

Interspecific Agonism and Foraging Competition Between *Coptotermes formosanus* and *Coptotermes gestroi* (Blattodea: Rhinotermitidae)

by

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ABSTRACT

We investigated interactions between *Coptotermes gestroi* (Wasmann) (formerly known as *C. vastator*) and *Coptotermes formosanus* Shiraki in forced encounters and in foraging competition. In agonistic assays, termites from each species, with a fixed worker-to-soldier ratio of 9:1, were placed in filter paper-lined petri dishes and allowed to interact over a 24-hour period. *Coptotermes gestroi* suffered more mortality in all but one interspecific encounter, although only one of these occurrences was statistically significant. There was no significance difference in mortality in any combination of intraspecific, intercolonial pairings within the same species. To investigate foraging competition, termites from colonies of both species were introduced into arenas with a single, centrally located wood food source. Neither species demonstrated an ability to monopolize the food source. There was significant mortality in trials containing both species in comparison to single-species controls; although there was no statistical difference in mortality when the two species were compared with each other.

INTRODUCTION

Coptotermes gestroi (Wasmann) (Blattodea: Rhinotermitidae [Eggleton *et al.* 2007, Inward *et al.* 2007]), under the name *Coptotermes vastator* Light, was apparently first introduced to Hawaii in 1918, in a shipment of banana stumps from Manila, Philippines (Erhorn 1934). In 1963, this termite was found infesting a single house in the Kapahulu neighborhood of Honolulu,

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Oahu, Hawaii (Bess 1966, 1970). This house was subsequently demolished during construction of the H1 highway, and *C. gestroi* (again as *C. vastator*) was not collected again in Hawaii until 1999, when it was found infesting two residential structures in Kalaeloa, Oahu (formerly Barbers' Point Naval Air Station), a hay barn at the nearby Barbers' Point Riding Stables, a residence in the adjacent community of Ewa Beach, and sea grape trees (*Cocoloba uvifera*) lining the perimeter of Ewa Beach Park (Woodrow *et al.* 2001). The area of infestation has continued to expand at a slow rate, with subsequent discoveries in two residences in the nearby community of Makakilo, and in a building at Hickam Air Force Base. With the exception of the earlier 1963 collection, all discoveries of *C. gestroi* in Hawaii have been within approximately 10 km of Kalaeloa / Barbers' Point.

As described by Acda (2004), *C. vastator* is the most economically important subterranean termite in the Philippines, and was thought by Light (1921, 1929) to be indigenous there. However, recent genetic studies have identified *C. vastator* Light as a junior synonym of *Coptotermes gestroi* (Wasmann) (Yeap *et al.* 2007), the same status now accorded *C. havilandi* Holmgren (Kirton & Brown 2003, Kirton 2005). Thus, with these recent synonymies, it appears that the southeast Asian species *C. gestroi* enjoys a worldwide tropical distribution, analogous to the subtropical distribution and pest status of *Coptotermes formosanus* Shiraki (Grace 2006). Although other locations may come to light, Taiwan (Republic of China), Hawaii, and Florida appear to be the only locations where both species occur together.

A number of comparative studies have been performed with *C. formosanus* and *C. gestroi*. Shelton & Grace (2003) noted greater mortality of *C. gestroi* than *C. formosanus* under desiccating conditions; and Grace *et al.* (2004) observed distinctly different tunneling patterns with these two species that suggested that *C. gestroi* employed a foraging strategy of intensive local search using a highly branched tunnel structure, while *C. formosanus* constructed longer tunnels with much less branching. In comparative studies of these two termite species in Hawaii, Uchima & Grace (2003a, b) concluded that *C. gestroi* had a lower feeding rate than *C. formosanus*, and generally smaller field colonies. One area where *C. gestroi* has demonstrated an advantage over *C. formosanus* is in resistance to attack by the nematode *Heterorhabditis indica*, although the basis of this is not known (Mankowski *et al.* 2005). It is

possible that the observed differences in cuticular hydrocarbons of these two *Coptotermes* species (Haverty *et al.* 2000) may influence both susceptibility to desiccation and nematode attachment.

