

141

#### 142 *Sampling and determination of colony characteristics*

143 The study site was a coastal forest in Amatsukominato, Chiba Prefecture,  
144 Japan. Samples were collected in early July in 1990 and late June in both 1991 and 1992.  
145 In each year, 17 (nested by 31 colonies), 17 (27 colonies) and 8 trees (17 colonies) were  
146 selected randomly within the study site, and all dead twigs attached to these trees were  
147 collected. Only twigs with *C. (C.) nipponicus* nests were transported to the laboratory,  
148 and they were broken open to collect the nest members. All nest members were counted  
149 with respect to their physical caste, and larvae were further classified into 3 size  
150 categories: (1) Small larvae; the larvae that did not reach 1.60 mm in their length. This  
151 size class could be regarded as broods that were produced after hibernation. (2) Sexu-  
152 als; the larvae that pupate as alate females and males. The sex of mature larvae can be  
153 discriminated from worker-destined by both their larger size and body shape (Hasegawa,  
154 1992). (3) Worker-destined larvae; the larvae that were not felled into the above two  
155 categories (1.60-3.50 mm in length), and they are regarded as overwintered and  
156 worker-destined individuals. Because of the nocturnal habit of *C. (C.) nipponicus*, all  
157 nest members could be captured during daytime collections. The total dry weight of all  
158 adult workers was used as an index of colony size. The total number of workers is not  
159 appropriate to represent the colony size in this species because there are two distinct  
160 worker subcastes with much different sizes. The total dry weight of workers in each nest  
161 was estimated from the regression equations of the pupal dry weight of each subcaste  
162 based upon the number of major workers in the nest (see Hasegawa, 1993a). Colony  
163 boundaries were determined by behavioral interactions of workers among nests (for the  
164 behavioral test, see Hasegawa, 1992). For polydomous colonies, all of the  
165 characteristics listed above were determined by compiling the data over all of the

166 satellite nests because there is no difference between queen-right and queen-less nests  
167 for reproductive characteristics.

168           The maximum longevity of a colony has a major effect on the optimal  
169 resource allocation between growth and reproduction (Stearns 1992). The maximum  
170 longevity of a colony was estimated from 1) the estimated growth curve of the colonies  
171 with age (Fig. 1), 2) size distributions of colonies in the reproductive season (June to  
172 August) in the three study seasons (Figs.2a-c) and 3) the negative regression curve of  
173 the number of nests to colony size (Fig. 3). In Figs. 2a-c, there is no difference between  
174 the slope of the regression line of the log-transformed colony numbers and colony size  
175 (for all possible pairs,  $p > 0.05$ , ANCOVA), and thus we combined the data to obtain the  
176 estimate of the decreasing curve presented in Fig.3. Fig. 3 shows that the number of  
177 colonies becomes less than 1 at a colony size of ca. 450-500 mg. A colony is estimated  
178 to reach to this size range after ca. 12-15 years from the colony founding (Fig. 1). Thus,  
179 we assumed that the maximum longevity of a colony is 15 years. Except for small  
180 colonies without sexual reproduction, ages of wild colonies are impossible to estimate  
181 because the different nutritional conditions for each colony will diversify the sizes  
182 among colonies with the same age. However, the productivity of larvae (the most  
183 important factor for allocation between workers (colony growth) and alates  
184 (reproduction)) must depend on colony size and not on age. Thus, in this study, we  
185 needed the estimate of the maximum longevity of a colony but not the estimate of each  
186 large colony.

187

### 188 **Statistical analysis**

189 The determination of how many cohorts were located in the small colonies (before the  
190 start of reproduction) was examined through Cassie's method (see below, and Cassie,  
191 1954, 1962), in which the examined colonies were classified into several classes, each  
192 of which had a normal distribution in colony size (see Fig. 1 in Hasegawa, 1993). Size  
193 or numerical differences were examined by *t*-test or two-sample *t*-test. When using *t*-test,  
194 we examined normality of distribution of the data. All statistical tests were performed  
195 by computer softwares (StatView 4.45.1 and R 3.2.1).

