Ambidextrous Mandibles in the Fire Ant *Solenopsis invicta*

DEBY L. CASSILL[1] AND DEVON SINGH[2]

Ann. Entomol. Soc. Am. 102(4): 713–716 (2009)

ABSTRACT The elongation and sharp teeth of ant mandibles are considered important adaptations that have contributed to ants successful colonization of terrestrial habitats worldwide. In extant ant species, mandibles function as hunting and defense weapons, as well as multipurpose tools for excavating soil, cutting leaves, capturing and butchering prey, harvesting seeds, and transporting brood. This article reports that the mandibles in the red imported fire ant, *Solenopsis invicta* Buren, are functionally ambidextrous. Individuals opened and closed each mandible in synchrony or independently depending on the requirement of the task at hand. Upon completion of a task, individuals were without a preference in the orientation of mandible overlap—right overlap or left overlap. Orientation of mandible overlap before and after performing a task was also examined in nine other ant species. No overlap orientation preference was observed in any of these ant species, suggesting that ambidextrous mandibles are a universal trait in ants. These findings add an increment of knowledge to the diverse functions of ant mandibles.

KEY WORDS functional morphology, grasping, fine motor skills, handedness

The family of ants (Formicidae) recently joined the families of preying mantids (Mantodea) and mantid lacewings (Neuroptera: Mantispidae) as insects that manipulate objects with grasping forelegs (Cassill et al. 2007). In combination with their forelegs, ants use their opposing mandibles for a diverse set of functions. For example, ants hold brood gently with their mandibles during grooming (Cassill et al. 2007) or while transporting brood from chamber to chamber inside the nest. Ants also use their mandibles for hard manual labor such as nest excavation (Cassill et al. 2002) and warfare, defense, hunting, foraging, or butchering prey (Hölldobler and Wilson 1990, Gronenberg 1995, Gronenberg et al. 1997, Cassill et al. 2005).

Among ant species, mandibles are highly diversified and a defining feature (Fisher and Cover 2007). In their primitive form, ants had short, curved mandibles with two teeth (Bolton 2003). Most modern ants have elongated mandibles with a wide masticatory margin, giving the mandible a distinctive triangular shape. Exceptions to the triangular mandible morphology are ants with short, narrow mandibles, long-toothed mandibles (Eisner et al. 1996), sickle-like mandibles (Gronenberg 1995), single-toothed mandibles for puncturing the soft cuticle of prey, or multiple-toothed mandibles for cutting or grinding the harder cuticle of plants and prey (Wilson 1980).

A serendipitous observation made during a study on the form and function of the red imported fire ant, *Solenopsis invicta* Buren, appendages (Cassill et al. 2007) found that their mandibles overlapped in two orientations—right overlap or left overlap (Fig. 1). This observation raised the question of whether individual ants had a "handedness" or preference for right or left-overlapping mandibles and whether the dexterity of mandible overlap was unique to fire ants. The purpose of this study was to test whether the mandibles of fire ant workers and queens were indeed ambidextrous, moving in synchrony or independently of each other as the task required, with no handedness or preference for the orientation of overlap (right or left overlap) within the same individual or within a population of individuals. We also recorded the mandible overlap orientation in nine other ant species before and after performing a task to determine how widespread ambidexterity in mandible use might be in ants.

Methods and Materials

Form. The heads of 36 fire ants (six mated queens, six virgin queens, six males, six large workers, six medium workers, and six small workers) were dissected and photographed using a 3500-N variable pressure scanning electron microscope (Fig. 1). Mandible width was measured from the tip of the first apical tooth to the tip of the fourth distal tooth using Quartz PCI software (Hitachi High Technologies America, Pleasanton, CA) (Fig. 1c and d).

Function. To quantify the dexterity of fire ant mandibles at the population level, 290 workers were randomly selected from five laboratory stock colonies and frozen (laboratory stock colonies were originally collected in August 2004 from fields in Pinellas County,

[1] Corresponding author: University of South Florida St. Petersburg, St. Petersburg, FL 33701 (e-mail: cassill@stpt.usf.edu).
[2] University of South Florida St. Petersburg, St. Petersburg, FL 33701.

