


Evolution of the optimal reproductive schedule in the ant *Camponotus (Colobopsis) nipponicus* (wheeler): a demographic approach

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Abstract. 1. Traits are hypothesised to optimise 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, it is shown that the reproductive schedule of the ant *Camponotus (Colobopsis) nipponicus* is tuned to maximise the lifetime 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 following 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 maximises lifetime alate production. The demographic data suggest a stable population, which is required for optimisation through this maximisation.

5. The observed reproductive schedule must be optimised, 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.

Key words. Ant, evolution, life history, reproduction, reproductive schedule.

Introduction

The optimisation theory predicts that traits of an organism must be optimised to maximise lifetime reproductive success (Stephens & Krebs, 1986; Parker & Maynard Smith, 1990; Williams, 1992). Life history is itself a trait that seriously affects the outcome of lifetime reproductive success (Stearns, 1992). Thus, several features of the life history of a species

(growth patterns, timing of reproduction, longevity, etc.) would be optimised 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 are enough demographic data, these parameters can be estimated (Rees & Woods, 1986; Preston *et al.*, 2000; Kéry *et al.*, 2005), 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. the 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 eclosures of the first workers, the life cycle shifts to the ergonomic stage.

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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 described three colonial stages annually. Whereas a part of the colonies of wasps and bees and all ants survive for more than 1 year, they produce alates perennially (Wilson, 1971; Ross & Matthews, 1991). In this condition, natural selection leads a colony to maximise for lifetime reproductive success. Thus, because the reproductive schedule has such major effects on lifetime reproductive success, several life-history characteristics must evolve to maximise lifetime 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 maximise alate reproduction in a colony as a whole? Oster and Wilson (1978) theoretically analysed 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 maximise 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. It should then invest a constant resource in colony maintenance and the rest to alate production in the following life period. They called this type of strategy the 'bang-bang strategy'. However, for non-social organisms, Stearns (1992) summarised 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 hypothesise that if the life history (i.e. reproductive schedule) has been optimised, a colony should allocate its resources to colony growth and alate production in order to maximise the lifetime production of alates (the expected lifetime 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 optimisation of life-history strategies.

Materials and methods

Biology of *Camponotus (Colobopsis) 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). *Camponotus (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 late June in the following year. The overwintered larvae grow rapidly after late March, and the sex of the 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 in the early summer should be developed from eggs laid after hibernation. *Camponotus (C.) nipponicus* has a polydomous nest system, but behavioural 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 eight 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 three size categories: (i) 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); (ii) sexuals – the larvae that pupate as alate females and males (the sex of mature larvae can be discriminated from worker-destined larvae by both their larger size and body shape; Hasegawa, 1992); and (iii) worker-destined larvae – the larvae that did not fall into the above two categories (1.60–3.50 mm in length); these 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 very 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 behavioural interactions of workers among nests (for the behavioural test, see Hasegawa, 1992). For polydomous colonies, all of the characteristics listed earlier 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

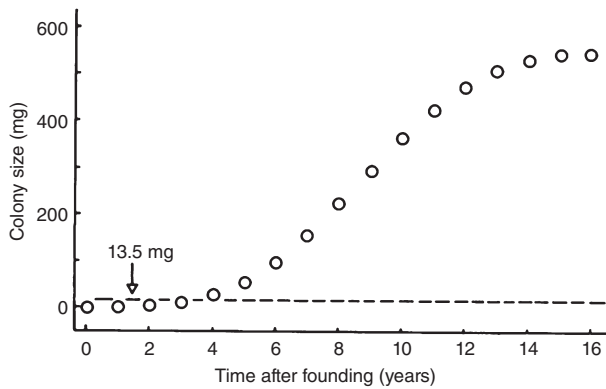


Fig. 1. The estimated colony growth pattern of *Camponotus (Colobopsis) nipponicus*. The horizontal line represents the threshold colony size for alate production. The colony size for the following year is calculated from the relationship between the number of worker brood and colony size in the colonies collected (see Fig. 4).

(Stearns, 1992). The maximum longevity of a colony was estimated from: (i) the estimated growth curve of the colonies with age (Fig. 1); (ii) size distributions of colonies in the reproductive season (June–August) in the three study seasons (Figs 2a–c); and (iii) 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. Figure 3 shows that the number of colonies becomes less than one at a colony size of c. 450–500 mg. A colony is estimated to reach to this size range c. 12–15 years after 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 the maximum longevity of a colony but not 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 later, 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, 1993b). 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 using STATVIEW 4.45.1 and R 3.2.1 software.

