Queen Succession Through Asexual Reproduction in Termites

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It is unknown how diverse the mating systems of termites, which include inbreeding and asexual reproduction, are and how they are maintained. Termite colonies are founded by one king and one queen, which produce the rest of the colony (*1*, *2*). In the subterranean termites (Rhinotermitidae), secondary neotenic reproductives are produced upon the death of the primary queen and/or king, which may engage in inbreeding for many generations (*3*).

We collected and censused 30 natural colonies of *Reticulitermes speratus* at five field sites. In all but one, the primary queen had been replaced by numerous secondary queens; in the exception, both the primary queen and 128 secondary queens were present (fig. S1 and S2) with 55.4 ± 12.4 (mean ± SEM, $n = 30$) queens present on average. All 1660 secondary queens collected were nymphoid, that is, neotenic reproductives with wing buds differentiated from nymphs (fig. S1). In contrast, 19 of 21 colonies had a single primary king; two had a single secondary king. These results suggest that primary kings live longer than primary queens and that replacement of the primary king may be rare.

Unmated primary queens of *R. speratus* can found colonies through thelytokous, automictic parthenogenesis with terminal fusion (*2*, *4*), but whether parthenogenetic reproduction is part of the breeding system in colonies containing a single king is unknown. Genetic analyses of seven representative colonies (Fig. 1) for different locations with five microsatellite loci (observed heterozygosities from 0.543 to 0.957) were used to genotype 135 secondary queens, one primary queen, six primary kings, one secondary king, 140 workers, and 40 alate nymphs. Nearly all of the secondary queens genotyped (131 of 135) were homozygous at all five loci for alleles from the primary queen (*5*), but none had alleles that could be attributed to the king. Hence, these secondary queens were produced by parthenogenesis (Fig. 1A). Additionally, secondary queens were related to their mother primary queen by one ($r = 0.99$, $SE_{jackknife} = 0.01$, $n = 7$ colonies) but were unrelated to the primary king from the same nest ($r = -0.07$, $SE_{jackknife} = 0.09$, $n = 7$ colonies). In contrast, 100% of the workers (140 of 140, Fig. 1B) and 95% of the alate nymphs (38 of 40, Fig. 1C) were produced by sexual reproduction. Thus, *R. speratus* colonies are composed of secondary queens that are almost exclusively produced parthenogenetically by the founding primary queens, whereas workers and alates are produced by normal sexual reproduction (Fig. 1).

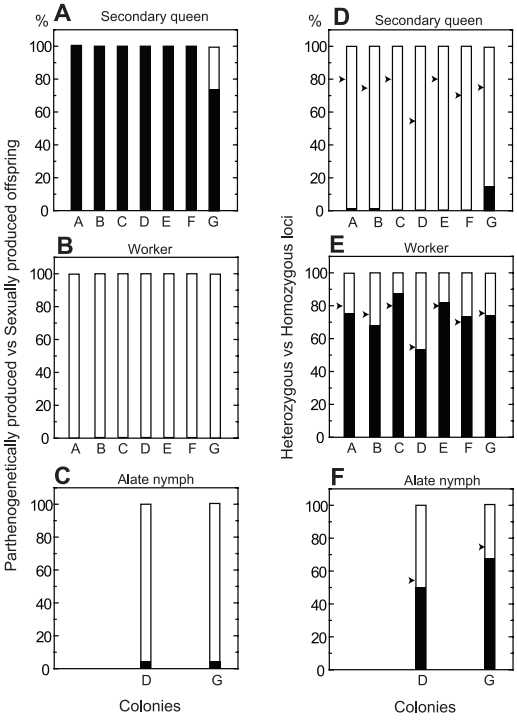

Fig. 1. Respective proportion of parthenogenetically produced offspring (black) and sexually produced offspring (white) in secondary queens (**A**), workers (**B**), and alate nymphs (**C**). Proportion of heterozygous loci (black) and homozygous loci (white) in secondary queens (**D**), workers (**E**), and alate nymphs (**F**). The amounts of heterozygosity expected for offspring produced by outcrossing of the primary king and the primary queen are indicated by arrowheads.

Heterozygosity of workers in colonies headed by secondary queens was as high ($H_o = 0.733$ over all loci) as that expected for offspring produced by outcrossing of the primary king and the primary queen ($H_e = 0.736$; G total = 8.63, df = 7, $P = 0.28$, G test; Fig. 1E). Likewise, there was no significant reduction of heterozygosity in nymphs produced in colonies with secondary queens ($H_o = 0.585$, $H_e = 0.65$; G total = 3.92, df = 2, $P = 0.06$; Fig. 1F), although occurrence of two parthenogenetic nymphs lowered overall heterozygosity somewhat. Further evidence for the lack of inbreeding in *R. speratus* colonies is provided by the low inbreeding coefficient of workers, which did not differ significantly from zero ($F_{IT} = 0.014$, $SE_{jackknife} = 0.048$, over all loci).

By using parthenogenesis to produce secondary queens, primary queens increase their reproductive output while retaining the transmission rate of their genes to descendants and maintaining genetic diversity in the workers and new primary reproductives even after they themselves are replaced (fig. S3). The lack of consanguineous matings in this breeding system may also benefit primary kings because the offspring produced by outcrossing between the king and parthenogenetic queens may have greater fitness than those produced by king-daughter inbreeding. These findings, together with similar reports from the phylogenetically distant ants (*6*–*8*), show that eusociality with its attendant caste structure and unique life histories can generate novel reproductive and genetic systems with mixed modes of reproduction that can provide important insights into the advantages and disadvantages of sexual reproduction.

References and Notes

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Supporting Online Material

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Materials and Methods
Figs. S1 to S3
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References

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