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Aggressive biting of human flesh by the worker caste is a unique behavioral characteristic of the *Nasutitermes nigriceps* complex (Termitidae: Nasutitermitinae) among termites from the United States and Mexico.

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ABSTRACT

We observed aggressive worker biting behavior (AWBB) in *Nasutitermes nigriceps* in which the worker caste rapidly, consistently, and persistently bit into, and clung tightly to human flesh causing a mild sting-like sensation. We used a forearm exposure test to evaluate how widespread this behavior was among termites in Mexico and the western United States. Among the termites tested, we determined that the behavior is limited to only the *Nasutitermes nigriceps* complex. We hypothesize that this presumably mammal–directed defensive behavior by the worker caste evolved in this group because their large arboreal nests are uniquely exposed to increased predation pressure from specialized arboreal mammals such as the tamanduas. Altruistic sacrifice for colony defense is normally a behavior limited to the soldier caste. However, in these "ultra-eusocial" termites the worker caste has also evidently evolved self-sacrificing altruistic colony defense behavior. Although the salivary glands exhibited no peculiar hypertrophy or modification, we suggest that the mild sting-like quality of the bite may be due to a molecular component in the oral secretion or crop content of the workers.

Key Words: Colony defense against vertebrate predators, aggressive worker biting behavior (AWBB), social insects, worker caste altruism, evolution of altruism, stinging bite of termite workers, venom, pain scale, Isoptera, Blattodea

INTRODUCTION

At the outset of a termite collecting trip to Mexico in 2017 we were startled to notice that worker termites, which crawled on our hands or forearms while we were collecting them from their large carton nests, bit fiercely into the skin causing a mildly painful sting-like sensation. This previously undocumented behavior seemed unusual in three respects. First, defensive behavior is usually the domain of the soldier caste, while workers normally retreat (Deligne et al., 1981). Second, despite extensive field experience collecting and handling termites, we had never before received a painful bite from a worker. Third, not only did the workers bite at the skin, but they clung persistently to the skin, with a grip which they could not be prodded to release. In fact, when wiped at, the termite's body became detached from the head and the decapitated head remained attached to the flesh, often eventually drawing a small amount of blood, and causing redness, a welt and itchiness to develop on the skin. We named this novel behavior Aggressive Worker Biting Behavior or AWBB and decided that for the duration of that trip we would document the extent of this behavior using a simple forearm exposure field test. Subsequently, on further collecting trips, we also tested other termite taxa as we encountered them, until we had tested representatives of all the families and subfamilies of the Nearctic region

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MATERIALS AND METHODS

Termites were collected using classical methods, primarily using a hatchet to break into wood or nests and tapping the host material to release termites onto a plastic or metal tray from which specimens could be easily collected. For the forearm exposure field test, we gently dumped the termites and associated debris onto the soft skin of the out-stretched right ventral forearm of the subject for at least one minute or until the pain of the bites caused the subject to brush away the termites (see Fig. 1). The test subjects consisted of the authors, numerous members of the Mexican Forestry Service who accompanied us, and in a few cases, local citizens who were curious about our work. Not all subjects were exposed to all species but at least a dozen individuals felt the stinging bite from workers of the *nigriceps* group. There was no attempt to quantify the number or life stages of the termites used in each test except that we tried to get many individuals (preferably more than 100) and as many life stages and castes (especially soldiers) as possible. Typically, the subject arm was positioned over a second collecting tray so that the remaining sample could be tested on another subject and specimens could be preserved in 80% ethanol for identification and other analyses. To ascertain the taxonomic range of AWBB we tested samples of most species collected during two trips to Mexico (combined duration 5 weeks in 2017, 2018) and several collecting trips in the Western United States encompassing parts of California, Nevada, Oregon, New Mexico, Arizona and Texas (approximately 6 weeks total in 2018 and 2019).

