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Foraging behavior in the ant genus *Messor* (Hymenoptera: Formicidae: Myrmicinae)

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Abstract

The genus *Messor* consists of 113 species of seed harvesting ants that are found in grasslands, semi-arid areas and savannahs in both the Old and New World. A full spectrum of foraging strategies occurs in *Messor*, ranging from individual to group foraging, with the latter having evolved several times. This paper reviews foraging strategies and the underlying behavioral mechanisms found in species of *Messor*. The glandular origin of trail pheromones in Old World species examined thus far come from Dufour gland secretions, whereas New World species use secretions from the poison gland. The constituents of poison and Dufour glands are known for several species, but biologically active components have not been identified. In addition, two New World group foraging species (*M. andrei*, *M. pergandei*) possess pygidial glands that function during initiation of group foraging. Overall, this diverse genus deserves further study because it contains examples of behavioral convergence both within the genus and with other seed harvesting genera, such as *Pogonomyrmex*.

Key words: Dufour gland, foraging columns, harvesting ants, poison gland, pygidial gland, recruitment, trunk trails, review.

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Introduction

In most arid regions there are ant species that have independently evolved harvesting behavior. Some species harvest liquids such as insect exudates (honeydew) and hemolymph, or plant nectars, e.g., honey pot ants in the genus *Myrmecocystus* in western North America (HÖLLDOBLER 1976a, SNELLING 1976), and *Camponotus inflatus* (BARRETT 1927) and *Melophorus bagoti* (CONWAY 1992, MUSER & al. 2005) in Australia. Other species collect the seeds of plants and store them in underground chambers. Genera of seed harvesting specialists include *Pogonomyrmex* (JOHNSON 2000a, 2001, MACMAHON & al. 2000), *Pheidole* (WHITFORD & al. 1981, JOHNSON 2000b), *Messor* (CREIGHTON 1953, BOLTON 1982), *Meranoplus* (ANDREW 1986), and to a lesser extent *Aphaenogaster* (MORALES & HEITHAUS 1998, MARTÍNEZ-DURO & al. 2010) and *Solenopsis* (CARROLL & RISCH 1984).

Harvesting ants are ecologically important because of their strong effects on plant communities, including seed dispersal, seed predation, nutrient cycling and microclimate modification (CRIST & MACMAHON 1992, BROWN & HUMAN 1997, MACMAHON & al. 2000, BOYD 2001, BOULTON & al. 2003, GRASSO & al. 2004, RETANA & al. 2004, AZCÁRATE & PECO 2007, MARTINEZ-DURO & al. 2010, MAJER & al. 2011). *Messor bouvieri* and several species of *Meranoplus* negatively impact seed banks (ANDREW 1986, MARTÍNEZ-DURO & al. 2010), and removal of harvester ant colonies in Sonoran Desert plots lowered the diversity of annual plants (INOUYE & al. 1980). The direct and indirect effects of *Pogonomyrmex* on their communities include changes in soil composition as well as the composition and density of plants (MACMAHON & al. 2000). *Messor andrei* enriches nutrients and biological diversity in serpentine soils (BROWN & HUMAN 1997, BOULTON & al. 2003, PETERS & al. 2005). Plant communities are also affected at the microscale because colony middens create micro-environments that influence the abundance, distribution, and diversity of plants (RISSING 1986, VORSTER 1989, BROWN & HUMAN 1997, AZCÁRATE & PECO 2007, SOLIDA & al. 2011b, NICOLAI & BOEKEN 2012). Overall, abundant information exists on the ecological significance of harvester ants, but little is known about foraging strategies for species of *Messor*. This paper examines the diversity of foraging behavior within the genus *Messor*, with emphasis on traits that correlate with the evolution of species differences. These mechanisms include pheromones, colony size, competition, and distribution of resources.

Messor is a moderate-sized genus of granivorous ants (subfamily Myrmicinae, tribe Pheidolini) consisting of 113 described species (BOLTON 2012). The genus occurs in the New and Old World, most commonly in arid and semi-arid areas, grasslands, and savannahs. Many species are polymorphic, but the genus also contains monomorphic and weakly polymorphic species (DÍAZ 1994, DETRAIN & TASSE 2000, AZCÁRATE & al. 2005, AZCÁRATE & PECO 2007, ARNAN & al. 2010). Several species have been the focus of studies on foraging, seed selection (RISSING 1987, JOHNSON 1991, BARONI URBANI 1992, AZCÁRATE & PECO 2007, SOLIDA & al. 2010, 2011a), and how environmental variation affects these behaviors (RISSING & WHEELER 1976, JOHNSON 1991, LÓPEZ & al. 1993a, 1993b, 1994, WILBY & SHACHAK 2000). Several polymorphic species have been examined for matching between worker size and size of the items that they harvest (RISSING 1981, WASER 1998, HEREDIA & DETRAIN 2005, AZCÁRATE & al. 2005).

Ant foraging strategies

Foraging strategies vary within and among ant species (HÖLLDOBLER 1976b, LIEFKE & al. 2001), but rarely does the entire spectrum of foraging strategies occur within a genus; exceptions include *Camponotus* (HÖLLDOBLER 1971a), *Polyrhachis* (LIEFKE & al. 2001), *Pogonomyrmex* (HÖLLDOBLER 1976b), and *Messor* (Tab. 1). The type of foraging behavior that a colony employs affects the pattern of resource retrieval (RETANA & al. 2004), and likewise the resource distribution affects the topography of foraging trails (in army ants, *Eciton*: FRANKS & al. 1991; in harvesting ants, *Messor*: DÍAZ 1994). Neighboring colonies also modify the activities and spatial parameters of foraging behavior (HÖLLDOBLER 1976b, 1981). Consequently, it is problematic to describe the foraging behavior of a species using one term (TRANIELLO 1989a). For clarity, we briefly describe recruitment mechanisms (tandem running, group recruitment, mass recruitment) and describe how these mechanisms are used to coordinate efforts in group foraging strategies such as trunk trails and foraging columns.

Individual or solitary foraging, as a strategy, implies foraging workers leave the nest independently, and when they return to the nest with food they do not recruit or lead nestmates to the location where the item was harvested. Individual foraging occurs when food items can be carried by individuals, but are distributed randomly and at a low density. Individually foraging species may have the capacity to recruit nestmates to new rich food sources. For example, the solitary foraging *Pogonomyrmex maricopa* lay recruitment trails to new seed patches with pheromones from the poison gland (HÖLLDOBLER 1976b), using the same major compounds as related trunk trail foragers such as *P. barbatus* and *P. rugosus* (HÖLLDOBLER & al. 2001). In this paper, we distinguish between species which primarily employ individual foraging versus those with some form of group foraging, where group foraging strategies involve multiple individuals coordinating their efforts to retrieve resources using various combinations of recruitment mechanisms.

Tandem running occurs when one ant leads another to a chosen location (WILSON 1959). The leader ant solicits a follower by chemical or tactile signals, and moves towards the targeted location (often following her own trail), waiting for tactile signals by the follower before resuming (HÖLLDOBLER & al. 1974, MÖGLICH & al. 1974, MÖGLICH 1978, JESSEN & MASCHWITZ 1986, LIEFKE & al. 2001, PRATT & al. 2002, FRANKS & RICHARDSON 2006).

Group recruitment is when a leader ant uses motor displays to induce 5 - 30 workers to follow a short-lived odor trail, such as occurs in several *Camponotus* species (HÖLLDOBLER 1971a), *Aphaenogaster cockerelli*, *A. albisetosus* (HÖLLDOBLER & al. 1978), *A. senilis* (CERDÁ & al. 2009), *Pheidole pallidula* (DETRAIN & al. 1991), and *Tetramorium caespitum* (COLLINGNON & DETRAIN 2010). This strategy leads more workers to a location with a lower risk of becoming lost or disoriented. Group recruitment is often employed to retrieve large prey items (HÖLLDOBLER & al. 1978). The behavior evolved in part as a counter-strategy to escape mass recruiting competitors that employ chemical repellants to take possession of prey.

Fig. 1: Trunk trail (runs vertically through photograph) cleared by a Nearctic *Messor*, *M. andrei*, California, USA (photograph by Nicola Plowes).

