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Evolution of Asexual Queen Succession System in Termites 【Review article】

無性生殖的白蟻蟻后繼承系統之演化【綜合論述】

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Received: 2011/04/17 Accepted: 2011/04/20 Available online: 2010/06/01

Abstract

The evolution and maintenance of sexual reproduction is believed to involve important tradeoffs. The queens of social insects are faced with a dilemma over the costs and benefits of sexual and asexual reproduction. Asexual reproduction by a queen doubles her contribution to the gene pool. However, overuse of asexual reproduction reduces the genetic diversity of the offspring and thus the ability of the colony to adapt to environmental stress. Recent research suggests that queens of some *Reticulitermes* termites can solve this tradeoff by the conditional use of sexual and asexual reproduction, whereby queens produce neotenic (secondary) queens by parthenogenesis but use sexual reproduction to produce workers and alates (sexual imagos). I also discuss proximate physiological mechanism and genetic background of the asexual queen succession system in the termites.

摘要

有性生殖的演化和維持被認為有重要的代價權衡參與其中，社會性昆蟲的王后必須在有性生殖與無性生殖的代價和利益中進行抉擇。王后可經由無性生殖加倍其貢獻至基因庫，然而過度的無性生殖將降低後代的遺傳多樣性，並因此降低群體對於環境壓力的適應能力。近年的研究顯示散白蟻屬 *Reticulitermes* 的一些蟻后可以有條件的運用有性與無性生殖來解決此代價權衡，蟻后經由孤雌生殖產生下一世代的蟻后，工蟻則經由有性生殖產生。我也將討論無性生殖的白蟻蟻后繼承系統可能的生理機制和潛在的遺傳背景。

Key words: thelytoky, caste differentiation, genetic diversity, queen succession, queen pheromone, sex ratio

關鍵詞: 產雌孤雌生殖、階級分化、遺傳多樣性、蟻后繼承、蟻后費洛蒙、性別比例。

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Evolution of Asexual Queen Succession System in Termites

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ABSTRACT

The evolution and maintenance of sexual reproduction is believed to involve important tradeoffs. The queens of social insects are faced with a dilemma over the costs and benefits of sexual and asexual reproduction. Asexual reproduction by a queen doubles her contribution to the gene pool. However, overuse of asexual reproduction reduces the genetic diversity of the offspring and thus the ability of the colony to adapt to environmental stress. Recent research suggests that queens of some *Reticulitermes* termites can solve this tradeoff by the conditional use of sexual and asexual reproduction, whereby queens produce neotenic (secondary) queens by parthenogenesis but use sexual reproduction to produce workers and alates (sexual imagos). I also discuss proximate physiological mechanism and genetic background of the asexual queen succession system in the termites.

Key words: thelytoky, caste differentiation, genetic diversity, queen succession, queen pheromone, sex ratio

Introduction

Kin selection and inclusive fitness theory predicts that high relatedness, possibly generated by genetic factors such as haplodiploidy, inbreeding, or clonal reproduction, is critical to the evolution of eusociality. However, relatedness among workers within colonies of some species is relatively low due to sexual reproduction, including outbreeding, multiple mating (polyandry), and multiple reproductive females (polygyny), which lowers the potential inclusive fitness gains for

altruistic members. Hughes *et al.* (2008) compared female mating frequencies in eusocial Hymenoptera and demonstrated that monandry was the ancestral state when eusociality arose in Hymenoptera and that mating by queens with multiple males is always derived. High levels of polyandry occur only in species whose workers have lost reproductive totipotency. Similarly, polygyny is also derived. This indicates that high relatedness has played a decisive role in the evolution of eusociality and strongly supports inclusive fitness theory.

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Living in social groups has not only advantages but also drawbacks. For example, infectious diseases can potentially spread more easily among group members than solitary-living individuals. Transmission is more likely in groups because individuals live at high densities and have frequent social contact. In addition, group members are close relatives and thus susceptible to the same parasite infections (Schmid-Hempel, 1998). This can be understood using an analogy to human agriculture (e.g., Muira *et al.*, 2008). Selective breeding of crops for desirable traits and against the undesirable ones leads to monocultures, or entire farms of nearly genetically identical plants. Little to no genetic diversity makes crops extremely susceptible to widespread disease. Low genetic variance and closely spaced individuals may be the reasons why the avian flu causes devastating effects on poultry farming and why plant hoppers wipe out acres of rice paddies at once. Both human agriculture and social insect colonies face risks associated with high density and low genetic diversity.

Perhaps the best solution to the dilemma over the costs and benefits of sexual and asexual reproduction is to use both modes of reproduction conditionally and therefore to experience the advantages of both. Indeed, recent studies have uncovered unusual modes of reproduction both in the ants *Cataglyphis cursor* (Pearcy *et al.*, 2004), *Wasmannia auropunctata* (Fournier *et al.*, 2005), and *Vollenhovia emeryi* (Ohkawara *et al.*, 2006), and in the termite *Reticulitermes speratus* (Matsuura *et al.*, 2009), in which advantage is taken of the social caste system to use sex for somatic growth, but parthenogenesis for germ line production.

The capability of parthenogenesis in Isoptera was first reported by Light in 1944. However, the reproductive biology of termite parthenogenesis has not been examined in detail beyond its notional documentation until recently. This is largely because parthenogenetic reproduction

has been regarded as an unusual case with little adaptive significance in nature. Even after the adaptive significance of termite parthenogenesis was recognized, researchers believed that the function of parthenogenesis in termites was no more than “the best of a bad job”, that is, females used parthenogenesis only when they failed to mate with males (Matsuura and Nishida, 2001; Matsuura *et al.*, 2002).

