

Review Article

Chemical Recruitment for Foraging in Ants (Formicidae) and Termites (Isoptera): A Revealing Comparison

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All termites secrete trail pheromones from their sternal gland, whereas ants use a variety of glands for this purpose. This and the diversity of chemical compounds that serve as trail pheromones among ants, and the uniformity of chemicals among termite trails, suggest a different evolutionary historical dynamics for the development of chemical mass recruitment in both taxa. Termites in addition show pheromonal parsimony. This suggests a single evolutionary origin of pheromone trails in Isoptera, whereas chemical mass recruitment among Formicidae seems to have evolved many times and in different ways. Despite these very different evolutionary histories, both taxa evolved chemical recruitment systems involving attractants and orientation signals, and at least two divergent decision making systems for recruitment. This evolutionary analogy suggests that chemical mass recruitment is constrained by fundamental physical dynamic laws. Artificial intelligence including “mass intelligence” and “ant intelligence”, emulates mass recruitment in interacting virtual agents in search of optimal solutions. This approach, however, has copied only the “Democratic” recruitment dynamics with a single compound pheromone. Ant and termite evolution shows more sophisticated recruitment dynamics which, if understood properly, will improve our understanding of nature and applications of artificial “swarm intelligence”.

1. Introduction

One of the great advantages of society is the use of large numbers of individuals to perform tasks that a lonely individual is unable to perform [2, 3]. One of the most studied group task in social insects is recruitment for food retrieval, after an individual discovers a food source that is much larger than what it can handle on its own. Some of the communication signals modulating this recruitment are based on auditory or visual signals, but the most important communication signal used in recruitment, in the great majority of ant and termite species, is chemical. In recruitment to food, these signals are at least of two different kinds as first detailed for ants [4]: one used to orient workers to the food source, that is trail pheromones; another to attract workers to the trail and thus to the food source, that is attractants for food recruitment. Some species use chemicals for only one of these signals and signal the other function by means of tactile or acoustic signals. An illustrative intermediate recruitment system is called “Tandem Running” [5], where

the scout physically carries a nestmate to the food source. In tandem calling [6], the recruiting workers lead nestmates to the newly discovered food source by physically guiding them to the source, sometimes using chemical trails to help orientate to the food. Other species lay chemical trails that fulfill both functions, requiring different chemicals for attracting and orienting ants [7, 8]. These intermediate stages in the evolution of chemical mass recruitment, starting from individual foraging, allow us to suggest phylogenies for recruitment systems illuminating the possible evolutionary history of chemical mass recruitment. Such comparisons suggest that the evolution of chemical recruitment seems to have happened several times, at least in ants [9].

Termites seem also to use both type of chemicals, attractants and orientation signals, in their foraging trails [10, 11], although the details of the chemical communication system used by termites are less well known than in ants.

As both, ants and termites, are terrestrial and arboreal, and that both use chemical mass recruitment, we can compare the different chemical recruitment systems known

among ants and among termite in order to extract some general rules.

2. Methods

We explored the existing literature collected by Pherobase [1] for publications on trail pheromones for ants and Isoptera and by Bordereau and Pasteels [12] for additional data on Isoptera. Pherobase, among many other things, reports for Isoptera and for Formicidae all publications mentioning chemicals that had been related to trail pheromones by the author of the publication. Pherobase provides, if available, the exact molecular structure of the chemical and the link to the reference where the trail pheromone was published, grouped by taxonomic or by chemical criteria. Thus, for more details of all references indicated in the Tables, the reader should consult Pherobase for ants and Isoptera, and Bordereau and Pasteels for Isoptera.

3. Results

3.1. Ants. Reports of the chemical nature of the communication signal used for recruitment in ants revealed an interesting pattern of chemical compounds. The summary of available data for ants is presented in Table 1. This table shows that, in many cases, the various compounds produced by a single species are very similar as they constitute small variants of a common chemical skeleton, as is the case for *Monomorium pharaonis*. We suggest that this might be due to the fact that in the biochemical process leading to the synthesis of one or a few active compounds, other chemicals are produced in the process. Indirect evidence for this suggestion comes from other insects where it was shown that synthesizing pure chemicals in pheromone secreting glands is very difficult, if not impossible [13]. In other cases, an adaptive purposeful chemical diversity seems to be present, as chemicals from completely different biochemical pathways are produced as a substrate for the chemical recruitment signal. This is the case for the *Atta* and *Acromyrmex* species and *Daceton armigerum*. In these cases, as shown in Table 1, some compounds have high carbon numbers and low volatility, and others have high volatility, appropriate for the fulfillment of different communication functions such as orientation and attraction.