196

197

### 198 **Results**

199 *Reproductive parameters of colonies*

200 To estimate the growth pattern of colonies, several reproductive parameters  
201 were estimated from the demographic data. Productivity for either the workers or alates  
202 was estimated as the regression of the number of produced individuals on the colony  
203 size (CS) (Fig.4; for workers (W),  $W=0.98CS+27.7$ ; for alate females (F),  
204  $F=0.19CS-1.67$ ; for males (M),  $M=0.31CS+1.87$ , where colony size is the total dry  
205 weight of all adult workers (mg)). In simulation analyses, these regression equations  
206 were used to predict the produced number of each class in a colony of a given size.

207 The mortality of workers is another important parameter for estimating a  
208 colony's demographic changes. Worker mortality was 60% for workers and 33% for  
209 majors in this population during the active season (Hasegawa unpubl.), and the number  
210 of workers did not decrease during winter (Hasegawa, 1992). Thus, the above mortality  
211 values were used as adult mortality through a year.

212 In this study, all of the estimations or simulations of demographic change in  
213 colonies were calculated by the above equations or values.

214

215 *Colony growth and start of reproduction*

216 Cassie provided a method by which data of size distribution of organisms can  
217 be classified into several groups each of which has a normal distribution. As size of a  
218 cohort of a species is assumed to have a normal distribution, this method allow us to  
219 estimate number of cohorts in a size data of an organism (Cassie, 1954, 1962). By using  
220 this method, incipient (no alate production) colonies of *C. (C.) nipponicus* could be  
221 classified into three groups, each of which had a normal distribution (see Fig. 1 in  
222 Hasegawa, 1993). The average colony size (dry weight of total workers) of each group  
223 is shown in Table 1. The founding queens make a small nest in a hollow dead twig in the  
224 late summer and overwinter only with the larvae (Hasegawa 1992). Thus, the first  
225 workers appear in the following year. The first group consisted of colonies containing a  
226 queen with only larvae, or a few normal workers. Thus, this group represents colonies at  
227 the founding stage. Therefore, this first cohort is the colonies after one year from the  
228 colony founding, and the second cohort is that after 2 years from the founding. The third  
229 cohort is the colonies after 3 years from the founding. These colonies did not contain any  
230 alates in the reproductive season, but the larger colonies contained alates. Thus, the  
231 production of alates must start from 4 years after the colony founding. This data also

232 indicates that the threshold size for reproduction is approximately 13.5 mg (Fig. 1). This  
233 size is much smaller than that of matured colonies (Fig. 1 and 3).

234 The average colony growth pattern was simulated by using the observed  
235 productivity and mortality values. In the simulation, the caste ratio was held at 20%  
236 throughout the lifetime because *C. (C.) nipponicus* colony workers are ca. 20% majors,  
237 regardless of colony size (Hasegawa, 1997). The results from the colony-growth  
238 simulation are shown in Fig. 1. The expected colony size of the 1st, 2nd and 3rd year  
239 colonies were compared with the observed value (Table 1). In addition, we also  
240 compared the expected size of a 15-year-old colony with the average size of the largest  
241 10 colonies in the field. Each observed size was not significantly different from the  
242 estimated size (*t*-test,  $p > 0.05$  for all the comparisons), showing that the simulation  
243 correctly estimates colony size in each year. Therefore, it was concluded that colonies  
244 start reproduction from the 4th year following the colony founding, at which time the  
245 colony is far smaller compared to its eventual maximum size.

