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Reproductive strategies and community structure of New Guinean arboreal nesting termites^{*,**}

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Abstract

Colonies of Microcerotermes biroï, an arboreal nesting termite, generally headed by a pair of dealated imagos (84% of colonies in coconut plantations), spread by large nuptial flights which allow a fast colonization of new habitats. Replacement reproductives, which are nymph-derived and transitorily worker-derived, were found in 16% of the colonies in the field and presumably differentiated in response to the death of the primary reproductives or to the isolation of a satellite nest from a parent nest (budding). M. biroï reproductive strategy allows it to preempt the habitat with many small colonies and to be the most common species in coconut plantations despite the fighting superiority of main competitor Nasutitermes princeps which exhibit a propensity to build very large nests and to propagate by budding. Differences in each species reproductive strategy was one of the major factor explaining the observed community structure.

Key words: Termites, Reproduction, Ecology, Papua New Guinea.

Introduction

The purpose of this paper is to show how it is possible to infer the mode of colony formation from the number and type of reproductives found in termite nests and to stress the importance of reproductive strategies in the shaping of a community structure. As an example, we will focus on the analysis of the reproductive mechanism of *Microcerotermes biroï*, a termite found in new guinean coconut plantation together with two other arboreal nesting termites: *Nasutitermes princeps* and *N. novarumhebridarum* (ROISIN *et al.*, 1987, LEPONCE *et al.*, 1995, 1996a).

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Fig. 1. Reproductive forms. A: *Microcerotermes biroi* alate; B: *Nasutitermes princeps* adultoids derived from alates in the nest (2 individuals on the left, notice the wing scales on thorax) or from precocious differentiation of nymphs (microimago, individual at center, notice the short wings), S: pear shaped head soldier; C: *M. papuanus* worker-derived replacement reproductive (ergatoid, notice the absence of wings and the dark pigmentation); D: Nymph-derived replacement reproductives (notice the wing buds) in *M. biroi*: K: king, Q: queens. Other castes: L1: first instar larva, L2: second instar larva, W: worker, S: mandibulate soldier, N: nymph.

Basically new termite colonies are founded by alates which leave an existing mature colony in swarms (Fig. 1A). After the nuptial flight alates pairs shed their wings and start to build a new nest. As a rule, new colonies are founded by a single pair of alates although in some species multiple alates are sometimes found (pleometrosis) (WEYER, 1930; NOIROT, 1985; THORNE, 1985; DARLINGTON, 1985, 1988; ROISIN, 1993). Imagos which found a colony after a nuptial flight (primary reproductives) are fully pigmented and have well cut wing scales (wings break across a suture during dealation). By contrast, secondary reproductives differentiate in their parental colony after the dead (replacement reproductives) or a drop in the fertility (supplementary reproductives) of the primary reproductives. In species where colonies are composed of multiple nests, secondary reproductives may differentiate in a satellite nest (budding) when the connection with the main nest is broken or when the distance from the main nest reduces the influence of the functional reproductives. Secondary reproductives may arise from alates in the nest (adultoids), nymphs (nymphoid neotenic) or workers (ergatoid neotenic). Adultoids are morphologically indistinguishable from primary reproductives although their wings are sometimes imperfectly shedded or shorter and their pigmentation weaker (Fig. 1B). Ergatoids differentiate from workers and therefore never develop wings (Fig. 1C). Nymphoids lack wing scales but are recognizable by the presence of wing buds (Fig. 1D). As a rule, secondary reproductives are generally present in large number especially at the beginning of the replacement process. The capacity of each caste to differentiate into secondary reproductives varies largely from one species to another.

M. biroi, *N. princeps* and *N. novarumhebridarum* build their nests on trees in New Guinea coconut plantations. They exclude each other from the coconut tree, used as nesting site and food source (ROISIN *et al.*, 1987; LEPONCE *et al.*, 1995, 1996b, 1997). *N. princeps* builds large nests which may reach up to 300 dm³ (LEPONCE *et al.*, 1995). One colony may be composed of several nests: a parent nest with reproductives (originally a pair of imagos) and one or more satellite nests (ROISIN *et al.*, 1987). *N. princeps* is characterized by an exceptional proportion of polygynous (multiple queen) colonies (60%) (ROISIN, 1987). Polygyny may result from the replacement of primary reproductives or from colony budding (ROISIN & PASTEELS, 1986a). Colony budding seems to be common in *N. princeps*: tests of antagonism between workers and analysis of the soldier defensive secretion coming from neighbor nests headed by reproductives often reveal a lack of antagonism and chemical similarities suggesting that these multiple nests are genetically very close and share a common origin (ROISIN *et al.*, 1987, LEPONCE *et al.*, 1997). Neotenic in *N. princeps* are adultoids or pseudimagos (nymphs which shortened their development to become replacement reproductives) (ROISIN & PASTEELS, 1986a, b). *N. princeps* caste composition includes a unique form of short winged alates, called microimagos (Fig. 1B) (ROISIN & PASTEELS 1985), unable to fly. *N. novarumhebridarum* builds smaller nests than *N. princeps* (maximum 85 dm³, LEPONCE *et al.*, 1997) and field colonies are always headed by a primary

pair (ROISIN & PASTEELS, 1987). Replacement reproductives in artificially orphaned colonies are worker-derived (ergatoids).