0013-8746/09/0713–0716$04.00/0 © 2009 Entomological Society of America

Downloaded from https://academic.oup.com/aesa/article/102/4/713/58025 by guest on 23 April 2024

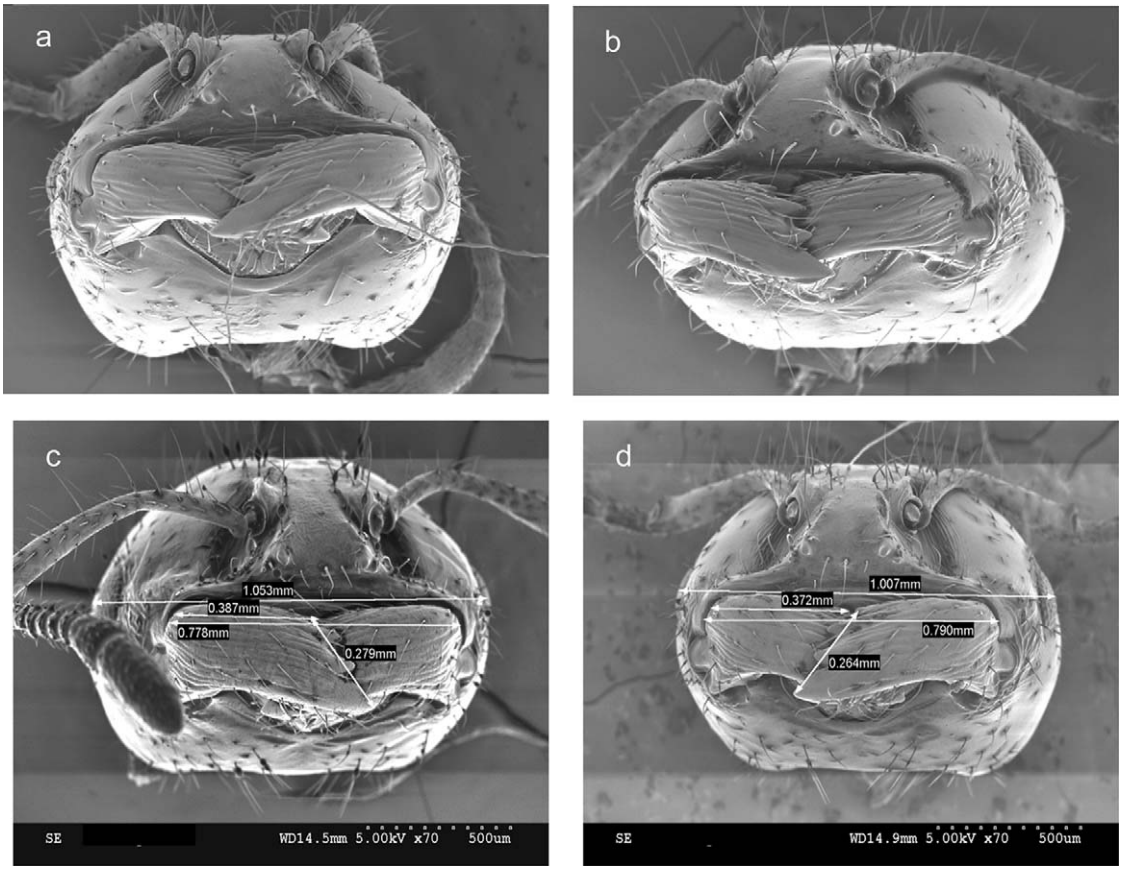

Fig. 1. Scanning electron micrograph images of ambidextrous mandibles of *S. invicta*. Workers with left-overlap (a) and right-overlap (b) mandibles. To determine mandibular symmetry (c and d), each overlapping mandible was measured from its apical to distal teeth using Quartz PCI software. Photos: WD12.1 mm, 4.90 kV × 250, 2 μm.