Most recently, however, it was revealed that parthenogenesis in some termite species plays a much greater role than has been previously understood. In the Japanese subterranean termite *R. speratus* (Matsuura *et al.*, 2009) and the North American subterranean termite *R. virginicus* (Matsuura and Vargo, in prep.), queens exclusively use parthenogenesis to produce secondary (neotenic) queens. On the other hand, queens produce workers and alates by outcrossing with the primary king. This model of asexual queen succession (AQS) or conditional use of sexual and asexual reproduction can be studied to understand the advantages and disadvantages of thelytoky in termites.

Thelytoky in eusocial insects

Thelytoky is a type of parthenogenesis in which females are produced from unfertilized eggs. Among the 12,500 ant and 2,400 termite species in the world, thelytoky has been reported in only nine ant species and seven termite species. Thus, the percentages of species with thelytokous capability are 0.07% and 0.29% in ants and termites, respectively. These values are much lower than 2%, which is the percentage of all insect species with thelytokous capabilities. By taking advantage of asexual reproduction, queens of eusocial insects are able to realize a twofold advantage over sexual reproduction by allowing the transmission of twice the number of genes to offspring. This leads to the very interesting question of why thelytoky is so rare among eusocial insects.

One possible explanation is that only a limited number of studies have carefully examined the possibility of thelytokous parthenogenesis in eusocial insects. Thelytoky may be more difficult to detect in eusocial insects than in other insects because its presence is sometimes concealed or suppressed by social structure; the mechanisms that cause this are described in the next section. Indeed, findings by L. Keller of the conditional use of asexual reproduction in ants arose by pure serendipity (Keller, 2007). Future studies may reveal thelytoky in many more eusocial species. Possibly the rarity of thelytoky in eusocial insects is attributable to the importance of genetic diversity among colony members. While asexual reproduction by a queen would increase within-colony relatedness, the resulting reduction in genetic diversity within colonies would lower homeostasis in colonies. For example, low genetic diversity colonies are more afflicted by disease than genetically diverse colonies in bumblebees (Baer and Schmid-Hempel, 2001), honeybees (Seeley and Tarpy, 2007) and leaf-cutting ants (Hughes and Boomsma, 2004). In honeybees, high-diversity colonies maintain more uniform temperatures in their brood nests than did the uniform ones due to a system of genetically based task specialization (Jones *et al.*, 2004). Thus, reduction in genetic diversity would render the colonies less resilient to environmental perturbation. A comprehensive survey of species capable of thelytokous parthenogenesis is a necessary next step in the effort to understand the costs and benefits of sexual and asexual reproduction for eusocial insects.

Mechanism of termite parthenogenesis

Research on chromosome numbers of Isoptera showed that higher termites (Termitidae) are karyotypically uniform ($2n = 42$), while lower termites are more variable, with diploid numbers ranging from 28 to 56 (Bergamaschi *et al.*, 2007).

Reticulitermes termites have a fixed number of chromosomes ($2n = 42$). Karyotypic chromosome observations showed that parthenogenetic offspring are diploid, with $2n = 42$ chromosomes in *R. speratus*. Although termite sex determination mechanisms are not completely understood, males commonly appear heterogametic in termites (Roisin, 2001). Interchange multiples (chains or rings of chromosome) in the male meiosis is common in termites (Syren and Luykx, 1977). Chromosome multivalents have been observed in male meiosis in *R. speratus*, generating a multiple-X, multiple-Y system (Matsuura, 2002). Because of the XY sex determination system, termite parthenogenesis produces only female progeny.

The genotypes of parthenogenetic offspring depend on the mode of parthenogenesis (Templeton, 1982). Thelytokous parthenogenesis can be categorized into two major cytological divisions, “apomixis (ploidy stasis)” and “automixis (ploidy restoration).” In apomictic parthenogenesis, known as clonal reproduction in aphids, the features of meiosis are either entirely or partially lacking. Only one maturation division takes place in the egg and this division is equational. The offspring retain the genetic constitution of the mother (excluding mutations), and heterozygosity is maintained in subsequent generations.

Importantly, parthenogenesis of termites is not clonal. Thelytoky in termites, such as *R. speratus* and *R. virginicus*, is accomplished by automixis with terminal fusion, in which two haploid pronuclei that divide at meiosis II fuse (Fig.1). Thus, offspring are homozygous for a single maternal allele at all loci that did not crossover, whereas offspring have the same genotype as their mother at loci where crossover occurred. This causes a rapid reduction of heterozygosity (Matsuura *et al.*, 2004).