The chemical survey presented in Table 1 reveals that the pattern of chemical compounds related to trail pheromones in ants correlates with what we know about the decision making behavior used during chemical mass recruitment to food [14]. We know that ants use either one of two decision making systems regulating chemical mass recruitment. The “Democratic” mass recruitment was described in detail for *Solenopsis invicta* [15] and the “Autocratic” system first described for *Atta cephalotes* [16]. The main difference is that in the Democratic system, all workers eventually perform all tasks as in *Solenopsis*; in the Autocratic system, workers specialize either in scouting or in food retrieval [17], as in *Atta*. The Democratic recruitment system is adapted for fast recruitment towards ephemeral food sources. Here all

workers participating in the recruitment process have the same responsibility and add a fixed amount of recruitment pheromone to the trail. The more trail pheromone, the stronger the signal, the more workers are recruited. This leads to an increase in the workforce allowing engaging the maximum worker strength in the shortest possible time, so as to collect a scarce resource (a recently discovered dead cockroach for example) before a competitor does.

The Autocratic recruitment system is adapted for the simultaneous exploitation of a diversity of durable food sources. Here workers specialize in chemical communication or in food retrieval. Communication specialists then visit different food sources and signal the palatability, quality, or quantity of a food source with varying levels of chemical concentrations. Thus, a very good food source will trigger trail laying with plenty of an attractive chemical, whereas food sources of low quality will be signaled with low amounts of this chemical laid on the trail. This system allows for the fine tuning of sophisticated recruitment activity such as described for several *Atta* species, where one group of workers recruit nestmates to the tree canopy where they cut large leaves at their base, so that they fall whole to the ground. There, another group of workers is recruited to each of the leaves that accumulate on the ground, where the workers cut the leave in smaller pieces and transport these pieces to intermediate sites, from where another group of workers transport the leaf fragments to the nest [18].

In both cases, the trail needs to be marked with a chemical that will orient workers towards the food source. If the food source is ephemeral in its existence, an efficient chemical mark does not need to last long. As soon as the food has been collected, the chemical evaporates and the trail disappears. For the simultaneous exploitation of several food sources, however, several longer lasting chemical signals could be very useful, as the source could be revisited fast after spots of inactivity due to rain, heat, cold, or other daily rhythmic patterns. Yet a long lasting chemical signal is not appropriate if it has to work also as an attractant, as any changes in the required workforce will take a long time to achieve if the long lasting chemical need, to evaporate first. Therefore in this later case, highly volatile chemicals, together with some of low volatility, are required to modulate recruitment. Species using chemicals to only attract or orient ants need only one—or a few—chemical compounds to perform this function, whereas species using chemical trails for both, attraction and orientation of nestmates, have to produce a range of chemicals for these two purposes.

As Table 1 shows, most ant species seem to use a few compounds as trail pheromone. Only 14 out of 57 species (25%) seem to use more than 3 chemicals, and only 10% of the species listed use six or more compounds. The use of a few compounds corresponds well to Tandem Calling or even to a Democratic recruitment system. In contrast, species such as the leaf cutting and fungus growing ants *Atta*, *Trachymyrmex*, and *Acromyrmex* secrete over six different chemicals on their trails. Other species using the Democratic system, such as *Solenopsis*, seem to produce much simpler trail pheromones from the standpoint of chemical diversity of compounds. The trail pheromone composition of

TABLE 1: Chemical compounds reported in trail pheromones of ants. All data were extracted from Pherobase [1].

Myrmicinae
<i>Acromyrmex octospinosus</i>
Cross JH 1982. J. Chem. Ecol. 8 : 1119
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
3me5me-2-ethylpyrazine
<i>Acromyrmex subterraneus subterraneus</i>
Do Nascimento RR 1994. J. Chem. Ecol. 20 : 1719
me-4me-pyrrole-2-carboxylate
<i>Aphaenogaster albisetosus</i>
Hölldobler B 1995 J. Insect Physiol. 41 : 739
4Sme-7-3Kt
4Rme-7-3Kt
<i>Aphaenogaster cockerelli</i>
Hölldobler B 1995. J. Insect Physiol. 41 : 739
1R-phenylethanol
4Sme-7-3Kt
<i>Aphaenogaster rudis</i>
Attygalle AB 1998b Naturwissenschaften 85 : 38
anabesine
anabaseine
2,3-bipyridyl
isopentyl-2-phenylethylamine
<i>Atta bisphaerica</i>
De Oliveira JS 1990 An. Soc. Entomol. Brasil 19 : 145
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2-phenylacetic acid
bornylene
8OH
<i>Atta cephalotes</i>
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2Ald
Riley RG 1974b J. Insect Physiol. 20 : 651
me-4me-pyrrole-2-carboxylate
<i>Atta laevigata</i>
De Oliveira JS 1990 An. Soc. Entomol. Brasil 19 : 145
me-4me-pyrrole-2-carboxylate
2-phenylacetic acid
bornylene
8OH
<i>Atta sexdens</i>
Robinson SW 1978 Bull. Entomol. Res. 68 : 159
me-4me-pyrrole-2-carboxylate
<i>Atta sexdens rubropilosa</i>
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate

TABLE 1: Continued.

