

The rapid mandible strike of a termite soldier

Marc A. Seid¹, Rudolf H. Scheffrahn² and Jeremy E. Niven^{1,3}

Arthropods use a remarkable variety of mechanisms to store energy for rapid ballistic movements [1–8]. These movements are primarily either for prey capture [1,2] or for predator evasion [3–5], although the mandible strike of the trap-jaw ant can produce both outcomes [6,7]. Soldiers of the termite *Termes panamaensis* (Snyder) also have a mandible strike [9]. We report that this mandible strike is a rapid, ballistic movement that functions neither for prey capture nor for predator evasion, but as a defence for the colony against insect invaders such as ants or other termite species. Unlike that of the trap-jaw ants [6,7], the mandible strike of *T. panamaensis* soldiers involves a scissor-like movement of highly elongated mandibles across one another, powered by energy stored in deformation of the mandibles, a mechanism convergent with the mandible strike of the ant *Myrmica* [8,10]. The velocity achieved during the *T. panamaensis* strike exceeds those reported for other ballistic movements in arthropods [1–8] and generates sufficient force upon impact that a single blow can kill invaders within the narrow confines of their tunnels.

Termites are eusocial insects that form colonies, some in excess of 1 million individuals, with specialized worker, soldier and reproductive castes [11]. In tropical rainforests termites, such as *T. panamaensis*, excavate extensive tunnel networks that ramify through the wood in which they feed. Soldiers, which may comprise as little as 1% of the colony, defend it against attacks from invaders, such as predatory ants and other termites with which they compete for resources. To enable them to defend the colony, soldiers' heads are modified to produce formidable weapons that in *T. panamaensis* take the form of highly elongated mandibles [9].

T. panamaensis soldiers were taken from colonies collected in Gamboa, Panama (9°7'N, 79°42'W) and placed in artificial tunnels that mimicked the dimensions of those in which they

live (Figure 1). The upper surface of these tunnels was transparent allowing the behaviour of the termites to be monitored by a high-speed video camera. In each trial a *T. panamaensis* soldier and a single invader of another termite or ant species were placed at either end of the artificial tunnels. Invaders were always of species obtained by sampling within or near *T. panamaensis* nests. Upon detecting an invader in the tunnel, the soldiers manoeuvred their mandibles into position next to or on the underside of the invader's head and released the strike (Figure 1B).

A single strike can kill workers and soldiers of competing termite species (Figure 1B), such as *Microcerotermes* sp., as well as predatory ant species such as *Azteca* sp. Typically, these encounters resulted in the death of >70% of the termite invaders and >60% of the ant invaders (see Table S1 in the Supplemental Data available on-line with this issue). Workers of invading termite and ant species died in 85% and 71% of encounters, respectively. Whilst both termites and ants were susceptible to the mandible strike, soldiers were significantly less susceptible than workers (G-Test, $p < 0.025$). The workers of some ant species such as *Gnamptogenys* sp. were, however, significantly more resilient to attacks (Fisher Exact Test, $p < 0.0001$). Examination of the heads of invaders after death did not reveal external damage that would occur if the mandibles pierced or tore the cuticle, suggesting that the force of the impact itself caused death. Those trials in which invaders were not killed usually ended in a stand-off or their retreat (84%); just 4.4% of all trials resulted in a *T. panamaensis* soldier dying.

Soldiers of *T. panamaensis* have a total body mass of 1.76 ± 0.15 mg (mean \pm standard deviation, $n = 14$ unless otherwise stated) and a total length of 4.98 ± 0.21 mm. Their head comprises 39.5% of the body mass and 28.1% of the length and the mandibles, which project forward from the head, are just 1.6% of the body mass but 29.8% of the length (Figure 2A; Table S2). Whilst in a resting position the mandibles are held with tips touching but separated at the base (Figure 1A). The mandibles are smooth, lacking the mechanosensory hairs that in some ants trigger mandible strikes (Figure 2A) [6,8]. Behavioural observations show that

antennal contact is sufficient to initiate the preparatory movements of the mandibles for the strike (Figure 1B). Consistent with these observations strikes can be initiated in restrained soldiers by touching the antennae. During a strike the antennae are either raised or make a dorsal deflection, presumably to prevent damage.