In the present study, we examined agonism and foraging competition between *C. formosanus* and *C. gestroi*, in order to shed light on the dynamics of their interactions in the field in Hawaii and the potential for greater spread of *C. gestroi* in the islands. Coexistence, competition for resources, and/or secondary pest occurrence following control of the primary pest species are all possible outcomes when multiple subterranean termite species occupy the same area. For example, studies in Florida (Su & Scheffrahn 1988), Louisiana (Cornelius & Osbrink 2000), and Japan (Wang & Sameshima 2002) have demonstrated the potential for *C. formosanus* to out compete and exclude *Reticulitermes* spp. With respect to secondary pest occurrence, observations in Guam have demonstrated that a *Schedorhinotermes* sp. (Rhinotermitidae) and a *Nasutitermes* sp. (Termitidae) will occupy subterranean termite control bait stations and presumably the adjacent gallery systems after elimination of *C. gestroi* (Yudin 2002).

MATERIALS AND METHODS

To investigate agonistic interactions, termites were collected from three field colonies of *C. gestroi* located in Kalaeloa on the island of Oahu, Hawaii and two *C. formosanus* colonies located on the campus of the University of Hawaii at Manoa, Oahu (Table 1). A straight-line distance of 40 km separates the Manoa campus of the University of Hawaii and Kalaeloa. Colony cv1 is separated from cv2 by a distance of 3.0 km, cv1 is 0.3 km away from cv3 and

Table 1. Termite field colonies. *Coptotermes gestroi* is identified here as “cv” due to the previous identification of this species in Hawaii as *C. vastator*.

Colony Identifier	Colony Location	Site Description	Species
cv1	Kalaeloa, Oahu, HI	Abandoned residence	<i>C. gestroi</i>
cv2	Kalaeloa, Oahu, HI	Horse stables hay storage	<i>C. gestroi</i>
cv3	Kalaeloa, Oahu, HI	Abandoned residence	<i>C. gestroi</i>
cf1	University of Hawaii	Near Gilmore Hall	<i>C. formosanus</i>
cf2	University of Hawaii	Near Miller Hall	<i>C. formosanus</i>

colonies cv2 and cv3 are 2.6 km away from each other. A distance of 0.4 km separates colonies cf1 and cf2. Agonism patterns of the two *C. formosanus* colonies have been previously reported (Shelton & Grace, 1997). Both interspecific agonism, and the intraspecific agonism patterns of the three *C. gestroi* colonies, were investigated in the current study.

Termites were collected from wooden box-type aggregation traps located at all sites using techniques modified from those of Tamashiro *et al.* (1973) and Su & Scheffrahn (1986). Due to the similarities in size and appearance of the two species under investigation, workers were stained with Fat Red 7B dye (Sigma Chemical Co.) in order to maintain species identification throughout the experiment. For termite soldiers, dye marking was restricted to the tip of the abdomen and required high concentrations and long periods of exposure to the dye marker (Su *et al.* 1983), but this was sufficient to allow identification during this short-term experiment.

Ten termites from one colony (9 workers and 1 soldier), mimicking normal caste proportions (Pangga 1936, Haverly 1977), were simultaneously introduced into a 60 x 15mm dish with ten termites (9 workers and 1 soldier) from another colony. In all cases, one colony was marked with dye and the other unmarked. Each trial included an equal number of replicates with stained and unstained pairings for each colony. A moistened piece of 42.5mm Whatman #2 filter paper was placed at the bottom of the dish to provide moisture prior to the introduction of the termites. The individual dishes were covered, placed on moistened paper towel lined trays; and the trays covered and placed in an unlighted incubator at 27°C for 24 hours. Mortality for each colony cross and control was recorded at the conclusion of the 24-hr period. Percentage mortality data were transformed by the arcsine of the square root and subjected to a two-sample *t*-test with a significance level of $\alpha=0.05$ (SAS Institute 1987). The combined percentage mortality data were also transformed by the arcsine of the square root, and subjected to an ANOVA using General Linear Models with means significant at $\alpha=0.05$ separated by the Ryan-Einot-Gabriel-Welsch Multiple Range Test (SAS Institute 1987).

