

Foraging strategies and defence mechanisms of termite species (Isoptera) in the Western Australian wheatbelt.

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Abstract

This study investigated the relationship between foraging strategies (reflecting exposure to predation) and mechanisms of defence for termite species in the Western Australian wheatbelt. Of 38 species studied, 17 were primarily harvesters (facing presumptive high levels of predation). All harvester species defended themselves with abundant soldiers using either chemicals (Nasutitermitinae), or a combination of chemicals and prominent mandibles (*Drepanotermes* sp., *Amitermes neogermanus*). Of 21 wood-eating species (facing presumptive lower levels of predation), the majority (71 %) relied on the mandible defences of relatively rare soldiers. Exceptions were wood-eating *Coptotermes* and *Schedorhinotermes* (Rhinotermitidae), and *Nasutitermes* and *Occasitermes* (Nasutitermitinae), which had more numerous soldiers with either a mixed chemical-mandibulate defence (Rhinotermitidae), or a chemical defence (Nasutitermitinae). Such defences are consistent with the defences of the rhinotermitids and nasutitermitids in general, regardless of foraging strategy. The relationship between predation risk and mechanism of defence is best exemplified by the endemic harvester genus *Drepanotermes*, which has evolved from the almost cosmopolitan, predominantly wood-eating, *Amitermes*. By filling the large harvester niche in arid and semi-arid Australia, *Drepanotermes* appears to have evolved large size in both workers and soldiers, and an abundant soldier caste displaying prominent mandibles as well as an effective means of chemical defence. The observed relationship between foraging strategies and defence mechanisms resembles observations made on South American species but does not necessarily apply to the termites in general. It also does not necessarily imply a causal relationship between foraging strategy and mechanism of defence. Potentially profitable areas of future research are identified.

Introduction

The diet of termites is often complex but consists principally of cellulose in various forms, be it living, dead but sound, or decomposed vegetation (including dung), humus or soil, or various combinations of the above (Wood 1978). However, from the view of susceptibility to predation, what is more important to termites than what they eat is how they obtain their food.

As in most organisms, foraging is associated with some risk of being eaten. Animals reduce the risk of predation by a variety of strategies such as choosing appropriate places and times for foraging, or by evolving morphological or chemical adaptations for defence. Defence strategies in termites are either mandibulate where soldiers are equipped with large mandibles (Deligne 1965); chemical, where secretions may be toxic, sticky or of repulsive odour (Quennedey 1975); or a combination of chemicals and mandibles (Blum *et al.* 1982). Most studies have emphasized chemical types of defence (see Prestwich 1988 for a review), as have most Australian investigations (Moore 1969, McMahan 1974, Eisner *et al.* 1976). Mandibulate, chemical and mixed chemical-mandibulate defence strategies are also prevalent in the termites of the Western Australian wheatbelt (Abensperg-Traun 1988, Abensperg-Traun *et al.* 1991).

Two broad termite foraging strategies are apparent. (1) Harvesting grass or other plant debris on the soil surface where exposure to predators such as ants and lizards is high; (2) *in situ* consumption of wood. By foraging within their

food source, to which predators are likely to have restricted access, such termites may experience lower levels of predation. If termites are as well defended as they need to be for the successful exploitation of such variably hostile foraging niches, one might expect termites that exploit such different niches to also differ in their mechanisms of defence.

Studies of the relationships between termite foraging strategies and their mechanisms of defence are scarce. Coles de Negret & Howse (1983) found that defence type corresponds with levels of predation for termites from parts of Brazil. Heavily predated harvester species have abundant soldiers with chemicals, whereas lightly-predated non-harvesters have few mandibulate soldiers. The relationship between foraging strategy and mechanism of defence in Australian termites has not been examined. Using the termites from the Western Australian wheatbelt, the present study tests two predictions: (1) harvester termites are heavily defended; (2) wood-eaters are lightly defended.

Study Area and Methods

Observations were made in Durokoppin (31°24'S, 117°45'E) and Kodj Kodjin (31°27'S, 117°47'E) Nature Reserves of the Western Australian wheatbelt during a study of the foraging ecology of the echidna from 1987 to 1989 (Abensperg-Traun 1990). Termite colonies were sampled in a variety of microhabitats (soil, timber, mounds), and observations regarding foraging strategy (harvesting, wood-eating) and defence mechanism were noted. Estimated numbers of colonies sampled are given for respective species. The

foraging strategy of wheatbelt termites has been discussed in earlier papers, as have been characteristics of the study area such as climate, vegetation and soils (Abensperg-Traun 1988, Abensperg-Traun 1991, Abensperg-Traun & De Boer 1990, Abensperg-Traun *et al.* 1991). By examining termites in the very broad harvester vs. non-harvester categories, I ignore potentially important, but unknown differences in the foraging strategies of individual species.