In mass recruitment, the number of workers leaving the nest is controlled by the quantity of recruitment pheromones emitted by foragers. Tests with *Solenopsis invicta* and other mass recruiting species, using artificial trails, have shown that the number of individuals leaving the nest is a linear function of the amount of trail pheromone deposited (WILSON 1962). Under natural conditions, worker outflow adjusts to the level needed at the food source (WILSON 1962, HANGARTNER 1969). If the first recruits find food or fill their crop, they will reinforce the recruitment trail, which leads to more recruits. Conversely, if the food source declines or is overcrowded, then returning ants are unsuccessful and do not deposit a trail pheromone. As recruitment pheromones are volatile, trail concentration quickly decreases below the response threshold, which leads to a rapid decline of responding ants. Nevertheless, CASSILL (2003) demonstrated that even in mass recruitment, the response of workers is finely regulated by motor displays performed by recruiters. In most cases, foraging trails are marked by multiple compounds which have different functions, such as short-lived signals that activate foragers and induce recruitment, and longer lasting markers that serve for orientation (reviewed in MORGAN 2009).

Tab. 1: Foraging strategies used by species of *Messor*.

Species	**Foraging strategy**
New World	
andrei	Foraging columns (Creighton 1953, Brown 1999)
chamberlini	Individual (Johnson 2000a), diurnal column forager (M. Bennett, pers. comm.)
chicoensis	Individual (Johnson 2000a; M. Bennett, pers. comm.)
julianus	Trunk trails (Creighton 1953, R.A. Johnson, unpubl.)
lariversi	Nocturnal individual forager (Creighton 1953; M. Bennett, pers. comm.)
lobognathus	Individual (Johnson 2000a), nocturnal (M. Bennett, pers. comm.)
pergandei	Foraging columns (Creighton 1953, Wheeler & Rissing 1975b), individual (Bernstein 1975)
smithi	Individual (Johnson 2000a), nocturnal (M. Bennett, pers. comm.)
stoddardi	No foraging column (Creighton 1953), solitary and crepuscular (M. Bennett, pers. comm.)
Old World	
aegypticus	Trunk trails (permanent and temporary trackways), foraging columns (Pickles 1944, Sheata & Kaschef 1971, Wehner 1992)
aciculatus	Individual (Onoyama & Abe 1982), individuals from different colonies may engage in ritualized duels without soliciting help from nestmates (Yamaguchi 1995)
arenarius	Individual and group (Steinberger & al. 1992, Wehner 1992)
barbarus	Trunk trails, stable system of permanent trails (Arnan & al. 2010, Pickles 1944), trails persist over winter, even when not being used (Acosta & al. 1995), shape of trail depends on resource (López & al. 1994), trails can be 30 m long (Cerdan & Délye 1988)
bouvieri	Foraging column, temporary seasonal trails (Azcárate & Peco 2003), frequently change direction (Arnan & al. 2010), trails 4 - 5 m long (Cerdá & Retana 1994)
capensis	Trunk trail, foraging trails many meters long, slow and deliberate movements (Brand & Mpuru 1993, Vorster 1989, Vorster & al. 1991)
capitatus	Individual (90% of the time) (Arnan & al. 2010, Cerdá & Retana 1994), some instances of group foraging (Arnan & al. 2010, Baroni Urbani 1991), trunk trails (Acosta Salmerón & al. 1985, Grasso & al. 1998)
ebeninus	Unclear if trunk trail or foraging column, described as long foraging trails (Coll & al. 1987)
minor	Foraging columns or trunk trails, can have more than one trail per day (Wehner 1992, Solida & al. 2010, 2011a; D.A. Grasso, pers. comm.)
medioruber	Trails, unclear if trunk trails (Wehner 1992)
structor	Foraging columns or trunk trails (unclear), irregular, broad trails (1 m wide) (Baroni Urbani 1991), individual foraging on widespread seeds, dense seeds exploited through recruitment (Hahn & Maschwitz 1985)
wasmanni	Foraging columns or trunk trails, can have more than one trail per day (Solida & al. 2010, 2011a; D.A. Grasso, pers. comm.)
hispanicus	Foraging columns or trunk trails (unclear), seasonal trails (Azcárate & Peco 2003)

Trunk trails persist for months to years (Rosengren 1971, Hölldobler 1974, 1976b, Wirth & al. 2003), and can be considered as part of the colony's territory (Hölldobler & Lumsden 1980). In areas with grass or debris, workers clear obstacles and vegetation from the trails, such that the trails are often conspicuous and can be recognized, even after rainfall (Fig. 1). In several species, trunk trails of neighboring colonies never cross and act to partition foraging territories. One colony may have several trunk trails originating from the nest entrance, but not all may be used simultaneously or with equal frequency. Trunk trails may branch, and the terminal branches are more subject to changing routes as a result of resource availability or competitive pressure (Hölldobler 1974, 1976b, Hölldobler & Möglich 1980, López & al. 1994).

Movement of foragers along trunk trails is well studied in some species of *Pogonomyrmex* (Hölldobler 1976b, Gordon & al. 2008), *Pheidole* (Hölldobler & Möglich 1980), *Atta* (Wirth & al. 2003, Roces & Bollazzi 2009, Bollazzi & Roces 2011, Röschard & Roces 2011), and several formicines (Traniello 1989b). In *Pogonomyrmex*, trails lead to relatively stable seed patches, facilitate the efficient retrieval of seeds, and serve as territorial partitioning between neighbors (Hölldobler & Lumsden 1980, Davidson 1977b). Trunk trails in *Pogonomyrmex* are marked with persistent colony-specific chemical trail guides

(HÖLLDOBLER & al. 2004). Some *Pogonomyrmex* species typically use trunk trails, but lay recruitment pheromone trails to rich food sources. Visual landmarks and celestial cues (sun compass) also stabilize the topography of the trunk trail system (HÖLLDOBLER 1976b). In fact, the first studies of celestial navigation in ants, the classic "mirror" experiments (where a mirror was used to reverse the direction of celestial cues), demonstrated that *Messor barbarus* use celestial cues when returning to the nest (SANTSCHI 1911). In *Messor semirufus*, when workers foraging individually were displaced to arenas devoid of sun or landmarks, they oriented correctly towards the nest when exposed to blue sky, but incorrectly when the sky was overcast (WEHNER 1981). On the other hand, when trail foragers were displaced, they oriented instead to the point on the trail from which they had been removed (WEHNER 1981).

In *P. barbatus*, returning foragers are recognized by their cuticular hydrocarbon pattern (GREENE & GORDON 2007a, STURGIS & GORDON 2012). Nestmates are triggered to move out along the trunk trails by the return of successful foragers. Artificial trails drawn with Dufour gland secretions direct foragers to particular trunk trails (GREENE & GORDON 2007b). Although it was found that trails drawn with Dufour gland secretion serve as trail guides in homing harvester ants (HÖLLDOBLER 1971b, HÖLLDOBLER & al. 2001), they do not function to recruit foragers when presented at the nest entrance of laboratory colonies (HÖLLDOBLER & WILSON 1970). In contrast, poison gland secretions, in particular 3-ethyl-2, 5-dimethyl pyrazine (EDMP), elicit an exodus of foragers (HÖLLDOBLER & WILSON 1970, HÖLLDOBLER & al. 2001). The comparative tests of poison gland secretion or EDMP and Dufour gland secretions were conducted with laboratory colonies, but once, during a dry summer with no foraging activity of *Pogonomyrmex* for weeks, foragers exited from field colonies in response to EDMP (HÖLLDOBLER & al. 2001). Moreover, it is difficult to test trail pheromones in the field, so it is surprising that GREENE & GORDON (2007b) obtained clear-cut results with directing foragers to a particular trunk route by applying the contents of one Dufour gland. Although it is certainly possible that encounters with returning foragers lower the response threshold to recruitment pheromones in nestmates, previous results suggest that the chemical recruitment signals derive from the poison gland, whereas the much more persistent components from the Dufour gland serve as chemical trail guides. In addition, the orientation of *Pogonomyrmex* foragers along the long-lasting trunk trail is aided by visual landmarks and sun compass orientation (HÖLLDOBLER 1976b).

