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Author(s)	Hasegawa, Eisuke; Watanabe, Saori; Murakami, Yuuka
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Title: Evolution of the optimal reproductive schedule in the ant *Camponotus (Colobopsis) nipponicus* (Wheeler): A demographic approach.

Running title: Reproductive schedule in an ant.

Authors:

Eisuke Hasegawa^{1†*}, Saori Watanabe², Yuuka Murakami³

Affiliations:

1. Department of Biology, Faculty of Science, Tokyo Metropolitan University.
Minamiohsawa 1-1, Hachioji-si, Tokyo 192-03, Japan.

2. Laboratory of Animal Ecology, Department of Ecology and Systematics, Graduate
School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan.

3. Graduate School of Medicine, Department of Neuropharmacology, Hokkaido University.
Sapporo 060-8638, Japan.

†Present Address: Laboratory of Animal Ecology, Department of Ecology and
Systematics, Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589,
Japan.

Corresponding author:

Eisuke Hasegawa

e-mail: ehase@res.agr.hokudai.ac.jp

Tel.: +81-11-706-3690

Fax: +81-11-706-2494

Abstract

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

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

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

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

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

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

Introduction

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

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

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

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

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

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

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

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

Materials and Methods

Biology of C. (C.) nipponicus

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

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

Sampling and determination of colony characteristics

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

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

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

Statistical analysis

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

Results

Reproductive parameters of colonies

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

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

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

Colony growth and start of reproduction

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

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

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

Population stability and decreasing rate of colonies

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

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

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

Timing of reproduction and mortalities of colonies

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

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

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

The optimal timing of reproduction

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

Discussion

Is the reproductive schedule optimized?

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

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

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

Why do small colonies decrease more rapidly than large colonies?

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

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

Is the reproductive schedule dependent on size or age?

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

Conclusion

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

interesting theme.

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Conflict of Interest

The authors declare no competing financial interests.

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Figure legends

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

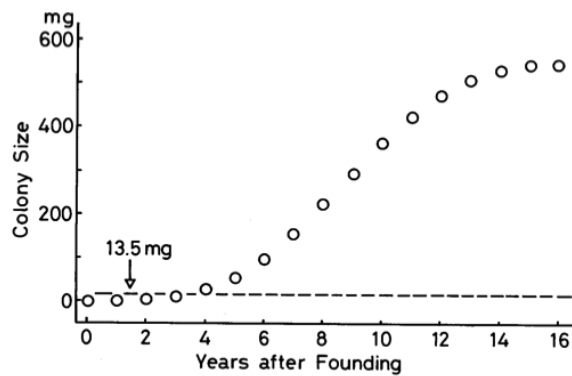


Figure 2. Size distribution of colonies in the three reproductive seasons (June - July). There is no difference in the shape of the distribution between the three years. (For all the pairs, the slope of the regression line of the log-transformed colony number on colony size was not different at $p=0.05$ level (ANCOVA). Thus, all the data were combined to estimate the average death rate of a colony at a size (see Figure 3).

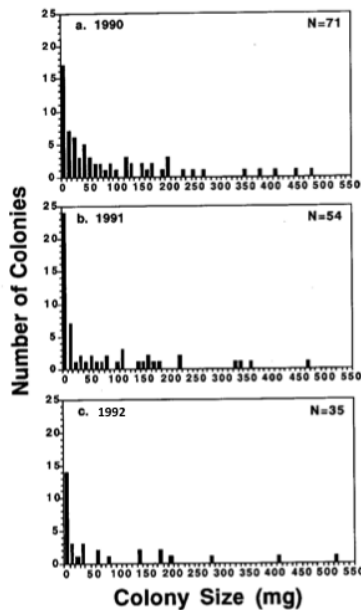
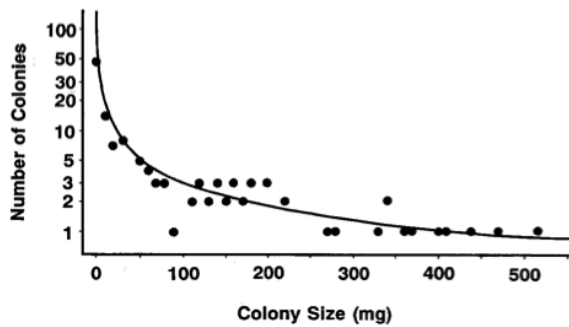
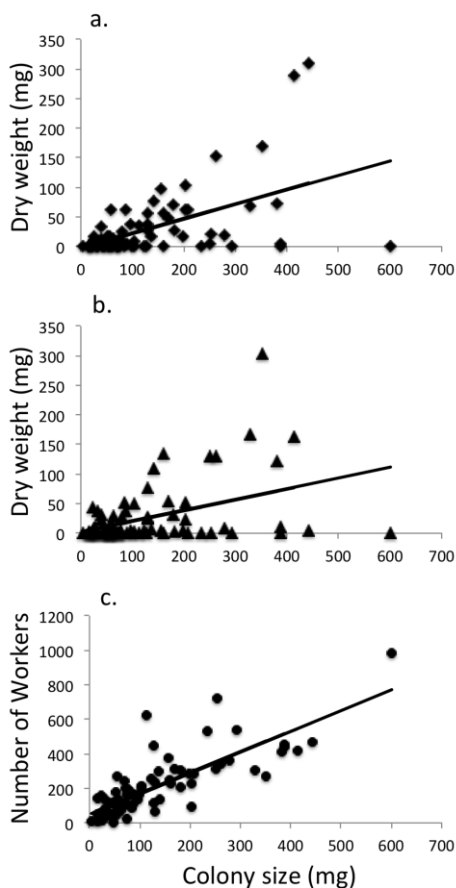