Myrmicinae
2me5me-3-ethylpyrazine
2Ald
Cross JH 1979 J. Chem. Ecol. 5 : 187
2me5me-3-ethylpyrazine
methyl phenylacetate
ethyl phenylacetate
me-4me-pyrrole-2-carboxylate
<i>Atta sexdens sexdens</i>
Billen J 1992 Ethol. Ecol. Evol. 4 : 197
2me5me-3-ethylpyrazine
me-4me-pyrrole-2-carboxylate
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2Ald
<i>Atta texana</i>
Tumlinson JH 1972b J. Insect Physiol. 18 : 809
me-4me-pyrrole-2-carboxylate
Sonnet PE 1972 J. Agric. Food Chem. 20 : 1191
me-4me-pyrrole-2-carboxylate
<i>Crematogaster castanea</i>
Morgan ED 2004 Chemoecology 14 : 119
R-dodecan-2-ol
<i>Daceton armigerum</i>
Morgan ED 1992 J. Chem. Ecol. 18 : 2161
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
delta9-23Hy
23Hy
delta9-25Hy
<i>Eutetramorium mocquerysi</i>
Tentschert J 2000 Naturwissenschaften 87 : 377
2me3me-5-2-methylpropylpyrazine
<i>Manica rubida</i>
Attygalle AB 1986a Physiol. Entomol. 11 : 125
2me5me-3-ethylpyrazine
<i>Mayriella overbecki</i>
Kohl E 2000 Naturwissenschaften 87 : 320
me-2-hydroxy-6me-benzoate
<i>Messor bouvieri</i>
Jackson BD 1989a Experientia 45 : 487
anabesine
2me5me-3-ethylpyrazine
<i>Messor capensis</i>
Brand JM 1993 J. Chem. Ecol. 19 : 1315
anabesine
anabaseine

TABLE 1: Continued.

Myrmicinae
<i>Messor ebeninus</i>
Coll M 1987 Z. Naturforsch. C 42 : 1027
anabesine
<i>Metapone madagascaris</i>
Hölldobler B 2002 Chemoecology 12 : 147
me-pyrrole-2-carboxylate
<i>Metapone madagascaris</i>
Hölldobler B 2002 Chemoecology 12 : 147
me-pyrrole-2-carboxylate
<i>Monomorium pharaonis</i> Linnaeus
Edwards JP 1978 Ann. Appl. Biol. 89 : 395
3-butyl-5me-octahydroindolizine
Ritter FJ 1977b Crop Prot. Agents : 195
monomorine I
Ritter FJ 1977a Tetrahedron Lett. 30 : 2617
faranal
Ritter FJ 1975b Uni. Dijon : 99
monomorine I
monomorine II
monomorine III
monomorine IV
monomorine V
<i>Pheidole pallidula</i>
Ali MF 1988c Physiol. Entomol. 13 : 257
2me5me-3-ethylpyrazine
<i>Pogonomyrmex barbatus</i>
Liu Y 2002 Fenxi Huaxue 47 : 369
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
2me5me-pyrazine
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
<i>Pogonomyrmex maricopa</i>
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
<i>Pogonomyrmex occidentalis</i>
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
<i>Pogonomyrmex rugosus</i>
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
<i>Solenopsis invicta</i>
Van der Meer RK 1983 Fla. Entomol. 66 : 39

TABLE 1: Continued.