246

#### 247 *Population stability and decreasing rate of colonies*

248 Fig. 3 shows the size distribution of colonies in the reproductive season over  
249 the three years. To test differences in the distribution pattern of colony sizes among  
250 years, a regression of colony number on the mode for each size class was calculated for  
251 log-transformed data in each year, and then the slopes of the regression lines were  
252 compared among years. There was no difference in the slopes among the three years (F  
253 test,  $P > 0.05$  for all 3 pairs). Thus, the size structure of *C. (C.) nipponicus* colonies in  
254 this population was stable during the examined period. In addition to the size structure,  
255 the population growth rate also has major effects on population dynamics and life  
256 history strategies (Stearns, 1992). Table 2 shows the average number of colonies per  
257 tree (=colony density) in the reproductive season of the three investigated years. The  
258 differences among the 3 years were not significant for all the pairs (two-sample *t*-test,  
259  $P > 0.05$ ). Thus, colony density did not fluctuate from year to year. From the above  
260 results, it was concluded that this population was a stable population.

261 Fig. 3 shows the log-transformed size distribution of *C. (C.) nipponicus*  
262 colonies in this population. Because this population can be regarded to be stable, all of  
263 the 3 data sets were combined for the analyses. The regression of colony numbers on  
264 colony size was calculated as a linear regression on the log-transformed data (the

265 decreasing curve in Fig. 3). In Fig. 3, although the Y axis was log-transformed, the  
266 regression line has a concave shape. This means that the decreasing rate of colonies  
267 (hereafter referred to as “mortality”) changes with colony size, i.e., the mortality is size  
268 dependent. This result allows us to estimate the instantaneous mortality at a given  
269 colony size as the differential coefficient for the regression curve at that size. Therefore,  
270 the concave shape of the regression curve suggested that mortality decreases with  
271 colony growth. It should be noted that the number of workers produced would be  
272 determined by the nutritional condition for the colony. Thus, with an exception for small  
273 colonies, colony sizes would diverge depending upon the nutritional condition for each  
274 colony over an age. Thus, we conducted these simulations for colony productivities  
275 based upon colony size and not based upon age.

276

#### 277 *Timing of reproduction and mortalities of colonies*

278 When a colony produced alates, a portion of the colony resources is  
279 inevitably allocated to them; therefore, the colony sacrifices a portion of its possible  
280 colony growth. As indicated above, the mortality of a colony decreases with its size.  
281 Thus, there is a trade-off between reproduction and colony survival. To know whether  
282 mortality has a major effect on the timing of reproduction or not, the instantaneous  
283 mortality at the actual size (after reproduction) was compared with that at the possible  
284 maximum size (if all resources were allocated to worker production). The mortality was  
285 calculated as the differential coefficient for the regression curve in Fig. 3 at a given size  
286 (see Fig. 4). The possible mortality was calculated as the differential coefficient for the  
287 same regression line at the possible maximum size of the colony. The subcaste ratio was  
288 assumed to be the same with the observed ratio.

289 Since mortality decreases with colony size (Fig. 3), colony growth necessarily  
290 results in decreasing mortality. In addition, the differential coefficient means that the  
291 slope of the contact line intersects at a given point (see Fig. 6). Thus, the improvement  
292 rate of mortality can be evaluated by the angle made by the two contact lines ( $\theta$  in Fig.  
293 5), and we can then estimate an amount of mortality improvement of a colony via  
294 abandoning reproduction as the tangent  $\theta$  (Fig. 5). Fig. 6 shows the relationship between  
295 the colony size and the possible improvement rate of mortality calculated by the above  
296 method. The regression line of actual alate production on the colony size is also shown  
297 in Fig. 6. The improvement rate decreased rapidly with colony size, and almost no

298 improvement is expected for large colonies even when they increase their colony size  
299 maximally by abandoning reproduction during the year. In nature, the production of  
300 alates is initiated from a threshold colony size (13.5 mg), at which the improvement rate  
301 becomes low (Fig. 6). Therefore, the colonies actually minimize the risk of  
302 reproduction.

