

Letter to the Editor

Soldier production strategy in lower termites: A simpler alternative hypothesis

1. Introduction

Horiuchi et al. (2002) put forward an interesting model related to the production of small soldiers in young colonies of the termite *Neotermes koshunensis* and large soldiers in older colonies. They use this model to “explain why higher termites produce soldiers from fixed instars” whereas more primitive termites (such as those in the family Kalotermitidae e.g. *N. koshunensis*) produce soldiers from variable different instars. In this article, we have three goals. Firstly, we commend Horiuchi et al. (2002) for highlighting some important but previously largely ignored questions in termite biology, including many aspects of the biology of kalotermitid termites which, unlike most social Hymenoptera, often live within a finite food source and have soldier and worker sizes progressively increasing with colony age (Grassé, 1982; Lenz, 1994). Secondly, we point out some shortcomings of the model of Horiuchi et al. (2002). Thirdly, we propose a simpler alternative explanation for why *N. koshunensis* produces small soldiers in young colonies and large soldiers in older colonies. For brevity, we will abbreviate “Horiuchi et al. (2002)” to “H.” in this article.

The issues in H. are complex, therefore we include some clarifying and background information here. *N. koshunensis* like nearly all species of the moderately basal (Eggleton, 2001) termite families Kalotermitidae and Termitidae are “one-piece termites” (Abe, 1987). That is, the workers spend their whole lives inside a single piece of wood. Workers do not go outside to forage. Colonies of one-piece termites rarely exceed 10,000 individuals (Lenz, 1994). However, in all the other major termite families (both phylogenetically basal and apical to one-piece termites (Eggleton, 2001), including the higher termites (family Termitidae)), workers do go outside the nest to forage (Abe, 1987), usually by underground or covered earthen galleries. Also, the maximum colony size is typically much larger, commonly being tens or hundreds of thousands of individuals and sometimes over a million (Lepage and Darlington, 2000).

1.1. The model of Horiuchi et al. (2002) for *N. koshunensis*

The two most important terms in H.’s model are “ l ” and “ c ”.

l The defensive power needed for each worker (see Appendix).

c “The contribution of each junior worker for producing and caring for eggs, which become young instars.” (p. 197).

1.2. Conclusions of the model of Horiuchi et al. (2002)

Conclusion 1—when l and c are large then small soldiers would be produced.

Conclusion 2—when l and c are small then large soldiers are produced.

1.3. Assumptions of H.’s model

Assumption I—as colonies of *N. koshunensis* grow then l declines.

Assumption II—as colonies of *N. koshunensis* grow then c also declines.

1.4. Evidence for “Assumption I”

To support this the only reference that H. cites is Maki and Abe (1986). Maki and Abe (1986) show that the ratio of numbers of soldiers (to numbers of “workers”) in the colony declines as the colony ages. However, soldiers become proportionately larger with colony age (Kalshoven, 1930; Horiuchi et al., 2002). When an organism or a colony has an option of investing resources in “Individual type A” or “Individual type B” or both, when A and B individuals are of different sizes, then relative biomasses are a much better estimate of relative investment (Porter and Tschinkel, 1986; Boomsma et al., 1995; Kaspari and Byrne, 1995). Simply comparing numbers of A vs. B (Maki and Abe, 1986) gives an inaccurate estimate (Oster and Wilson, 1978). In this case, the issue is whether or not investment in defense decreases. Because neither H. nor Maki and Abe (1986) tested to see whether the relative biomass of the soldiers to workers actually decreased with colony

age then it cannot be assumed that defensive power declines.

1.5. Evidence for “Assumption II”

The only direct evidence that H. offers to support Assumption II is a single reference by Shellman-Reeve (1997). H. p. 200 states “In *Zootermopsis* (Termopsidae), Shellman-Reeve (1997) showed that, as the colony is filled with many colony members, offspring gained per allop parent per year decreases from 5.00 to 0.60 in six years. This phenomenon corresponds to the decrease of the parameter c in the model.” We present Shellman-Reeve’s (1997) data in Table 1 of this paper.

We remain unconvinced that Table 1 shows a gradual decline from years 1 to 6. If the 7th year is removed from Table 1, then there is no significant decrease in the number of offspring gained per allop parent per year during years 1 to 6 ($p = 0.39$, Spearman’s rank order correlation test; Zar, 1996).

