REPRODUCTIVE PLASTICITY IN THE NEOTROPICAL TERMITE *NASUTITERMES CORNIGER*

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SUMMARY

Colonies of the arboreal Neotropical termite *Nasutitermes corniger* display an exceptionally diverse combination of reproductive patterns. Colonies can be monogynous or polygynous. Independent alates can initiate nests, or daughter colony «buds» can split from a parent nest. A dead queen or king is replaced either by alates within the nest, or by ergatoid reproductives developed from workers. This degree of intraspecific plasticity is a new finding among the Termitidae, and such marked flexibility is rare among the eusocial insects as a whole.

RESUMEN

Plasticidad reproductiva en la termita neotropical *Nasutitermes corniger*

Las colonias de termitas arboreas neotropicales *Nasutitermes corniger*, despliegan una combinación exceptionalmente diversa de patrones reproductivos. Las colonias pueden ser monogénicas o poligénicas. Aladas independientes pueden iniciar nidos, o los jóvenes de la colonia hija pueden dispersarse del nido de sus padres. Una reina o un rey muerto

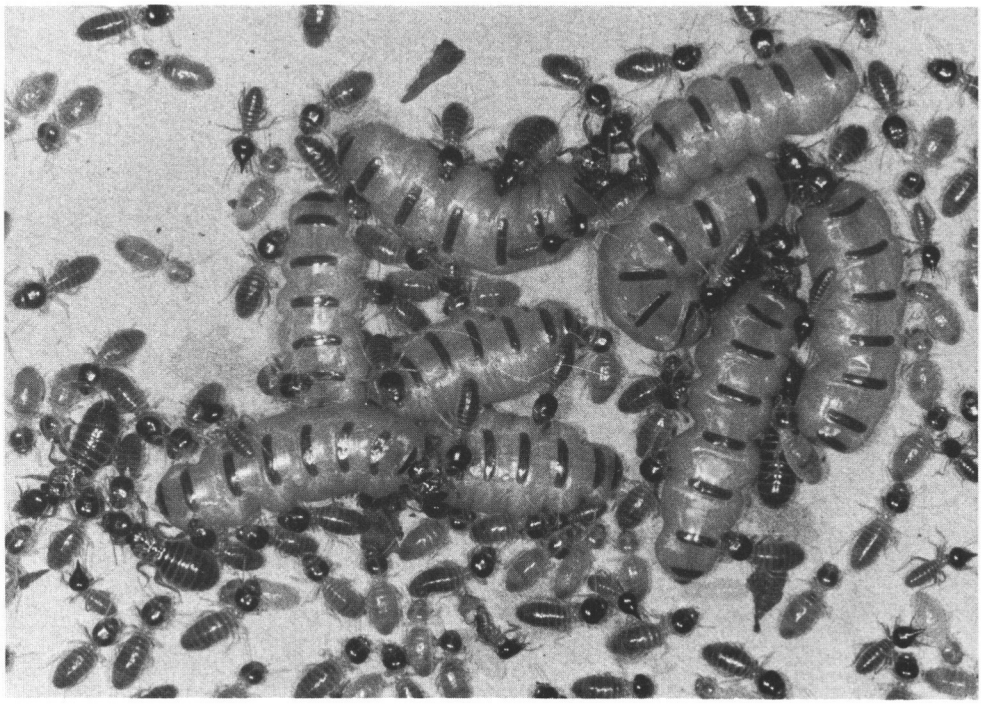

Fig. 1 – Nine primary queens and four primary males found in a *Nasutitermes corniger* colony collected May 22, 1980 in Frijoles, Republic of Panama.

Fig. 1 – Nueve reinas primarias y cuatro machos primarios encontrados en una colonia de *Nasutitermes corniger* colectada el 22 de mayo de 1980 en Frijoles, República de Panama.

pueden ser remplazados ya sea por alados dentro del nido o por suplementos (ergatoid) reproductivos desarrollados a partir de obreras. Este grado de plasticidad intraespecífica es nuevo desenvolvimiento dentro de los *termitidea* y esta marcada flexibilidad es rara dentro de los insectos eusociales como un todo.