### 303 *The optimal timing of reproduction*

304 To estimate the optimal timing of reproduction, the expected number of alate  
305 females and males through the life-time was calculated for a putative average colony  
306 that grows by following the growth pattern of Fig. 1. This colony was given all of the  
307 observed reproductive parameters in this population, but the start year of reproduction  
308 was changed from 2 to 9. In this sensitivity test, we assumed the production of a single  
309 male in 2-year-old colonies and that of two males in 3-year-old ones. When the start of  
310 reproduction was delayed, all resources were assumed to be invested back into colony  
311 growth until the start of reproduction; then, the colony was assumed to allocate  
312 resources to alates in the actual ratio at that size. The longevity of the colony was  
313 assumed to be 15 years from the observed data (see above). The result of this sensitivity  
314 test is shown in Fig. 7. The simulation showed that a colony can maximize its life-time  
315 alate production by starting reproduction from 4 years after the colony founding. As  
316 demonstrated previously, wild colonies start their reproduction from 4 years old  
317 (Hasegawa, 1993b). Therefore, it was suggested that the reproductive schedule of *C.*  
318 (*C.*) *nipponicus* colonies is optimized in this population.

319

## 320 **Discussion**

### 321 *Is the reproductive schedule optimized?*

322 This study showed that *C. (C.) nipponicus* colonies start reproduction from a threshold  
323 size (ca. 13.5 mg) that the colony attains at 4 years following the colony founding. The  
324 result of the reproductive simulation suggests that this schedule is the best way to  
325 maximize the expected life-time production of alates (=life-time fitness). Age or size at  
326 maturity is affected by population dynamics (Stearns, 1992). When a population  
327 continues to grow and generations are overlapped, individual fitness must be  
328 represented by a contribution to the intrinsic rate of increase and not by the life-time  
329 reproductive success (Stearns 1992). In such a case, early reproduction results in high  
330 fitness (Maynard-Smith, 1989; Stearns, 1992). However, the population in this study

331 can be regarded as at an equilibrium state, i.e., the population has a stable colony size  
332 distribution and a stable colony density in every year. If a population is at an  
333 equilibrium state, individual fitness is consistent with life-time reproductive success  
334 (Stearns, 1992). Therefore, the observed reproductive schedule would be optimized in  
335 this population.

336           Contrary to the prediction of the bang-bang theory, *C. (C.) nipponicus*  
337 colonies started reproduction from a far smaller size when compared to that of matured  
338 colonies. Why does the "bang-bang theory" break down? If delayed maturity results in  
339 additional growth with high initial fecundity (as would be the case for social insect  
340 colonies), then delaying reproduction is favored when juvenile mortality is low (Stearns,  
341 1992). In such a case, reproduction will be delayed until the fitness gain through  
342 increased fecundity is balanced by the fitness loss through lower survival to maturity.  
343 Thus, the "bang-bang strategy" is favored in an environment in which mortality of  
344 juveniles is low. The size distribution of colonies in *C. (C.) nipponicus*, however,  
345 suggests that the mortality of colonies changes with its size, i.e., smaller colonies suffer  
346 higher mortality than larger colonies (Fig. 3). In addition, the colonies start reproduction  
347 from a point at which an advantage in mortality improvement by abandoning  
348 reproduction becomes relatively low (Fig. 6). Considering these facts, the high mortality  
349 of small colonies seems to be a major factor affecting the reproductive schedule in *C.*  
350 *(C.) nipponicus*. Thus, the "bang-bang strategy" would break down due to the high  
351 mortality of small colonies in *C. (C.) nipponicus*.