Figure 3. Relationship between log-transformed number of colonies and size classes.

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



512
 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 they 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.



517
 518
 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

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

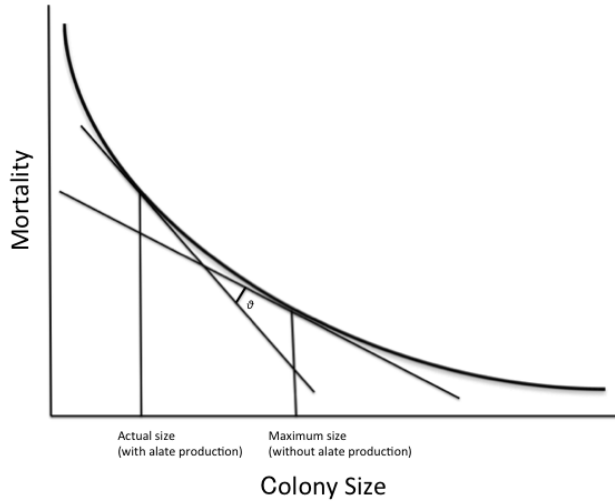


Figure 6. Relationship between the observed colony size and the possible improvement in mortality. The straight line represents the observed regression between colony size and alate production (see Figure 5). Colonies start reproduction from a point (13.5mg) where possible mortality improvement becomes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

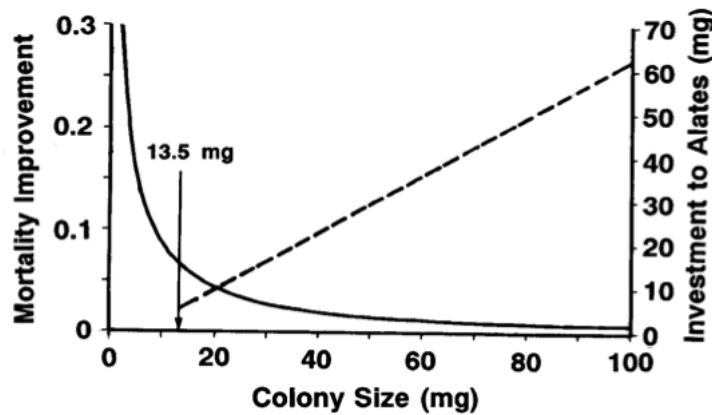


Figure 7. Estimated relationship between start year of reproduction and life-time reproductive success. When starting reproduction after 4 years from the colony founding, a colony can maximize their life-time production of alates in both sexes.

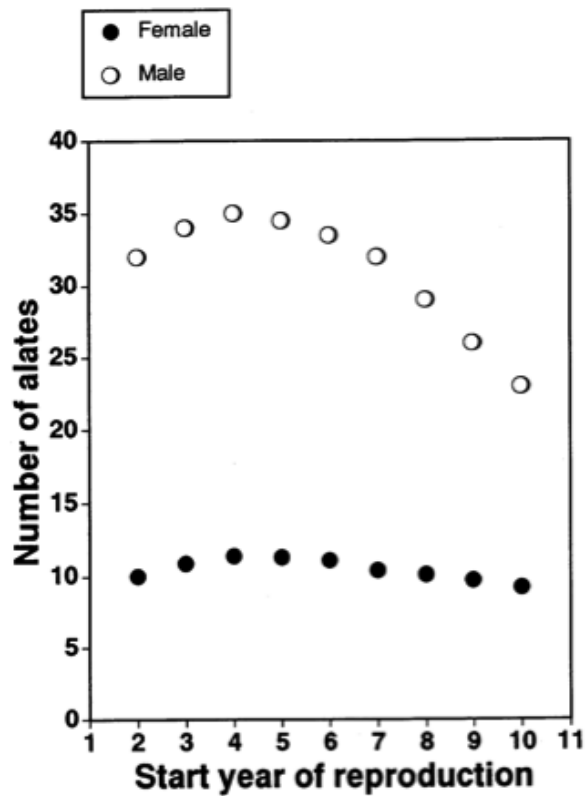


Table 1. Comparison between the observed (mean $\pm$ S. D.) and expected size of each class of colonies in *C. (C.) nipponicus*

	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

	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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