Myrmicinae
Z,E-alpha-farnesene
E,E-alpha-farnesene
Z,E-alpha-homofarnesene
Z,Z-alpha-homofarnesene
17Hy
Z,Z,Z-allofarnesene
Williams HJ 1981b Experientia 37 : 1159
Z,Z,Z-allofarnesene
Van der Meer RK 1981 Tetrahedron Lett. 22 : 1651
Z,E-alpha-farnesene
E,E-alpha-farnesene
Z,E-alpha-homofarnesene
Z,Z-alpha-homofarnesene
<i>Tetramorium caespitum</i>
Attygalle AB 1984J. Chem. Ecol. 10 : 1453
2me5me-pyrazine
2me5me-3-ethylpyrazine
Attygalle AB 1983b Naturwissenschaften 70 : 364
2me5me-pyrazine
2me5me-3-ethylpyrazine
<i>Tetramorium impurum</i>
Morgan ED 1990 J. Chem. Ecol. 16 : 349
me-2-hydroxy-6me-benzoate
Morgan ED 1987 Naturwissenschaften 74 : 596
me-2-hydroxy-6me-benzoate
<i>Tetramorium meridionale</i> Emery
Jackson BD 1990c Naturwissenschaften 77 : 294
2me-pyrazine
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
Formicinae
<i>Camponotus atriceps</i>
Haak U 1996 Chemoecology 7 : 85
6-butyl-tetrahydro-3me5me-pyran-2Kt
nerolic acid
<i>Camponotus balzani</i>
Kohl E 2003 Chemoecology 13 : 113
8-hydroxy-3me5me7me-isochromanone
<i>Camponotus castaneus</i>
Kohl E 2003 Chemoecology 13 : 113
6-butyl-tetrahydro-3me5me-pyran-2Kt
<i>Camponotus floridanus</i>
Haak U 1996 Chemoecology 7 : 85
6-butyl-tetrahydro-3me5me-pyran-2Kt
nerolic acid
<i>Camponotus herculeanus</i>
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984
2Sme4Rme5S-5-hexanolide
Payne TL 1975 Ann. Entomol. Soc. Am. 68 : 385

TABLE 1: Continued.

Formicinae	
me-2-hydroxy-6me-benzoate	
mellein	
Hölldobler B 1965 Z. vergl. Physiol. 50 : 551	
me-2-hydroxy-6me-benzoate	
mellein	
10me-12Acid	
<i>Camponotus inaequalis</i>	
Bestmann HJ 1997 Angew. Chem. 36 : 395	
3,4-dihydro-8-hydroxy-3me5me7me-isocoumarin	
<i>Camponotus ligniperda</i>	
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984	
2Sme4Rme5S-5-hexanolide	
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984	
2Sme4Rme5S-5-hexanolide	
<i>Camponotus rufipes</i>	
Uebler E 1995 Naturwissenschaften 82 : 523	
mellein	
<i>Camponotus sericeiventris</i>	
Kohl E 2003 Chemoecology 13 : 113	
8-hydroxy-3me5me7me-isochromanone	
<i>Camponotus silvicola</i>	
Uebler E 1995 Naturwissenschaften 82 : 523	
8-hydroxy-3me5me7me-isochromanone	
<i>Camponotus socius</i>	
Kohl E 2001 Chemoecology 11 : 67	
2Sme4Rme5S-5-hexanolide	
2,3-dihydro-3,5-dihydroxy-6me-pyran-4Kt	
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984	
2Sme4Rme5S-5-hexanolide	
<i>Formica rufa</i>	
Bestmann HJ 1992 Angew. Chem. 31 : 795	
R-mellein	
<i>Lasius fuliginosus</i>	
Kern F 1997 J. Chem. Ecol. 23 : 779	
mellein	
2,3-dihydro-3,5-dihydroxy-6me-pyran-4Kt	
Akino T 1996 Jap. J. Appl. Entomol. Zool. 40 : 233	
caproic acid	
enanthic acid	
caprylic acid	
pelargonic acid	
caprinic acid	
lauric acid	
Huwylar S 1975 J. Insect Physiol. 21 : 779	
caproic acid	
enanthic acid	
caprylic acid	
pelargonic acid	
caprinic acid	
lauric acid	

TABLE 1: Continued.