352

353 *Why do small colonies decrease more rapidly than large colonies?*

354           Small colonies show a higher mortality than large colonies (Fig. 3). What is  
355 the reason for this difference? Hasegawa (1993b) showed that there is a strong  
356 intraspecific competition for nest sites in *C. (C.) nipponicus*, and major workers are  
357 necessary for colony survival because the defensive abilities of major workers are  
358 essential to defend the nest site from competitors. As shown in Table 1, the first-year  
359 colonies contained no major workers, and thus, they decreased more rapidly than the  
360 other year colonies due to the weak defensive abilities existing in these colonies. In  
361 addition, if a colony lost a single worker, the total damage to the colony as a whole  
362 would be far more serious in small colonies than in large colonies because they lost a  
363 larger proportion of their worker force. For these reasons, small colonies would be weak

364 and vulnerable to predation or nest site competition. It should be noted that after the  
365 appearance of the first soldier, the effect of this competition would decrease  
366 significantly because Hasegawa (1993b) has also shown that a soldier per nest entrance  
367 is enough to protect a nest from competitors (see Fig. 2 in Hasegawa 1993b). Thus, the  
368 existence of intraspecific competition for nest sites has little effect on the life history  
369 strategy in large colonies.

370

371 *Is the reproductive schedule dependent on size or age?*

372 In this study, whether the selection that shaped the reproductive schedule is  
373 dependent on size or age cannot be determined because size and age cannot be  
374 separated when a colony became large. Different nutritional conditions for colonies will  
375 diverge the sizes of the colonies of the same age over a long period. During the same  
376 period, colonies under rich nutritional conditions become larger faster than those under  
377 poor nutritional conditions. Thus, we could estimate the age of colonies within a few  
378 years after the colony founding by a cohort analysis. Thereafter, an estimation of colony  
379 age would be impossible. However, the above-mentioned size effect is dependent only  
380 upon the colony size and not upon age. A major factor affecting the reproductive  
381 schedule seems to be the high mortality of small colonies. In addition, most of  
382 reproductive parameters of a colony, such as brood productivity, mortality, and resource  
383 storing ability, seem to depend on the colony size only and not on the age. Nonetheless,  
384 the maximum longevity of a colony is required and, in fact, crucial to estimate the  
385 life-time alates production for a colony. We estimated this parameter as 15 years from Fig.  
386 1 & 3. Therefore, it is considered that the reproductive schedule of *C. (C.) nipponicus*  
387 has been shaped mainly depending on its size and not on its age.

388

389 *Conclusion*

390 This study showed that demographic data enables us to estimate the required parameters  
391 to examine the evolution of life history. Although there are several excellent studies on  
392 this issue (Burns *et al.*, 2010; Phillips *et al.*, 2010; Swain, 2010; Agrawal, 2013), most  
393 of them require a great deal of effort and time. As far as we know, there is no other study  
394 that adopt the analytical ways using demographic data as in this study. Since the  
395 evolution of life history is an important viewpoint in evolutionary biology, the  
396 demographic approach provided here would be a good tool for future studies on this

397 interesting theme.

398

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406

### 407 **Conflict of Interest**

408 The authors declare no competing financial interests.

409

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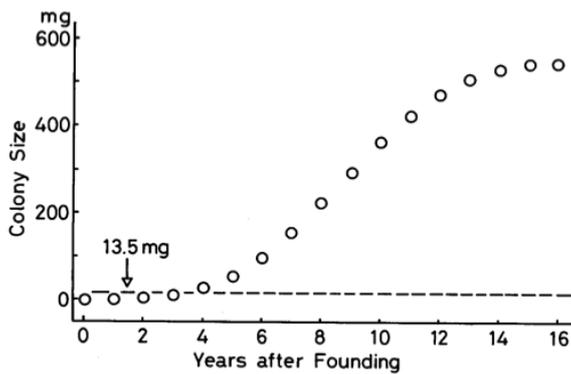
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496 **Figure legends**

497

498 Figure 1. The estimated colony growth pattern of *C. (C.) nipponicus*. The vertical line  
499 represents the threshold colony size for alate production. The colony size of the next  
500 year is calculated from the relationship of number of worker brood on colony size in the  
501 collected colonies (see Figure 4).