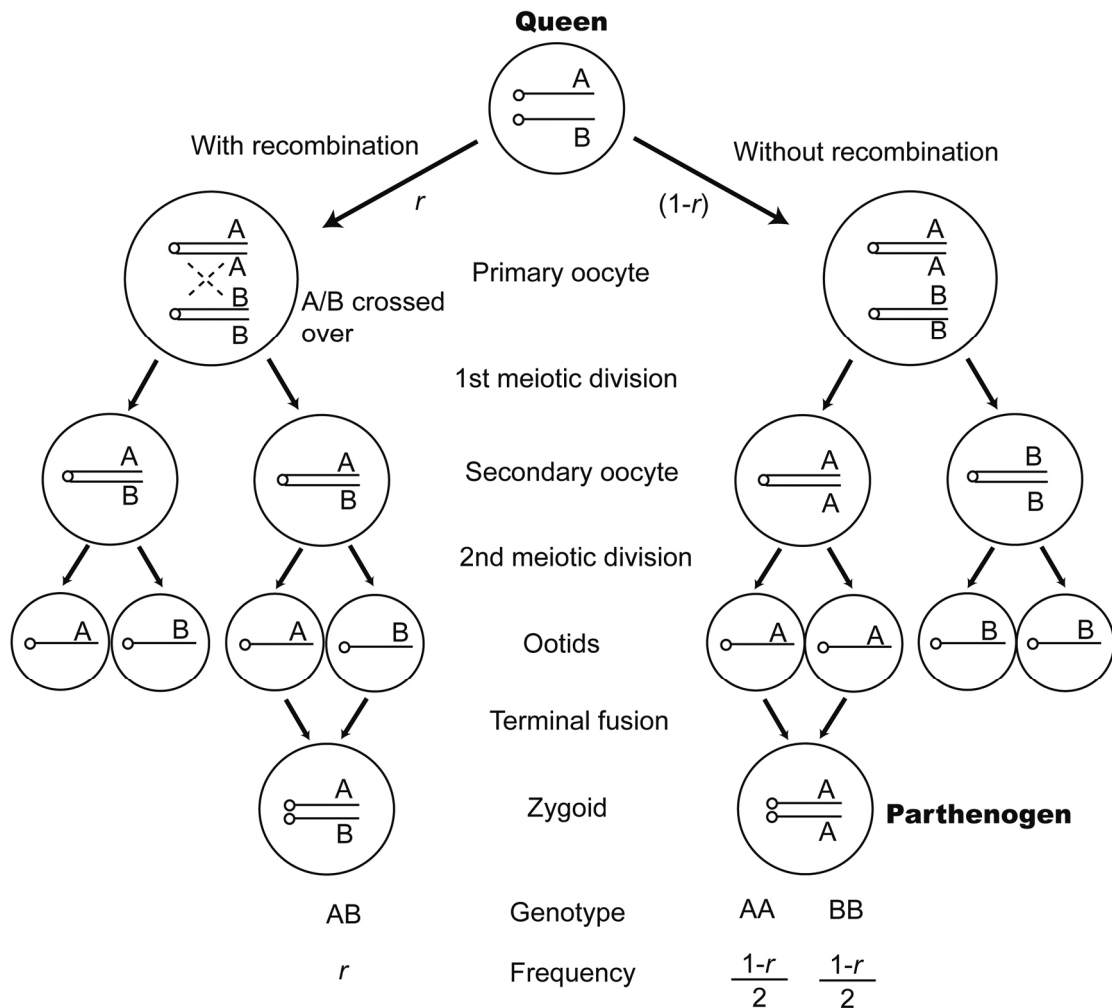


Fig. 1. Scheme of ploidy restoration by automixis with terminal fusion. This type of parthenogenesis results in rapid reduction of heterozygosity. r : recombination rate. From Matsuura *et al.* (2004).

Asexual queen succession (AQS) in *Reticulitermes speratus*

In most termite species, one king and one queen usually found colonies. In termites, especially in lower termites, it has long been believed that the inbreeding cycles of generations of neotenic reproductives propagate the colony after the death of the primary king and queen (Bartz, 1979). Evidence for inbreeding depression in termites is mounting, such as higher mortality in inbred incipient

colonies and lower lifetime fecundity in inbred colonies. Like most subterranean termites, *Reticulitermes* species have cryptic nesting habits with transient, hidden royal chambers underground or deep inside wood, making it difficult to reliably collect reproductives. Therefore, the breeding system of subterranean termites has been primarily estimated by genotyping workers or culturing laboratory colonies rather than censuses of field colonies.



Fig. 2. A royal chamber of *Reticulitermes speratus*, where a single primary king (PK: arrowed) and dozens of secondary queens reproduce.

Reticulitermes speratus is the most common termite in Japan. To obtain reproductives from a sufficient number of natural colonies, we collected more than 1,000 nests in the field. We successfully found the royal chambers, where reproductives and young broods were protected, of 55 colonies. In nearly all cases, primary kings were continuously present but primary queens had been replaced by an average of 62.73 ± 8.54 (mean \pm s.e.m, $n = 55$) secondary queens (updated after Matsuura *et al.*, 2009; Fig. 2). These results indicate that primary kings live much longer than primary queens; replacement of the primary king is rare, whereas replacement of the primary queen is the rule at a certain point in colony development. All of the 3,450 secondary queens collected from field colonies were nymphoid, i.e., neotenic reproductives with

wing buds differentiated from nymphs (updated after Matsuura *et al.*, 2009; Fig. 3).