Eusocial insects exhibit a diverse array of reproductive patterns. Colonies can be founded by one or more reproductives (*independent founding*) or by reproductives joined by a group of sterile workers (*budding* or *swarming*). Some mature colonies have a single queen (*monogyny*), others have two or more fecund queens concurrently (*polygyny*). The number of queens may change over the life cycle of the colony (Hölldobler & Wilson, 1977 ;

Oster & Wilson, 1978 ; West-Eberhard, 1978a, b). If the queen dies, she may be replaced by a young reproductive, or members of the worker caste may develop functional ovaries and become egg layers. Despite the plasticity across the eusocial insects as a whole, the reproductive organization within any single species of ant, bee, wasp or termite is usually restricted. Frequently there is no intraspecific flexibility in mode of colony foundation : species with independent founders may not be capable of swarming, and vice versa (Evans & West-Eberhard, 1970 ; Spradbery, 1973 ; Hölldobler & Wilson, 1977 ; West-Eberhard, 1978b). Many species are obligately monogynous (Hölldobler & Wilson, 1977 ; West-Eberhard, 1978b). Queen replacement is often solely via young reproductives because workers in a number of species are irreversibly sterile (Wilson, 1971).

This paper describes the first case of a higher termite with intraspecific expression of the entire diversity of principal reproductive options. Colonies of the Neotropical termite *Nasutitermes corniger* (Motschulsky) studied in second growth areas of the Republic of Panama (Frijoles and the Gigante Peninsula, former Canal Zone) are sometimes founded by mating pairs and sometimes by buds from a parent nest. Reproductively mature colonies have from 1-22 fully physogastric primary queens, and occasionally more than one king (Dudley & Beaumont, 1889a, b, 1890 ; Dietz & Snyder, 1923 ; Thorne, 1982)[1] (see Figure 1). Available data suggest that in polygynous colonies the number of queens is reduced over time. Colonies can be re-queened or re-kinged with young reproductives, or less frequently, ergatoid (third-form) reproductives develop from workers (Thorne & Noirot, 1982). These broad alternatives in reproductive method and organization give *N. corniger* a marked ecological flexibility (see Figure 2).

The ellipsoidal nests of *Nasutitermes corniger* are constructed of a network of carton galleries surrounding a very dense queen cell. Large workers, small workers and nasute soldiers compose the non-reproductive «neuter» castes. A large *N. corniger* nest harbors a neuter population of from 500,000 - 800,000 individuals[2]. Alates, the fertile winged reproductives, are produced once a year and fly during the early rains of the wet season (April - June) (Dudley & Beaumont, 1889b ; Dietz & Snyder, 1923 ; personal observation). Independent founding is the most common mode of colony foundation in *N. corniger*. Alates fly from the parent nest, land to find a mate, drop their wings and depart to search for a nest site where they will start new colonies. Alternatively, new *N. corniger* colonies can be formed by budding, a process described only rarely in the order Isoptera (reviewed in Nutting, 1969). In four cases, mature *N. corniger* colonies were observed to form daughter «satellite» nests located within 2 m of the original nest, and initially connected by covered trails to the parent colony. The young satellite nests expanded