Foraging columns last from hours to days, and do not have cleared paths like trunk trails. In addition, over periods of weeks, columns from neighboring colonies may overlap foraging areas, but neighboring columns avoid foraging in the same area simultaneously. Most ants leaving the nest follow the column to its terminus, and then leave the column to search for food items individually. When ants have completed their foraging bout or have a food item to bring back to the nest, they return to the column and then follow the chemically marked column trails to the nest. In most cases, foraging columns are initiated by one to several leader ants emitting recruitment and orientation pheromones. In army ants (*Eciton* spp.), thousands of ants leave their bivouac simultaneously in a swarm. The swarm advances, and a column forms between the nest and the swarm (SCHNEIRLA 1934, CHADAB & RETTENMEYER 1975, KRONAUER 2009). Each day the columns can form in a different direction, allowing the colony to find resources in a new patch of forest (FRANKS & FLETCHER 1983). In dulotic ants, columns may also lead brood-raiders (e.g., *Polyergus* spp.) to target nests (COOL-KWAIT & TOPOFF 1984, MORI & al. 1991, GRASSO & al. 1997).

In general, group foraging strategies (trunk trails, foraging columns, short-lived mass recruitment trails) are considered adaptations for high density, patchy resources (DAVIDSON 1977a, MULL & MACMAHON 1997). The ancestral foraging behavior is likely to have been similar to solitary foundress wasps and primitive ponerine ants which forage individually, while group foraging strategies are derived states that evolved independently several times within the Formicidae (BARONI URBANI 1993, HÖLLDOBLER & WILSON 2009). Group foraging strategies are correlated with increased colony size (BECKERS & al. 1989). Contributing factors in the evolution of larger group sizes may be that larger colonies are more resistant to losses of workers in extreme environments (KASPARI & VARGO 1995), and that larger groups are theoretically more efficient at exploiting food sources than small groups (NICOLIS & al. 2003).

Biogeography and taxonomic considerations

The genus *Messor* is presumed to have evolved in the Palearctic region and later spread to Africa and Asia; North American species are presumed to have arrived via the Bering land bridge (BENNETT 2000). Old World *Messor* are distributed in a wide belt that includes southern Europe, Africa and Madagascar, eastward throughout Asia and Japan, and northward into southern Russia; the genus is absent from Southeast Asia and areas further south (BOLTON 1982, GUÉNARD & al. 2010). The majority of species occur in the Palearctic region (70 - 80 species), with the highest number of species in the Mediterranean area (BOLTON 1982). There are twelve Afrotropical species, one species in Madagascar, several species in Asia, and one species in Japan (BOLTON 1982, ONOYAMA & ABE 1982, YAMAGUCHI 1995).

The nine New World species of *Messor* are restricted to the Nearctic region, and they occur throughout western North America, along the coast from southern Oregon to northern Mexico and west throughout the Great Basin and Sonoran Deserts (BENNETT 2000, JOHNSON 2001). One species, *M. lobognathus*, occurs eastward into northern Colorado and western portions of the Dakotas (WHEELER & WHEELER 1944, WHEELER & WHEELER 1956, 1959, 1965, 1967, JOHNSON 2000a).

Messor was first described as a subgenus of *Aphaenogaster* based on the Old World species *Messor barbarus* (FOREL 1890). It was later transferred to a subgenus of *Stenamma* (EMERY 1895) before it was raised to generic status by BINGHAM (1903). FOREL (1917) later transferred all New World species of *Messor* to the new subgenus *Veromessor*. WHEELER (1922) raised *Veromessor* to generic status, but it was later placed as a junior synonym of *Messor* (BOLTON 1982), where it currently stands.

The taxonomic status of *Messor* is likely to change again, given that New World *Messor* may be more closely related to a small group of New World *Aphaenogaster* (BENNETT 2000, WARD 2005) than to Old World species of *Messor*. Using morphological characters of workers and males, BENNETT (2000) reconstructed a phylogeny which suggests that New World *Messor* are monophyletic and that the *Aphaenogaster albisetosa* group (formerly *Novomessor*) is the sister group to these species. Additional support for this hypothesis would result in resurrecting the genus *Veromessor* for New World species. Such a taxonomic change would also indicate strong morphological and behavioral convergence between *Veromessor* and *Messor*.

The phylogenetic reconstruction by BENNETT (2000) suggested that the Nearctic *Messor* consists of two clades. The first clade consists of the group foragers, *M. pergandei* and *M. julianus*, and three individual foragers, *M. lariversi*, *M. smithi*, and *M. lobognathus*. The second clade has one group foraging species, *M. andrei*, and three individual foraging species, *M. chamberlini*, *M. chicoensis*, and *M. stoddardi*. Palearctic *Messor* formed a monophyletic sister group to the Nearctic *Messor* and related *Aphaenogaster* species.

Recently, an integrative approach was used to study the relationship between three sympatric Mediterranean *Messor* species: *M. capitatus*, *M. minor*, and *M. wasmanni* (STEINER & al. 2011). The authors found genetic evidence for hybridization between *M. minor* and *M. wasmanni*, as well as backcrosses between hybrids and parental species. In addition, mixed species colonies were found, including colonies consisting of *M. capitatus* and *M. minor / M. wasmanni* hybrids. These may arise from brood raiding between incipient colonies of different species, or social parasitism during colony founding (e.g., RACZKOWSKI & LUQUE 2011). The pattern of hybridization is different than that of *Pogonomyrmex*, where ancient hybridization resulted in genetic caste determination (HELMS CAHAN & al. 2002, JULIAN & al. 2002, VOLNY & GORDON 2002, HELMS CAHAN & KELLER 2003).

Foraging behavior in Old World *Messor*

Foraging behavior has been described for few of the 104 Old World species of *Messor* (BOLTON 2012). Ten species have been described as "group foragers": *M. aegypticus*, *M. arenarius*, *M. barbarus*, *M. bouvieri*, *M. capensis*, *M. ebeninus*, *M. minor*, *M. structor* (= *rufitarsis*), *M. wasmanni*, and *M. hispanicus* (Tab. 1). *Messor barbarus* uses trunk trails, while the remaining species use ephemeral foraging columns, or are too poorly known to be classified. Three species are known to forage individually: *M. aciculatus*, *M. capitatus*, and *M. structor* (Tab. 1).

Messor barbarus is the best studied group foraging species. It is a polymorphic species that has temporary and permanent components to its trails (PICKLES 1944) (Fig. 2a). The description of permanent foraging trails having "vegetation and other obstacles found by workers… cleared" (DETRAIN & al. 2000) fits our definition of trunk trails. Trail length ranges from 1 - 30 m (REYES 1986, CERDAN 1989, DETRAIN & al. 2000). Claire Detrain (pers. comm.) describes trails as about 10 - 20 cm wide, and they are often branched (LÓPEZ & al. 1993a, 1993b, 1994). More branching and shorter links develop after a productive season, whereas an unproductive season results in longer links and fewer branches (LÓPEZ & al. 1994). This change in topology adjusts the search area to the resource level.

Fig. 2: Old World *Messor*: a) A major worker of *M. barbarus* carries a seed of *Planatus hybrida* in Sevilla, Spain (photograph by Fernando Amor). b) A laden *M. structor* forager (photograph by Jiří Bohdal).

Colonies of *M. barbarus* have multiple nest entrances with trunk trails arising from each entrance. One-third of the colonies in a Spanish population had trails between nest entrances that functioned to increase communication and food transfer throughout the colony (LÓPEZ & al. 1993b). Along the length of foraging trails, size matching between individuals and their harvested items was negatively correlated with distance from the nest entrance (REYES-LÓPEZ & FERNÁNDEZ-HAEGER 2001). Seed selectivity, which is the abundance of specific species of seeds retrieved by ants compared to the relative abundance of those seeds in the environment, was positively correlated with trail length, but not with seed density (DETRAIN & al. 2000). Workers chose smaller items when provided with various sizes of the same food (oats) (HEREDIA & DETRAIN 2005). This may result from the advantage of increased information transfer, where returning more rapidly to recruit foragers provides the colony with a mechanism to increase food gathering rates (ROCES & BOLLAZI 2009, BOLLAZZI & ROCES 2011).