Authorities on population growth in social insects (Brian, 1965; Wilson, 1971; Lepage and Darlington, 2000) emphasize a logistic growth phase in worker production occurs soon after the nest is initiated. This has also been demonstrated in *Neotermes* (Kalshoven, 1930). In one-piece termites and most ants this phase typically lasts a number of years. Then alates start to be produced, initially in small and then increasing numbers (Heath, 1927; Heath and Wilbur, 1927; Kalshoven, 1930; Brian, 1965; Wilson, 1971; Lepage and Darlington, 2000; Korb and Lenz, 2004). There is no slow down in colony activity, merely increasing resources are devoted to producing alates. The result is that the total number of workers in a colony starts to level off (Brian,

1965; Wilson, 1971; Lepage and Darlington, 2000). Therefore, we suggest that a tailing off in the rate of worker increase in one-piece termites (Table 1, year 7) is not an indication that there is less work for each junior worker to do. On the contrary, with the colony producing large numbers of alates there is much work for each worker to do. Therefore, we see no reason why in H. parameter c should progressively decline as the colony goes through its logistic and mature growth phases.

1.6. Constraint in egg production concept associated with “Assumption II”

Inbuilt in Assumption II is a concept assumed by H. (p. 200) that the one-piece termite “queen cannot produce enough eggs for each worker’s workload in a large colony because of her limited egg productive capacity”. H. uses this as one of the reasons to explain what is argued as a progressive decline in c as the colony grows.

H.’s concept here conflicts with what is known from studies with other social insects. These indicate that it is the size of the workforce (which feeds the queen, raises her young, forages, etc.) and not the physical capacity of the queen to lay sufficient eggs that limits the rate of colony growth (Brian, 1953; Michener, 1964; Spradbery, 1965; Wilson, 1974; Oster and Wilson, 1978, p. 34; Karsai et al., 1996).

Furthermore, the concept that one-piece queens might not be able to produce sufficient eggs for the colony to reach its optimum size seems contrary to current knowledge of evolutionary biology which demonstrates very strong selection pressure for animals to maximize reproductive output (Horn, 1978; Trivers, 1985; Promislow and Harvey, 1990; Krebs and Davies, 1997; Futuyama, 1998). Hence, there would be very strong selection pressure for physogastry (enlarged queen abdomen) and/or the colony to produce additional neotenic queens *if* this was really the factor limiting colony growth. Both these options, which can dramatically increase egg production, are found among some species in families phylogenetically both basal and apical to one-piece termites (Coaton, 1958; Coaton and Sheasby, 1974; Grassé, 1984; Watson and Abbey, 1985; Thorne, 1998; Myles, 1999), and the latter option (multiple neotenic queens) is indeed found in a few one-piece termites (Mensa-Bonsu, 1976; Lenz, 1985; Thorne and Lenz, 2001).

The higher termite queen can always produce sufficient eggs for the colony needs (p. 201), whereas H. argues that the one-piece queen cannot. H. uses this to help explain why higher termites “produce soldiers from fixed instars” (p. 202). We disagree because we disagree with the assumptions of the model.

Table 1

Offspring produced per allop parent as a function of colony age in the one-piece termite *Zootermopsis nevadensis* (Table from Shellman-Reeve (1997) compiled using data from Heath (1927).)

Year of production	Median number (range) of residents	Offspring gained per allop parent per year ^a
1	10 (0–20)	5.00
2	40	3.75
3	100	2.14
4	400	5.17
5	953 (789–1120)	1.86
6	2547 (2213–2881)	2.89
7	3500	0.60

^aThe estimated offspring number per allop parent (either soldier or worker morph) is obtained by the following formula: offspring earned, year₁ = residents₁/2 parents; offspring earned, year₂ = (residents₂ – residents₁)/(residents₁ – 2 parents); offspring earned, year₃ = (residents₃ – residents₂)/(residents₂ – residents₁); offspring earned year₄ = (residents₄ – residents₃)/(residents₃ – residents₂), and so on (Shellman-Reeve, 1997).

2. Alternative simpler explanation

2.1. Key “Fact X” to explain

Why small colonies of the termite *N. kosshunensis* produce small soldiers and large colonies produce many large soldiers.

Below, we compare H.’s model with our explanation for “Fact X”.

2.2. H.’s model

(1) H.’s model explains “Fact X” using a hypothesis found in the discussion of Maki and Abe (1986) (see H. p. 200, paragraphs 1 and 3).

(2) In the young soldier strategy [Fig. 1(a)] junior soldiers live for period of time “Y” and senior soldiers live for period of time “Z”. In the old soldier strategy [Fig. 1(b)] only senior soldiers, which live for period of time Z, are produced. So the young soldier strategy results in more soldiers in the colony (Y + Z) than the old soldier strategy (Z only).

(3) Therefore, H.’s model explains key “Fact X” by saying that according to Maki and Abe’s (1986) hypothesis small colonies need proportionately more soldiers to defend the suggested greater surface area volume ratio of their smaller nest. Therefore, small soldiers are produced because Fig. 1(a) results in more soldiers (Y + Z).