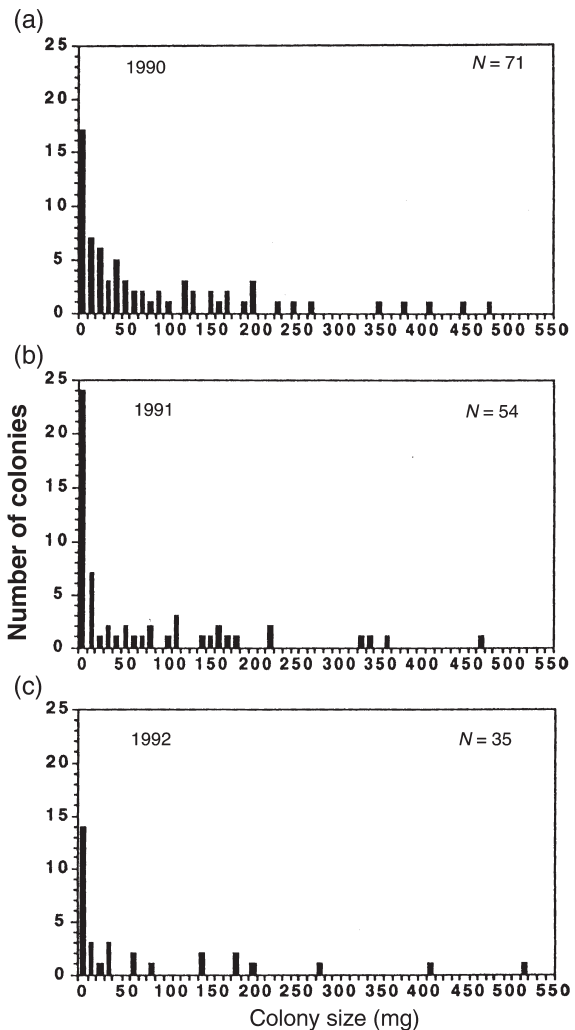


Fig. 2. Size distribution of colonies in the three reproductive seasons (June–July). There is no difference in the shape of the distribution between the 3 years. For all the pairs, the slope of the regression line of the log-transformed colony number on colony size was not different at the $P = 0.05$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

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), $W = 0.98 \times CS + 27.7$; for alate females (F), $F = 0.19 \times CS - 1.67$; for males (M), $M = 0.31 \times CS + 1.87$, where colony size is the total dry weight of all adult workers (mg)]. In simulation analyses, these regression equations were used to predict the number produced of each class in a colony of a given size.

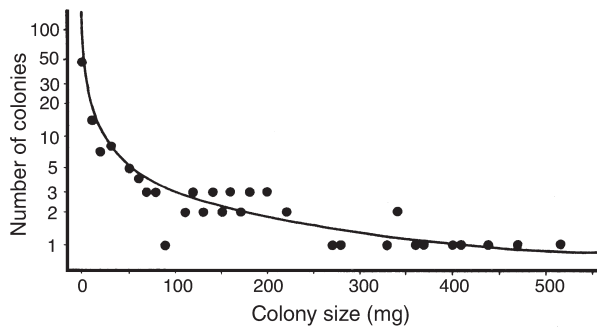


Fig. 3. Relationship between log-transformed number of colonies and size classes. The fitted curve can be regarded as the decreasing number of colonies with colony growth in this population.

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 calculated 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 using the described equations or values.

Colony growth and start of reproduction

Cassie provided a method by which data concerning the 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 allows us to estimate number of cohorts in the 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, 1993b). 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 consists of colonies at 1 year after the colony founding, and the second and third cohorts comprise colonies at 2 and 3 years after the founding, respectively. 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. These data also indicate that the threshold size for reproduction is approximately 13.5 mg (Fig. 1). This size is much smaller than that of matured colonies (Figs 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