Formicinae	
<i>Lasius niger</i>	
Bestmann HJ 1992 Angew. Chem. 31 : 795	
3,4-dihydro-8-hydroxy-3me5me7me-isocoumarin	
<i>Linepithema humile</i>	
Greenberg L 2000 J. Econ. Entomol. 93 : 119	
Cordova YL 1998 Eur. J. Entomol. 95 : 501	
sulcatone	
sulcatol	
13-2Kt	
Z9-16Ald	
Van Vorhis Key SE 1982 J. Chem. Ecol. 8 : 3	
Z9-16Ald	
Cavill GWK 1979 Experientia 35 : 989	
Z9-16Ald	
Dolichoderinae	
<i>Dolichoderus thoracicus</i>	
Attygalle AB 1998a Naturwissenschaften 85 : 275	
Z9-18Ald	
Z9-16Ald	
<i>Tapinoma simrothi</i>	
Simon T 1991 Insectes Soc. 38 : 17	
iridodial	
iridomyrmecin	
Ectatomminae	
<i>Ectatomma ruidum</i>	
Bestmann HJ 1995 Naturwissenschaften 82 : 334	
geranylgeraniol acetate	
geranylgeraniol	
<i>Gnamptogenys striatula</i>	
Blatrix R 2002 J. Chem. Ecol. 28 : 2557	
4-methylgeraniol	
bishomoggeraniol	
E2,4S6-3me4me7me-octadienyl decanoate	
E2,4S6-3me4me7me-octadienyl dodecanoate	
Ponerinae	
<i>Leptogenys diminuta</i>	
Kern F 1993 Naturwissenschaften 80 : 424	
3R4Sme-heptan-3-ol	
Attygalle AB 1991b Naturwissenschaften 78 : 90	
isogeraniol	
Attygalle AB 1988c Naturwissenschaften 75 : 315	
3R4Sme-heptan-3-ol	
isogeraniol	
<i>Leptogenys peuqueti</i>	
Janssen E 1997b Naturwissenschaften 84 : 122	
1-ethyl-4me-heptyl acetate	
1-isopropyl-4me-heptyl acetate	
1-propyl-4me-heptyl acetate	
4me-dodecan-7-ol	
3me9me-dodecan-6-ol	

TABLE 1: Continued.

Ponerinae	
	1-pentyl-4me-heptyl acetate
	4me-tridecan-7-ol
	4me10me-tridecan-7-ol
	4me-tetradecan-7-ol
	3me-hexyl-4me-heptyl acetate
	3me-hexyl-octyl acetate
	heptyloctyl acetate
	4me-hexadecan-7-ol
	3me-hexyl-decyl acetate
<i>Megaponera foetens</i>	
Janssen E 1995 J. Chem. Ecol. 21 : 1947	dimethyluracil
	actinidine
Longhurst C 1979 J. Chem. Ecol. 5 : 703	1me2me-disulfane
	1me3me-trisulfane
	benzyl methyl sulfane
Longhurst C 1979 J. Chem. Ecol. 5 : 703	11Hy
	13Hy
<i>Pachycondyla tarsata</i>	
Janssen E 1999 Chemoecology 9 : 9	17-9Kt
<i>Rhytidoponera metallica</i>	
Meinwald J 1983 Naturwissenschaften 70 : 46	isogeraniol
	3-hydroxybenzaldehyde
Aenictinae (dorylinae)	
<i>Aenictus sp</i>	
Oldham NJ 1994, Experientia 50 : 763	methyl anthranilate
	methyl nicotinate

Solenopsis invicta recalls the case of *Monomorium pharaonis* discussed above. Although over 5 different chemicals can be recognized in Table 1, all these chemicals have the same chemical skeleton. Thus, the Autocratic chemical recruitment system could be associated to a more advanced chemical signaling. The case of the hunting and recruiting foragers of *Daceton armigerum* [19] that use a multitude of recruitment strategies is interesting. Table 1 shows that its trail pheromone has many chemical compounds, hinting to a sophisticated diverse chemical communication system.

Many ant species in the subfamily Myrmicinae with large colonies and a sophisticated social structure, use carboxylates and pyrazines to lay their pheromone trail. These are semivolatile compounds. The Myrmicinae, *Atta*, and *Acromyrmex*, for example, need to constantly recruit many workers to supply big colonies with a great quantity of leaves which they use as a substrate to grow their fungus. In contrast, ants with less developed societies living in smaller colonies, such as species of the subfamily Ponerinae,

use alcohols and acetate, which are more volatile and thus might serve as chemical attractants to trigger foraging to collect ephemeral food sources. Ponerinae individuals feed opportunistically on dispersed food items. This requires quick recruitment of workers, and, as a consequence, the compounds of the pheromone trail are more volatile and less permanent in time, compared to the carboxylates of the leaf cutter ants. In some species of Ponerinae, chemical trails also regulate nest moving [20].

The Formicinae ants are mostly predators but differ from Ponerinae by their greater social complexity, larger colonies, and more diverse worker castes or polymorphism. The trail pheromones of Formicinae species use a mix of compounds that are more complex than that of Ponerinae, probably due to a more elaborate recruitment system. Table 1 reflects this showing among Formicinae, compounds with elevated molecular weights, such as mullein, in addition to compound of low molecular weight and probably low volatility. Formicinae trail pheromone chemistry seems to be closer to the Myrmicinae than the Ponerinae. This suggests trails with both short-term attractant and long-term orientation function. In the case of Dolichoderinae species, the information is scarcer. In the Argentine ant, *Linepithema humile*, a tramp species with supercolonies of hundreds of thousands of workers, the trail pheromone has short-chain volatile aldehydes, suggesting a foraging strategy with fast short term bouts of recruitment. The continuous reinforcement of a trail made with short lasting volatiles can last long if it is reinforced by hundreds of workers.