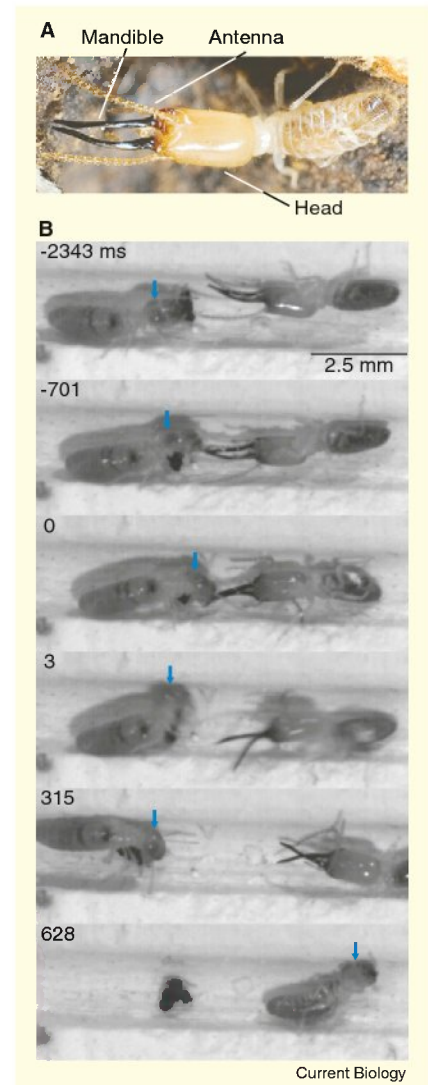


Figure 1. *Termes panamaensis* soldier termites defend the colony against attack from invaders.

(A) Photograph of a soldier termite. (B) A video sequence showing an encounter between a soldier termite and an invading worker termite (*Microcerotermes* sp.). Following detection of the invader (–2343 ms), the soldier termite rolls onto its back positioning the mandibles underneath the invader's head (0 ms). The strike is triggered propelling both termites backwards in the tunnel (3 ms). After contact with the strike the invader walks a few steps but dies (628 ms). The blue arrow indicates the position of the invader's head.

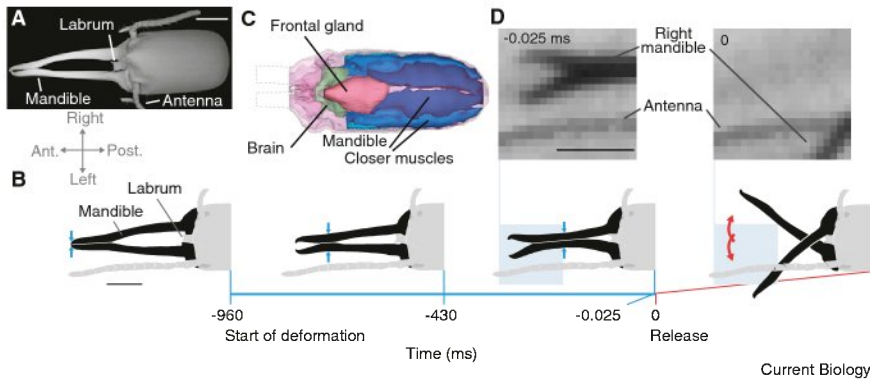


Figure 2. The mandible strike of the *Termes panamaensis* soldier termite.

(A) A scanning electron micrograph of the head of a soldier termite. (B) A schematic of mandible movements before and during a strike. Before the strike, the mandibles bend, their point of contact (blue arrows) moving towards the head. The strike is executed when the mandibles cross (red arrows). The region captured by the high speed video camera in (D) is indicated by a pale blue box. (C) A serial reconstruction of the head including the muscles, brain and frontal gland. The position of the mandibles is indicated by a grey dashed outline. (D) Sequential images from high speed video taken at 40,000 frames per second showing the rapid crossing of the mandibles during the strike. Scale bars indicate 0.5 mm.

Before a strike the mandibles are pushed against one another causing them to bend and their point of contact to move towards the head (see Supplemental Movie S1). During a strike the mandibles slide over one another, crossing in less than 0.025 ms (Figure 2B,D). The mandible tips rotate through $53.8 \pm 8.53^\circ$ ($n = 10$) with a mean velocity of $56.0 \pm 8.87 \text{ m}\cdot\text{s}^{-1}$, though individual strikes can exceed $67 \text{ m}\cdot\text{s}^{-1}$. Thus, although *T. panamaensis* are just 15% of the body mass of trap jaw ants, the velocity of their strike is greater [7]. Modelling the mandible as a thin rod (see Supplemental Experimental Procedures), the mean force exerted by the strike on a potential invader is of the order of 54 mN. Generating an average *T. panamaensis* strike requires 0.15 mJ of energy, giving an estimated power output of 1.5 W (assuming acceleration is applied within 0.01 ms). The mandibular closer muscles (Figure 2C), which pull the mandibles towards one another, weigh $0.15 \pm 0.08 \text{ mg}$ and have a cross-sectional area of 0.17 mm^2 , giving a specific power output of the order of $11 \text{ MW}\cdot\text{kg}^{-1}$ and generating an equivalent of $3 \text{ MN}\cdot\text{m}^{-2}$ of muscle.