To investigate foraging competition, *C. formosanus* and *C. gestroi* were again collected from field colonies on the island of Oahu, HI using the same techniques. *Coptotermes formosanus* termites were collected from a colony

located on the campus of the University of Hawaii at Manoa, and *C. gestroi* termites were collected from a colony located at the horse riding stable at Kalaeloa, Oahu.

A foraging arena (Fig. 1) was constructed from three 12-dram (30mm diameter by 70mm high) plastic snap cap vials and two 2.5cm long glass tubes (0.5mm inside diameter and 0.8mm outside diameter). Holes were drilled into the sides, near the bottom of the plastic vials, to allow insertion of the glass tubes. The arena was stabilized and secured with hot glue. 20g of silica sand (Fisher Chemical) were placed into each of the three vials of the arena. For moisture, 250ml of distilled water were added to each vial at least two hours prior to the introduction of termites. Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) blocks (13 x 13 x 6mm) were dried for 24 hours at 90°C, cooled in a dessicator, and weighed. A Douglas fir block was placed into the center vial of each feeding arena. Additionally, a 1cm square of paper towel was placed into each of the two outer vials as an initial food source just prior to the introduction of the termites.

Termites from both species were stained in order to allow species identification in the interspecific replicates. Termites were stained with Fat Red 7B (Sigma Chemical Co.) by being force-fed stained filter paper (1 % wt/wt

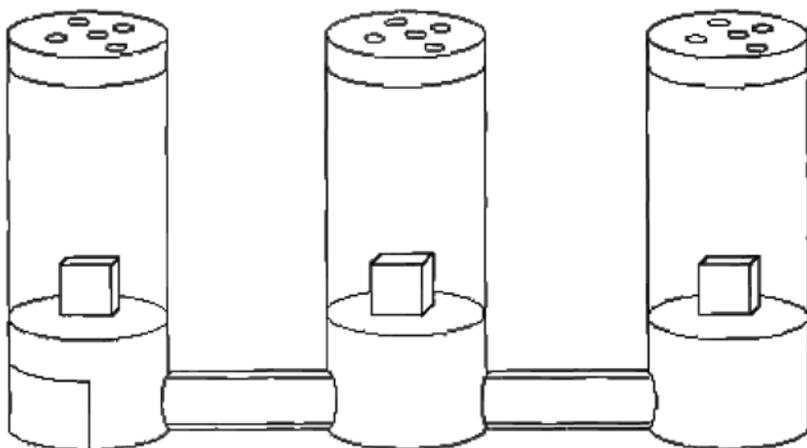


Fig. 1. Competitive foraging arena, consisting of 3 plastic vials connected serially with glass tubing, with a Douglas-fir block in the center vial and 1cm paper squares in the outer vials. Termites (50 of each test species, with 10% soldiers) were introduced into each end vial.

solution on 90mm diameter Whatman #2 filter paper). Soldiers were not used in this experiment since they do not stain appreciably for studies longer in duration than a single day (Su *et al.* 1983). All single-species control replicates included 50% stained and 50% unstained termites. The interspecific pairings each consisted of an equal number of replicates with both combinations of stained and unstained termites.

Fifty workers were placed into the end vials of each arena. The arenas were covered and placed into plastic bins lined with moist paper towels. The plastic bins were covered and placed in unlighted incubators set at 27°C for 72 hours. Qualitative observations were made at 24-hour intervals for a period of 72 hours to determine which species was exploiting the food source in the center vial. The experiment was completed at the end of the third observation. At the completion of the experiment, the arenas were dismantled, surviving termites counted and the wood blocks from the center vials were cleaned, oven-dried and weighed.