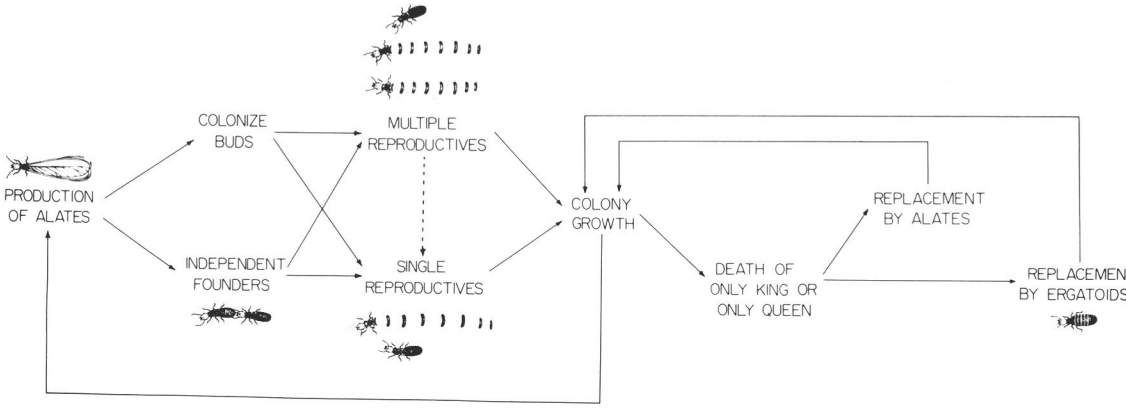

Fig. 2 —Life history flexibility in *Nasutitermes corniger*. Not all pathways are followed with equal frequency. The number of queens in polygynous colonies may decrease as individual queens grow larger, but that transition line is tentative (dashed) because there is only circumstantial evidence of its occurrence.

Fig. 2 – Flexibilidad de la historia natural de *Nasutitermes corniger*. No todas las secuencias son seguidas con la misma frecuencia. El número de reinas en las colonias poliginas puede decrecer pero en este caso son individualmente más voluminosas ; la línea de transición es tentativa (discontinua) porque solamente hay evidencias circumstanciales de su ocurrencia.

rapidly, the population growth being accelerated by immigration of neuters from the original nest[3]. Alates were produced in three of the parent colonies[4]. One or more alates of each sex did not fly, and instead moved into the new nest bud, apparently to assume reproductive status[5]. In a separate case, an *N. corniger* colony of unknown history was collected six weeks after the alate flights in 1979. It was full of mature soldiers and workers, but had no eggs, no immatures, and five young de-winged alates (three females ; two males). The nest was small and constructed of thin carton. That colony was probably a bud as well.

Independent founders can disperse to distances far from the parent nest. As a consequence, they do not draw away energetically costly mature neuters from their mother's colony. Alates joining buds begin their colonies with a pre-existing neuter support staff capable of getting food, defending and expanding the nest, and caring for new brood. For these reasons, the growth rate and probability of survival of the buds may be significantly higher than in colonies of the same age founded by independent alates.

Formation of satellite buds in *N. corniger* is ecologically distinct from «accidental» fracture of a colony and subsequent maturation of neotenics in the queenless portion, a process occurring in a number of termite species (reviewed in Nutting, 1969). *N. corniger* budding is an active, deliberate division (similar to the «sociotomy» reported in *Anoplotermes* sp. and *Trinervitermes bettoniamus* Sjöstedt by Grassé and Noirot, 1951). The reproductives which head the newly budded *N. corniger* nests are dewinged alates (primary reproductives).

Most termite species are reported to be exclusively monogynous and monoandrous : colonies have a single pair of primary reproductives, the queen and the king. Of 69 dissected *Nasutitermes corniger* nests with *at least one* queen, 21 colonies had *multiple* primary queens, and two had multiple primary kings[6]. Polygyny involving primary queens has been documented only rarely among the Isoptera (reviewed in Thorne, 1982), and never in the relatively high frequency found in *N. corniger*. Reproductives in each *N. corniger* colony were always found in the same queen cell, either all in the same chamber or divided among adjoining chambers. Each queen in a polygynous association is a functional egg-layer. Mature (alate producing) colonies can be polygynous. No signs of aggression have been observed between queens from a single colony, although laboratory observation conditions are not comparable to the nest environment. Monogyny is not found exclusively in large colonies ; polygyny is not restricted to small colonies.