Direct muscle contractions could not generate the mandible movements over the short distances and times available [4,5]. Instead, the deformation of the mandibles before the strike, which lasts $0.78 \pm 0.25 \text{ s}$ ($n = 66$), stores energy from muscle contraction, released probably when the forces exerted

exceed a threshold allowing the mandibles to slide over one another. A modified mouthpart, the labrum, lies between the mandibles (Figure 2A) and is compressed between the mandibles during the strike. Following a strike, the mandibles return to their resting position. The labrum is necessary for resetting the mandibles. Removal of the entire labrum, or raising it out of the plane of the movement, caused the mandibles to rotate further during the strike (Figure S1). Following this excess rotation, the mandibles were jammed together and could not be reset. Thus the labrum is required to prevent extreme rotation of the mandibles.

Both crustaceans [1,2] and insects [3–7,8] produce rapid movements that rely on the storage of energy in advance of the execution of the movement. Insects use a variety of mechanisms in which energy is stored by cuticular deformation prior to the generation of rapid movements. These energy storage mechanisms may allow the generation of large forces without paying the substantial costs associated with maintaining and carrying large muscles. This strategy has evolved numerous times within the insects and is involved in the production of jumping and kicking [3–5] and the mandibular strike of the trap jaw ant [6,7]. *T. panamaensis* soldiers generate the fastest known mandible strike by a mechanism that is convergent with that of *Myrmium* ants, which also store energy in mandible deformation and lack a distinct trigger mechanism

[8,10]. The function of the *Myrmium* mandible strike is uncertain but it may be for defensive purposes like that of the *T. panamaensis* soldiers [8,10]. The termite soldiers do not employ stealth or surprise as tactics because they are facing their adversary. Instead, the high velocities achieved during their mandible strike are crucial for generating sufficient force upon impact within the narrow confines of a tunnel that the invader is totally disabled.

Supplemental Data

Supplemental data are available at [http://www.current-biology.com/supplemental/S0960-9822\(08\)01261-X](http://www.current-biology.com/supplemental/S0960-9822(08)01261-X).

Acknowledgments

Thanks to M. Burrows, S. Rogers, J. Scharlemann, G. Sutton and W. Wcislo for comments on the manuscript and advice. Supported by the STRI Laboratory of Evolutionary Behaviour and Neuroscience/Levinson Family Foundation (M.S., J.E.N.) and Royal Society (J.E.N.).

References

- Burrows, M. (1969). The mechanics and neural control of the prey capture strike in the mantid shrimps *Squilla* and *Hemisquilla*. *Z. Vergl. Physiol.* 62, 361–381.
- Patek, S.N., and Caldwell, R.L. (2005). Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp *Odontodactylus scyllarus*. *J. Exp. Biol.* 208, 3655–3664.
- Evans, M.E.G. (1973). The jump of the click beetle (Coleoptera, Elateridae) -energetics and mechanics. *J. Zool. Lond.* 169,181–194.
- Bennet-Clark, H.C. (1975). The energetics of the jump of the locust, *Schistocerca gregaria*. *J. Exp. Biol.* 63, 53–83.
- Burrows, M. (2003). Biomechanics: Froghopper insects leap to new heights. *Nature* 424, 509.
- Gronenberg, W., Tautz, J., and Hölldobler, B. (1993). Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science* 262, 561–563.
- Patek, S.N., Baio, J.E., Fisher, B.L., and Suarez, A.V. (2006). Multifunctionality and mechanical origins: Ballistic jaw propulsion in trap-jaw ants. *Proc. Natl. Acad. Sci. USA* 103, 12787–12792.
- Gronenberg, W., Hölldobler, B. and Alpert, G.D. (1998). Jaws that snap: control of mandible movements in the ant *Myrmium*. *J. Insect Physiol.* 44, 241–253.
- Deligne, J., Quennedy, A. and Blum, M.S. (1982). The enemies and defense mechanisms of termites. In Hermann, H.R. ed. *Social Insects Vol. II* (New York: Academic Press).
- Moffett, M. (1986). Mandibles that snap: notes on the ant *Myrmium camillae* Emery. *Biotropica* 18, 361–362.
- Abe, T., Bignell, D.E. and Higashi, M. (2000). *Termites: Evolution, Sociality, Symbioses, Ecology* (Boston: Kluwer Academic Publishers).

¹Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá. ²University of Florida Research & Education Center, 3205 College Avenue, Fort Lauderdale, FL 33314, USA. ³Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.
E-mail: jen22@cam.ac.uk