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Rare production of nymphs in an Asian subterranean termite (Isoptera: Rhinotermitidae) incipient colony

Thomas Chouvenc, Aaron J. Mullins, and Nan-Yao Su*

Termite colonies have a long life cycle, wherein the colony needs to mature before being able to invest in reproduction (Nutting 1969). Alate production occurs through several instars of nymphs (Raina et al. 2004, Chouvenc & Su 2014), and in the Asian subterranean termite, *Coptotermes gestroi* (Wasmann) (Isoptera: Rhinotermitidae), it can take up to 8 yr for a colony to mature (Costa-Leonardo et al. 2005). Nymphs are found primarily in mature colonies that are in the process of producing alates for dispersal flights (Lenz et al. 1988; Roisin & Lenz 1999; Raina et al. 2004; Albino & Costa-Leonardo 2011; Chouvenc & Su 2014). Occasionally, a few of these nymphs may become secondary or replacement reproductives within their native colony (Myles 1999). Although the replacement of primary reproductives was described from mature colonies after artificial orphaning in some *Coptotermes* species (Lenz & Barret 1982; Lenz & Runko 1993; Roisin & Lenz 2002), the production of such nymphs in young *Coptotermes* colonies has received little documentation. The only previous study, by Costa-Leonardo et al. (2004), showed that some 3-yr-old orphaned colonies of *C. gestroi* were able to produce nymphs, with the condition that larvae were present at the time of orphaning. In addition, Costa-Leonardo et al. (2004) observed that replacement by brachypterous nymphs occurred in two 3-yr-old colonies that naturally lost a primary reproductive. All nymphs obtained in the study by Costa-Leonardo et al. (2004) were apparently reproductively non-functional. This is presumably because the colonies were too immature and lacked resources to produce functional replacement reproductives. To our knowledge, it has not been observed that *Coptotermes* colonies younger than 3 yr old have the ability to produce nymphs.

In Mar 2014, 380 colonies of *C. gestroi* were established in the laboratory using the protocol described by Chouvenc et al. (2015). Briefly, 1 male and 1 female *C. gestroi* dealates were paired in a vial (8 × 2.5 cm diameter) with soil, wood, and agar. Between 9 and 10 mo after foundation, 250 colonies were opened to count all individuals. During the census, we observed that 76% of the colonies had successfully established (i.e, with both surviving primary reproductives, plus eggs, larvae, workers, and soldiers, and no nymphs observed). In the 60 colonies that were "unsuccessful," there was either no brood, no eggs, or at least one missing primary reproductive. In one of these 10-mo-old failed colonies, we observed nymphs present. This colony contained 1 male (primary reproductive), no eggs, no larvae, 43 workers, 5 soldiers, and 5 nymphs (Fig. 1). All nymphs were females and had wing buds. All individuals were transferred to a new vial, which was re-opened after 12 mo to check again for eggs or larvae, but none were found.

In a different experiment initiated in 2013, twelve 1-yr-old colonies of *C. gestroi* were orphaned by removing the queen. We observed that 1 yr after removal, 8 of the 12 colonies produced 1 or 2 neotenic females displaying visible physogastry. However, none of the 2-yr-old orphaned colonies had eggs or larvae, and all contained only visibly old individuals. In both observations, the absence of eggs and larvae in colonies that produced neotenic females suggests that, as previously observed by Costa-Leonardo et al. (2004), young *Coptotermes* colonies may not have the ability to produce fully functional replacement reproductives, possibly due to the lack of resources (Roisin & Lenz 2002) or the accelerated development of individuals (Chouvenc et al. 2014, 2015).

When compared with caste developmental plasticity of *Reticulitermes* species or other lower termites (Grassé & Noirot 1957; Buchli 1958; Greenberg & Stuart 1982), it has been established that *Coptotermes* species do not possess the flexibility to change their developmental pathway outside of particular environmental and internal cues (Chouvenc & Su 2014). The physiological trigger to produce nymphs and replacement reproductives from larvae in cases of orphaning, as previously described in mature *Coptotermes* colonies (Lenz & Runko 1993), is also true in incipient colonies (< 10 mo old), although rare. As observed in the current study and by Costa-Leonardo et al. (2004), as the colony grew older, orphaned young colonies (1–3 yr old) produced nymphs more often than orphaned incipient colonies. However, none of the neotenics observed in both studies displayed reproductive functionality. The non-functional neotenic females in incipient *Coptotermes* colonies may represent a vestigial trait wherein the pathway still exists but has lost its function, whereas it was conserved in termites such as *Reticulitermes* (Pawson & Gold 1996; Myles 1999). Such function may be regained by mature *C. gestroi* colonies that have enough resources to use such developmental pathway efficiently in order to insure the survival of the colony when in a precarious situation.