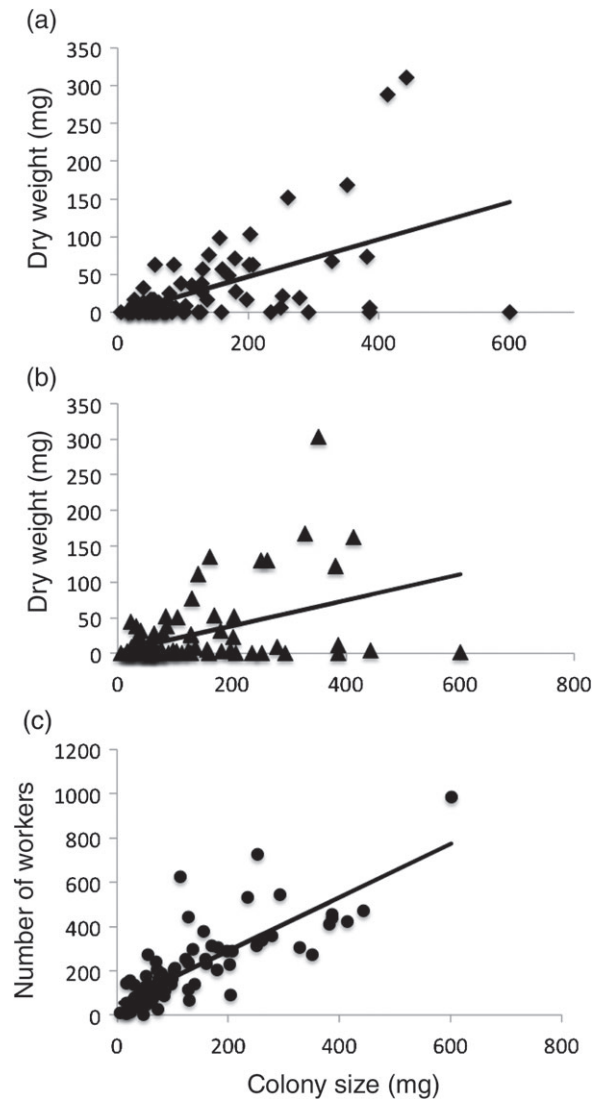


Fig. 4. Relationships between colony size and production of workers (a), alate females (b) and males (c). The line in each figure represents the liner regression of the workers, alate-females and males on their colony size, respectively. The estimated productivities from these regressions are used in the following simulations for colony growth or alate production as a function of colony size.

because *C. (C.) nipponicus* colony workers are *c.* 20% majors, regardless of colony size (Hasegawa, 1997). The results from the colony-growth simulation are shown in Fig. 1. The expected colony sizes of the first-, second- and third-year colonies were compared with the observed values (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 fourth year after the colony founding, at which time the colony is far smaller than its eventual maximum size.

Table 1. Comparison between the observed (mean \pm SD) and expected sizes of each class of colonies in *Camponotus (Colobopsis) nipponicus*.

	Class of colonies			
	First year (<i>n</i> = 49)	Second year (<i>n</i> = 9)	Third year (<i>n</i> = 11)	The largest 10 (<i>n</i> = 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

Table 2. Average number of colonies nested per tree in the three study seasons.

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

Standard error is shown with the mean.

Population stability and decreasing rate of colonies

Figure 3 shows the size distribution of colonies in the reproductive season over the 3 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 the slopes of the regression lines were then compared among years. There was no difference in the slopes among the 3 years (*F*-test, $P > 0.05$ for all three 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 three 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 these results, it was concluded that this was a stable population.

Figure 3 shows the log-transformed size distribution of *C. (C.) nipponicus* colonies in this population. Because this population can be regarded as stable, all three datasets 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 of the colony. Thus, with the exception of 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 produces 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 earlier, the mortality of a colony decreases with 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.

As 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 the amount of mortality improvement of a colony via abandoning reproduction as the tangent θ (Fig. 5). Figure 6 shows the relationship between the colony size and the possible improvement rate of mortality calculated by this 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 minimise the risk of reproduction.

The optimal timing of reproduction

To estimate the optimal timing of reproduction, the expected number of alate females and males throughout a colony's lifetime was calculated for a putative average colony that follows the growth pattern in Fig. 1. This colony was given all of the observed reproductive parameters in this population, but the start year of reproduction was changed from two to nine. 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 earlier). The result of this sensitivity test is shown in Fig. 7. The simulation showed that a colony can maximise its lifetime

