SCIENTIFIC NOTE

STICKY-BUSINESS: A UNIQUE CHEMICAL DEFENCE STRATEGY IN NASUTE TERMITES

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Summary

Predation is a strong selective force driving the evolution of complex antipredator traits. Antipredator defences in the form of morphological or chemical weaponry, or behavioural traits, increases a prey organism's chance of survival when faced with a predator. Termites are a group of social insects that possess an arsenal of mechanical and chemical weapons to thwart attacks from vertebrate and invertebrate predators. The soldier caste of termites have a range of mandibular modifications, including snapping, piercing and crushing mandibles. Some taxa, however, have undergone mandibular regression and are entirely reliant on chemical defence. The nasute termites are one such group that have lost their mandibles and instead have a specialised cephalic appendage in which they use to eject as viscous defensive secretion. The chemical and morphological aspects of some termite defences are well-studied, but often the behavioural components of complex antipredator traits are often neglected in current studies. Thus, improving our understanding of the underlying biological and behavioural mechanisms of termite defence systems will allow us to increase our current knowledge of the evolutionary history of a complex social insect taxon.

Keywords: Isoptera, termites, defence, antipredator adaptations, weaponry

Predator-prey interactions are commonly seen throughout the animal kingdom, with predation being an important selective force driving the evolution of anti-predator defences (Endler, 1991). If prey cannot effectively defend themselves from a predator, then they are more likely to end up as the predator's next meal. As such, prey have evolved a suite of defence mechanisms, from spikes and armour, to warning colouration and complex chemical defences, to increase their chances of survival when faced with a predator (Edmunds, 1974; Endler, 1991). Defensive adaptations can be morphological, behavioural, or chemical, with some species employing a range of tactics to ensure the highest level of protection against predators (Emlen, 2008; Ruxton et al. 2019).

When we think of well-defended animals, termites are typically not the first thing that comes to mind. Termites are a group of social insects that are closely related to cockroaches (Inward et al. 2007; Legendre et al. 2008). These soft-bodied insects exist in high densities in relatively static communities within a nest structure (Eggleton, 2011). The colony is divided into several castes, including soldiers, workers, reproductives and typically a king and queen, each with different functional roles within the colony. Termites are particularly vulnerable to predation from a wide variety of vertebrate and invertebrate predators. Termites provide a tasty meal for several animals such as anteaters and echidnas, and many arthropods such as predatory ants (Deligne et al. 1981; Eggleton, 2011). So how do termites protect their colonies given that they seem to be a target for so many predatory species? The first line of defence for termites stems from their sheltered lifestyle. They are hidden away in complex tunnels and galleries within nests and therefore termites can minimise the risk that they'll be detected (and eaten) by predators (Perna et al. 2008). If this fails, however, termites have an arsenal of secondary defences they can employ (Eggleton, 2011).

Termites are well-equipped with a variety of morphological, chemical, and behavioural traits to assist in thwarting predator attack. The soldier caste is primarily responsible for colony defence and exhibit the highest degree of morphological variation compared to the other castes (Eggleton, 2011). Often, the heads of soldiers are enlarged and highly sclerotised. The mandibles of termite soldiers are highly modified for a variety of purposes including biting, crushing, snapping and piercing. Those species with snapping mandibles can produce rapid strikes that can inflict serious injury, or even death to small arthropod predators whilst some species can bite or latch onto approaching predators in attempt to deter them from breaching the nest (Prestwich, 1984; Seid et al. 2008). Most of these mandibular adaptations, in which are referred to as mechanical defence strategies, are often accompanied by some form of chemical defence. This can be in the form of secretions exuded from specialised glands, the production of alarm pheromones or even toxic substances being ejected from specialised structures (Mill, 1983; Prestwich, 1979a,1984; Šobotník et al. 2010). There are examples of some termite species that exhibit suicidal altruism, in that they give their life for the benefit of the colony, through a process known as autothysis. This process sees an individual soldier (or in some species, this strategy is employed by workers), essentially commit suicide by rupturing internal glands and releasing a sticky secretion that coats the predator, thereby protecting the rest of colony from a predator attack (Bordereau et al. 1997; Prestwich, 1984; Šobotník et al. 2012). Autothysis is definitely one of the more extreme defensive measures we see termites exhibiting as a means of stopping predator attacks.

