Detecting Nestmate Recognition Patterns in the Fission-Performing Ant *Aphaenogaster senilis*: A Comparison of Different Indices

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In this paper, we compare three indices for nestmate recognition behaviors in the ant *Aphaenogaster senilis* within and among colonies and populations: the classical Aggression Index, a multidimensional Principal Component Analysis (PCA) Behavioral Index incorporating all observed behaviors, and a Chemical Profile Index for cuticular hydrocarbon composition. With these indices, we quantified nestmate recognition behaviors between workers from a parent nest and between those from independent colonies. The PCA Behavioral Index performed as well as or better than the classical Aggression Index in distinguishing small differences in nestmate recognition. Correlation analysis of the PCA Behavioral Index with the Chemical Profile Index may assist in identifying the occurrence of colony fissions. The PCA Behavioral Index correlated strongly with the Chemical Profile Index, suggesting that hydrocarbon profiling may be used as an alternative to nestmate recognition assays. This correlation also suggests that nestmate recognition in *A. senilis* is a graded response rather than a threshold one.

KEY WORDS: aggression; ant; budding; cuticular hydrocarbon profile; nestmate recognition.

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INTRODUCTION

Since Crozier and Dix (1979) proposed the individualistic and Gestalt models for nestmate recognition in social insects, nestmate recognition has been widely studied in various social insects. The Gestalt model is commonly supported in species that establish larger colonies (Carlin and Hölldobler, 1986; Dahbi et al., 1997; Lenoir et al., 2001c), while the individualistic model is generally supported in species such as primitive ponerine ants, which establish small colonies (Soroker et al., 2003). Recognition behaviors are presumably determined by the spectrum of cuticular hydrocarbons (Vander Meer and Morel, 1998; Lenoir et al., 2001b). A nest-specific spectrum of odors, termed the “gestalt,” is generated. The gestalt odor is established through hydrocarbons regurgitated from the postpharyngeal gland (Soroker et al., 1994; Lahav et al., 1999, 2001) and exchanged with other colony members by allo-grooming, trophallaxis, or body touching (Dahbi et al., 1999; Boulay et al., 2000; Lenoir et al., 2001a; Boulay et al., 2004; see also Blomquist and Howard, 2003). Each member of the colony learns this common odor as an internal representation called the “template.” When encountering another insect, she compares the odor of encountered animals with her template to determine if it belongs to her colony.

There are two possible models for the responses of ants encountering odors different from the template. The threshold model (Reeve, 1989) predicts that if the difference between the template and the encountered odor spectrum is above a threshold, the insects will behave aggressively. According to the threshold model, the aggression based on the chemical profile will be an “all-or-none” response. The graded model, on the other hand, proposes that ants may vary their level of aggression according to the difference between the template and the encountered odors (Lenoir et al., 1999; see also Cassill and Tschinkel, 1999). Thus, a linear regression is expected under the graded model if both behavior and the chemical profile difference are properly quantified.

The classical Aggression Index defines the degree of nestmate recognition by scoring individual aggressive behaviors (e.g., Carlin and Hölldobler, 1987; Hefetz et al., 1996; Stuart and Herbers, 2000, Roulston et al., 2003). The Aggression Index may not correctly scale intermediate levels of recognition such as those found in ants that perform nest fission. Colony fission is when a social insect colony divides into new colonies and it is different from “budding,” which occurs in polygynous societies (Bourke and Franks, 1995). Worker recognition responses between the two fissioning nests gradually alter, from peaceful to “skeptic” to aggressive over time (e.g., Dahbi and Lenoir, 1998; Boulay et al., 2000; Lahav et al., 2001, 2001c). For such species, multi-dimensional statistical methods in which all behaviors are incorporated, such as the Principal Component Analysis (PCA), might be