RESULTS

Table 1 lists the four termite families, nineteen termite genera, and 35 termite species that were tested for aggressive worker biting behavior using the forearm exposure test. As can be seen in Table 1, all species scored negative for AWBB except for species of *Nasutitermes. Nasutitermes corniger* and *N. ephratae* gave a weakly positive biting reaction in some cases, while *Nasutitermes nigriceps* and *N. colimae* consistently gave a strongly positive test response. In the majority of other taxa, neither the workers nor soldiers showed any reaction to human skin. They exhibited no apparent alarm or excitation. They simply wandered around on the skin as if it was any inert substrate, and eventually tumbled off. The only exceptions were *Coptotermes testaceus* and the two other species of *Nasutitermes* we tested. *N. corniger* and *N. ephratae.* In our forearm tests, a few *Coptotermes* soldiers managed to bite into the skin, but they did not draw blood and were easily brushed away. In the Nasutitermitinae, two tested genera *Tenuirostritermes* and *Parvitermes* showed no biting reaction, while in *N. corniger* and *N. ephratae* the worker biting reaction was weak to non-apparent. In both species a few bites by workers did occur but without the stinging sensation or a noticeable irritation of the skin.

DISCUSSION

At first, we considered AWBB to be such an unusual behavior that we wondered if worker biting was a response to the insect repellent that we were using. In subsequent days, we specifically refrained from using insect repellent and continued to observe the same behavior. We then considered whether biting was due to some unique individual odor. To control for this possibility, we allowed all our guests and field staff to participate in the forearm exposure test (at least a dozen different people). All experienced the same stinging pain which invariably produced, yelping, flinching and efforts to wipe the termites off as quickly as possible. The pain was certainly more intense than a mosquito bite, but much less than a honey bee sting. Arizona entomologist, Dr. Justin Schmidt has developed a pain scale for measuring the intensity of insect stings (summarized in Schmidt, 2016). Based on our observations, on the Schmidt scale, *N. nigriceps* worker stinging bites would probably rate no more than ½ to 1 on a scale of 1-4 where a western honeybee rates a 2.

Although, AWBB was novel to us and our colleagues in Mexico, another colleague (preferring to remain anonymous) confirmed that she also observed what we are calling AWBB during her studies of *N. nigriceps* in Panama and while studying *Nasutitermes acajutlae* in the Caribbean, stating that:

"….it is well known among locals, at least where I've worked in Panama and the Caribbean, that the "large termite" (*N. nigriceps* or *N. acajutlae*) can "hang on" to human skin. In fact, that's a way that residents differentiate nasute species (in addition to nest appearance)." (email communication, January 6, 2021).

Although this colleague seems to have observed AWBB, she did not recall that the bites were particularly sting-like. We acknowledge that the stinging sensation is not delivered by a stinger, like the modified ovipositors of the Hymenoptera, but we hypothesized that the stinging sensation may be the result of a chemical in the saliva or oral secretions. We dissected numerous specimens but could find no specialized gland and no particular hypertrophy of the salivary glands or salivary reservoirs of *N. nigriceps* compared to other termites. We also noted the ability of the workers not only to bite, but to bite and gnaw, thus clinging to the skin. The continuous gnawing often resulted in drawing blood (Fig. 2 & 3). Soldiers are much smaller than workers and almost immediately fell off the arm. It was easy to associate individual workers, which are much larger than soldiers with individual bites.

In addition, we observed that even when brushed at, the thorax and abdomen of the termite worker would usually detach so that just their head stays attached to the subject (Fig. 4). This equates to the phenomenon of "stinger autotomy" as in the honey bee and some other social Hymenoptera, where the stinger mechanism detaches from the bee's body, sacrificing the worker bee's life, to keep venom pumping into the mammal attacking the colony (Hermann, 1971). As with the honey bee stinger, effort was required to detach the termite head from the subjects arm often leaving a drop of blood followed by the development of welts and a period of itchiness.

As pointed out by Schmidt (2016), the induction of pain in vertebrate predators has an important adaptive function. It is a particularly important aspect of colony defense by social insects against long-lived mammalian predators, so that they are taught by the painful experience, to avoid further predatory behavior in the future. It seems likely that the bite alone is an inadequate defense by the workers, if not for the pain also delivered.