Seed depots, locations along a trail where large numbers of foragers drop their seeds, are found on ~ 20% of *M. barbarus* paths (DETRAIN & TASSE 2000). Seed depots are not an adaptive behavior for sequential load transport, but rather they are a consequence of the fact that longer trails are more likely to have patches of terrain that are more difficult for a laden ant to negotiate, and foragers are more likely to drop seeds at these locations (C. Detrain, pers. comm.).

Messor barbarus prefer seeds that range from 4 - 50 mg in mass regardless of seed density, and only a subset of species in the plant community are used, resulting in differential predation of seeds (DETRAIN & PASTEELS 2000). AZCÁRATE & al. (2005) found that *M. barbarus* also choose forage items based on length (in addition to mass). This pattern of foraging constitutes a time-saving strategy as opposed to an energy-efficiency strategy (which predicts that seeds would be selected based on mass), because seeds that are longer are found more easily and are less likely to be buried.

Messor bouvieri is a group foraging species in southern Europe and North Africa (JACKSON & al. 1989). Colonies have narrow trails that vary from 1.5 - 26 m long (CERDÁ & RETANA 1994, WILLOTT & al. 2000). Trails rotate around the nest entrance, sometimes moving within one day (CERDÁ & RETANA 1994). However, it is unclear if the entire trail slowly shifts, or if new trails form and become more heavily used while the original trail decays. A moderate degree of size matching is found, where 21 - 32% of the variability in collected items is due to ant size, but size of harvested seeds does not correlate with distance from the nest entrance (WILLOTT & al. 2000).

Colonies of *M. capensis*, found in South Africa, have from four to eight trunk trails leading from the nest (VORSTER & al. 1991). Trails extend 9.55 m ± 6.75 m from the nest entrances. This species shows monophasic allometry, and did not display size matching between worker head width and food particle mass (VORSTER 1989, VORSTER & al. 1991).

Messor ebeninus, *M. minor*, and *M. wasmanni* have been described as trunk trail foragers that may produce more than one column per day (WEHNER 1992, WARBURG & STEINBERGER 1997, SOLIDA & al. 2010, NICOLAI & BOEKEN 2012). However, the dynamics, topology, and mechanisms underlying trail formation are unknown. In *M. minor* and *M. wasmanni*, there is strong evidence for size matching between the dry mass of food items and head width (SOLIDA & al. 2007). *Messor arenarius* and *M. ebeninus* have been alternatively categorized as "usually individual" (WARBURG & STEINBERGER 1997) and as usually "group forager" (WILBY & SHACHAK 2000), illustrating the occurrence of intraspecific variation in foraging behavior (HÖLLDOBLER 1976b, TRANIELLO 1989a). Resources are heterogeneously distributed in areas in which *M. arenarius* and *M. ebeninus* are found, and colonies adapt their foraging behavior via seasonal changes in the type of seeds collected and the amount of time spent in different patches (WILBY & SHACHAK 2000). Steven W. Rissing (pers. comm.) has observed size matching between workers and seeds in *M. arenarius*, but not in *M. ebeninus* or *M. rugosus*.

Messor aciculatus and *M. structor* (= *rufitarsis*) are primarily individual foragers that have been observed to recruit to rich experimental resources (ONOYAMA & ABE 1982, HAHN & MASCHWITZ 1985, CERDÁ & RETANA 1994). *Messor structor* has been alternatively described as having broad trails (more than 1 m wide) with low densities of foragers (BARONI URBANI 1991) (Fig. 2b). On these broad trails, workers drop seeds which are later recovered, but not at specific seed depots (BARONI URBANI 1991). Both *M. aciculatus* and *M. structor* foragers show strong site fidelity, where individuals return on subsequent foraging trips to areas they have just searched (ONOYAMA & ABE 1982, HAHN & MASCHWITZ 1985). Foraging areas, the maximum area covered by all individual foragers, show considerable overlap between neighboring nests in *M. aciculatus*. Encounters between neighboring colonies result in ritualized dyad fights without soliciting aid from nestmates (YAMAGUCHI 1995).

Messor capitatus is a highly polymorphic species that has a flexible foraging strategy (ACOSTA SALMERÓN & al. 1985, BARONI URBANI 1991, CERDÁ & RETANA 1994, GRASSO & al. 1998, ARNAN & al. 2010). BARONI URBANI (1991) describes *M. capitatus* as having long narrow trails that are less than 10 cm wide, and that workers drop seeds at depots along the trail. The direction that a trail takes is affected by the presence of neighboring colonies and their trails (ACOSTA SALMERÓN & al. 1985). Trail direction can be stable for multiple days in the absence of perturbation by neighboring colonies. Workers of *M. capitatus* deposit colony-specific secretions (anal spots) around the nest and possibly also mark trails (GRASSO & al. 2005). This provides a mechanism by which colonies segregate foraging areas and minimize interactions with neighbors.

A comparison of how head width in *M. capitatus* correlated with the volume and mass of artificial seeds (lead weighted Styrofoam coated with sugar and flour) found no preference for different sized "seeds" of equivalent mass (BARONI URBANI & NIELSEN 1990). A preference for "seeds" of moderate mass (400 mg) was found when size was held constant (5 - 5.5 mm diameter). When presented with various sizes of crushed wheat seeds, those with smaller dimensions were preferred, but there was no preference for any particular mass. Distance from the nest did not affect seed preference. BARONI URBANI & NIELSEN (1990) concluded that this species probably does not optimize energy intake. Calculations suggest that one ant carrying a grain of wheat over 20 m would use less than 1 Joule of energy. Thus, a negligible amount of energy is needed for food transport (FEWELL 1988, NIELSEN & BARONI URBANI 1990). BARONI URBANI (1992) suggested that true harvester ants (those that feed on seeds rather than elaiosomes) should select seeds with heavier masses to maximize energy storage.

Foraging behavior in New World *Messor*

Three species of Nearctic *Messor* have been described as "group foragers": *M. andrei*, *M. julianus*, and *M. pergandei* (JOHNSON 2001). The other six species are described as having "solitary foraging with recruitment" or with "limited recruitment", which is considered to be the ancestral state (JOHNSON 2001). Nearctic *Messor* are nocturnal, except for *M. andrei*, *M. chamberlini* and *M. pergandei*, which are primarily diurnal or crepuscular, depending on the season (COLE 1966, GORDON 1978, JOHNSON 2001) (Fig. 3a).

Little is known about the individual foraging Nearctic *Messor*, in part due to their nocturnal behavior (GREGG 1955, WHEELER & WHEELER 1956, 1959, 1965, 1967, COLE 1963). Colonies have approximately 500 workers (JOHNSON 2000a, COLE 1963). *Messor chamberlini* have a foraging method intermediate to solitary and group foraging because they can form recruitment trails to rich food resources (JOHNSON 2000a).

The three group foraging species of *Messor* have parapatric distributions with narrow zones of overlap (JOHNSON 2000a). Colonies of all three species (*M. andrei*, *M. julianus*, *M. pergandei*) have several thousands of workers (JOHNSON 2000a). Proposed phylogenetic relationships