M. biroi is the most common species in the habitat (relative abundance: 87% of the arboreal nesting termites, *N. princeps*: 10%, *N. novarumhebridarum*: 3%; LEPONCE *et al.*, 1995) despite the aggressive superiority of the two *Nasutitermes* species, especially of *N. princeps* which usually invades neighbor *M. biroi* nests during the expansion of its territory (LEPONCE *et al.*, 1997). The fact that *M. biroi* is the most common species in the habitat and that its nests are secondarily invaded by main competitor species *N. princeps* and, to a lesser extent, *N. novarumhebridarum* suggest that *M. biroi* is the first colonizer of the habitat. To test this hypothesis *M. biroi* dispersal ability was investigated. To estimate the relative importance of nuptial flights and budding in colony propagation it was necessary to determine the ability of *M. biroi* to replace its reproductives in parent nests and in satellite nests and to compare the type and number of reproductives obtained under these conditions with those found in field colonies. Additionally, dynamics of colonization and colony growth were studied by monitoring a coconut plantation initially devoid of arboreal nesting termites.

Methods and results

Ability of *M. biroi* to replace its reproductives

Fourteen nests headed by a pair of imago were orphaned (removal of the reproductives). The royal cell was first localized by cutting the lateral edges of the nest with a machete and looking for the presence of the nursery, always near the royal cell, where eggs and young larvae are concentrated. The royal cell was then removed and the reproductives collected together with a sample of the nest population fixed in FAA (formaldehyde: alcohol: acetic acid) and preserved in ethanol 70%. Twelve months later, 11 out of the 14 (79%) nests were found containing replacement reproductives: mainly nymphoids sometimes accompanied by ergatoids. Adultoids never differentiated even in nests initially containing alates. One nest died and 2 others were found without replacement reproductives.

To test if replacement reproductives would develop in satellite nests (without reproductives), all nests containing reproductives were entirely removed from a one-hectare quadrat. A sampling of each satellite nest population at that time revealed that some contained nymphs and/or alates additionally to the neuter population of workers and soldiers. Sixteen out of the 29 (55%) satellite nests revisited 9 months later were found containing secondary reproductives: mainly nymphoids sometimes accompanied by ergatoids.

Frequency of the reproductive forms in field colonies

All nests were systematically dissected in two one-hectare quadrats. A pair of imago (a king and a queen) were found in 114/136 (84%) of the

nests containing reproductives. The others 22 nests contained nymphoids. Ergatoids were never observed.

Dynamics of colonization of the habitat by *M. biroi*

A young, 10 years old, coconut plantation initially devoid of arboreal nesting termites was monitored. In 3 1/2 year 63% of the trees were colonized by *M. biroi*. Neither *N. princeps* nor *N. novarumhebridarum* colonies were observed during this period.

Discussion

M. biroi showed a good ability to replace its primary reproductives in the parent or even in satellite nests demonstrating the possibility of colony budding. Secondary reproductives differentiated from nymphs and also sometimes from workers at the beginning of the replacement process. Since adultoid replacement reproductives never differentiated in *M. biroi* colonies artificially deprived of their reproductives, the imaginal pair found heading 84% of the field colonies can be interpreted with confidence as the primary reproductives. The 16% of colonies left, which contained nymphoids, were either buds or colonies where the primary pair was replaced. *M. biroi* thus seems to rely much more on nuptial flights than on budding to propagate its colonies. The fast colonization of the site initially devoid of arboreal nesting termites (63% of the trees colonized in less than 3 1/2 years) and the fact that *M. biroi* was the sole species present support the hypothesis that *M. biroi* is a pioneer species.

Occasional competitor *N. novarumhebridarum* also reproduces by nuptial flights but is attracted by dead trees (ROISIN & PASTEELS, 1987; LEPONCE *et al.*, 1995), a resource rare in coconut plantations, and even scarcest in young plantations, probably explaining why this species despite an effective dispersal strategy is not widespread in the habitat. *M. biroi*' main competitor *N. princeps* tends to build very large colonies produced by polygynous (multiple-queen) associations of adultoids and invests on budding to propagate its colonies as illustrated by the presence of microimagos, unable to fly but ready to become functional reproductives in the parent colony. This strategy added to its superior aggressivity allow this late colonizer to establish and expand in an habitat already largely preempted by *M. biroi*. In conclusion, the reproductive strategy of each species appear as a key component to understand the community structure.

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