Sexual reproduction can lead to important conflicts between sexes and within genomes. In monogamous termites, conflicts between the primary king and queen can arise over parental investment and genetic contribution to offspring. Our finding that primary queens are replaced much earlier than primary kings in *R. speratus* leads to a paradox if the secondary queens are the daughters of the primary king. King-daughter inbreeding should result in uneven genetic contribution to the secondary offspring (offspring of secondary queens) by the primary king and queen. The life-for-life relatedness of a primary king to the secondary offspring produced by king-daughter inbreeding is $5/8$, while relatedness of the primary

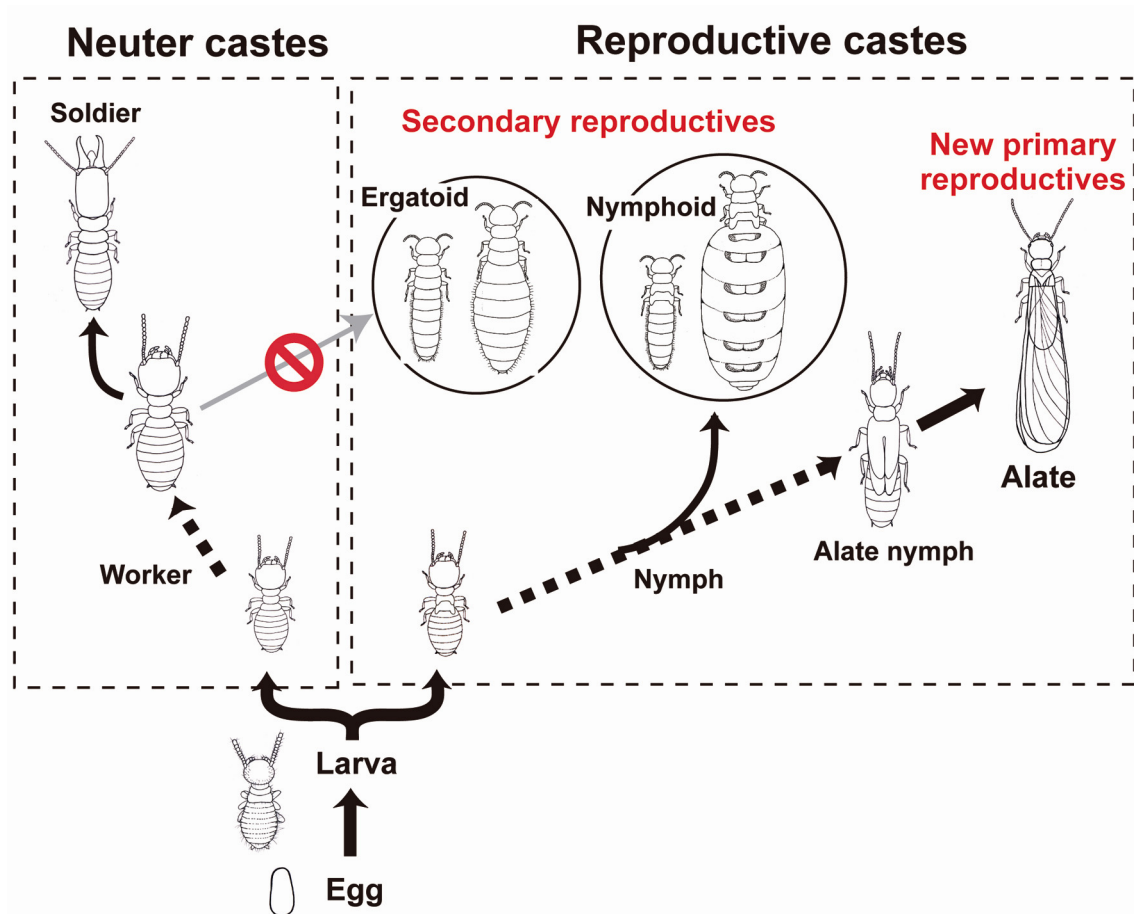


Fig. 3. Differentiation pathways of primary and secondary reproductives in the genus *Reticulitermes*. In field colonies of *R. speratus*, secondary queens always differentiate from nymphs but never from workers.

queen to the secondary offspring is $1/4$ when the primary king and the primary queen are unrelated. Because male primary reproductives are 2.5 times more related to offspring than is the primary queen under this system, colonies are expected to bias alate (new primary reproductives that disperse) production in favor of males. Contrary to this prediction under this breeding system, the alate sex ratio is slightly but significantly female-biased in this species (numerical ratio of male = $0.43 \pm 0.02_{SE}$). Because of the larger size of females relative to males, the biomass sex ratio was even more biased

toward females (Investment ratio of male: $0.415 \pm 0.02_{SE}$). This inconsistency between king-daughter inbreeding and sex investment ratio in alate production suggests that there is a different breeding system in which the king and queen have more equal genetic contributions to offspring.

Together with Edward L. Vargo, we examined the genotypes within nests of *R. speratus* and uncovered an extraordinary mode of reproduction (Matsuura *et al.*, 2009). Secondary queens are almost exclusively produced parthenogenetically by the founding primary queens, whereas workers and alates were produced by