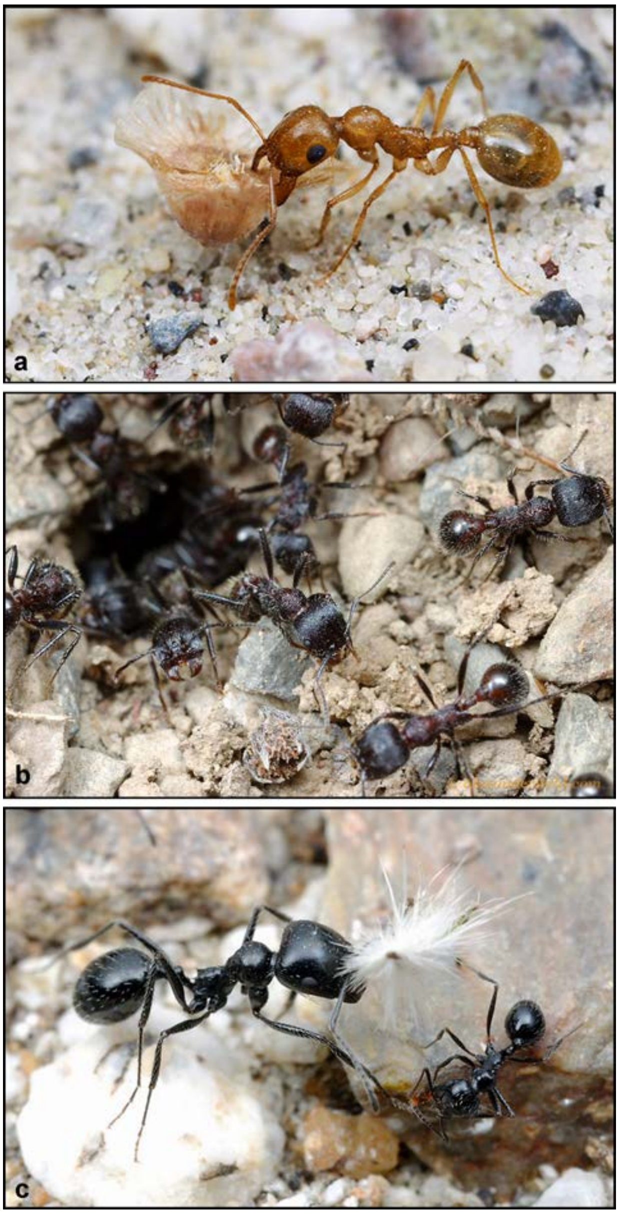

Fig. 3: New World *Messor*: a) Nocturnal species of *Messor* are pale in color, like this *M. lariversi* forager. b) Monomorphic *M. andrei* exiting a nest entrance, California, USA. c) Polymorphic *M. pergandei* workers carrying seed along a trail. (Photographs by Alex Wild.)

among these three species suggest that group foraging has evolved at least twice in New World *Messor* (BENNETT 2000, JOHNSON 2001).

Messor andrei is a monomorphic, crepuscular species that occurs from northern Baja California to southern Oregon (JOHNSON 2000a, 2001) (Fig. 3b). Foraging columns are described as a "stream of ants leaving the nest, when more than 5 ants crossed … approximately 25 cm from the nest in 30 s", and most foraging occurs within 5 m of the nest (BROWN 1999). Each colony can have multiple foraging columns per day, with columns extending up to 20 m from the nest (BROWN & GORDON 2000). Total number of foraging trips for a colony was estimated to range from 2684 to 3933 per day (BROWN 1997). Once ants reach the end of the trail they move out into a foraging fan to search for food. The foraging fans of neighboring colonies frequently overlap, resulting in foragers fighting with low incidence of mortality (BROWN & GORDON 2000). To test the effect of an encounter on a colony's subsequent choice of direction, colonies which had two foraging columns had 50 enemy ants added to one foraging fan. The next day, colonies were more likely to return to the foraging fan which had non-nestmates added the previous day. Length of time that a column persists in the same direction in the absence of enemies is unknown (BROWN & GORDON 2000). *M. andrei* colonies recruit to artificial food sources (*Microseris douglasii*) placed 3.5 m from nest entrances (BROWN & GORDON 2000).

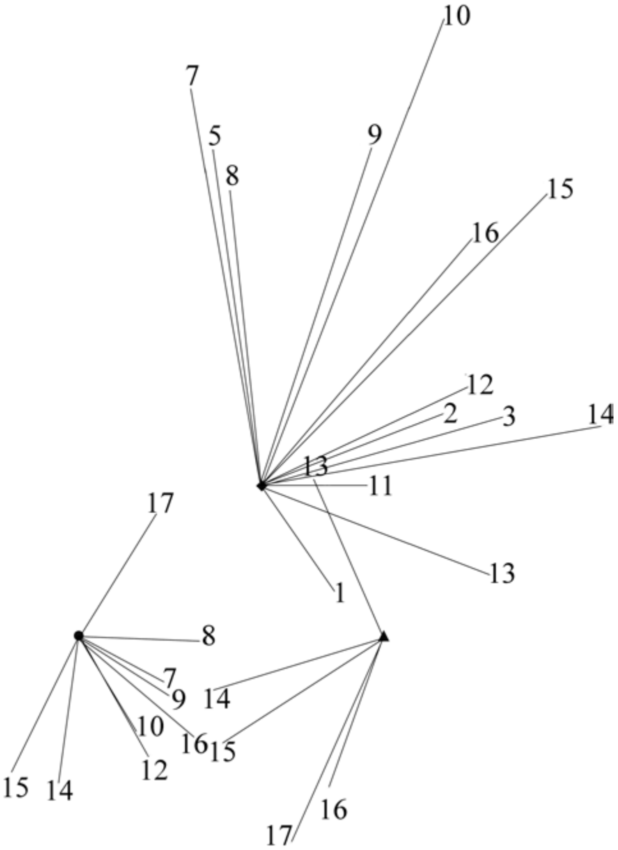

Fig. 4: Foraging direction taken by three neighboring colonies of *Messor pergandei* over 17 days. Numbers refer to the observation day. On day 13, two colonies had columns that intersected, which led to internidal hostility (N.J.R. Plowes, R.A. Johnson & B. Hölldobler, unpubl.).

Messor julianus is a monomorphic species that is an endemic to the Baja California peninsula of Mexico (JOHNSON 2000a, JOHNSON & WARD 2002). Foraging columns are much more populous than in *M. andrei*, consisting of thousands of workers in long columns that are comparable in length to those of *M. pergandei* (JOHNSON 2000a). Foraging parameters such as colony density, topography of foraging columns, and behavioral and chemical mechanisms are unknown.

Messor pergandei occurs in the Sonoran and Mohave Deserts (TEVIS 1958, WHEELER & RISSING 1975a) (Fig. 3c). Colonies form foraging columns that travel in different directions, sometimes changing direction every day (WHEE-

LER & RISSING 1975b, RISSING & WHEELER 1976, RISSING & POLLOCK 1989) (Fig. 4). Foraging trails contain 17,000 to 35,000 individuals (WENT & al. 1972, WHEELER & RISSING 1975b) and range from 3 to 40 m long (BERNSTEIN 1975, WHEELER & RISSING 1975b). The ants move out individually into a foraging fan at the end of the foraging column (N.J.R. Plowes, R.A. Johnson & B. Hölldobler, unpubl.).

The spatio-temporal dynamics of foraging columns in *M. pergandei* are driven by colonies at high densities interacting aggressively when foraging columns intersect (WENT & al. 1972, WHEELER & RISSING 1975b). WENT & al. (1972) reported that column direction changed by 15° increments, based on observations of one colony. BERNSTEIN (1971) measured foraging direction for two consecutive mornings, finding that the mean change averaged 32° (n = 39, range = 0 - 160°).

Resource abundance and distribution has been hypothesized to drive column rotation (the change in foraging direction between two successive foraging bouts) in *M. pergandei* (BERNSTEIN 1975, RISSING & WHEELER 1976, RYTI & CASE 1986, 1988, JOHNSON 1989). When resources are scarce, colonies are expected to modify their foraging dynamics to search for higher quality or higher density food patches. Several changes might occur: colonies may change column direction more frequently, column length can increase or decrease, or they can change the angle between subsequent foraging columns (larger angles result in surveying colony surroundings more rapidly).

To address the question of column rotation, BERNSTEIN (1975) assumed that seed density was correlated with elevation and season. Her data collection regime included observing whether columns rotated clockwise or counterclockwise, and the "rate of rotation" based on the change in direction over two days. She collected data on nine colonies located at 500 m elevation and 10 - 11 colonies at 700 m elevation in May and June. In May at 500 m, the average rotation was 29°, whereas at 700 m the average rotation was 14°. In June at 500 m, the average rotation was 71°, whereas at 700 m the average rotation was 22°. BERNSTEIN (1975) assumed that food abundance was lower at 500 m than 700 m (due to increased rainfall at higher elevations), and concluded that rate of rotation increases with decreasing food density. Column length was also positively correlated with food density (BERNSTEIN 1975). These results are unlikely to be conclusive because GORDON (1978) found both long and short columns during all seven months of observations. Indeed, RISSING (1987) found no alteration of column length with changing resources.