Termite mortality data were converted to percentages, transformed by the arcsine of the square root and subjected to a two-sample *t*-test (SAS Institute 1987). Wood consumption data were subjected to an ANOVA, using General Linear Models, with means significant at $\alpha=0.05$ separated by the Ryan-Einot-Gabriel-Welsch Multiple Range Test (SAS Institute 1987). Chi-square analysis was used to compare the species occupancy of the center vial (SAS Institute 1987).

RESULTS

The mean percentage mortalities of the colony pairings after the 24-hour exposure period in the agonistic interactions experiment are summarized in Table 2. The highest mortality rates occurred in the interspecific trials, while the lower mortality rates occurred in the intraspecific colony pairings. The lowest mortality rates occurred in the single-colony control pairings, although only the single-colony control cf1 evidenced no mortality in all replicates. In every other single-colony control, at least one replicate evidenced at least one termite death. It is worth noting that no overlap exists between the ranges of mortality for the intraspecific and interspecific pairings. Intraspecific colonial pairings experienced mortality no higher than 20.5% (the pairing cv1-cv3) while 64.5% (the pairing cv2-cf1) was the lowest percent mortality

any interspecific colonial pairing experienced. The highest combined percent mortality observed was 87.0% with the cv3-cf1 combination.

Table 3 summarizes the agonism pattern among the five colonies under investigation in this experiment. Percent mortality in all but one pairing did not differ significantly at $\alpha=0.05$. The combination of cv2-cf2 did demonstrate a significant difference in their respective percentage mortalities ($t=2.538$, $df=18$, $Pr>t=0.021$), with *C. gestroi* suffering the greatest mortality.

Table 4 shows the survival data from the foraging competition experiment. Both termite species suffered significantly higher mortality (at $\alpha=0.05$) in the cross treatments versus their respective

controls. However, the difference in mortality for the two species in the crosses when compared with one another was not significant at $\alpha=0.05$ ($t=-0.285$, $df=17.98$, $Pr>t=0.779$; df expresses the assumption that the variances are not equal). Likewise, the occupancy of the center vial in the crosses did not differ significantly from that of the controls ($\chi^2=0.04$, $df=1$, $P=0.85$) and competition did not significantly affect the mean consumption of wood by either species ($F=2.13$, $df=3$, $Pr>F=0.12$). Arenas were not used in the center-vial-occupancy and wood consumption data analysis if the central food source vial exhibited the following: (1) neither species attempting to tunnel to the food source, (2) evidence of heavy fighting was found and neither species maintained active access to the food source vial or (3) fighting occurred with subsequent combat survivors remaining in the center vial but isolated from conspecifics.

Table 2. Mean total percentage mortality (\pm standard deviation) in *C. gestroi* and *C. formosanus* colony pairings (ten replicates per pairing).

Colony Pairing	Mean Percent Mortality*
cv1-cv1	0.030 \pm 0.048 b
cv1-cv2	0.160 \pm 0.284 b
cv1-cv3	0.205 \pm 0.272 b
cv1-cf1	0.730 \pm 0.379 a
cv1-cf2	0.795 \pm 0.315 a
cv2-cv2	0.040 \pm 0.052 b
cv2-cv3	0.065 \pm 0.088 b
cv2-cf1	0.645 \pm 0.398 a
cv2-cf2	0.755 \pm 0.370 a
cv3-cv3	0.020 \pm 0.042 b
cv3-cf1	0.870 \pm 0.178 a
cv3-cf2	0.690 \pm 0.201 a
cf1-cf1	0.000 \pm 0.000 b
cf1-cf2	0.015 \pm 0.037 b
cf2-cf2	0.010 \pm 0.032 b

*Means followed by the same letter do not differ significantly at $\alpha=0.05$ (ANOVA of percentage data transformed by the arcsine of the square root, Ryan-Einot-Gabriel-Welsch Multiple Range Test; SAS Institute 1987).