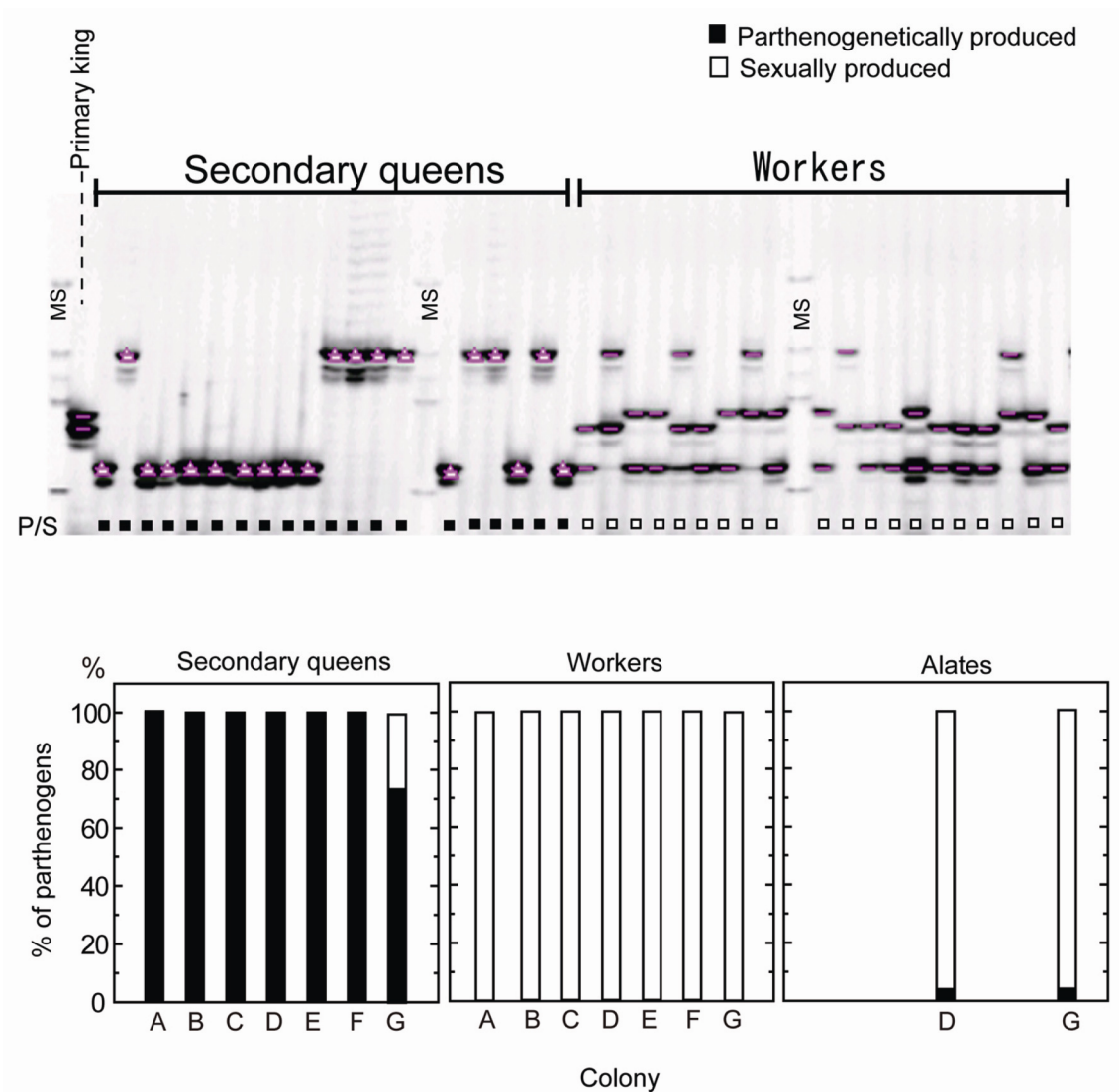


Fig. 4. Proportion of parthenogenetically produced offspring (black) and sexually produced offspring (white) in secondary queens, workers and alates. Secondary queens have only maternal (primary queens') alleles, while workers and alates have both maternal and paternal alleles indicating conditional use of sexual and asexual reproduction. MS: molecular standard. From Matsuura *et al.* (2009).

sexual reproduction (Fig. 4, 5). By using parthenogenesis to produce secondary queens, primary queens are able to retain the transmission rate of their genes to descendants while maintaining genetic diversity in the workers and new primary reproductives even after the primary queen is replaced. The relatedness of the

primary queens to workers ($r = 0.49$, $SE_{jackknife} = 0.04$) and to alate nymphs ($r = 0.58$, $SE_{jackknife} = 0.079$) is not significantly different from 0.5, the value expected between a female and her sexual offspring. This is twice the expected genetic contribution queens would make to colony members under king-daughter inbreeding