3.2. Termites. Termite species also show diverse ecological life types. We know species that live and feed in the same piece of wood, and species that have their nest separated from their food source [21]. But even the “one-piece” life type species possess trail pheromones which they use to recruit workers for defense or nest moving. Termites of “one-piece” life type do not require orientation systems a priori. Secretions of their sternal gland are considered to function in the recruitment of nestmates to source disturbance within the nest. These termites might also use trail following pheromones to colonize new food sources to where they move their nest [22, 23]. Most termites forage on relatively durable food sources containing cellulose. In addition, most termite species forage on several food sources simultaneously, suggesting a recruitment system closer to the above described Autocratic chemical recruitment system, which seem to be the case in the only termite species where this has been explored so far [24]. Table 2 presents what we know about the chemicals used in trail pheromones by termites. The available data shows that pheromone trails among each termite species are constructed with one or a few compounds among a total of 8 chemicals. For the families where chemical trail pheromones have been reported, the Rhinotermitidae, Termitidae, and Kalotermitidae seem to use mainly neocembrene and a dodecatrienol; *Nasutitermes corniger* uses in addition to these two compounds trinervitatriene; whereas Mastotermitidae and Termopsidae use a trimethylundecadienol for trail following. That is, all trail pheromones in Isoptera are synthesized from a much

TABLE 2: Chemical compounds reported from trail pheromones of termites. All data were extracted from Pherobase [1], and from Bordereau and Pasteels [12].

Mastotermitidae	
<i>Mastotermes darwiniensis</i>	
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol
Termopsidae	
Porotermitinae	
<i>Porotermes adamsoni</i>	
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol
Stolotermitinae	
<i>Stolotermes victoriensis</i>	
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol
Termopsinae	
<i>Zootermopsis angusticollis</i>	
Greenberg SL 1986 Int. J. Insect Morphol. Embryol. 15 : 283	Heneicosano
	Tricosane
Bordereau C. et al. 2010 Biol J Linn Soc 100 : 519–530	4,6-dimethyldodecanal
<i>Zootermopsis nevadensis</i>	
Karlson P. et al. 1968 J. Insect Physiol. 14 : 1763	n-Hexanoic acid
	Caproic acid
Bordereau, C. et al. 2010 Biol J Linn Soc 100 : 519–530	4,6-Dimethyldodecanal
Kalotermitidae	
<i>Cryptotermes brevis</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Cryptotermes darlingtonae</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Cryptotermes pallidus</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Incisitermes tabogae</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Kalotermes flavicollis</i>	
Klochkov and Zhuzhikov 1990. Advances in life science. Birkhäuser, Basel, pp 41–43	Nonanol
	Decanol
	Undecanol
	dodecanol

TABLE 2: Continued.

Kalotermitidae	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	
	(Z)-dodec-3-en-1-ol
<i>Neotermes holmgreni</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Postelectrotermes howa</i>	
Sillam-Dussès et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Procryptotermes falcifer</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
<i>Procryptotermes leewardensis</i>	
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108	(Z)-dodec-3-en-1-ol
Rhinotermitidae	
Prorhinotermitinae	
<i>Prorhinotermes canalifrons</i>	
Sillam-Dussès D. et al. 2005 Chemoecology 15 : 1–6	Neocembrene A
<i>Prorhinotermes simplex</i>	
Sillam-Dussès D. et al. 2005 Chemoecology 15 : 1–6	Neocembrene
Sillam-Dussès D. et al. 2009 J. Insect Physiol 55 : 751-757	Neocembrene A
	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Coptotermitinae	
<i>Coptotermes formosanus</i>	
Tokoro M. et al. 1994 J. Chem. Ecol. 20 : 199	(Z,E,E)-dodeca-3,6,8-trien-1-ol
<i>Coptotermes gestroi</i>	
Arab A. et al. 2004 Sociobiology 43 : 377	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Sillam-Dussès D. et al. 2006 Proceedings XV IUSI. Washington 100-101	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Heterotermitinae	
<i>Heterotermes tenuis</i>	
Arab A. et al. 2004 Sociobiology 43 : 377	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Sillam-Dussès D. et al. 2006 Proceedings XV IUSI. Washington 100-101	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Reticulitermes flavipes</i>	
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147	(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Matsumura F. et al. 1968 Nature 219 : 963	(Z,Z,E)-dodeca-3,6,8-trien-1-ol

TABLE 2: Continued.