Defence mechanisms (chemical, mandibulate or mixed chemical-mandibulate) of the study species are based largely on published data which are comprehensive for the majority of taxa discussed. For instance, all Nasutitermitinae (*Tumulitermes*, *Nasutitermes*, *Occasitermes*) have chemical defence (Prestwich 1988), whereas *Coptotermes*, *Schedorhinotermes* and *Drepanotermes* combine large mandibles with chemical secretions (Moore 1969, Quennedey 1975; Blum *et al.* 1982). My observations on soldier defence were directed at detecting chemical secretions at sampling time. Droplets of soldier secretions from the fontanelle, an opening on the forehead, are either clearly visible (when carried between the mandibles, or after solidifying when placed into 75 % ethanol), or are apparent by odour. The abundance of termite soldiers for respective species at collection time was ranked from 1 (scarce) to 4 (abundant) rather than counted because reliable, accurate caste ratios are difficult to obtain, particularly for rare species, and generally require destructive methods such as the excavation of the entire colony. The approximations as given here are sufficient for the purpose of the present study. Mean head capsule widths of soldiers and workers, as a measure of body size, were determined from five specimens for each study species. Only those species are discussed for which adequate foraging and defence data are available.

Results

Harvester termites

Numbers of colonies of harvester termites sampled range from < 20 colonies for rare *Tumulitermes* sp. to > 100 for three *Drepanotermes* sp. and *Amitermes neogermanus* (Table 1). All harvester termites were heavily defended, upholding the study prediction. Of the 38 species studied (Table 1), 12 *Tumulitermes* sp., four *Drepanotermes* sp. and *Amitermes neogermanus* (Termitidae) were harvesters, and all possessed a chemical defence with either small but very abundant soldiers (*Tumulitermes* sp.) or a mixed chemical-mandibulate defence with abundant but larger soldiers (*Drepanotermes* sp.) (Fig 1). Harvesters made up 45 % of the species studied, although three species also ate wood. Defence in *Tumulitermes* soldiers (indeed in all nasutitermitids) involved the shooting of a sticky thread from the nasus (Fig 2A). Similar to *Drepanotermes* sp., *Amitermes neogermanus* soldiers readily secreted a droplet of clear fluid from the fontanelle, which was carried between the mandibles. However, the secretion was only mildly odorous, unlike that of *Drepanotermes* soldiers which is strong, reminiscent of oranges. The workers and soldiers of the endemic obligate harvester *Drepanotermes* sp. were larger than their caste equivalents of the predominantly wood-eating *Amitermes* from which they originally evolved (Fig 1).

Wood-eaters

Numbers of colonies of wood-eaters sampled (Table 1) range from < 10 colonies (*e.g.* *Amitermes heterognathus*) to > 100 colonies (*e.g.* *Coptotermes acinaciformis*). Of the 21 termite species known to be predominantly wood-eating, 15 species (71 %) were lightly defended, depending on mandibulate soldiers for colony defence (Table 1). Such soldiers were both intermediate in size (Fig 1), and rare (Table 1). Their mandibles (Fig 2) were either short and stout (*Amitermes* sp., *Coptotermes* sp., *Heterotermes* sp., *Microcerotermes* sp., *Schedorhinotermes* sp.), or long and slender (*Ephelotermes argutus*, *Paracapritermes kraepelini*, *Xylochomitermes occidualis*). Species that were more heavily defended, and thus did not uphold the study prediction, had either more numerous, larger soldiers with a mixed chemical-mandibulate defence (Rhinotermitidae), or very abundant, but small soldiers with a chemical defence (Nasutitermitinae). *Coptotermes* soldiers secreted a droplet of milky fluid when disturbed. Chemical defence in *Schedorhinotermes* was not detected. A single soldier each of the common wood-eaters *A. obeuntis* (> 100 colonies sampled), *A. dentosus* (> 50 colonies) and *A. calabyi* (> 50 colonies), respectively, was observed to secrete chemicals from the fontanelle at collection time; their secretions solidified into a whitish mass when placed into 75 % ethanol.