FL). In addition, >100 workers per species from nine other ant species were collected in Pinellas County, FL, during May 2008. Workers were collected along foraging trails or in leaf litter with an aspirator and thus were likely from a single colony. Workers were frozen within several hours after collection. Workers (n = 100) from each ant species were placed under a microscope, one at a time, to record the orientation of mandible overlap—right overlapping or left overlapping.

To quantify the dexterity of worker mandibles at the individual level, 62 fire ant workers were temporarily narcotized with CO_2 and divided into two groups. Workers with right-overlapping mandibles were placed in one group; workers with left-overlapping mandibles were places in a second group. When workers revived, each group was placed in an artificial nest containing soil to encourage the use of mandibles for excavation. Excavations were videotaped at 20× for 2 h to record mandible use. After 24 h, each group of workers was frozen and the orientation of the postexcavation mandible overlap for each worker was recorded.

To quantify the dexterity of queens at the individual level, videotapes of five newly mated queens were analyzed to determine the sequence of change in the overlap of mandibles during self-grooming and egg manipulation. Ten sequences were recorded on each of the five queens.

Data Analysis. Data were analyzed using JMP IN statistical software (Sall and Lehman 2005). Data were checked for independence and normality of error effects and for homogeneity of error variance. Data transformations were not required. Regression, analysis of variance (ANOVA), t-tests and chi-square tests were used as experimental design and data type dictated.

Results

Form. When comparing right and left mandibles on the same worker, no significant difference in the length of their toothy edges was found ($t_{35} = 0.68$, $P = 0.716$). Right and left mandibles were symmetrical for this parameter.

Function. In fire ants, there was no significant difference in an ant's handedness or preference for mandible overlap at the population level (53.7% were right overlap; $\chi^2 = 2.44$, df = 289, $P = 0.517$) or at the individual level (51.4% of individual excavating work-

Downloaded from https://academic.oup.com/aesa/article/102/4/713/58025 by guest on 23 April 2024

Table 1. Overlap orientation of the mandibles among workers of nine Florida ant species (n = 100 per species)

Ant species	% workers with right-overlapping mandibles (n = 100)
Paratrechina longicornis (Latreille)	45
Paratrechina bourbonica (Forel)	50
Brachymyrmex obscurior (Forel)	47
Prenolepis imparis (Emery)	47
Pheidole moerens (Wheeler)	51
Camponotus floridanus (Buckley)	48
Crematogaster ashmeadi (Emery)	53
Dorymyrmex bureni (Trager)	53
Forelius pruinosus (Roger)	47

ers changed the overlap orientation of their mandibles; $\chi^2 = 1.49$, df = 61, $P = 0.626$). Likewise, no significant difference was found in an ant's preference for a right or left mandible overlap in the other nine ant species ($\chi^2 = 1.91$, df = 8, $P = 0.984$) (Table 1).

Video analysis of excavating fire ant workers revealed that they opened and closed their mandibles independently depending on the angle of excavation. Video analysis of individual fire ant queens showed no preference or handedness in the orientation of mandible overlap when resting ($\chi^2 = 3.21$, df = 4, $P = 0.533$). Queens switched the orientation of mandible overlap repeatedly, grooming their right fore-tarsus between the right mandible and tongue, and their left fore tarsus between the left mandible and tongue. For example, 10 overlap sequences of one queen followed an "r l l l r r l l l r" pattern. In summary, fire ants used their mandibles independently or in synchrony depending on the requirements of the task at hand rather than individual preference.

Discussion

This study adds an increment of knowledge to the functionality of ant mandibles, demonstrating that fire ant mandibles were morphologically symmetrical and functionally ambidextrous. Fire ants used their mandibles in synchrony or independently depending on the task at hand. Queens and workers showed no handedness or preference for mandible overlap at the completion of a task.