Table 3. Direct comparison of mean percentage mortality of pairings between *C. gestroi* and *C. formosanus* colonies.

Colony Pairing	Colony 1	Colony 2	<i>t</i> -Test Results
cv1-cv1	0.020±0.048	0.040±0.055	<i>t</i> =-0.632, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.545
cv1-cv2	0.150±0.324	0.170±0.254	<i>t</i> =-0.324, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.750
cv1-cv3	0.270±0.327	0.140±0.201	<i>t</i> =0.809, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.429
cv1-cf1	0.710±0.348	0.750±0.425	<i>t</i> =-0.403, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.692
cv1-cf2	0.880±0.312	0.710±0.311	<i>t</i> =1.446, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.165
cv2-cv2	0.040±0.055	0.040±0.055	<i>t</i> =0.000, <i>df</i> =18, <i>Pr</i> > <i>t</i> =1.000
cv2-cv3	0.070±0.106	0.060±0.070	<i>t</i> =-0.068, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.947
cv2-cf1	0.730±0.371	0.560±0.425	<i>t</i> =1.124, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.276
cv2-cf2	0.900±0.221	0.610±0.321	<i>t</i> =2.538, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.021
cv3-cv3	0.000±0.000	0.040±0.055	<i>t</i> =-1.633, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.141
cv3-cf1	0.890±0.191	0.850±0.172	<i>t</i> =0.830, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.418
cv3-cf2	0.740±0.395	0.640±0.381	<i>t</i> =0.799, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.435
cf1-cf1	0.000±0.000	0.000±0.000	*
cf1-cf2	0.010±0.032	0.020±0.042	<i>t</i> =-0.600, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.556
cf2-cf2	0.000±0.000	0.020±0.045	<i>t</i> =-1.000, <i>df</i> =18, <i>Pr</i> > <i>t</i> =0.347

*No statistical analysis conducted due to no mortality in any replicates.

Table 4. Mean termite survival in competitive foraging arenas.

Species Pairing	N*	Percent Survivorship (± SD)	
		<i>C. formosanus</i>	<i>C. gestroi</i>
Cf-Cf	10	96.8±2.1	-
Cv-Cv	10	-	96.4±1.1
Cf-Cv	20	68.9±20.5	66.1±20.8

*100 termites per replicate (50 of each pair, with 10% soldiers).

DISCUSSION

In the agonistic interactions experiment, *C. gestroi* and *C. formosanus* from colonies at Kalaeloa and the University of Hawaii campus, respectively, demonstrated a pattern of agonism towards one another. This laboratory outcome is similar to that of field interactions reported between *C. formosanus* and *R. flavipes* in Florida (Su & Scheffrahn 1988). The level of this agonism and the ability of one species to out compete the other are questions yet to

be addressed. *Coptotermes formosanus* has not eliminated the presence of the native subterranean termite in Louisiana, *R. flavipes*, in over 40 years of coexistence (Cornelius & Osbrink 2001). From the results of this experiment, *C. formosanus* appeared to be the species better able to survive forced one-on-one encounters in a laboratory environment, and *C. gestroi* suffered a higher rate of mortality in five of six interspecific pairings. In combination with the lower feeding rate of *C. gestroi* noted by Uchima & Grace (2003b), these results suggest that *C. gestroi* may remain in limited distribution in the Hawaiian Islands, with the pattern of slow expansion noted to date. However, *C. gestroi* certainly has the potential to become a serious secondary pest at sites where *C. formosanus* colonies have been eliminated by bait applications. In Guam, *C. gestroi* has been found to be the species responsible for structural damage once attributed to *C. formosanus* (Su 1994, Su & Scheffrahn 1998).

The clustered distribution of *C. gestroi* on Oahu on or near former military installations suggests that it was introduced to Hawaii by military traffic, possibly with either Guam or the Philippines. The lack of intraspecific agonism displayed by the three colonies of *C. gestroi* also suggests that *C. gestroi* has been introduced once, or from a single foreign location, although agonism is a poor indicator of colony relatedness (Husseneder & Grace 2001), and can be influenced by environmental factors (Shelton & Grace 1997).