Rhinotermitidae
<i>Reticulitermes hesperus</i>
Zhong CM 1979 Sci. Silvae Sin. 15 : 15
Z3-4-phenyl-4OH
<i>Reticulitermes lucifugus grassei</i>
Wobst B. et al. 1999 J. Chem. Ecol. 25 : 1305
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Reticulitermes santonensis</i>
Wobst B. et al. 1999 J. Chem. Ecol. 25 : 1305
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Laduguie N. et al. 1994 J. Insect Physiol. 40 : 781
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Reticulitermes speratus</i>
Tokoro M. et al. 1990 J. Chem. Ecol. 16 : 2549
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Yamaoka R. et al. 1987 J. Chromatogr. 399 : 259
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Reticulitermes tibialis</i>
Bernklau EJ 2005 J. Econ. Entomol. 98 : 476
CO ₂
Zhong CM 1979 Sci. Silvae Sin. 15 : 15
Z3-4-phenyl-4OH
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Reticulitermes virginicus</i>
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Tai A. et al. 1969 J. Org. Chem. 34 : 2180
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Matsumura F. et al. 1968 Nature 219 : 963
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Rhinotermitinae
<i>Rhinotermes marginalis</i>
Sillam-Dussès D. et al. 2006 Proc. XV Congress IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Schedorhinotermes lamianus</i>
Sillam-Dussès D. et al. 2006 Proc. XV Congress IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
Termitidae
Macrotermitinae
<i>Ancistrotermes pakistanicus</i>
Robert A. et al. 2004 Naturwissenschaften 91 : 34–39
(Z,Z)-dodeca-3,6-dien-1-ol
<i>Macrotermes annandalei</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
Peppuy A. et al. 2001 J. Insect Physiol. 47 : 445

TABLE 2: Continued.

Termitidae
(Z)-dodec-3-en-1-ol
<i>Macrotermes barneyi</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
<i>Macrotermes bellicosus</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
<i>Macrotermes subhyalinus</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
<i>Odontotermes formosanus</i>
Deng XJ. et al. 2002 Acta Entomol. Sin. 45 : 739
(Z,Z)-dodeca-3-6-dien-1-ol
Du TY 1982 Acta Entomol. Sin. 25 : 172
(Z,Z)-dodeca-3-6-dien-1-ol
<i>Odontotermes hainanensis</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
<i>Odontotermes maesodensis</i>
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(Z)-dodec-3-en-1-ol
<i>Pseudacanthotermes militaris</i>
Bordereau C. et al. 1993 Actes Coll. Insectes Soc. 17 : 2177
(Z,Z,E)-dodeca-3,6,8-trienol-1-ol
<i>Pseudacanthotermes spiniger</i>
Bordereau C. et al. 1991 J. Chem. Ecol. 17 : 2177
(Z,Z,E)-dodeca-3,6,8-trienol-1-ol
Termitinae
<i>Cubitermes</i> sp.
Sillam-Dussès D. et al. 2006 Proc. IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Drepanotermes perniger</i>
Sillam-Dussès D. et al. 2006 Proc. IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Termes hispaniolae</i>
Sillam-Dussès D. et al. 2006 Proc. IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Amitermes evuncifer</i>
Kotoklo E. et al. 2010 Sociobiology 55 : 1-10
Dodecatrienol
Neocembrene A
Syntermitinae
<i>Cornitermes bequaerti</i>
Sillam-Dussès D. et al. 2006 Proc. IAUSS, Washington, DC, 100–101
(Z,Z,E)-dodeca-3,6,8-trien-1-ol

TABLE 2: Continued.

Termitidae
<i>Cornitermes cumulans</i>
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101 (Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Cornitermes snyderi</i>
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101 (Z,Z,E)-dodeca-3,6,8-trien-1-ol
<i>Syntermes grandis</i>
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101 (Z,Z,E)-dodeca-3,6,8-trien-1-ol
Nasutitermitinae
<i>Constrictotermes cyphergaster</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Nasutitermes corniger</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A Trinervitatriene
<i>Nasutitermes diabolus</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Nasutitermes ephratae</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Nasutitermes exitiosus</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
Birch AJ 1972 J. Chem. Soc. 1 : 2653 Neocembrene-A
<i>Nasutitermes graveolus</i>
Moore P 1966 Nature 211 : 746–747 Neocembrene-A
Birch A. et al. 1972 J Chem Soc Perkin Trans 1 : 2653–2658 Neocembrene-A
<i>Nasutitermes guayanae</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Nasutitermes kemneri</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol

TABLE 2: Continued.