Discussion

Harvesters

As predicted, all harvester termites were heavily defended. *Tumulitermes* sp. soldiers have evolved the highly specialized chemical defence (typical, and exclusive to Nasutitermitinae), of squirting a viscid secretion from their nozzle-like frontal gland (Fig 2A). Soldiers thus need not make physical contact with the predator to transmit the chemical. The soldiers are very small (Fig 1), each weighing as little as 1 mg fresh weight (Abensperg-Traun 1990), but (as in all species of Nasutitermitinae) comprise a significant proportion of the colony population (Haverty 1977). Reliable soldier: worker ratio estimates for Australian "nasute" termites (species in which the head-capsule forms a nasus) are limited to wood-eating *Nasutitermes exitiosus* in which the natural proportion of soldiers is estimated at ~ 15 % (Moore 1969); this is within the upper range of soldier:worker ratios of known species (Haverty 1977).

Gay & Calaby (1970) state that all species of *Tumulitermes* are harvesters. Evidence from the Western Australian wheatbelt supports this, although some species have a mixed diet of harvested material and wood, eaten *in situ* (Table 1). There are no published soldier:worker ratio estimates for harvester *Tumulitermes* sp. For one of its southern African ecological equivalents, the harvester *Trinervitermes trinervoides* (Nasutitermitinae), soldiers make up ~ 32 % of the foraging termites, which is significantly higher than their proportion within the nest (Skaife 1955, Richardson 1987).

Other (non-nasute) harvesters were also heavily defended by combining prominent mandibles with chemical secretions of abundant soldiers. They included four species of *Drepanotermes* and *A. neogermanus*. All known species of *Drepanotermes* are obligate harvesters (Watson & Perry 1981). *Amitermes neogermanus* is predominantly a harvester (storing

Table 1.
Foraging strategies and defence mechanisms of
termite species in the Western Australian wheatbelt.

TERMITE SPECIES	FORAGING STRATEGY	DEFENCE MECHANISM			SOLDIER ABUNDANCE
		Mandi- bulate	Chemical	Mixed chemical- mandibulate	
Rhinotermitidae					
<i>Coptotermes acinaciformis</i> Froggatt (>100)	W			x	2
<i>Coptotermes frenchi</i> Hill (>50)	W			x	2
<i>Heterotermes occiduus</i> Hill (>100)	W	x			2
<i>Heterotermes paradoxus</i> Froggatt (>50)	W	x			2
<i>Schedorhinotermes actuosus</i> Hill (<10)	W			x	2
<i>Schedorhinotermes reticulatus</i> Froggatt (>100)	W			x	2
Termitidae					
<i>Amitermes calabyi</i> Gay (>50)	W	x			1
<i>Amitermes capito</i> Hill (>20)	W	x			1
<i>Amitermes dentosus</i> Hill (>50)	W	x			1
<i>Amitermes hartmeyer</i> Silvestri (>50)	W	x			1
<i>Amitermes heterognathus</i> Silvestri (< 10)	W	x			1
<i>Amitermes neogermanus</i> Hill (>100)	H, W			x	3
<i>Amitermes obeuntis</i> Silvestri (>100)	W	x			1
<i>Amitermes perarmatus</i> Silvestri (>50)	W	x			1
<i>Amitermes westraliensis</i> Hill (<10)	W	x			1
<i>Drepanotermes gayi</i> Watson & Perry (>20)	H			x	4
<i>Drepanotermes perniger</i> Froggatt (>100)	H			x	4
<i>Drepanotermes rubriceps</i> Froggatt (>100)	H			x	4
<i>Drepanotermes tamminensis</i> Hill (>100)	H			x	4
<i>Ephelotermes argutus</i> Hill (>100)	W	x			1
<i>Microcerotermes distinctus</i> Silvestri (>50)	W	x			1
<i>Microcerotermes newmani</i> Hill (>100)	W	x			1
<i>Paracapritermes kraepelinii</i> Silvestri (>100)	W	x			1
<i>Xylochomitermes occidialis</i> Gay (>100)	W	x			1
Nasutitermitinae					
<i>Nasutitermes exitiosus</i> Hill (>100)	W		x		4
<i>Occasitermes occasus</i> Silvestri (>50)	W		x		4
<i>Tumulitermes comatus</i> Hill (>20)	H		x		4
<i>Tumulitermes dalbiensis</i> Hill (>100)	H		x		4
<i>Tumulitermes peracutus</i> Hill (>100)	H, W		x		4
<i>Tumulitermes petilus</i> Hill (>100)	H, W		x		4
<i>Tumulitermes</i> sp. "AI" (<20)	H		x		4
<i>Tumulitermes</i> sp. "AJ" (<20)	H		x		4
<i>Tumulitermes</i> sp. "AK" (<20)	H		x		4
<i>Tumulitermes</i> sp. "B" (<20)	H		x		4
<i>Tumulitermes</i> sp. "MT" (<20)	H		x		4
<i>Tumulitermes</i> sp. "O" (<20)	H		x		4
<i>Tumulitermes</i> sp. "V" (<20)	H		x		4
<i>Tumulitermes</i> sp. "W" (<20)	H		x		4