(4) Furthermore, H. suggests large colonies produce large soldiers because this [Fig. 1(b)] is the best strategy for having fewer soldiers (Z only). According to Maki and Abe’s (1986) hypothesis the nests of large one-piece colonies have a relatively smaller surface area volume ratio and therefore would need proportionately fewer soldiers to defend them.

2.3. The passageway-width explanation

(1) We propose this hypothesis to explain “Fact X”.

(2) Rather than just two ages of soldiers (“junior and senior soldiers” in H.’s model) in reality in *Neotermes* and other one-piece termites there are several different sizes of soldiers (Kalshoven, 1930; Grassé, 1982; Noirot, 1985). Evidence suggests that this is due to a combination of two factors. (i) As the colony ages soldiers of larger size, developing from successive different instars of workers, are increasingly produced in one-piece termites (Grassé, 1982; Noirot, 1989; Roisin, 2000). This is indicated by the progressively increasing wide range of antennal joint number in H.’s Figs. 2 and 3, which indicates successive instars (Kalshoven, 1930; Buchli, 1958; Myles and Chang, 1984). (ii) Soldiers of instar X (with antennal segment number Y) tend to be larger in large termite colonies than in small colonies (Kalshoven, 1930; Darlington, 1991; Grace et al., 1995).

(3) It has been shown in *Neotermes* (Kalshoven, 1930) as well as in other termites (Darlington, 1991; Grace et al., 1995) that as well-established (i.e. non-incipient) termite colonies age the workers become progressively larger.

(4) One-piece termites like many other wood-nesting termites and some soil nesters employ static rather than mobile warfare in defending their nests (Deligne and Pasteels, 1982; Leponce et al., 1997; Noirot and Darlington, 2000). Nests are commonly composed of many small chambers connected by small openings (Deligne and Pasteels, 1982; Noirot and Darlington, 2000). These openings are few and of one particular minimal size; they allow only one termite to pass through at a time (Deligne and Pasteels, 1982; Noirot and Darlington, 2000; Matsuura, 2002). Furthermore, the chamber openings fit exactly the maximum diametrical dimensions of the workers’ abdomens and of the soldiers’ heads (Deligne et al., 1981; Deligne and Pasteels, 1982). The reason for this is thought to be because the soldiers of many termite genera behave phragmotically without having typical phragmotic morphology (Deligne et al., 1981; Noirot and Darlington, 2000; Matsuura, 2002). This is certainly likely to include *Neotermes* which is confined to wood. This phragmotic behavior is an important defense against intruders that are potentially devastating to termite colonies (Noirot and Darlington, 2000; Thorne et al., 2003).

(5) Therefore, in the passageway-width explanation we propose that as the colony ages and the workers become larger then the passage points between galleries become larger, so the workers can get through.

(6) We suggest that this is the reason why many of the soldiers gradually become progressively larger as the colony grows. When colonies are old, small soldiers might now be too small to individually fully plug up the now larger passageways between galleries and therefore might be of less use.

(7) When colonies are young and the workers are small, a large soldier would be too large to fit through the narrow passageways between galleries. It not only would provide a poor plug defense but it would be unable to move freely around the nest to the site of the intruders’ attack.

(8) H. hints at the passageway-width explanation in three sentences of their discussion. However, we believe that a much fuller description, like above, is necessary to explain to the reader that this explanation might be a better alternative to H.’s model.

(9) Recent work in a one-piece termite has shown that colonies that were presumed to be older, because they contained soldiers with larger head-widths, did indeed have significantly larger minimum gallery diameters (Roux, E.A., Roux, M. & Korb, J. unpublished, submitted), which supports our hypothesis.

Further research is necessary to determine whether the progressive average increase in soldier and worker size with colony age in termites after the incipient colony is just a side-effect of colony age or whether specific adaptive advantages can be determined.

One excellent thing that the study of Horiuchi et al. (2002) has helped highlight, is how little the world knows about colony development in one-piece termites, which include some economically very important species (Edwards and Mill, 1986). Furthermore, Horiuchi et al. (2002) highlight a potentially very interesting theory by Maki and Abe (1986) that has previously been little explored, in addition to other important questions in termite biology which as Horiuchi et al. (2002) show may have implications for other animal societies.

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Appendix

The definition of “ l ” in H ’s model

l = the defensive power needed for each worker

Below are three indications from H . that support this definition of “ l ”.

(1) “As the colony needs more defensive power for each worker, l is larger.” (p. 198).

(2) “With a high value of l , the colony needs a relatively high number of soldiers.” (p. 200).

(3) $b = d \times l$ (p. 198). Therefore, $l = b/d$.

d = “the strength of each small soldier” (p. 197).

From H . we understand that this is a constant. Because d is a constant, and $l = b/d$ then l is directly proportional to b , which is “the defensive strength needed for one worker” (p. 197).

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