

Invasive Termites Revisited: *Coptotermes gestroi* meets *Coptotermes formosanus*

by

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Abstract

Coptotermes gestroi (Wasmann) and *Coptotermes formosanus* (Shiraki) represent the most widely distributed subterranean termites (Rhinotermitidae) in the world. The wide distribution of *C. gestroi* has only come to light in the past decade, as numerous junior synonyms for this tropical termite have been resolved. With *C. gestroi* found in the equatorial zone, and *C. formosanus* in the subtropics and warm temperate regions, the distributions of these two invasive termites currently overlap in only three locations in the world: Taiwan, Hawaii and Florida. Comparative studies have identified a number of biological and behavioral differences between the two species, such as greater desiccation tolerance in *C. formosanus*, as well as a possible variation in aggressiveness related to the origin of different *C. gestroi* populations. The tunneling patterns of *C. gestroi* and *C. formosanus* are quite distinct, and appear to reflect both the distribution of woody resources in the ecological zones inhabited by each species and selection of different optimal foraging strategies.

Key Words: Asian subterranean termite, Formosan subterranean termite, Blattodea, Rhinotermitidae, invasive species, termite foraging strategies

Introduction

In a 2006 presentation to the (USA) National Conference on Urban Entomology, Grace (2006) summarized the information available at the time on two invasive subterranean termites (Rhinotermitidae) in Hawaii under the title “When invasives meet: *Coptotermes formosanus* and *Coptotermes vastator* in the Pacific.” Native to southern China, *Coptotermes formosanus* Shiraki (the

Formosan subterranean termite) is widespread throughout the subtropical and adjacent warm temperate regions of the world, and has been recognized for many years as a very serious invasive pest (Evans et al. 2013). *Coptotermes formosanus* is a long-time resident of Hawaii, originally introduced in the late 1800's or very early 1900's (Yates and Tamashiro 1999, Swezey 1914). On the other hand, *C. vastator* Light (the Philippine milk termite) was a new immigrant to Hawaii (Woodrow et al. 2001), known to occur only in the Pacific Basin, and very rarely in the same location as *C. formosanus*. Since 2006, however, our knowledge of *C. vastator*, now known to be a synonym for *Coptotermes gestroi* (Wasmann) (the Asian subterranean termite) (Yeap et al. 2007), has greatly expanded. We now know that *C. gestroi* is the tropical equivalent of *C. formosanus* in terms of its current and potential worldwide distribution (Evans et al. 2013, Li et al. 2013).

The Rise of *Coptotermes gestroi*

Originally thought to be native to the Philippines (Light 1929), and thus one of very few island endemic termites (Evans et al. 2013), *C. vastator* was mentioned by Kirton (2005) as one of several *Coptotermes* species in neighboring regions that were so similar to *C. gestroi*, the Asian subterranean termite, that they “could be the same species described under different names.” Soon after, Yeap et al. (2007) demonstrated conclusively that *C. vastator* was indeed a junior synonym for *C. gestroi*.

Originally described from Myanmar (formerly Burma) (Wasmann 1902), *C. gestroi* was originally thought to occur only in that region, Northern India, and Thailand (Roonwal and Chhotani 1962). In fact, it has taken over 100 years for the incredibly widespread distribution of this invasive tropical termite to be recognized (Li et al. 2013). Synonyms were created and adopted in India, Pakistan, Southeast Asia and the Pacific islands. First described as *C. vastator*, and then under the name *Coptotermes havilandi* Holmgren, *C. gestroi* spread from Asia to Brazil in 1936, into the Caribbean (Araujo 1970), and into peninsular Florida (Su et al. 1997).

Along with the creation of junior synonyms for *C. gestroi* such as the destructive *Coptotermes heimi* (Wasmann) (Yeap et al. 2010), misidentification and confusion with other valid *Coptotermes* species has also commonly occurred. In parts of Southeast Asia, *C. gestroi* was sometimes misidentified as *Coptotermes travians* (Haviland), while the true *C. travians* was also wrongly identified as *C. havilandi* in peninsular Malaysia (Kirton and Brown 2003). In the Pacific, *C. gestroi* was wrongly identified as *Coptotermes formosanus* Shiraki in Guam (Su 1994, Su and Scheffrahn 1998).

As described by Li et al. (2013), the following are all now considered to be junior synonyms for *Coptotermes gestroi*: *C. heimi* (Wasmann), *C. parvulus* Holmgren, *C. havilandi* Holmgren, *C. vastator* Light, *C. pacificus* Light, *C. javanicus* Kemner, *C. obliquus* Xia and He, and *C. yaxianensis* Li. In

addition, although it has yet to be formally synonymized, *C. ceylonicus* Holmgren from Sri Lanka was also considered part of the *C. gestroi* complex by Kirton (2005), and similar enough in morphology to *C. gestroi* to possibly be the same species.