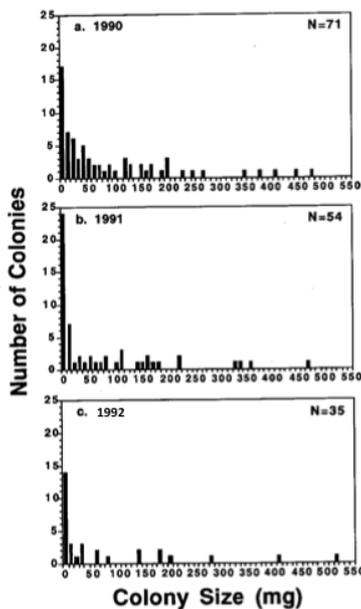


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504 Figure 2. Size distribution of colonies in the three reproductive seasons (June - July).

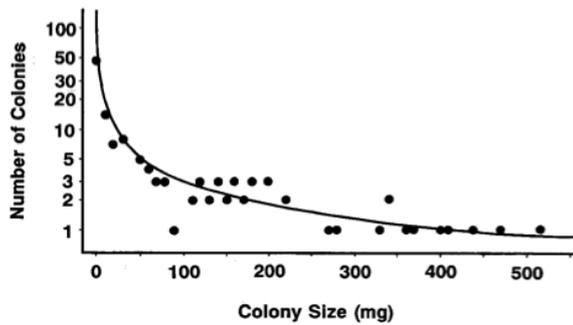
505 There is no difference in the shape of the distribution between the three years. (For all  
506 the pairs, the slope of the regression line of the log-transformed colony number on  
507 colony size was not different at  $p=0.05$  level (ANCOVA). Thus, all the data were  
508 combined to estimate the average death rate of a colony at a size (see Figure 3).



509

510 Figure 3. Relationship between log-transformed number of colonies and size classes.

511 The fitted curve can be regarded as a decreasing curve of colonies in this population.

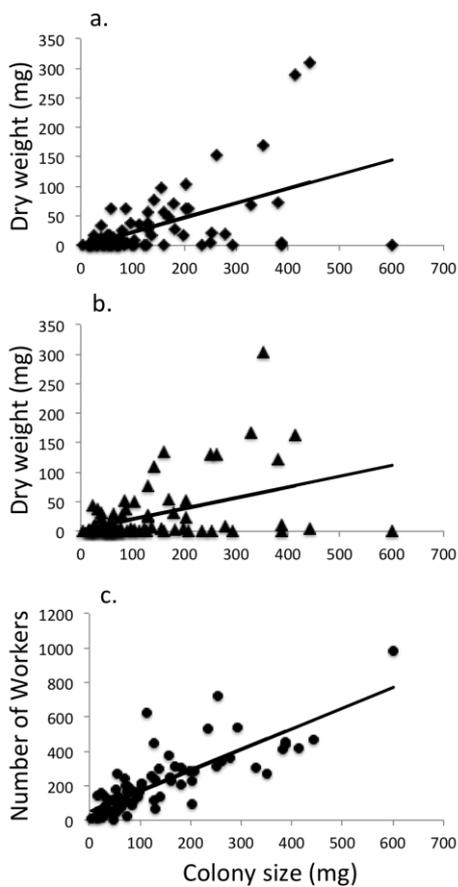


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513 Figure 4. Relationships between colony size and production of workers (a), alate  
514 females (b) and males (c). The lines are the linear regressions of them on colony size.

515 The estimated productivities from these regressions are used in the following

516 simulations for colony growth or alate productions at a colony sizes.