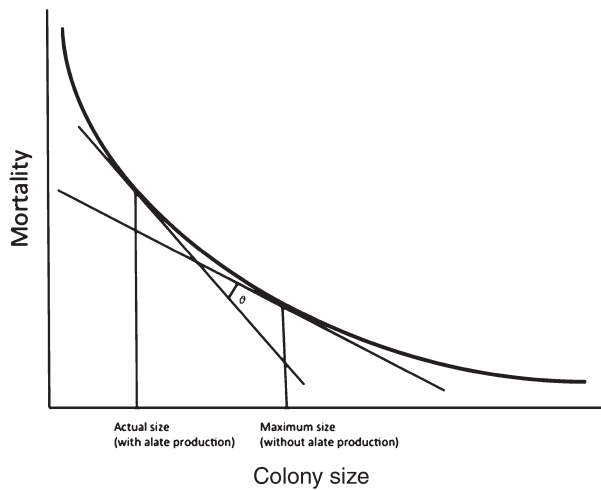


Fig. 5. A scheme explaining how to estimate the improvement in a colony's mortality by abandoning alate production for a year. A colony has two options: (i) all its resources are invested in worker production to realise the maximum possible colony size that maximises survival to the next year; (ii) a portion of the resources is invested in alate production by sacrificing colony growth rate (does not maximise colony survival). The improvement rate between the two strategies can be represented by $\tan\theta$ in the figure.

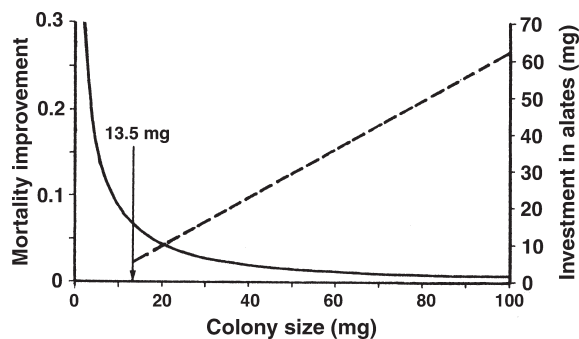


Fig. 6. Relationship between observed colony size and the possible improvement in mortality. The straight line represents the observed regression between colony size and alate production (see Fig. 5). Colonies start reproduction at a point (13.5 mg) where possible mortality improvement becomes low.

alate production by starting reproduction at 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 optimised in this population.

Discussion

Is the reproductive schedule optimised?

This study showed that *C. (C.) nipponicus* colonies start reproduction from a threshold size (c. 13.5 mg) that the colony attains at 4 years after the colony founding. The result of the reproductive simulation suggests that this schedule is the

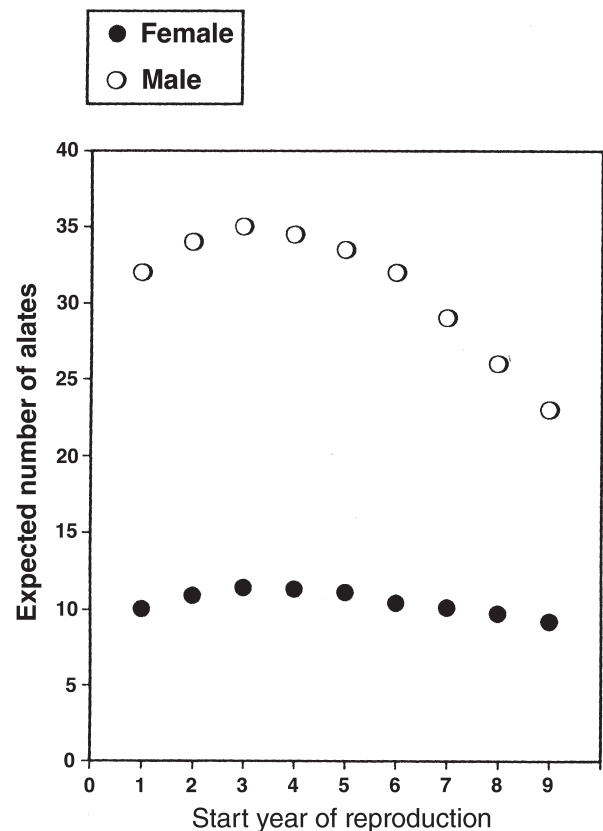


Fig. 7. Estimated relationship between start year of reproduction and lifetime reproductive success. When starting reproduction 4 years after the colony founding, a colony can maximise its lifetime production of alates in both sexes.

best way to maximise the expected lifetime production of alates (lifetime 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 lifetime 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 being in 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 in an equilibrium state, individual fitness is consistent with lifetime reproductive success (Stearns, 1992). Therefore, the observed reproductive schedule would be optimised in this population.