In the foraging competition experiment described here, neither *C. formosanus* nor *C. gestroi* displayed the ability to monopolize a food source. Additionally, the presence of the other species did not significantly affect the feeding rate of the species that occupied the center food source vial. A similar experiment, utilizing larger arenas and longer exposure periods, found that when a sole food source was placed in the center arena, *C. formosanus* and *Reticulitermes flavipes* (Kollar) both occupied the food source arena 60% of the time, with the two termite species maintaining partitioned foraging areas within the arena (Cornelius & Osbrink 2000). Investigations with larger arenas may demonstrate a similar situation with *C. formosanus* and *C. gestroi*.

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REFERENCES

- Acda, M. N. 2004. Economically important termites (Isoptera) of the Philippines and their control. *Sociobiology* 43: 159-169.
- Bess, H. A. 1966. Notes and exhibitions: *Coptotermes vastator* Light. Proceedings of the Hawaiian Entomological Society 19: 136.
- Bess, H. A. 1970. Termites of Hawaii and the oceanic islands. Pp. 449-476 in *Biology of Termites*, Volume 2 (K. Krishna & F. M. Weesner, editors). Academic Press: New York.
- Campora, C. E. & J. K. Grace. 2001. Tunnel orientation and search pattern sequence of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* 94: 1193-1199.
- Cornelius, M. L. & W. L. A. Osbrink. 2000. Interspecific interactions between *Coptotermes formosanus* and *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) in laboratory bioassays. *Journal of Insect Behavior* 13: 757-770.
- Eggleton, P., G. Beccaloni & D. Inward. 2007. Response to Lo *et al.* *Biology Letters* 3: 564-565.
- Ehrhorn, E. M. 1934. The termites of Hawaii, their economic significance and control and the distribution of termites by commerce. Pp. 321-333 in *Termites and Termite Control* (C. A. Kofoid, editor). University of California, Berkeley, California.
- Grace, J. K. 1991. Response of eastern and Formosan subterranean termites (Isoptera: Rhinotermitidae) to borate dust and soil treatments. *Journal of Economic Entomology* 84: 1753-1757.
- Grace, J. K. 2006. When invasives meet: *Coptotermes formosanus* and *Coptotermes vastator* in the Pacific. Proceedings of the 2006 National Conference on Urban Entomology. Raleigh-Durham, North Carolina; 21-24 May, 2006. Pp. 92-94.
- Grace, J. K., M. Aihara-Sasaki & J. R. Yates. 2004. Differences in tunneling behavior of *Coptotermes vastator* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology* 43:153-158.
- Haverty, M. I. 1977. The proportion of soldiers in termite colonies: a list and a bibliography. *Sociobiology* 2: 199-219.
- Haverty, M. H., R. J. Woodrow, L. J. Nelson & J. K. Grace. 2000. Cuticular hydrocarbons of the termites (Isoptera: Rhinotermitidae) of Hawaii. *Journal of Chemical Ecology* 26: 1167-1191.
- Husseneder, C. & J. K. Grace. 2001. Evaluation of DNA fingerprinting, aggression tests and morphometry as tools for colony delineation of the Formosan subterranean termite. *Journal of Insect Behavior* 14: 173-186.