Code initials for undescribed species as in Abensperg-Traun (1988, 1991) and Abensperg-Traun & De Boer (1990). W = wood-eating, H = harvesting. Soldier abundance ranges from 1 (scarce) to 4 (abundant). Values in brackets following species are estimated numbers of colonies sampled.

finely comminuted forage) but also eats the decayed surfaces of woody litter and logs, under the protective cover of soil-sheeting (Gay & Calaby 1970, M A-T personal observations). I was unable to locate published reference to chemical defence in *A. neogermanus*. Unlike *Amitermes* conspecifics which are lightly defended, *A. neogermanus* has evolved heavier defences

and exploits the (presumptive) high-risk harvesting niche. The above species have no nasus, hence soldiers need to make physical contact with the predator to transmit the secretion (Deligne 1971). The only available information on the proportion of soldiers in populations of such species in the wheatbelt comes from unpublished observations by H.

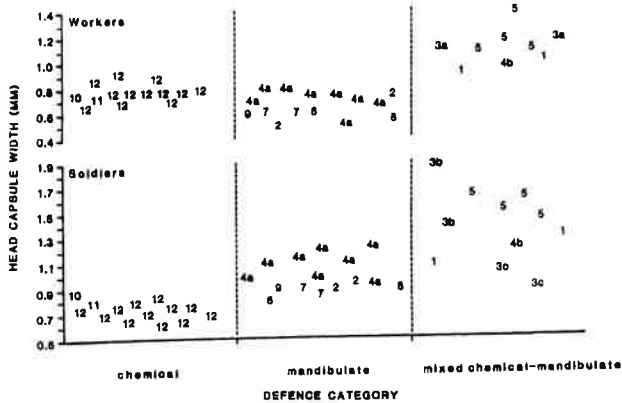


Figure 1. Soldier and worker head-capsule widths (as a measure of body size) of 38 termite species from the Western Australian wheatbelt. Species are categorized by their cephalic defence capabilities: mandibulate, chemical, mixed chemical-mandibulate (see Table 1). Measurements were carried out on the authors' reference material (mean of measurements on five specimens for each species). 1 *Coptotermes* sp.; 2 *Heterotermes* sp.; 3A *Schedorhinotermes* sp.; 3B *Schedorhinotermes* sp. major soldiers, 3C *Schedorhinotermes* sp. minor soldiers; 4A *Amitermes* sp. (excl. *A. neogermanus*); 4B *Amitermes neogermanus*; 5 *Drepanotermes* sp.; 6 *Ephelotermes argutus*; 7 *Microcerotermes* sp.; 8 *Paracaprithermes kraepelinii*; 9 *Xylochomitermes occidualis*; 10 *Nasutitermes exitiosus*; 11 *Occasitermes occasus*; 12 *Tumulitermes* sp.

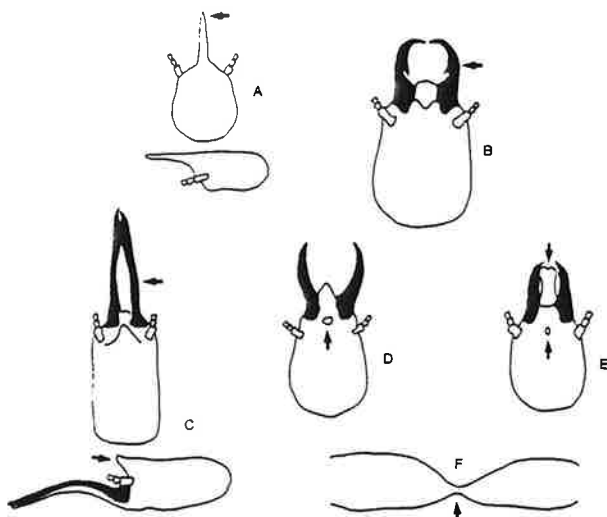


Figure 2. Defence mechanisms in termites from the Western Australian wheatbelt.