Thus, we expect that educating mammalian predators would be more effective if there was also some pain inducing quality of the saliva or oral secretion. For example, we hypothesize that an adaptation as simple as a slight increase in the acidity of the saliva (e.g. lower pH), could produce the pain associated with the bite. Anyone who has experienced vinegar (acetic acid) or lemon juice (citric acid) poured into an open cut will realize the painful effect, thereby induced. Unfortunately, we were not equipped at the time to make a comparative evaluation of the acidity of termite worker saliva. However, it has long been known that the foregut of termites is a slightly acidic environment (Randall and Doody, 1934). Tokuda et al., (1997) showed that cellulases are endogenously produced in the salivary glands and midgut and that the optimal pH for cellulase activity is in the range of 4.4 -6.0 for various termites (66% of glucosidase activity is in the salivary gland, 90% of the glucanase activity is in the midgut). Furthermore, Khademi et al. (2002) demonstrated that the salivary glands, foregut, and midgut of *Nasutitermes takasagoensis* are all acidic in the pH range from 2.6-5.6 for the enzyme catalyzed hydrolysis by endogenous cellulases. Thus, it seems likely that any oral secretion would likely be somewhat acidic and therefore might induce the sting-like effect we witnessed.

Perhaps the most important question to consider is why has AWBB evolved in only the *N. nigriceps* group of the Nasutitermitinae. We hypothesize that it is because the *N. nigriceps* group represents the intersection between two sets of morphological and behavioral characters; soldier mouthpart morphology and colony structure. First, it is well known that in termites the soldier caste defends the colony (except in Apicotermitinae where most species are soldierless). This is mostly accomplished using elongated, blade-like mandibles that work in a scissoring motion to dismember invaders such as ants. In the highly derived Nasutitermitinae, chemical defense has replaced mechanical defense, and the soldier head capsule is modified to form a nozzle-like structure. Internally, the frontal gland is modified into a pipette-like structure which enables them to shoot or squirt defensive secretions at enemies. In *N. nigriceps,* the defensive secretion consists of a cocktail of 10 different volatile and non-volatile components (Valterova et al., 1991). This chemical defense is effective against small invertebrates but may be less so against a much larger mammalian predator. Second, we characterize colony structure after the 4-tiered hierarchy of sociality (Myles, 2003). The species in the lowest tier, pro-eusociality, as seen in Archotermopsidae and Kalotermitidae consists of small colonies limited to excavations in logs or dead branches. In the second tier, meso-eusocialty, termites in Mastotermitidae and Rhinotermitidae are subterranean and have large populations but no defined nest. In the third tier, meta-eusociality, as in most species of Termitidae, there is a small but distinct nest structure, and in the fourth and most advanced tier, ultra-eusociality, colonies make a very large nest often exceeding 1 meter in diameter, which is usually conspicuously present above ground as a large mound or as a very large arboreal nest. *Nasutitermes nigriceps* and *N. colimae* are the only Nearctic termites, that meet the criteria of being ultra-eusocial that also have soldiers that use chemical defense. In other words, their nests are extremely conspicuous (Thorne, 1980; Thorne et al.,1996) exposing them to specialized vertebrate predation by termitophilous mammals such as oppossums, tamanduas, and silky anteaters (Redford, 1987; Emmons and Freer, 1990; Oyarzun et al., 1996) yet the termite soldier mouthparts are modified to defend against small invertebrates. We suggest that this combination of factors has led to selection for aggressive worker biting behavior for colony defense against mammalian predators. We hope that this documentation of AWBB will stimulate further research looking for putative chemical factors causing the sting-like sensation and helps to differentiate significant phylogenetic and adaptive differences within the large genus *Nasutitermes*.