Termitidae
Neocembrene-A
<i>Nasutitermes lujae</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Nasutitermes walkeri</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Neocembrene-A
<i>Nasutitermes voeltzkowi</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Trinervitermes bettonianus</i>
McDowell PG and Oloo G. 1984 J. Chem. Ecol. 10 : 835 Neocembrene-A
<i>Trinervitermes geminatus</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A
<i>Trinervitermes trinervoides</i>
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20 Dodecatrienol Neocembrene-A

conserved metabolic route eventually leading to a compound with the same carbon skeleton as that of a dodecatrienol, where two subfamilies have diverged somewhat from the rest in that they synthesize trimethylundecadienol instead of dodecatrienol as the rest of termite species does.

In the case of termites, volatile chemicals for modulating the recruitment of workers are most likely to be used outside the nest or outside the covered galleries. This seems natural if we take into account that most termites forage in galleries which orient workers to their food sources. Very volatile chemicals are of little use in closed environments where they cannot disperse. Long-lasting, low-volatility chemicals may be useful for trail orientation outside the nest and might form the substrate around which galleries are built [25]. Thus, other signals seem to be more appropriate here in modulating communication. Many termite species add feces, saliva, and other secretions to the trail. This explains foraging trails that are reused after several years. A different situation may occur among termites foraging on grasses or leaves in open habitats and foraging at the end of their galleries where they can display very sophisticated foraging and recruitment strategies [26]. When recruitment behavior was explored in an open setting in a Nasutitermitinae [24], the decision making systems used to modulate the recruitment dynamics conformed to the Autocratic kind described for *Atta*.

4. Discussion

This paper is based only on published reports, and many more compounds used as trail pheromones are surely to be discovered in the future. For example, it is very likely that *Atta texana* uses a larger pool of compounds as trail pheromones as that reported in Table 1, as it is unlikely to differ very much from other *Atta* species in this regard. Thus, results in the Tables are biased towards species that have drawn more attention from researchers. Another cautionary remark regards the assessment of volatility based on chemical structure alone. In general, compounds of the same kind of lower molecular weight are more volatile than the ones of higher molecular weight or longer carbon chains. Biologically relevant volatility, however, depends not only on the compound but also on the substrate on which the chemical is secreted, on its concentrations on the substrate, and on the humidity and temperature of the surrounding air. Thus, simple direct correlations between molecular weight, assumed volatility, and behavioral function of a compound should be avoided.

The work behind the literature used for this study, evidently, was not performed with our objectives in mind, but it is unlikely that methodological limitations explain the lack of more chemical compound associated with trail pheromones among termites than among ants. Despite many possible limitations of this study, the large extend of the research effort explored and the large number of species covered guarantee a minimum of robustness that makes drawing conclusion from these data reasonable.

Despite these and other limitations of this paper, we might suggest two basic trends: (1) evolutionary history of the evolution of ant and termite trails is very different, and (2) the dynamics of interacting individuals achieving a recruitment process mediated by chemicals follow basic rules.

4.1. Different Evolutionary Histories between Ants and Termites. The diversity of chemical structures among ant trail pheromones and the uniformity of chemical compounds among termite trails suggest a different evolutionary history for the development of chemical mass recruitment in both taxa. In termites, often trail pheromone compounds are synthesized also by other exocrine glands and are used as sex pheromones. This pheromonal parsimony seems to be characteristic of termites [12] and is not common among ants.

Chemical mass recruitment among ants seems to have evolved at least 8 times [9], whereas chemical mass recruitment among termites seems to be a more conservative phenomenon where all species seem to share a common ancestor that had already developed chemical recruitment. This explains also the large difference between ants and termites in the glands responsible for the secretion of the trail pheromones. Many different glands are used by different species among ants [27], whereas only the sternal gland is used by termites [12]. Another factor explaining this difference is the ecological diversity of ant species, each

exploring different food source. Termites in contrast exploit more uniform ecological niches in their search for cellulose.

4.2. Basic Rules Govern the Recruitment Dynamics. The main conclusion from this study is that despite the fact that the evolutionary history of the chemical mass recruitment of ants and termites is different, a similar recruitment dynamics has evolved in both groups. This evolutionary analogy suggests that chemical mass recruitment is constraint by basic physical-dynamic laws. This would explain the convergence to chemical mass recruitment in the two evolutionary processes studied. A third convergence towards similar solution for the modulation of mass recruitment dynamics is nowadays repeated in the development of artificial intelligence, where the “mass intelligence” of ants copied in the interaction of simple virtual computer agents is in search of optimal solutions. Artificial intelligence, however, has copied only the simple recruitment dynamics named here as the Democratic system with a single compound pheromone. More sophisticated modeling could bear fruits to artificial intelligence that might echo the fruits chemical mass recruitment that has brought to social insect species evolving them.

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