***Coptotermes gestroi* in Hawaii**

Under the name *C. vastator*, *C. gestroi* was apparently first intercepted in 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, Oahu, Hawaii (Weesner 1965; Bess 1966, 1970). This house was subsequently demolished during construction of the H1 highway, and *C. gestroi* 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 uvifara*) 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 on the island of Oahu.

A comparative study of field sites occupied by *C. formosanus* and *C. gestroi* in Hawaii found that *C. gestroi* favored warmer locations (27-33 °C, annual mean 30 °C) than *C. formosanus* (23-30 °C, annual mean of 27 °C), and was most active in foraging at the soil surface in the late spring and summer months, while *C. formosanus* was more active than *C. gestroi* during the cooler winter period (Hapukotuwa and Grace 2012a). The preference of *C. gestroi* for warmer locations is also reflected in the relative distribution of these two species in Taiwan, where *C. gestroi* has been found only in the southern portion of the island (Li et al. 2009). A mark-release-recapture study of two *C. gestroi* field colonies in Hawaii yielded foraging population estimates of 0.2 million and 0.7 million termites, and estimated foraging areas of 10.5 m² and 287 m², respectively (Uchima and Grace (2003a). These are in the same range as estimates in the Philippines of 60,000 to 1.5 million termites and foraging areas averaging 20 m² (Yudin 2002), suggesting that *C. gestroi* colonies may be slightly smaller than those of *C. formosanus*.

Alate flight periods for these two species overlap in Hawaii (largely April - July) (Tong et al. 2013), as has also been observed in Taiwan (Li et al. 2009).

Biological and Behavioral Differences

In addition to the ecological differences observed between *C. gestroi* and *C. formosanus* field colonies in Hawaii, biological and behavioral differences have also been noted. Although both species exhibited similar feeding preferences for different types of lumber (Hapukotuwa and Grace 2011a) and bamboo (Hapukotuwa and Grace 2011b), *C. gestroi* was found to have a slower feeding rate than *C. formosanus* (Uchima and Grace 2003b). *Coptotermes gestroi* also suffers greater mortality than *C. formosanus* under desiccating conditions (Shelton and Grace 2003). 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.

Co-occurrence and Competition

The relative worldwide distributions of *C. gestroi* and *C. formosanus* (Evans et al. 2013, Li et al. 2013), the temperature and seasonal activity differences observed between field colonies in Hawaii (Uchima and Grace 2003a), and the reduced desiccation tolerance of *C. gestroi* (Shelton and Grace 2003) all point to the fact that *C. gestroi* is most comfortable in the warm and humid equatorial zone, while *C. formosanus* is subtropical in nature. Their distributions overlap only in Hawaii, Taiwan (Tsai and Chen 2003, Li et al. 2009, Yeap et al. 2009), and Florida (Scheffrahn and Su 2005). Although both species are also found within the territorial boundaries of Japan, they occur in completely different locations, with *C. gestroi* found only on Minami Torishima (Marcus Island), most likely due to former American military operations on that island (Morimoto and Ishii 2000, Yeap et al. 2009).

Despite the somewhat lower feeding rate of *C. gestroi* (Uchima and Grace 2003b), Florida *C. gestroi* colonies were found to dominate and kill *C. formosanus* in forced interactions in the laboratory (Li et al. 2013). Similar studies of interspecific agonism in Hawaii also demonstrated consistent battles, but the winning species was inconclusive (Uchima and Grace, 2009). Many factors, such as environment and diet (Shelton and Grace 1997), can influence termite agonistic behavior, but the different results observed with Florida and Hawaii colonies may reflect genetic differences. Florida *C. gestroi* have been found to be more closely related to SE Asian (Malaysia) populations (Jenkins et al. 2007, Li et al. 2009), while Hawaii *C. gestroi* are instead more closely related to those in Taiwan and the Philippines (Li et al. 2009, Yeap et al. 2009)

Tunnel Patterns and Optimized Foraging Strategies

Grace et al. (2004) observed that *C. gestroi* and *C. formosanus* have distinctly different tunneling patterns. Tunnels created by *C. gestroi* are thin and highly branched, with the overall pattern appearing similar to a mosaic or jigsaw puzzle. *Coptotermes formosanus* tunnels, on the other hand, are wider and far less branched. Numerous laboratory examinations of *C. formosanus* tunneling have been performed (e.g., Campora and Grace 2001, 2009), and while these reach beyond *C. formosanus* to help illuminate general principles of subterranean termite foraging to a certain extent, they shed little light on the selection pressures influencing the tunneling behavior of termite species originating in different regions. Comparative studies with termite species from different environments have this potential, but are difficult to perform since termites with different ecological requirements would very rarely be found in the same research location. Thus, the overlapping distributions of *C. gestroi* and *C. formosanus* in Hawaii, Taiwan and Florida create a unique situation for comparative studies.