- Inward, D., G. Beccaloni & P. Eggleton. 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters* 3: 331-335.
- Kirton, L. G. 2005. The importance of accurate termite taxonomy in the broader perspective of termite management. Pp. 1-7 in *Proceedings of the 5th International Conference on Urban Pests* (C.-Y. Lee & W. H. Robinson, editors), Singapore, 10-13 July 2005.
- Kirton, L. G. & V. K. Brown. 2003. The taxonomic status of pest species of *Coptotermes* in Southeast Asia: Resolving the paradox in the pest status of the termites *Coptotermes gestroi*, *C. havilandi* and *C. travians* (Isoptera: Rhinotermitidae). *Sociobiology* 42: 43-64.
- Light, S. F. 1921. Notes of Philippine termites II. *Philippine Journal of Science* 19: 23-63.
- Light, S. F. 1929. Notes on Philippine termites, III. *Philippine Journal of Science* 40: 421-52.
- Mankowski, M.E., H.K. Kaya, J.K. Grace & B. Sipes. 2005. Differential susceptibility of subterranean termite castes to entomopathogenic nematodes. *Biocontrol Science and Technology* 15: 367-377.
- Pangga, G. A. 1936. A biological study on some common Philippine termites. *Philippine Agriculture* 25: 233-265.
- Puche, H. & N.-Y. Suo 2001. Tunnel formation by *Reticulitermes flavipes* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in response to wood in sand. *Journal of Economic Entomology* 94: 1398-1404.
- SAS Institute. 1987. *SAS/SAT guide for personal computers*. Version 6 edition. SAS Institute, Inc. Cary, NC, USA. 1028 pp.
- Shelton, T. G. & J. K. Grace. 1997. Suggestion on an environmental influence on intercolony agonism of Formosan subterranean termites (Isoptera: Rhinotermitidae). *Environmental Entomology* 26: 632-637.
- Shelton, T. G. & J. K. Grace. 2003. Comparative cuticular permeability of two species of *Coptotermes* Wasmann (Isoptera: Rhinotermitidae). *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 134: 205-211.
- Su, N.-Y. 1994. A case of mistaken identity: all the evidence pointed to the Formosan subterranean termite, but closer inspection proved it wasn't so. *Pest Control* 62(10): 7980.
- Su, N.-Y. & R. H. Scheffrahn. 1986. A method to access, trap and monitor field populations of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in the urban environment. *Sociobiology* 12: 299-304.
- Su, N.-Y. & R. H. Scheffrahn. 1988. Foraging population and territory of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in an urban environment. *Sociobiology* 14: 353-359.
- Su, N.-Y. & R. H. Scheffrahn. 1998. *Coptotermes vastator* Light (Isoptera: Rhinotermitidae) in Guam. *Proceedings of the Hawaiian Entomological Society* 33: 13-18.
- Su, N.-Y., J. P. La Fage & G. R. Esenther. 1983. Effects of a dye, Sudan red 7B, on the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *Material und Organismen* 18: 127-133.

- Tamashiro, M., J. K. Fujii & P.-Y. Lai. 1973. A simple method to observe, trap and prepare large numbers of subterranean termites for laboratory and field experiments. *Environmental Entomology* 2: 721-722.
- Uchima, S. Y. & J. K. Grace. 2003a. Characteristics of *Coptotermes vastator* (Isoptera: Rhinotermitidae) colonies on Oahu, Hawaii. *Sociobiology* 41: 281-287.
- Uchima, S. Y. & J. K. Grace. 2003b. Comparative feeding rates of *Coptotermes vastator* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology* 41: 289-294.
- Wang, J. & K. Sameshima. 2002. Behavior analyses on *Reticulitermes speratus* (Kolbe) and *Coptotermes formosanus* Shiraki in nature - on foraging pattern, territory, competition and colony size. *Shiroari* 127: 2-11.
- Woodrow, R. J., J. K. Grace & S. Y. Higa. 2001. Occurrence of *Coptotermes vastator* (Isoptera: Rhinotermitidae) on the island of Oahu, Hawaii. *Sociobiology* 38: 667-73.
- Yeap, B.-G., A. S. Othman, V. S. Lee & C.-Y. Lee. 2007. Genetic relationship between *Coptotermes gestroi* and *Coptotermes vastator* (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* 100: 467-474.
- Yudin, L. 2002. Termites of Mariana Islands and Philippines, their damage and control. *Sociobiology*. 40: 71-74.