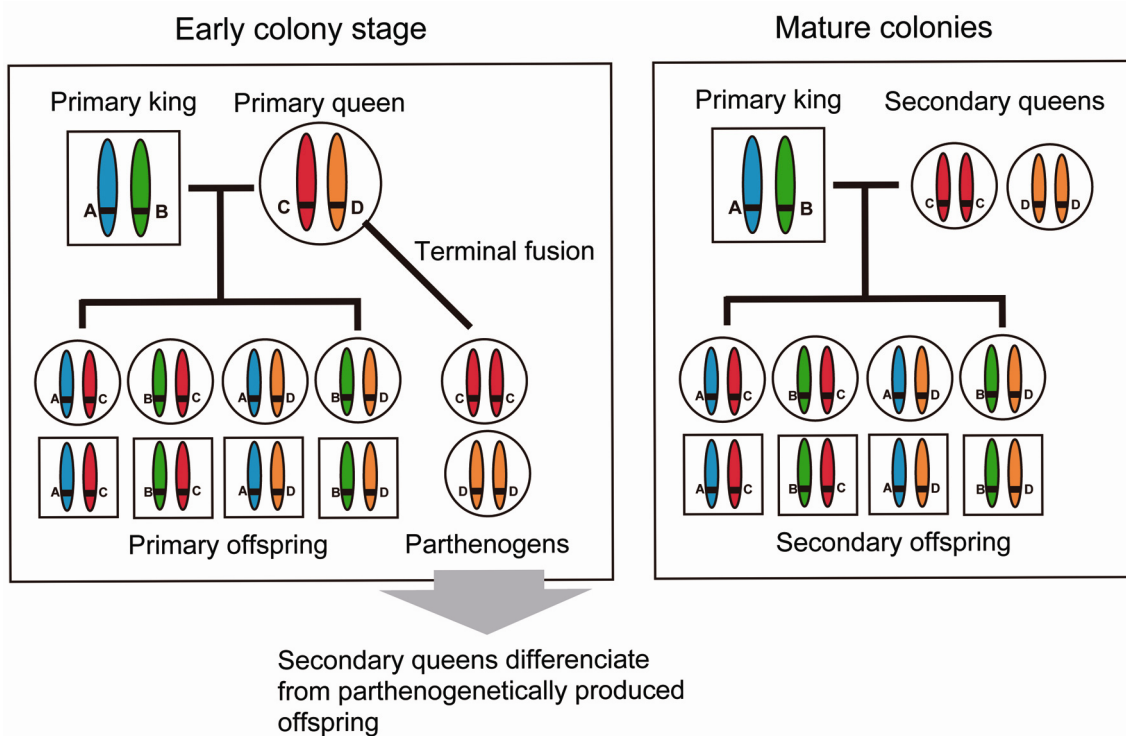


Fig. 5. Scheme for the breeding system with asexual queen succession in termites. This breeding system enables the primary queen to maintain her full genetic contribution to the next generation, while avoiding any loss in genetic diversity from inbreeding.

($r_{\text{primary queen to king-daughter offspring}} = 0.25$).

Parthenogenetic production of secondary queens allows *R. speratus* to undergo queen succession without inbreeding (Fig. 5). Heterozygosity of workers in colonies headed by secondary queens was as high ($H_o = 0.733$) as that expected for offspring produced by outcrossing of the primary king and the primary queen ($H_e = 0.736$; Fig. 6). Likewise, there was no significant reduction of heterozygosity in alate nymphs produced in colonies with secondary queens (Fig. 6). Further evidence of the lack of inbreeding in *R. speratus* colonies is provided by the low inbreeding coefficient of workers, which did not differ significantly from zero ($F_{IT} = 0.014$, $SE_{\text{jackknife}} = 0.048$, over all loci). The lack of consanguineous mating in this breeding system may also benefit primary kings.

The offspring produced by outcrossing between the king and parthenogenetic queens may have greater fitness than those produced by king-daughter inbreeding.

The production of secondary queens through conditional parthenogenesis effectively extends the reproductive life of the primary queen, greatly expanding her reproductive capacity (Fig. 7). This process of queen succession allows the colony to boost its size and possibly its growth rate without suffering any loss in genetic diversity or diminishing the transmission rate of the queen's genes to her grand offspring, feats that would not be possible if secondary queens were produced by normal sexual reproduction.

Purging: another benefit of AQS

A faster rate of accumulation of



Fig. 6. Proportion of heterozygous loci (black) and homozygous loci (white) in secondary queens, workers and alates. The amount of heterozygosity expected for offspring produced by outcrossing of the primary king and the primary queen are indicated by arrowheads. From Matsuura *et al.* (2009).

deleterious mutations is a major cost of asexual reproduction. In haplodiploid organisms, deleterious alleles are directly exposed to selection each generation in the haploid males, and there is no masking effect of dominance. Therefore, purging selection will cause a more rapid decrease in the frequency of deleterious alleles at haplodiploid loci than at comparable loci in diploid organisms (Goldstein, 1994).

In termites, paradoxically, asexual queen succession can function to purge deleterious mutations. Parthenogenetic offspring are homozygous for a single maternal allele at all loci due to terminal fusion. Therefore, deleterious recessive genes are exposed to selection in homozygous parthenogens. Parthenogens carrying homozygous recessive deleterious alleles should not be able to survive or develop into functional secondary queens. The obligate occurrence of parthenogenesis in the normal life cycle of this species can eliminate recessive deleterious genes in every generation, much like the genetic purging that haploid males of Hyme-

noptera undergo, eliminating the transmission of deleterious recessive alleles to the sexual offspring.

Genetic caste determination and AQS

The question of how reproductives and sterile workers differentiate within eusocial groups has long been a core issue in the study of social insects. Recent studies have shown that not only environmental factors but also genetic factors affect caste differentiation. Genetic influences on queen-worker differentiation are essential to the conditional use of sexual and asexual reproduction. In the termite *R. speratus*, parthenogens are strongly biased to develop into secondary queens, suggesting that differentiation into this caste is genetically influenced, possibly by whether individuals are heterozygous or homozygous at certain loci. The AQS system can work only if parthenogens have priority to become secondary queens. Why is it that nymphs produced by parthenogenesis can exclusively differentiate into secondary queens when there are numerous sexually

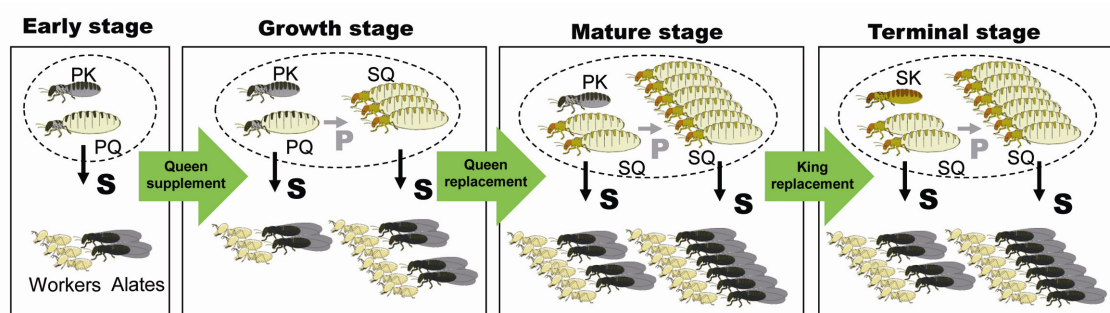


Fig. 7. Schematic diagram of asexual queen succession. PK: primary king, PQ; primary queen. SQ: secondary queen. SK: secondary king. P: parthenogenesis. S: sexual reproduction. Modified from Matsuura (2010).