The initial qualitative visual observations of the differences between *C. gestroi* and *C. formosanus* tunneling patterns were confirmed as quantitatively different tunneling systems by Hapukotuwa and Grace (2012b). *Coptotermes gestroi* constructed thin, highly branched tunnels, while *C. formosanus* tended to construct wider and less branched tunnels. Tunnels of *C. gestroi* showed more spatial dispersion than those of *C. formosanus*, and this species constructed a larger number of tunnels compared to *C. formosanus*. As has been reported by other researchers (Arab and Costa-Leonardo 2005), the presence or absence of wood within the arena did not influence the tunneling pattern of either species.

Since tunneling patterns reflect foraging strategies, these differences suggest that *C. gestroi* and *C. formosanus* may have each evolved to forage most efficiently in different ecological habitats. If trees are more densely and evenly distributed near the equator, then an equatorial termite like *C. gestroi* may find food (wood) more efficiently by an intensive search of the immediate area where food has already been found, rather than by moving further away from that location and searching for more distant food. Since termites forage for food by tunneling, an intensive local search would be facilitated by creating a highly branched network of short tunnels.

By comparison, if fallen wood becomes a rarer occurrence as the distance from the equatorial zone increases, and trees tend to be separated rather than clustered tightly together, a more efficient method of finding food in subtropical and temperate regions might be to strike out in all directions with long and unbranched tunnels until intersecting a new piece of wood, rather than waste time and energy searching intensively in a single location for more wood. Such straight tunnels are characteristic of *C. formosanus*, which inhabits the subtropics and the warm temperate regions. Lee et al. (2009) demonstrated that restricting the number of primary tunnels to five or six, consistent with empirical observations of *C.*

formosanus tunneling in laboratory arenas, maximized food transportation efficiency within the gallery system.

To test this relationship between a particular pattern of tunnel excavation and increased foraging efficiency under specific environmental conditions, Hapukotuwa and Grace (2012c) used a laboratory arena that mimicked the more widely separate, or clumped, distribution of woody resources that might occur in subtropical and temperate regions. A single piece of wood was placed at either end of a foraging arena, and either *C. gestroi* or *C. formosanus* workers and soldiers released in the center. The hypothesis of this experiment was that the presence of widely separated resources in the arena would favor *C. formosanus*, with its long, straight tunnels, and disadvantage *C. gestroi*, with its highly branched tunnel network. Thus, *C. gestroi* would be expected to take longer to find the first piece of wood at one end of the arena than *C. formosanus*. Even if the two termite species did not differ in the time taken to find the first piece of wood, which was possible since the arenas were fairly small, the longer and straighter tunnels constructed by *C. formosanus* would be expected to give it an advantage in discovering the second piece of wood at the opposite end of the arena, since *C. gestroi* would be expected to construct a dense network of tunnels around the first piece of wood discovered rather than immediately striking out across the arena. As predicted, *C. formosanus* did indeed locate the first piece of wood in the arenas an average of one day faster than *C. gestroi* (2.5 vs. 3.5 days), and then discovered the second piece of wood at the opposite end of the arena an average of 2.5 days faster as well (6 vs. 8.5 days) (Hapukotuwa and Grace 2012c).

Yeoh and Lee (2007) also observed that the dense and heavily branched tunneling networks of *C. gestroi* and *C. curvignathus* Holmgren contrasted with the straight and relatively unbranched tunnels of *C. kalshoveni* Kemner. This suggests that selective factors other than wood distribution in different environments may also influence subterranean termite foraging behavior. Computer simulation by Lee et al. (2008) using a lattice model of tunnel structure, demonstrated two possible strategies for optimizing subterranean termite food encounter rates, one based on a searching distance effect (SDE) characterized by long primary tunnels with short branches, and a second based on a searching area effect (SAE), that balances tunnel length with branch length in order to cover a broad area. These strategies reflect the empirical results extremely well, indicating that *C. gestroi* has optimized food encounter rate through a SAE strategy most appropriate for the distribution of woody resources in its native environment, while *C. formosanus* employs a strategy based on SDE.

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