A *Tumulitermes petilus* (chemical); B *Amitermes obeuntis* (mandibulate); C *Ephelotermes argutus* (mandibulate); D *Coptotermes acinaciformis* (chemical-mandibulate); E *Schedorhinotermes reticulatus* (chemical-mandibulate); F termite chamber constriction. Arrows in D and E indicate the position of the fontanelle from which chemicals are secreted in *Coptotermes* and *Schedorhinotermes*, and applied via the labrum in *Schedorhinotermes* (E). Head-capsules were redrawn from Hill (1942) and Miller (1991). Drawings are not to scale.

Park (personal communication). His mound excavations of *Drepanotermes tamminensis* colonies indicate that colony populations have ~ 16 % soldiers, which is comparable to figures reported for nasute species (Moore 1969, Haverty 1977).

The relationship between high-risk foraging, as in harvesting termites, and the need for an effective mechanism of defence, is best demonstrated with reference to the endemic *Drepanotermes* species, which have evolved within Australia from the predominantly wood-eating, almost cosmopolitan, smaller-bodied *Amitermes* (Watson & Perry 1981; Watson 1982; Watson & Gay 1991). Unfortunately, nothing is known about the appearance of the species from which it originally evolved. However, considering extant species of *Amitermes*, it appears that, in order to fill the large harvester niche in arid and semi-arid Australia, *Drepanotermes* has evolved large size in both workers and soldiers (Fig 1), and an abundant soldier caste (Table 1), displaying not only prominent mandibles but also an effective chemical defence (Moore 1969, Abensperg-Traun *et al.* 1991). *Amitermes neogermanus* shows similar adaptations.

Wood-eaters

Unlike harvesters, the large majority of wood-eating termites that rely on mandibulate defences, like those discussed here, live entirely within subterranean galleries and chambers, or within surface wood and thus rarely if ever venture into the open (Wood & Johnson 1986). Given that their interaction with surface predators such as ants and lizards is likely to be lower than that of the harvester species, their need for heavy soldier defence is also likely to be lower. This prediction is supported by the data because the majority of non-harvesters were lightly defended.

Moore (1969) reported the soldier caste of many Australian *Amitermes* species to represent < 0.1 % of total colony individuals (as against ~ 15 % for nasutitermitids and *Drepanotermes*). Many of their subterranean chambers contain a narrow entrance / exit at either or both ends (Fig 2F). In the case of a gallery breach, a single soldier, poking its prominent mandibles through the narrowed space, can effectively prevent the advance of ants. Mandibles of *E. argutus*, *P. kraepelinii* and *X. occidualis* can also be locked in a crossed position. The shield-like structure on the front of the head-capsule of soldiers assists in blocking chamber constrictions (Fig 2C), a habit known as phragmosis, which is seen most prominently in the wood-inhabiting Kalotermitidae (e.g. *Cryptotermes*; Gay & Watson 1982). However, harvester termites also incorporated such constricted spaces into their gallery and chamber systems (e.g. *Drepanotermes*, *A. neogermanus*). In the case of *A. obeuntis*, which has few soldiers (Table 1), the protective efficiency of its hard mound may have rendered the soldier caste largely redundant. The species is also known to frequently co-habit with *D. tamminensis* whose mounds are well defended by virtue of its hard surface and the abundant soldiers it contains (Abensperg-Traun 1988).

The relationship between predation risk and defence is taken to its extreme manifestation in the soldierless termites (Sands 1972). The absence of the soldier caste frequently occurs in soil-eating termites (Mill 1982); I interpret this to reflect their infrequent interaction with predatory ants, lizards and small mammals. Miller (1984, 1991) lists the northern

Australian *Invasitermes inermis* and *I. insitivus* as soil-eating and soldierless. Possibly reflecting their lack of soldier defence but some pressure from predation, their colonies are frequently housed in the protective mounds of *Amitermes laurensis*. In revising the Australian *Termes-Capritermes* branch of the Termitinae, Miller (1991), lists several genera as humus and soil-eating, although these do not entirely lack a soldier caste (see also Watson & Gay 1991). However, soil-eating is restricted to high moisture habitats in humid forests and savannas (Wood *et al.* 1982), and is thus unlikely to be an important foraging strategy in the dry and infertile soils of the semi-arid wheatbelt. All known species of the revised *Termes-Capritermes* complex (*E. argutus*, *P. kraepelinii*, *X. occidentalis*), were eating wood in advanced stages of decay.