The contention that seed density increases with elevation is based on the assumption that higher seed densities are found in areas with increased rainfall, and that rainfall increases consistently with elevation (BERNSTEIN 1975). The actual seed density may not follow the predicted pattern because rainfall in desert systems is patchy and unpredictable. Our observations on *M. pergandei* (following approximately 80 colonies for several weeks), indicate that some colonies forage consistently in one or two general directions, whereas others foraged in almost all directions (N.J.R. Plowes, R.A. Johnson & B. Hölldobler, unpubl.).

A study following two nests of *M. pergandei* (in 1974) and four nests (in 1973) found that there was no consistent rotation rate (RISSING & WHEELER 1976). The authors suggested that the change in column direction was related to seed production, because in 1973 (a year with high seed recruitment) the frequency histogram was more skewed (the angles between successive foraging columns were smaller) than in 1974. They also commented that there were colony-level patterns to foraging trail directions, where a colony would exhibit a "characteristic clockwise or counterclockwise fashion". A similar argument correlating rainfall, seed density, and rotation rate was proposed by JOHNSON (1989). Over three years, the mean rotation rate was 48°, 28° and 29°, and was suggested to be negatively correlated with winter rainfall in those same years (4.2 cm, 8.1 cm, 5.2 cm), which was used as a proxy for seed density. The approach of RISSING & WHEELER (1976) does not account for other reasons that a colony might change foraging direction (e.g., presence of neighbors). Another issue is that their histograms describe the number of degrees between two foraging bouts, but do not consider a single colony's behavior over several days. To illustrate this point, consider if one colony had the following compass directions over four days: 0°, 15°, 30°, 45° and another colony had these directions: 0°, 345°, 0°, 15°. Both colonies would have the same frequency histogram, but the first colony uses a much larger foraging area. The data in Figure 1 indicate that both different approaches to that of RISSING & WHEELER (1976) and larger sample sizes are necessary to support their hypothesis. Our data on approximately 80 colonies suggest that colonies change foraging direction rapidly, and that there is no characteristic clockwise or counterclockwise motion (GORDON 1978; N.J.R. Plowes, R.A. Johnson & B. Hölldobler, unpubl.) (Fig. 4).

Descriptions of a spatially explicit, predictable group behavior in *M. pergandei* led to developing a model that used individual level behaviors to generate the movement of foraging columns (GOSS & DENEUBOURG 1989). The model included successful foragers laying trails when they return to the nest, and recruited foragers following the most heavily marked trail when leaving the nest. The foraging area is divided into sectors which start out with similar abundances of food. As a sector's food supply diminishes through foraging, the relative abundance of preferred food types is higher in neighboring sectors, and foraging shifts to adjacent sectors. Thus the foraging trail moves across the foraging area as food decreases. To bring GOSS & DENEUBOURG's (1989) model in line with our data would necessitate modifying variables such as probability that an individual ant visits a sector that is not currently marked, and providing terms to allow that ant to induce sufficient recruitment to rapidly shut down foraging in the currently chosen direction. Foraging also occurs in bouts such that the column direction must be determined at the beginning of each bout (CREIGHTON 1953, BERNSTEIN 1974, RISSING & WHEELER 1976).

The diet and foraging range of eight *M. pergandei* colonies followed over several seasons showed no significant difference in mean maximum foraging distance between seasons with different food abundance, suggesting that columns function both for food acquisition and territorial interactions (RISSING 1988). New colonies establish further from mature conspecific nests than would be expected if nests establish randomly (RYTI & CASE 1984). Despite this pattern for young colonies, the authors document little evidence for competition between mature colonies. Other authors (including ourselves) have noticed internidal hostility with mortality when foraging columns intersect (WENT & al. 1972, WHEELER & RISSING 1975b). If information about mortality risk accompanies positive signals of food presence or abundance, as in *Lasius pallitarsis* (NONACS 1990), then fights between colonies could contribute to the dynamics of foraging columns, as occurs in *Pogonomyrmex* (HÖLLDOBLER 1976b).

The influence of neighbors on *M. pergandei* colonies was evaluated by describing the foraging direction and distance taken by a colony with respect to its nearest neighbor ("Relative Territory Use"- RTU) (RYTI & CASE 1986). Using their RTU statistic, the authors found that colonies avoided foraging toward their nearest neighbor (NN). Experimental manipulation of food sources, where seeds were placed equidistant between neighbors (n = 4 paired colonies) versus away from neighbors (n = 3 paired colonies) resulted in colonies foraging on the equidistant baits approximately two days later than seeds placed away from NN.

That colonies of *M. pergandei* also compete intraspecifically was demonstrated by manipulating resources and neighboring competitors (RYTI & CASE 1988). Resources were manipulated by adding seeds to four non-neighboring *M. pergandei* colonies in amounts equivalent to a colony's average monthly calorific intake (GORDON 1978). Competitors were removed from four focal colonies. Responses measured included numbers of foragers returning per minute, RTU, and number of alates produced as a proportion of the population. Foraging activity did not differ between colonies treated by feeding or neighbor removal. RTU of control colonies was correlated with rainfall, from which RYTI & CASE (1988) concluded that under low resource availability colonies forage away from NN. Removal of neighbors and supplemental feeding increased the number of alates produced per worker (RYTI & CASE 1988).

Colonies of *M. pergandei* that received food supplements during the laying of reproductive brood produced more female alates than unfed colonies. Additionally, colonies produced the fewest alates when resources were decreased by removing workers when queens were laying eggs destined to be reproductives. This suggests that behaviors that increase resource acquisition or decrease worker loss have fitness consequences (ODE & RISSING 2002).

Messor pergandei workers are highly polymorphic (RISSING & POLLOCK 1984), but either show no significant size matching of individuals to forage items, or the correlation is significant but weak (GORDON 1978, RISSING 1987, RISSING & POLLOCK 1984, WASER 1998). The distribution of worker sizes changes seasonally (RISSING 1987), and is assumed to be constrained by interspecific competitors (DAVIDSON 1978, WASER 1998), but this assumption has been criticized by JOHNSON (2001). Sampling frequency at seed baits placed on foraging columns increased as foragers moved further along the column from the nest (RISSING & POLLOCK 1984). Distance from the nest did not affect the mass of harvested seeds, but the mean mass of harvested seeds was significantly higher than that of offered seeds (RISSING & POLLOCK 1984). The number of seeds handled by individual workers was compared across different inferred seed densities and as seed density increased, so did the number of seeds sampled before an item was harvested (JOHNSON 1991). Another test demonstrated that sampling seeds functioned to convey information about the seeds because seeds that were sampled and dropped weighed less than random seeds, while those that were harvested were heavier than random seeds (JOHNSON 1991).

Seed distribution has been proposed to determine whether a colony engages in group or individual foraging (BERNSTEIN 1975). To test this, BERNSTEIN compared seven colonies that were provided with two, four, eight, or 16 tablespoons of rye seeds spread evenly around a circumference 3 m from the nest entrance (treatment) with seven colonies that remained unfed (control). Column length of control colonies averaged 16.3 m whereas treatment colonies' columns were only 4.4 m long. As a treatment colony was followed through a foraging bout, individuals initially followed a column, but over three hours the column disappeared as individuals moved out in all directions towards the food bait.

Foragers gain experience in their foraging environment. Seed handling time decreases over time with exposure to novel food sources in *M. pergandei* and *P. rugosus* (JOHNSON 1991, JOHNSON & al. 1994). In *M. pergandei*, workers increased their efficiency by reducing the number of items handled before harvesting. Evidence for learning came from the difference in rate of acquisition and loss of efficiency after exposure to novel seeds. Foraging efficiency indices in *M. pergandei* fell to a pre-exposure baseline after 12 days (JOHNSON 1991). Alternatively, seed recognition allowed a colony-level "memory" to exceed forager longevity, leading to the suggestion that workers were exposed to olfactory odors of seeds stored in the nest (JOHNSON & al. 1994).