produced nymphs at the same time? Without any genetic influence on caste differentiation, it seems impossible for this to happen. A genetic system of homozygous advantage to be secondary queens makes it possible. In addition, a stable AQS system requires the genetic advantage to be determined by an independent (unlinked) multilocus genotype. A single locus system cannot discriminate parthenogens and sexually produced offspring, and thus AQS is impossible, if the founding pair had the same allele at the locus. A multilocus system provides a rigorous mechanism by which only parthenogens can develop into secondary queens, because terminal fusion yields progeny of near-total homozygosity.

An analysis of the relationship between the reproductive dominance of female neotenic obtained from experimentally orphaned colonies and their genotypes at five microsatellite loci showed that homozygosity at two loci influenced the priority to differentiate into neotenic (Yamamoto and Matsuura, submitted data). These results suggest the existence of a multilocus queen determination system and explain why parthenogens have genetic priority to become neotenic in this termite species.

Termite queen pheromone and AQS

The hallmark of social insects is their caste system: reproduction is primarily monopolized by queens while workers

specialize on the other tasks required for colony growth and survival. Pheromones produced by reigning queens have long been believed to be the prime factor inhibiting the differentiation of new reproductive individuals. However, there has been very little progress in the chemical identification of such inhibitory pheromones. Recently, I and my colleagues identified a volatile inhibitory pheromone produced by female neotenic (secondary queens) that acts directly on target individuals to suppress the differentiation of new female neotenic (Matsuura *et al.*, 2010). We identified n-butyl-n-butyrate and 2-methyl-1-butanol as the active components of the inhibitory pheromone. An artificial pheromone blend consisting of these two compounds had a strong inhibitory effect similar to live neotenic. Surprisingly, the same two volatiles are also emitted by eggs, playing a role both as an attractant to workers and an inhibitor of reproductive differentiation. This dual production of an inhibitory pheromone by female reproductives and eggs probably reflects the recruitment of an attractant pheromone as an inhibitory pheromone and may provide a mechanism ensuring honest signaling of reproductive status with a tight coupling between fertility and inhibitory power. Most recently, we found that the queen pheromone also functions as a signal regulating colony-level egg production (Yamamoto and Matsuura, in

press).

From the view point of queen pheromone, the most parsimonious evolutionary origin of AQS might be a loss of the receptor of queen pheromone in homozygous progenies at a certain locus. In other words, the origin of the queen succession gene might be a recessive deleterious gene. The individuals with homozygous sets of the gene lose the queen pheromone receptor and thus have the developmental priority to differentiate into neotenics.

Thelytoky and alate sex ratio in termites

In *R. speratus*, females that fail to pair with males found colonies cooperatively with female partners or even alone, and reproduce by parthenogenesis (Matsuura and Nishida 2001, Matsuura *et al.*, 2002). The diploid female progeny reproduced by thelytokous parthenogenesis develop in the same way as sexually produced offspring. Parthenogenetic reproduction is advantageous, even if ultimately it may be inferior to sexual reproduction in terms of long term fitness. It enables females to reproduce in the event that a mating partner cannot be found. Therefore facultative parthenogenesis, where both sexual and asexual colony foundation is sometimes possible, may explain why alate sex ratio is female biased in some termite species.

Contrary to the intuitive expectation, an ESS model predicts that maleless colony foundation does not cause female-biased alate sex ratios (Matsuura and Dobata, in prep.). We consider a situation where F females found colonies in a population. We assume that one female is a mutant and $F-1$ females are resident. The sex ratio of alates produced by a colony is determined by the genotype of the founder female. Founder females produce alates by sexual reproduction and thelytoky at the proportion of x and $1-x$, respectively. The total numbers of alates produced by the foundresses' sexual repro-

duction and thelytoky are m and $(1-c)m$, respectively, where c is the cost of thelytoky. The number of male M_m and female M_f alates produced by the colony founded by the mutant female are given by

$$M_m = xms$$

$$M_f = xm(1-s) + (1-x)(1-c)m$$

where s is the sex ratio (male ratio) of alates produced by the mutant colony. The number of male R_m and female R_f alates produced by the colonies founded by the resident females are given by

$$R_m = (F-1)xms^*$$

$$R_f = (F-1)xm(1-s^*) + (F-1)(1-x)(1-c)m$$

where s^* is the sex ratio of alates produced by the resident colonies.

The alates of the next generation form P monogamous pairs (a male and a female) and reproduce sexually. The proportion of mutant males in the P pairs is equal to the proportion of mutant males in the total number of males in the population. Therefore, The number of mutant males and mutant females which formed monogamous pairs are $P M_m / (M_m + R_m)$ and $P M_f / (M_f + R_f)$, respectively.