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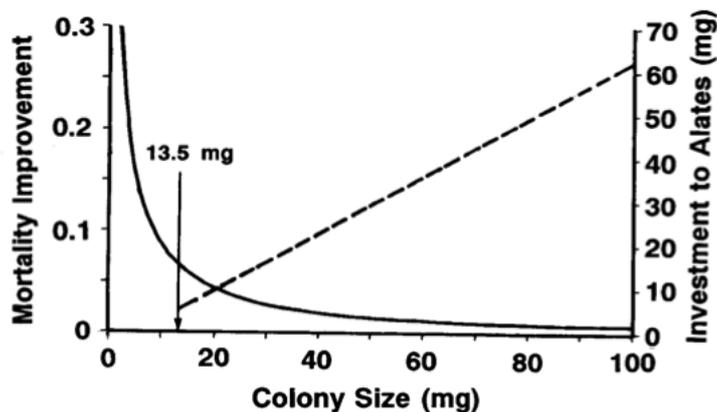
519 Figure 5. A scheme to explain the way to estimate the improvement of mortality of a  
520 colony by abandoning alate production for a year. A colony has two options; 1) all their

521 resources invest into worker production to realize the possible maximum colony size  
 522 that maximized the survival to the next year, 2) a part of resources invests to alate  
 523 production by sacrificing colony growth rate (=do not maximize colony survival). The  
 524 improvement rate between two strategies can be represented by  $\tan \theta$  in the Figure.



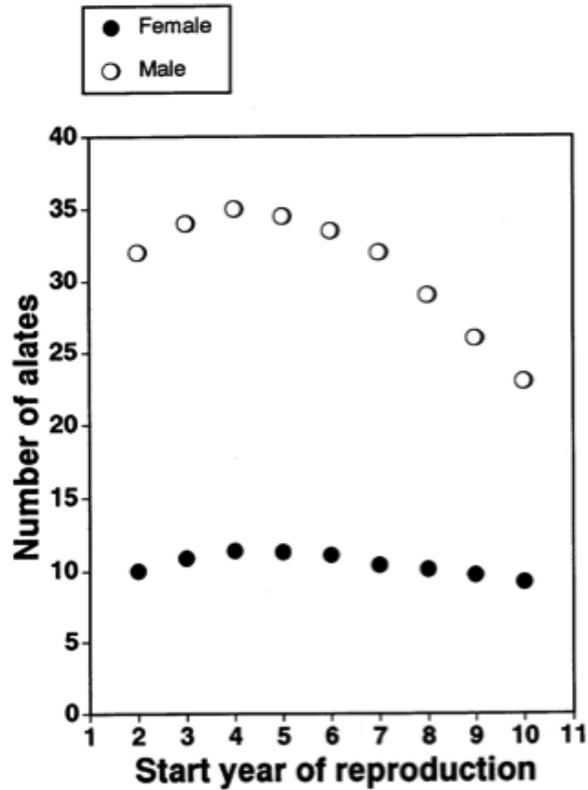
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527 Figure 6. Relationship between the observed colony size and the possible improvement  
 528 in mortality. The straight line represents the observed regression between colony size  
 529 and alate production (see Figure 5). Colonies start reproduction from a point (13.5mg)  
 530 where possible mortality improvement becomes low.



531  
 532

533 Figure 7. Estimated relationship between start year of reproduction and life-time  
 534 reproductive success. When starting reproduction after 4 years from the colony  
 535 founding, a colony can maximize their life-time production of alates in both sexes.



536

537

538 Table 1. Comparison between the observed (mean  $\pm$  S. D.) and expected size of each  
 539 class of colonies in *C. (C.) nipponicus*

540

	Class of colonies			
	1st-year (n=49)	2nd-year (n=9)	3rd-year (n=11)	The largest 10 (n=10)
Observed size	0.66 $\pm$ 0.38	3.46 $\pm$ 1.77	10.83 $\pm$ 2.70	529.6 $\pm$ 115.8
Estimated size	0.85	3.47	10.52	545.2

541

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543

544 Table 2. Average number of colonies nested per tree in the three study seasons. Standard  
 545 error is shown with the mean.

546

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	Year		
	1990	1991	1992
Number of colonies nested on a tree	3.50±0.27	3.17±0.66	3.88±0.58

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