Recruitment and chemical ecology of foraging in *Messor*

The known function of gland extracts in *Messor* and related species of *Aphaenogaster* are summarized in Table 2. In *M. barbarus*, Dufour gland extracts elicited significantly greater recruitment than poison gland extracts along a 10 cm radius circular trail with 1.5 gland equivalents (HEREDIA & DETRAIN 2000). The chemical constituents of *M. barbarus* poison and Dufour glands have not been described. Recruitment in *M. barbarus* involves chemical signals and is augmented by stridulation (CERDAN 1989).

Messor bouvieri colonies can recruit to rich artificial food sources (CERDÁ & RETANA 1994). To test trail following behavior, individual ants were placed on circular tracks of 5 cm radius marked with hexane extracts of one poison or one Dufour gland. There was no difference in the median distance travelled between tracks with poison gland or Dufour gland extracts (JACKSON & al. 1989). Trail following was induced by laying artificial trails of 3-ethyl-2,5-dimethylpyrazine, which was subsequently identified from the poison gland (JACKSON & al. 1989). We think this work needs to be confirmed because it would be the only Old World *Messor* species that preferably follows poison gland contents (Tab. 2).

In *M. capitatus*, *M. minor*, *M. structor*, and *M. wasmanni*, recruitment involves Dufour gland secretions and stridulation (HAHN & MASCHWITZ 1980, 1985, SCHILLIGER & BARONI URBANI 1985, BARONI URBANI & al. 1988, GRASSO & al. 1998, 1999). An experiment that used nests that either damped or transmitted vibratory signals showed that stridulation in *M. capitatus* increased the speed of recruitment, but not the number of individuals recruited (BARONI URBANI & al. 1988) in a similar fashion to *A.*

Tab. 2: Function of poison and Dufour glands in *Messor* and related species of *Aphaenogaster*. Recruitment refers to the ability to elicit trail following, alarm refers to the ability to attract and cause excitement among nest mates. † data based on few samples.

Genus	**Species**	**Poison gland**	**Dufour gland**
New World			
Aphaenogaster	*albisetosus*	Recruitment (HÖLLDOBLER & al. 1978)	–
	cockerelli	Recruitment (HÖLLDOBLER & al. 1978)	–
Messor	*pergandei*	Recruitment (BLUM 1974)	–
Old World			
Aphaenogaster	*fulva*	Alarm (WHEELER & al. 1981)	–
Messor	*barbarus*	Alarm / defense (HEREDIA & DETRAIN 2000)	Recruitment (HEREDIA & DETRAIN 2000)
	bouvieri	Recruitment (JACKSON & al. 1989)†	Recruitment (JACKSON & al. 1989)
	capensis	Alarm (BRAND & MPURU 1993)	
	capitatus	Recruitment + alarm (GRASSO & al. 1998)	Recruitment (GRASSO & al. 1998, 2002)
	ebeninus	–	Recruitment (COLL & al. 1987)
	foreli	–	Recruitment (MASHALY 2011)
	meridonalis	–	Recruitment (MASHALY 2011)
	minor	Recruitment + alarm (GRASSO & al. 1999)	Recruitment (GRASSO & al. 1999, 2002)
	structor	Alarm (HAHN & MASCHWITZ 1985)	Recruitment (HAHN & MASCHWITZ 1985)
	wasmanni	Recruitment + alarm (GRASSO & al. 1999)	Recruitment (GRASSO & al. 1999, 2002)

cockerelli and *A. albistetosus* (MARKL & HÖLLDOBLER 1978). Extracts of Dufour glands from *M. capitatus* persist for approximately 30 minutes after reinforcement has ceased, and are not colony specific (GRASSO & al. 1998). Poison gland extracts have been shown to elicit excitation and alarm in *M. capitatus*, *M. structor*, *M. minor*, *M. wasmanni*, and possibly in *M. capensis* and *M. ebeninus* (HAHN & MASCHWITZ 1985, COLL & al. 1987, BRAND & MPURU 1993, GRASSO & al. 1998, GRASSO & al. 1999).

In summary, Old World species of *Messor* typically use Dufour gland secretions for recruitment trails (HAHN & MASCHWITZ 1985, COLL & al. 1987, BRAND & MPURU 1993, GRASSO & al. 1998, 1999, HEREDIA & DETRAIN 2000, GRASSO & al. 2002, MASHALY 2011), whereas Nearctic *Messor* use poison gland secretions (BLUM 1974, HÖLLDOBLER & al. 1978). Our experimental work supports this pattern, where trail following in *M. barbarus* and *M. lusitanicus* is released by the Dufour gland (B. Hölldobler, N.J.R. Plowes & R.A. Johnson, unpubl.), while the poison gland is the source of trail pheromone in *M. pergandei* (BLUM 1974; B. Hölldobler, N.J.R. Plowes & R.A. Johnson, unpubl.). Also, for *M. andrei* and *M. smithii* we identified the poison gland as source of the recruitment trail pheromone. The only Nearctic species for which gland chemistry has been analyzed is *M. lobognathus* (DO NASCIMENTO & al. 1993; Tab. 3), but behavioral assays did not test for glandular origin or active components.

Large pygidial glands with reservoirs occur in *M. pergandei* and *M. andrei*, with the secretions functioning to reduce worker thresholds to follow recruitment pheromones during the initiation of columns (HÖLLDOBLER & ENGEL 1979; B. Hölldobler, N.J.R. Plowes & R.A. Johnson, unpubl.). The probable sister species to the Nearctic *Messor*, *A. albisetosa*, also possesses a large pygidial gland (HÖLLDOBLER & ENGEL 1979); therefore, these well-developed pygidial glands probably represent a synapomorphy to this group of species. Group foragers in both of BENNETT's (2000) clades (*M. pergandei*, *M. andrei*) have pygidial glands with large reservoirs, which suggests that the other group foraging species, *M. julianus*, also has a large pygidial gland. In contrast, the two Palearctic column foragers that have been examined (*M. barbarus*, *M. lusitanicus*) do not appear to have pygidial glands (B. Hölldobler, N.J.R. Plowes & R.A. Johnson, unpubl.). Behavioral assays on *M. minor* and *M. wasmanni* show that extracts from the last three abdominal tergites elicit excitement and stereotypical aggressive behavior such as biting and gaster flexing (GRASSO & al. 1999). The structure and identity of putative tergal glands are unknown (D.A. Grasso, pers. comm.).

Key species for future research on gland chemistry and function are Nearctic *Messor* (including *M. pergandei*, *M. andrei*, and *M. julianus*). Sympatric species of *Messor* s.str. (e.g., *M. capitatus*, *M. minor*, *M. wasmanni*) respond to interspecifically derived Dufour gland extracts (GRASSO & al. 2002), but demonstrate variability in preference (*M. capitatus* is the most selective). The components of Dufour glands in *M. minor* and *M. wasmanni* show considerable overlap, with several likely candidates for a common trail pheromone (e.g., n-tridecane; Tab. 3), but the biological activity of the constituents has not been studied (DI TULLIO & al. 2003). Further studies on the exocrine chemistry of these three species will prove interesting, as *M. minor* and *M. wasmanni* are group foragers, whereas *M. capitatus* has multiple foraging strategies (ACOSTA SALMERON & al. 1985, GRASSO & al. 1998, ARNAN & al. 2010, SOLIDA & al. 2010).

Tab. 3: Major chemical constituents of poison and Dufour glands in *Messor* and closely related species of *Aphaenogaster*. ‡ based on whole body extracts.