By far, the most unique and morphologically specialised defence mechanism of termites is seen in that of the group Nasutitermitinae, a taxon that relies solely on chemical defence. The 'nasute' soldiers have undergone mandibular regression, in that they have reduced or lost their mandibles entirely. Rather, they have evolved a specialised cephalic appendage, known as the nasus (Prestwich, 1979b, 1984; Šobotník et al. 2010). This structure resembles an elongated rostrum and acts as a deployment mechanism for the soldier's defensive secretion. The nasus essentially acts as a biological gun. When faced with a potential threat, typically in the form of predatory ants, nasute soldiers will eject a toxic, glue-like secretion from the nasus, that entangles the predator (Eisner et al. 1976). Due to the viscous and rapidly hardening nature of the secretion, predators often experience impaired movement, blocked spiracles and sensilla and even death. The secretion induces grooming behaviour in ants, causing the sticky secretion to be further spread across the ant's body. There are 81 genera of nasutes worldwide, all of which possess a nasus and defensive secretions (Cuezzo and Nickle, 2011).

The defensive secretion utilised by nasute termites is produced by a large, unpaired sac known as the frontal gland, which is located within the head capsule. This specialised gland is unique to the most advanced termite families and is one of the most studied termite organs. Within nasutes, the secretion itself may represent up to one-tenth of soldier's fresh body (Šobotník et al. 2010).

The defensive secretion produced by nasute soldiers is chemically complex, and possesses some novel diterpenes, unique only to termites (Prestwich, 1979b). The frontal gland secretion is known to contain a mixture of diterpenes and monoterpenes, typically along with other compounds such as alcohols and ketones (Goh et al. 1990; Prestwich, 1979b). Often, the chemical composition of the defensive secretions is species-specific (Goh et al. 1990; Gush et al. 1985). Diterpenes are the chemical constituent thought to be primarily responsible for the physical properties of the secretion, namely the congealment of the secretion when exposed to air but are also poisonous. The monoterpene hydrocarbons in the mixture are thought to enhance the stickiness and irritancy of the secretion, whilst also acting as a topical poison (Prestwich, 1979b; Šobotník et al. 2010).

As if the nasute termite's defensive secretion wasn't already complex enough, the monoterpenes in the secretion also serve as an alarm pheromone and a deterrent to other potential predators in the area (Costa-Leonardo et al. 2009). Once sprayed by an individual soldier, the defensive secretion causes the rapid recruitment of other soldiers to the area (Prestwich, 1984; Roisin et al. 1990). Soldiers will typically surround the predator, holding a defensive stance, but will only spray their secretion if they are directly attacked by the predator (Eisner et al. 1976; Lubin and Montgomery, 1981). Therefore, the secretion is an effective alarm signal and also acts to repel other threats around the nest. The presence of the secretion in the environment has the potential to deter even mammalian predators (Eisner et al. 1976; Šobotník et al 2010).

It seems that termites are not as vulnerable as we once thought. With an impressive arsenal of weapons and defensive tactics, termites are more than capable of preventing an impending predator attack. Nasutes, in particular, are an example of how predation can drive the evolution of highly complex and specialised adaptations, with chemical modes of defence playing an important role in colony survival. The chemical and morphological aspects of some termite defences are well-studied, but often the behavioural components of complex antipredator traits are often neglected in current studies. Understanding the biology and behaviour underlying termite defence systems is an important step towards increasing our understanding of the evolutionary history of a complex social insect.

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