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Table 1. List of termite families and species tested for Aggressive Worker Biting Behaviour (AWBB) by the forearm exposure test. (Subfamilies after Hellemans et al., 2024)

Family	Species	AWBB	Notes
Archotermopsidae			
	1. *Zootermopsis laticeps*	negative	
	2. *Zootermopsis angusticollis*	negative	
	3. *Zootermopsis nevadensis*	negative	
Kalotermitidae			
	4. *Pterotermes occidentis*	negative	
	5. *Marginitermes hubbardi*	negative	
	6. *Paraneotermes simplicornis*	negative	
	7. *Incisitermes minor*	negative	
	8. *Incisitermes marginipennis*	negative	
	9. *Incisitermes fruticavus*	negative	
	10. *Cryptotermes fatulus*	negative	
Heterotermitidae			
	11. *Reticulitermes hesperus*	negative	
	12. *Reticulitermes tibialis*	negative	
	13. *Heterotermes aureus*	negative	
	14. *Heterotermes orthognathus*	negative	
	15. *Coptotermes testaceus*	negative	a few soldiers penetrated skin
Termitidae (Amitermitinae)			
	16. *Amitermes californicus*	negative	
	17. *Amitermes wheeleri*	negative	
	18. *Amitermes beaumonti*	negative	
	19. *Amitermes silvestrianus*	negative	
	20. *Amitermes emersoni*	negative	
	21. *Amitermes ensifer*	negative	
	22. *Amitermes cryptodon*	negative	
	23. *Gnathamitermes grandis*	negative	
	24. *Hoplotermes amplus*	negative	
Termitidae (Termitinae)			
	25. *Termes* sp.	negative	
Termitidae (Microcerotermitinae)			
	26. *Microcerotermes septentrionalis*	negative	
	27. *Microcerotermes gracilis*	negative	
Termitidae (Apicotermitinae)			
	28. "*Anoplotermes*" spp.	negative	
Termitidae (Syntermitinae)			
	29. *Cahuallitermes intermedius*	negative	
Termitidae (Nasuitermitinae)			
	30. *Tenuirostritermes tenuirostris*	negative	
	31. *Parvitermes mexicanus*	negative	
	32. *Nasutitermes corniger*	partial	a few bites, not sting-like
	33. *Nasuitermes ephratae*	partial	a few bites, not sting-like
	34. *Nasutitermes colimae*	positive	rapid aggressive stinging bite
	35. *Nasutitermes nigriceps*	positive	rapid aggressive stinging bite

Figure 1. Demonstration of forearm exposure test. Exposure of forearm to termites (with nest debris).

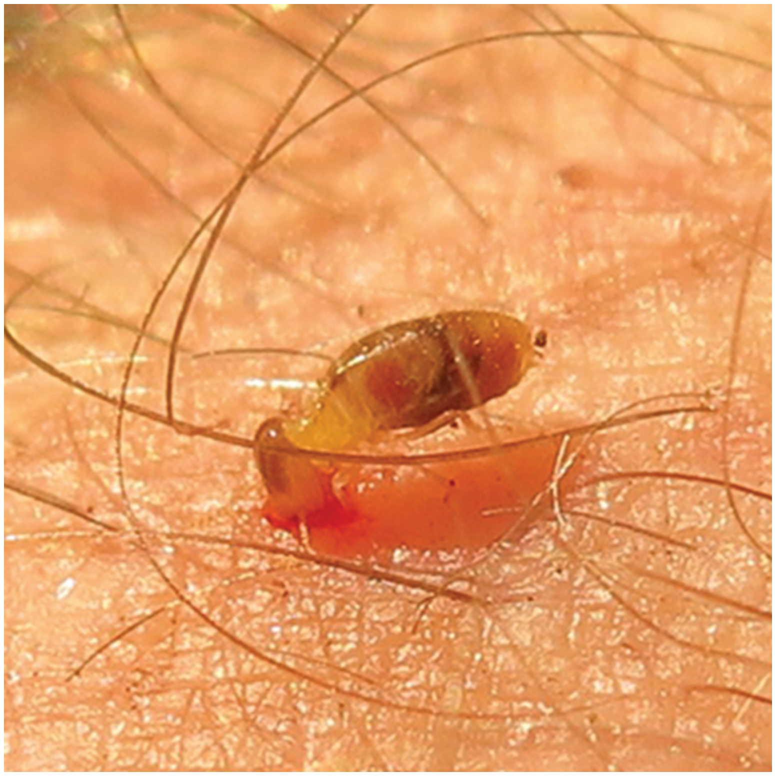

Figure 2. *Nasutitermes nigriceps* termite worker biting into and clinging to human skin.