The maximum wet weight recorded for a monogynous *N. corniger* queen was 0.5565 gms. The largest queen found in a polygynous nest weighed 0.3114 gms. In polygynous colonies with small queens (arbitrarily defined as $\leqslant 0.15$ gms), all females are of approximately the same size and weight. However, as the mean weight of queens within a polygynous group increases, so does the difference between their weights ($r = 0.676$; $p < .001$). When large numbers of queens are found in a single nest, all are usually small. Eight of the eleven polygynous colonies with a queen under 0.15 gms contained from 3-22 queens. Polygynous nests with larger queens tend to have fewer of them. Of the 10 polygynous colonies containing at least one queen weighing over 0.15 gms, only one had more than two queens. These data suggest that as individual queen size increases in polygynous colonies, the number of queens may be reduced[7].

The method of formation of polygynous *N. corniger* colonies, and thus the kin relationship among multiple reproductives, remains unclear. Available data imply that polygynous colonies can be initiated either by multiple independent founders or by a group of alates colonizing a bud. Three polygynous nests (containing 9, 10 and 18 queens respectively) were collected in Frijoles in April - June 1980. None of these nests were observed a year earlier in

an area I frequented constantly during the study. Each nest was isolated (> 150 m) from the nearest mature conspecific colony. All three nests were small to moderate in size ; none had dense carton construction (hard, heavily reinforced carton indicates an older nest). These colonies were probably initiated by a group of alate foundresses. Kin relationships among the queens are unknown. In the lab, alates from the same colony (sibs) or from different colonies will occupy lesions in wood (nesting sites) in groups of more than a single male-female pair. Successful colony initiation was never achieved in such experiments, but in one compartment in the center of a piece of wood I found 93 *N. corniger* alates (fungus growth present at the time of monitoring obscured genitalia and prevented a count of sex ratio). In a nest choice experiment involving only sibs, 20 male and 15 female alates were found in the same cavity. Because of the technical difficulties involved in following the ontogeny of a single colony over time without destructive sampling, precise tracking of polygynous associations is impossible. Nevertheless, it appears that colony foundation by a group of alates is possible as one route to polygyny. Buds seeded with more than one female alate may also form polygynous colonies. In such cases, all queens are definitely sibs, or half-sibs if the parent colony was itself polygynous (see Thorne 1982 for a related example in *N. ephratae*).

N. corniger colonies respond to king or queen death in one of several ways. If the neuter population size is small, the colony may not be able to replace a reproductive. Even if an alate egg or nymph is present, its development process takes several months. During that time colony health may be in jeopardy because no eggs are produced to replace the declining neuter population. If the king or queen dies when a mature colony has alates (or alate nymphs), it is probable that one or more of the alates will succeed the dead parent (such replacement reproductives are termed *adultoid* reproductives (Noirot, 1969)). Queen replacement by daughters has been documented in several species of Termitidae (reviewed in Noirot, 1969 ; Darlington, unpublished data). To unambiguously demonstrate this process, one must induce it experimentally (by queen removal : Coaton, 1949 ; Noirot, 1969 ; Darlington, unpublished data) or chance upon replacement in progress at the time of colony dissection.

I have circumstantial evidence for offspring replacement of parents (adultoid reproductives) in *N. corniger*. Of 29 colonies with at least one king, collected within six weeks of the major alate flights, seven (24.14 %) had from 2-13 de-winged males in or near the queen chamber. Four of these colonies were monogynous. The frequency of multiple males fell off sharphy in colonies dissected out of alate season (October - January). Of 31 nests with at least one king collected during that interval, only two (6.45 %) contained

multiple males. Both colonies also had small multiple queens. The marked increase in number of colonies with multiple male during alate season suggests that the additional males are temporary. Several male alates remain in the nest after the alate flights : eventually one will replace the old or dead king.

Several colonies seemed to be in the process of queen replacement at the time of dissection. Occasionally a relatively small queen is found in a large colony, or several de-winged female alates are found in a queenless colony. However, unambigous succession of a mother by her daughter in *N. corniger* must be demonstrated experimentally.