Many arthropods, especially crabs, have feeding appendages that are asymmetrical. Asymmetrical appendages perform different tasks. For example, the blue crab has asymmetrical claws; one claw has sharp incisor-like teeth for tearing flesh, and the other has rounded molar-like teeth for crushing (Blundon and Kennedy 1982, Laughlin 1982). The fiddler crab male has asymmetrical claws; a small claw for feeding and a grossly enlarged claw for signaling his gender, his social status and his availability for mating (Hyatt and Salmon 1978, Salmon 1984). If appendage asymmetry is an indicator of specialization and division of labor, then appendage symmetry is likely an indicator of a generalized function. To our knowledge, no ant species exhibit asymmetrical mandibles. Thus, symmetrical ant mandibles probably serve a generalized function with ants using both mandibles to complete a task.

In summary, although fire ant workers are polymorphic and prone to specialize in different tasks based on size (Cassill and Tschinkel 1999), their mandibles are generalist tools. Findings on the lack of handedness in the fire ant were confirmed in nine other ant species, suggesting that ambidextrous mandibles might be a universal trait in ants.

Acknowledgments

We thank Xuefeng Wang, Anthony Greco, and David Brodosi for technical assistance in image acquisition. We thank Kyle Raycraft and Megan Davis for capturing, identifying and recording mandibular overlap in nine local ant species other than the fire ant. We thank Mark Deyrup for identifying the ant species. Last, we thank the editor Ann M. Fraser for editorial guidance and encouragement and two anonymous reviewers for comments that greatly improved the manuscript. Experiments conducted on these organisms comply with the current laws of the country in which they were performed. This project was funded in part by the Environmental Science, Policy, Geography (ESPG) Program of Distinction at University of South Florida St. Petersburg.

References Cited

Blundon, J. A., and V. S. Kennedy. 1982. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. J. Exp. Marine Biol. Ecol. 65: 47–66.

Bolton, B. 2003. Synopsis and classification of Formicidae. Memoirs of the American Entomological Institute, vol. 71. Gainesville, FL.

Cassill, D. L., and W. R. Tschinkel. 1999. Task selection by workers of the fire ant, *Solenopsis invicta.* Behav. Ecol. Sociobiol. 45: 301–310.

Cassill, D. L., W. R. Tschinkel, and S. B. Vinson. 2002. Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta.* Insectes Soc. 49: 158–163.

Cassill, D. L., J. Butler, S. B. Vinson, and D. E. Wheeler. 2005. Cooperation in prey digestion between workers and larvae in the ant, *Pheidole spadonia.* Insectes Soc. 52: 339–343.

Cassill, D. L., A. Greco, R. Silwal, and X. Wang. 2007. Opposable spines facilitate fine and gross object manipulation in fire ants. Naturwissenschaften 94: 326–332.

Eisner, T., M. Eisner, and M. Deyrup. 1996. Millipede defense: use of detachable bristles to entangle ants. Proc. Natl. Acad. Sci. U.S.A. 93: 848–851.

Fisher, B. L., and S. P. Cover. 2007. Ants of North America: a guide to the genera. University of California Press, Los Angeles, CA.

Gronenberg, W. 1995. The fast mandible strike in the trap-jaw ant *Odontomachus.* J. Comp. Physiol. A 176: 399–408.

Gronenberg, W., J. Paul, S. Just, and B. Hölldobler. 1997. Mandible muscle fibers in ants: fast or powerful? Cell Tissue Res. 289: 347–361.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.

Hyatt, G. W., and M. Salmon. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax:* a quantitative analysis. Behaviour 65: 182–211.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola Estuary. Fla. Bull. Mar. Sci. 32: 807–822.

Downloaded from https://academic.oup.com/aesa/article/102/4/713/58025 by guest on 23 April 2024

Sall, J., and A. Lehman. 2005. JMP start statistics: a guide to statistics and data analysis using JMP and JMP IN software. Duxbury Press, Albany, NY.

Salmon, M. 1984. The courtship, aggression and mating system of a" primitive" fiddler crab (*Ucavocans:* Ocypodidae). Trans. Zool. Soc. Lond. 37: 1–50.

Wilson, E. O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). Behav. Ecol. Sociobiol. 7: 143–156.

Received 4 January 2009; accepted 2 April 2009.

Downloaded from https://academic.oup.com/aesa/article/102/4/713/58025 by guest on 23 April 2024