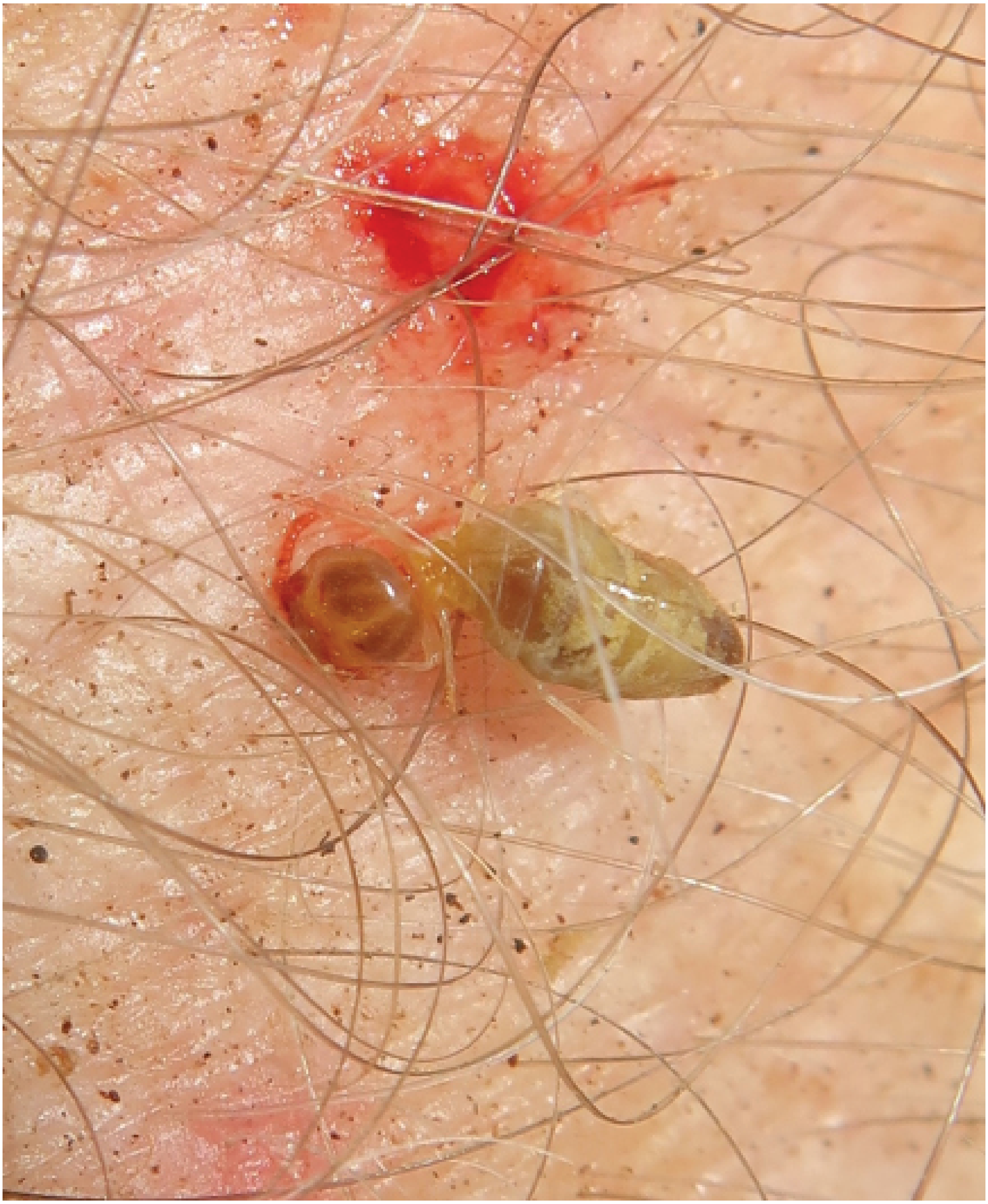

Figure 3. Close up of *Nasutitermes nigriceps* worker termite biting into arm and drawing blood.

Figure 4. *Nasutitermes nigriceps* worker head still embedded, clinging, and gnawing into the skin even after its body was rubbed off (notice the redness and developing welt on the skin).