The presence of a frontal gland, and a pore (fontanelle) on the forehead for secretion of a chemical, is typical for both the Rhinotermitidae and the Termitidae (Watson & Gay 1991). Moore (1969) detected traces of chemical secretions in a small number of *Amitermes* sp. (e.g. *A. laurensis*) where soldiers are few and mandibulate. I have made similar observations involving three species of *Amitermes*. However, the scarcity of soldiers in such species is likely to make chemical soldier defence largely ineffective (Moore 1969).

There were six exceptions to the predicted relationship between wood-eating and low soldier defence. Consistent with all nasutid termites, the wood-eating *O. occasus* and *N. exitiosus* were defended by large numbers of small chemical soldiers. Such a defence appears appropriate in colonies of *N. exitiosus* which are housed in soft and thus easily breached mounds, readily exposing the colony to vertebrate predators such as echidnas which do, in fact, avoid mound-inhabiting *N. exitiosus* in the wheatbelt (Abensperg-Traun 1988). Wilson (1971) suggests that the optimal proportion of termite soldiers has evolved through selection to maximize (at minimal cost) the production of virgin males and females, as well as adequate defence of the colony. In that light, it seems odd that *O. occasus* retains what appears to be an unnecessarily large soldier caste which is expensive to maintain because soldiers need to be fed by the workers.

Consistent with other rhinotermitids, soldiers of *Schedorhinotermes* and *Coptotermes* were moderately abundant (Table 1) with chemical defence capabilities, in addition to prominent mandibles (Quennedey & Deligne 1975; Blum *et al.* 1982). The clear secretions of *Schedorhinotermes* sp. soldiers are applied by means of an extended labrum, or "daubing brush" (Fig 2E), whereas *Coptotermes* soldiers emit a milky latex from a fontanelle when disturbed (Fig 2D). Although I was unable to detect secretions in *Schedorhinotermes* sp. soldiers, chemical defence in this taxon is well known and documented (Quennedey 1975). *Heterotermes* species also have a small fontanelle, but it is not known whether this is functional.

Future Research

Whereas the general study predictions were upheld by the data, differences in predation levels between harvesters and non-harvesters remain to be substantiated. Although the scarcity of soldiers among most wood-eaters may have alternative explanations, the most plausible explanation is a low risk foraging environment. Clearly, much remains to be discovered not only about the foraging behaviour of particular

species, especially the rarer ones which comprise the majority (Abensperg-Traun & De Boer 1990; Abensperg-Traun 1991), but also about the evolutionary forces that may have shaped the morphological and chemical adaptations seen in termites today (Hare 1937). For instance, with an increase in food quality (C:N ratio), the fecundity of termite colonies may also increase (Waller & La Fage 1987). With high fecundity, heavy investment in colony defence (e.g. a high soldier:worker ratio) to compensate for predation losses may be unnecessary. Whether relatively fecund termites (possibly those inhabiting nutrient-rich environments) are less heavily defended than less fecund species (possibly those inhabiting nutrient-poor environments) is poorly known and would provide interesting research.

There are other aspects that need to be considered when discussing interactions between termite foraging strategies and their mechanisms of defence, but relevant observations are lacking. For instance, the proportion of soldiers within colonies may vary significantly with season and age of the colony (Bouillon 1969), and this may relate in some way to foraging requirements. The size of the cephalic gland, and the chemical composition of secretions often differs between genera and even between congeneric species (Bouillon 1969, Prestwich 1979, Blum *et al.* 1982). Some species possess a dimorphic soldier caste, with major and minor forms that differ significantly in size (e.g. *Schedorhinotermes* sp.; Fig 1). How these factors complement each other in defence of foraging parties remains poorly understood.

The wider question of the effects of predation on termite populations, partially related to foraging strategy and the efficiency of defence mechanisms, is poorly understood. In Nigerian savanna, for instance, annual predation on *Macrotermes* sp. by one species of ant alone is 2.7-fold the standing crop of workers and soldiers (Longhurst *et al.* 1978). Although no Australian ants are known to be termite-specialists (A N Andersen and S Higashi, personal communications), species of *Iridomyrmex* ants in particular appear to be important termite predators (Greenslade 1970, Higashi & Ito 1989, Holt 1990). Given the significant ecological role attributed to termites, particularly in tropical and subtropical Australia (Stafford Smith & Morton 1990) where termites may compete with livestock for food (Watson *et al.* 1973), a detailed investigation into the effects of predation on termite populations is likely to be rewarding. The question that may be posed is whether termite populations are limited by predation, or other factors such as food and competition.

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