The males which failed to mate with females die, whereas the females which failed to mate with males still found colonies by alone or by female-female pairs and reproduce by thelytoky (Matsuura and Nishida, 2001). The number of females which reproduce by thelytoky in maleless colonies is $P(1-x)/x$, and thus the total number of mutant females reproducing by thelytoky is given by

$$P[(1-x)/x][M_f / (M_f + R_f)]$$

Then the monogamous pairs produce m alates by sexual reproduction. On the other hand, females of the maleless colonies produce $(1-c)m$ alates. In sexual reproduction, a parent male and female share the genetic contribution to the alates of the next generation. Therefore, the expected genetic contribution (i.e., fitness) of a mutant to the next generation is given by

$$W(s, s^*) = 1/2 [P M_m / (M_m + R_m)]m + 1/2 [P M_f / (M_f + R_f)]m + P [(1-x)/x][M_f /$$

$(M_f + R_f)](1-c)m$

$W(s, s^*)$ achieves its maximal value with respect to s when $s = s^*$, yielding the ESS condition

$$\left. \frac{\partial W(s, s^*)}{\partial s} \right|_{s=s^*} = 0$$

As a consequence, the ESS sex ratio is $s^*=1/2$.

This ESS model shows that the occurrence of maleless colony foundation does not cause sex-asymmetric fitness values of alates regardless of pairing efficiency, although thelytoky enables females to found colonies even when they failed to mate with males.

This result provides an important implication that the actual female-biased alate sex ratio of *R. speratus* cannot be explained by maleless colony foundation but should be explained by any other mechanism.

An alternative hypothesis for the female-biased alate sex ratio in AQS species is that the relatedness asymmetry caused by sex-specific parent-offspring mating biases investment toward the sex of inbred parent (Kobayashi *et al.* in prep). AQS system balances the genetic contribution to the next generation between the primary king and the primary queen for as long as the primary king is alive. However, inbreeding is inevitable after the primary king's death, and should result in uneven genetic contribution to the offspring by the primary king and queen. Thus even a small bias in genetic contribution to next generation can cause an unequal alate sex ratio (Kobayashi *et al.* in prep).

Comparison of the conditional use of thelytoky between ants and termites

Asexual royal succession in *R. speratus* is in some ways analogous to the conditional use of sex found in the ants *C. cursor*, *W. auropunctata*, and *Vollenhovia emeryi*. In these ant and termite species,

queens do not require sperm from mates to produce diploid (female) offspring. Nevertheless, they retain sexual reproduction for production of workers and have thus the genetic diversity in the worker force is maintained. By using alternative modes of reproduction for the queen and worker castes, genetic diversity in the worker population can be maintained.

As discussed above, reduced genetic diversity in the worker force may be detrimental for the colony because it leads to reduced defense against parasites, less efficient division of labor, and a decreased range of environmental conditions that a colony can tolerate. These costs are akin to those thought to lead to the instability of parthenogenetic reproduction in nonsocial organisms. Thus, sexual reproduction might have important benefits for colony function through increased defense against parasites, more efficient division of labor, and an increased range of environmental conditions that a colony can tolerate. Queens of these species take advantage of the social caste system to use sex for producing workers, which amounts to somatic growth but parthenogenesis, which does not involve the evolutionary cost of sex is used for germ line production.

In *R. speratus*, only the non dispersing neotenic (secondary) queens that develop within established colonies are produced asexually, whereas alates (adult primary queens) are produced sexually. Parthenogenesis with terminal fusion results in near complete homozygosity, which should reduce the viability and fitness of the secondary queens. However, the consequences for secondary queens in this termite species may be minimal, because secondary queens stay in the natal nest protected and cared for by the existing worker force, unlike independent colony founding by the primary king and queen. Contrary to neotenic queens, alates of termites disperse and found colonies independently, and are thus subjected to a number of environmental contingencies in

which genetic diversity is likely to be advantageous.

Although conditional use of sexual and asexual reproduction is currently known only in three ants and a single termite species, breeding systems involving conditional parthenogenesis may occur in other eusocial insects. To date, the ability to reproduce parthenogenetically has been reported in unmated females in seven termite species from four different families, in which the production of neotenic replacement reproductives is common. This raises the possibility that the conditional use of sex and parthenogenesis could be widespread within this ecologically and economically important group of social insects. In addition, the genetic system of homozygous advantage to secondary queens may provide an ideal opportunity to identify the queen determination gene in termites.

Acknowledgments

I thank C. Himuro, T. Yokoi, Y. Yamamoto and T. Yashiro for research assistance; K. Tsuji, E. L. Vargo, S. Dobata, E. Hasegawa, J. Yoshimura and K. Kobayashi gave helpful advices. This work was supported by the Japan Society for the Promotion of Science and the Program for Promotion of Basic Research Activities for Innovative Biosciences.

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- Received: April 17, 2011**
Accepted: April 20, 2011

無性生殖的白蟻蟻后繼承系統之演化

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摘 要

有性生殖的演化和維持被認為有重要的代價權衡參與其中，社會性昆蟲的王后必須在有性生殖與無性生殖的代價和利益中進行抉擇。王后可經由無性生殖加倍其貢獻至基因庫，然而過度的無性生殖將降低後代的遺傳多樣性，並因此降低群體對於環境壓力的適應能力。近年的研究顯示散白蟻屬 *Reticulitermes* 的一些蟻后可以有條件的運用有性與無性生殖來解決此代價權衡，蟻后經由孤雌生殖產生下一世代的蟻后，工蟻則經由有性生殖產生。我也將討論無性生殖的白蟻蟻后繼承系統可能的生理機制和潛在的遺傳背景。

關鍵詞：產雌孤雌生殖、階級分化、遺傳多樣性、蟻后繼承、蟻后費洛蒙、性別比例。

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