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Summary

Coptotermes colonies usually produce nymphs when a colony reaches maturity. In this study, we describe a rare case of nymph production from a 10-mo-old colony that previously had lost a primary reproductive. Such replacement reproductives are not functional. We suggest that the unusual developmental plasticity we observed may be the result of a vestigial developmental pathway that may partially regain its functionality in mature colonies.

Key Words: *Coptotermes*; replacement reproductive; neotenic; developmental plasticity

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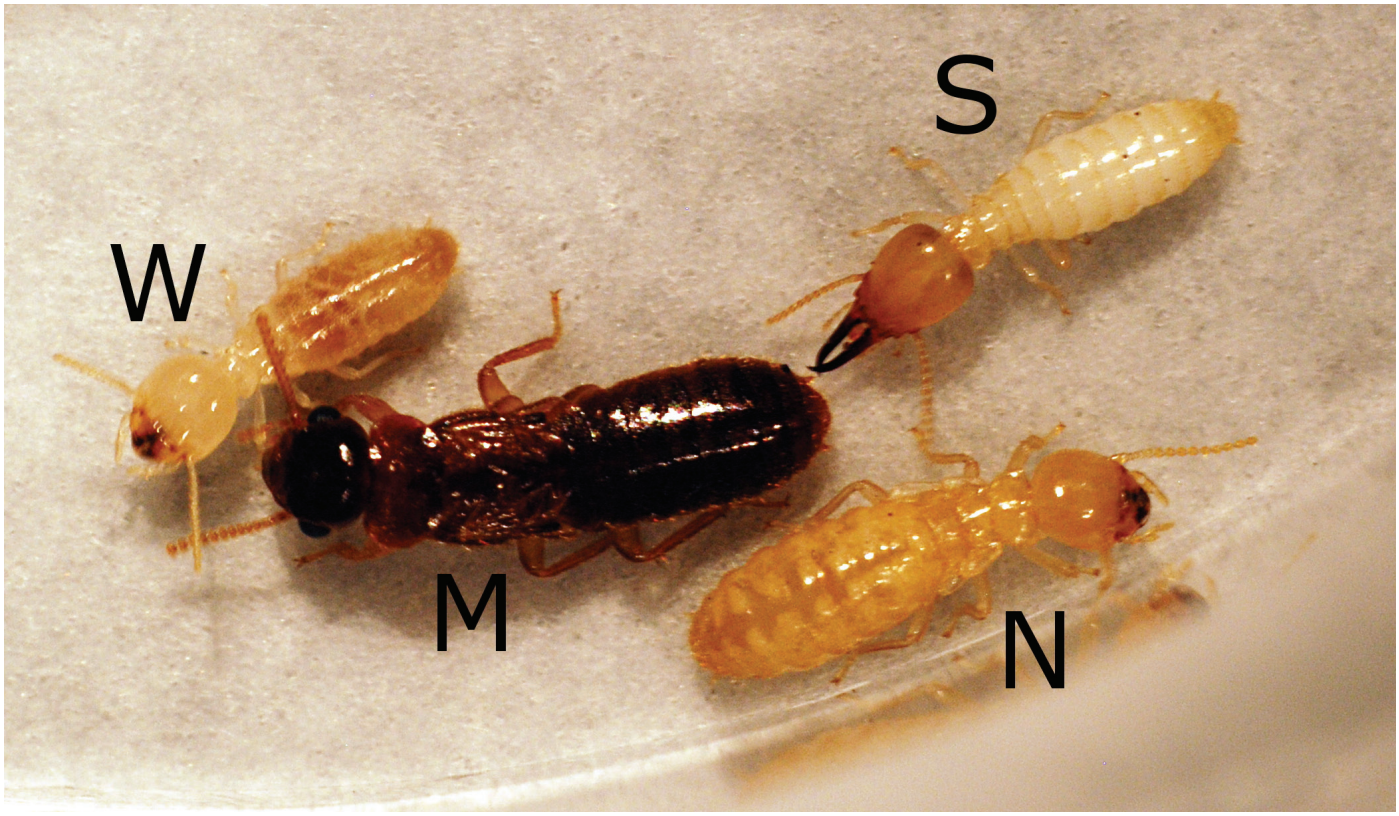


Fig. 1. Group of *Coptotermes gestroi* individuals from the only incipient colony (10 mo old) that produced nymphs in this study. W = worker, S = soldier, M = male (primary reproductive), N = nymph (with wing buds).

Sumario

Colonias de *Coptotermes* suelen producir ninfas cuando la colonia alcanza la madurez. En este estudio, se describe un raro caso de producción de ninfas por una colonia de 10 meses de edad, que anteriormente habían perdido su estado reproductivo primario. Tales reproductoras de reemplazo no son funcionales. Sugerimos que la plasticidad del desarrollo no usual que observamos puede ser el resultado de una manera de desarrollo vestigial que puede recuperar parcialmente su funcionalidad en las colonias maduras.

Palabras Clave: *Coptotermes*; reproductiva de reemplazo; neoténico; plasticidad del desarrollo

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