Genus	**Species**	**Poison gland**	**Dufour gland**
New World			
Aphaenogaster	*albisetosus*	R and S 4-methyl-3-heptanone, 3-ethyl-2, 5-dimethyl-pyrazine (Hölldobler & al. 1978)	–
	cockerelli	1-phenylethanol, 4-methyl-3-heptanone (Hölldobler & al. 1978)	–
	rudis	N-isopentylphenylethylamine, anabasine, anabaseine, 2,3'-bipyridyl (Attygalle & al. 1998)	–
Messor	*lobognathus*	tridecane, pentadecane, 3-methyltridecane, 5-methyltridencane, dodecane (do Nascimento & al. 1993)	tridecane, 6 and 7-pentadecene (Do Nascimento & al. 1993)
Old World			
Aphaenogaster	*fulva*	anabaseine (Wheeler & al. 1981)	–
	miamiana	(2'R)-anabasine (Leclercq & al. 2001)	–
	subterranea	anabasine, anabaseine (Leclercq & al. 2001)	–
Messor	*angularis*	anabasine, pentadecane (Co & al. 2003)‡	–
	arenarius	pentadecane, anabasine, 2,3' bipyridyl, anabaseine; glandular components varied among individuals (Cruz-Lopez & al. 2006)	pentadecane, tridecane, nonadecane (Co & al. 2003)
	barbarus	no anabasine or anabaseine (Leclercq & al. 2001, Co & al. 2003)	1-pentadecene; 1-nonadecene, nonadecene, tridecane, pentadecane, 1-heptadecene, heptadecane (Co & al. 2003)
	bouvieri	3-ethyl-2, 5-dimethlypyrazine, anabasine, anabaseine, 2,3'-bipyridyl (Jackson & al. 1989, Co & al. 2003)	6,9-heptadecadiene, undecane (Jackson & al. 1991), tridecane, 1-pentadecane, pentadecane, heptadecane (Co & al. 2003)
	capensis	anabasine (Brand & Mpuru 1993)	n-pentadecane (Brand & Mpuru 1993)
	capitatus	–	n-pentadecane, n-tridecane, n-heptadecane (Di Tullio & al. 2003)
	ebeninus	anabasine (Coll & al. 1987, Co & al. 1993, Cruz-Lopez 2006)	1-pentadecene, 1-heptadecene, tridecane, pentadecane (Co & al. 2003)
	galla	(E)-4-phenyl-3-buten-2-one (Olagbemiro & al. 1988)	–
	lusitanicus	heptadecane, 1-heptadecane, pentadecane, 1-pentadecene tridecane, 1-nonadecene, nonadecane (Co & al. 2003)	pentadecane, 1-pentadecene, nonadecene 1-heptadecene, heptadecane, tridecane (Co & al. 2003)
	marocanus	anabasine, tridecane, 1-pentadecane (Co & al. 2003)	–
	mediorubra	anabasine (95%) (Cruz-Lopez & al. 2006)	–
	minor	–	n-nonadecane, nonadecane, n-tridecane, heneicosene (Di Tullio & al. 2003)
	rugosus	heptadecane (Co & al. 2003), anabasine, N'-methylanabasine, anabaseine (Cruz-Lopez & al. 2006)	heptadecane (Co & al. 2003)
	sanctus	(2'S)-anabasine (Leclercq & al. 2001)	–
	semirufus	anabasine (Cruz-Lopez & al. 2006)	–
	structor	no anabasine or anabaseine (Leclercq & al. 2001)	–

Synthesis

A rich variety of foraging behaviors occurs in the genus *Messor*, including several species with sophisticated group foraging strategies. It is likely that group foraging evolved multiple times within this group, which allows comparing behavioral mechanisms and ecology both within the genus and with other seed harvesting ants (e.g., *Pogonomyrmex*).

Do foraging columns or trunk trails in *Messor* behave similarly to *Pogonomyrmex*, where trails of intraspecific neighbors rarely cross and appear to thus partition the foraging areas? Evidence suggests that this might be the case for several species of both Palearctic *Messor* (ACOSTA SALMERÓN & al. 1985, WEHNER 1992, WARBURG & STEINBERGER 1997, SOLIDA & al. 2010) and Nearctic *Messor* (RYTI & CASE 1984, 1986, 1988, BROWN & GORDON 2000), but further work is needed to understand the interplay between resources and competition. There are non-mutually exclusive hypotheses for the utility of trunk trails that include avoidance of competitors (HÖLLDOBLER 1976b, HÖLLDOBLER & LUMSDEN 1980), minimizing energetic costs (FEWELL 1988), and increasing harvesting success (WEIER & FEENER 1995). If competitors contribute to the formation of trunk trails, then we would expect to see partitioning of foraging areas, where trails would intercalate but not overlap, as is found in *Pogonomyrmex* (HÖLLDOBLER 1976b). If competition plays a lesser role, a higher degree of foraging overlap would be found, and the trail network system would be expected to be optimized to minimize either distance or time, or to maximize size of the foraging area. An individual based foraging model in *P. occidentalis* found that cooperative foraging resulted in higher harvest rates when resources were distributed heterogeneously, but no difference in harvest rates between cooperative foraging and individual foraging simulations when resources were distributed homogeneously (CRIST & HAEFNER 1994).

Environmental variability, primarily through changes in density and distribution of food resources, has strong effects on group foraging behavior (RISSING & WHEELER 1976, JOHNSON 1991, LÓPEZ & al. 1993a, 1993b, 1994, WILBY & SHACHAK 2000). Individual ants following the same behavioral repertoire can generate different group-level behaviors through the interaction with the environment (FRANKS & al. 1991). Species-specific foraging behavior emerges when a species adapts to environmental conditions. Two group foraging *Messor* species, *M. barbarus* and *M. pergandei*, show behavioral flexibility to environments which have patchy or unpredictable resources. During times of food scarcity, *M. barbarus* trails become longer with fewer branches (LÓPEZ & al. 1993a, 1993b, 1994). This extends the range of each colony, and is a strategy that promotes discovery of new resources. This behavior parallels the two-fold expansion in distance travelled by *Pogonomyrmex rugosus* foragers during a drought season (RISSING 1988). *Messor pergandei* colonies maintained constant foraging distances over the same environmental conditions (RISSING 1988). In both *P. rugosus* and *M. pergandei*, colonies respond to changes in resource availability by changing the direction of foraging (RISSING & WHEELER 1976, HÖLLDOBLER 1976b). In *M. pergandei*, columns are more sedentary when food resources are plentiful, and move more frequently when food resources are low (BERNSTEIN 1975, RISSING & WHEELER 1976, RYTI & CASE 1986, 1988, JOHNSON 1989).

Several *Messor* species show behavioral flexibility, and can switch between individual foraging and recruitment to bonanza food resources, including *Messor aciculatus*, *M. capitatus* and *M. structor* from the Old World, and *M. chamberlini* from the New World (ONOYAMA & ABE 1982, HAHN & MASCHWITZ 1985, CERDÁ & RETANA 1994, JOHNSON 2000a). Individual foraging is an adaptation to low levels of homogeneously distributed resources. However, colonies benefit from being able to concentrate their foraging on the rare occasion that a dense resource becomes available. This behavioral pattern is similar to individual foraging *Pogonomyrmex*, such as *P. maricopa*, which lay recruitment trails to new seed patches (HÖLLDOBLER 1976b). We expect that like *Pogonomyrmex*, individual foraging *Messor* species use the same major compounds as those employed by group foraging species (HÖLLDOBLER & al. 2001).

Little is known about the determinants of caste in *Messor*, except that in *M. pergandei* fluctuations in resources directly affect the production of large workers (RISSING 1987). In mature colonies, smaller workers are produced when resources are reduced, suggesting that worker number is more important than worker size. There is no association between foraging strategy and polymorphism across the genus *Messor*. Most Nearctic species are monomorphic (*M. lobognathus, M. smithi, M. chamberlini*), including two column foraging species (*M. andrei* and *M. julianus*) (BENNETT 2000, JOHNSON 2001). BENNETT (2000) proposed that polymorphism had evolved twice in the Nearctic *Messor*, once in *M. pergandei* and once in the group containing *M. chicoensis* and *M. stoddardi*, which are both individual foragers (JOHNSON 2001).

Further work should document foraging behavior, chemical ecology, and sociometry (TSCHINKEL 2011) of additional group foragers (including *M. julianus* and *M. andrei*). For example, evidence for recruitment in *M. andrei* would include data showing that the forager population increases at baits over time. In addition, if baits were placed away from foraging columns / fans, this would indicate that some proportion of the worker force act as scouts and move independently of the fan. We need to know what circumstances lead to switches in foraging styles within species, and what differences in resource structure (diversity, density, distribution, rate of replenishment) and colony size are found between species that primarily use individual foraging versus those that forage in groups.

Studies of group foraging in *Messor* have potential to develop spatial models of collective behavior (GOSS & DENEUBOURG 1989). With additional behavioral data, these models can be used to explore self-organized systems and to generate hypotheses for group behaviors that occur under different individual behavioral rules and / or ecological conditions.

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