Contrary to the prediction of the bang-bang theory, *C. (C.) nipponicus* colonies started reproduction from a far smaller size than 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 favoured 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 favoured

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 do 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 did colonies in other years, 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 becomes large. Different nutritional conditions for colonies will cause the sizes of the colonies of the same age to diverge over a long period. During the same period, colonies under rich nutritional conditions become larger at a faster rate 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 becomes 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 the 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 lifetime

of alate production for a colony. We estimated this parameter as 15 years, from Figs 1 and 3. Therefore, it is considered that the reproductive schedule of *C. (C.) nipponicus* has been shaped mainly by its size and not by its age.

Conclusion

This study showed that demographic data enable 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 *et al.*, 2013), most of them require a great deal of effort and time. As far as we know, there is no other study that has adopted the analytical methods using demographic data that have been used in this study. As 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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References

- Agrawal, A.A., Johnson, M.T.J., Hastings, A.P. & Maron, J.L. (2013) A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedbacks to seed predator populations. *The American Naturalist*, **181**, S35–S45.
- Brian, M.V. (1957) The growth and development of colonies of the ant *Myrmica*. *Insectes Sociaux*, **4**, 177–190.
- Burns, J.H., Blomberg, S.P., Crone, E.E., Ehrlen, J., Knight, T.M., Pichancourt, J.-B. *et al.* (2010) Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *Journal of Ecology*, **98**, 334–344.
- Cassie, R.M. (1954) Some uses of probability paper in the analysis of size frequency distributions. *Australian Journal of Marine Freshwater Research*, **5**, 513–522.
- Cassie, R.M. (1962) Frequency distribution models in the ecology of plankton and other organisms. *Journal of Animal Ecology*, **31**, 65–92.
- Hasegawa, E. (1992) Annual life cycle and timing of male egg production in the ant *Colobopsis nipponicus* (Wheeler). *Insectes Sociaux*, **39**, 439–446.
- Hasegawa, E. (1993a) Caste specialization in food storage in the dimorphic ant *Colobopsis nipponicus* (Wheeler). *Insectes Sociaux*, **4**, 261–271.
- Hasegawa, E. (1993b) Nest defense and early production of the major workers in the dimorphic ant *Colobopsis nipponicus* (Wheeler) (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **33**, 73–77.

- Hasegawa, E. (1994) Sex allocation in the ant *Colobopsis nipponicus* (Wheeler). I. Population sex ratio. *Evolution*, **48**, 1121–1129.
- Hasegawa, E. (1997) The optimal caste ratio in polymorphic ants: estimation and empirical evidence. *The American Naturalist*, **149**, 706–722.
- Imai, H.T., Kihara, A., Kondoh, M., Kubota, M., Kuribayashi, S., Ogata, K. et al. (2003) *Ants of Japan*. Gakken, Tokyo, Japan.
- Kéry, M., Gregg, K.B. & Schaub, M. (2005) Demographic estimation methods for plants with unobservable life-states. *Oikos*, **108**, 307–320.
- Maynard Smith, J. (1989) *Evolutionary Genetics*. Oxford University Press, Oxford, U.K.
- Oster, G.F. & Wilson, E.O. (1978) *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, New Jersey.
- Parker, G.A. & Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature*, **348**, 27–33.
- Phillips, B.L., Brown, G.P. & Shine, R. (2010) Life-history evolution in range-shifting populations. *Ecology*, **91**, 1617–1627.
- Preston, S., Heuveline, P. & Guillot, M. (2000) *Demography: Measuring and Modeling Population Processes*. Wiley-Blackwell, London, U.K.
- Rees, P. & Woods, R. (1986) Demographic estimation: problems, methods and examples. *Population Structure and Models: Developments in Spatial Demography*. (ed by Wood, R., Rees, P.), pp 301–343. George Allen and Unwin, Boston, Massachusetts.
- Ross, K.G. & Matthews, R.W. (1991) *The Social Biology of Wasps*. Cornell University Press, Cornell, New York.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, U.K.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Swain, D.P. (2010) Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evolutionary Applications*, **4**, 18–29.
- Tschinkel, W.R. (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecological Monograph*, **63**, 425–457.
- Williams, G.C. (1992) *Natural Selection: Domain, Levels and Challenges*. Oxford University Press, Oxford, U.K.
- Wilson, E.O. (1971) *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

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