King replacement is expected to be more frequent than queen replacement. The wet weight of a mature king ($\bar{x}$ = .0102 gms., s = 0.0012, N = 31) is only slightly more than the wet weight of a male alate ($\bar{x}$ = 0.0097 gms.[8]). In contrast, the size of an *N. corniger* queen increases markedly from alate wet weight ($\bar{x}$ = 0.0121 gms.[8]) to size of maximum fecundity (largest queen wet weight found in this study = 0.5565 gms.). The time and energy investment in a physogastric queen is significant. When a large queen is replaced by a young alate, egg production drops dramatically (Thorne, 1982). The high rate of egg production will be restored only after a costly time lag accomodating the new queen's growth.

One queenless colony of *N. corniger* was collected on December 14, 1979 on the eastern side of Gigante peninsula while both large and small workers (approximately 770 individuals) were in the process of differentiating into ergatoid reproductives (large workers are females ; small workers are males). The remaining neuter population (estimated to include approximately 20,600 workers, soldiers and immatures) were phenotypically unchanged. Histological analysis (Thorne & Noirot, 1982) revealed that none of the ergatoids had reached maturity at the time of collection, although immature sexual organs were distinct. Ergatoid reproductives have been found only rarely in the Nasutitermitinae (Noirot, 1956). The environmental conditions inducing ergatoid formation in *N. corniger* are unknown, but it is significant that this developmental channel is open in this species.

DISCUSSION

The termite *Nasutitermes corniger* has an exceptionaly plastic intraspecific reproductive repertoire. Colony foundation can involve alates alone, or both alates and neuters in satellite buds from an established nest. Both monogyny and polygyny occur in this species. The number of queens in polygynous colonies appears to decrease as individual queens grow larger. Queens and kings can be replaced either by young alates or by ergatoid

(worker-derived) reproductives. Thus all major binary «either/or» gates for eusocial insect reproductive cycles are open in *N. corniger*. Some pathways are followed more frequently than others, but the developmental and ecological flexibility present in the system is remarkable. It is hypothesized that the exceptional plasticity of this phylogenetically advanced termite has enabled colonies to successfully adjust to variable microhabitats, disturbed conditions, and to recover from individual historical accidents.

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Footnotes

1 Primary (first-form) reproductives develop from mature alates. Second-form (brachypterous) reproductives common in some species of termite are unknown in *Nasutitermes corniger*.

2 These and other nest data given in this paper are based on complete dissections of entire *N. corniger* nests, excluding foragers outside the nest. Colonies were collected, sealed in large plastic bags, and refrigerated to induce torpor in the termites. Estimates of population size and caste composition were made from volumetric subsamples. Standard errors were consistently less than 10 % of the estimates.

3 Members of the parent and satellite nests do not fight when placed together. This compatability demonstrates that they are members of the same colony (reviewed in Thorne, 1982).

4 It is possible that the alate brood in the fourth parent colony was aborted after formation of the bud commenced. The satellite nest connected with that colony stopped expanding after a few months, and was relatively small at the time of dissection.

5 At the time of nest dissections none of the young reproductives in any of the buds had begun laying eggs, although many had shed their wings and were clustered around a crude queen cell (probably of recent construction). Since nest dissection is irreversibly destructive, it is impossible to follow the progress of the satellite colonies after sampling. All colonies were dissected after the peak alate flights of *N. corniger*, but apparently sexual maturation of alates inhabiting buds occurs well after that time.

Young alates of the closely related sympatric species *N. ephratae* did develop functional ovaries in a queenless colony composed of workers and soldiers (Thorne, 1982).

6 Colonies with multiple males considered to be in the process of king replacement are excluded from this count, and are discussed later in the paper.

7 Because no data exist on the relationship between queen size and age, it is difficult to obtain an exact description of this process. However, since egg production is proportional to queen weight (Thorne, 1982), selection will favor large queens (assuming that the ratio of alate : neuter eggs is constant or increasing with weight). The method of queen reduction is completely unknown.

8 Calculated as the mean of the average weight of alates from 10 colonies.

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