

Research article

Life history traits of a European *Messor* harvester ant

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Abstract. We present life history traits of a Central European harvester ant, *Messor* cf. *structor*, determined by gyne and male dissections, behavioural assays, standardised brood photography and laboratory rearing of brood. *Messor* cf. *structor* is polygynous and builds up unicolonial populations. Sexuals develop from hibernated larvae in a univoltine cycle and become adult from late summer to late autumn. Neither intra- nor extranidal mating was observed in autumn, even though gynes and males were mature. In spring, after hibernation, intranidal mating without swarming flight took place, even though the flight muscles of alate sexuals were still fully developed.

Keywords: *Messor*, queen number, colony delimitation, development of sexuals, mating and dispersal strategy.

Introduction

The application of life history analysis to social insects in general and ants in particular is still in its infancy (Bourke and Franks, 1995: p. 325). The life histories of only a small number of model species have been investigated in detail (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). In the last ten years, efforts were focussed on gathering data on the social structure of ants by molecular methods. Life history data are indispensable to establish a general life history theory for social insects (Tschinkel, 1991; Bourke and Franks, 1995). They also serve as a backbone for several other studies, for example for molecular population studies

(Ross, 2001), including related fields such as conservation genetics (Hedrick, 2001).

Harvester ants are species that regularly store collected seeds in underground granaries (Hölldobler and Wilson, 1990), thus shaping the physical, chemical and hydrological properties of the soil (Cammeraat et al., 2002). Being major seed consumers in xeric habitats (Azcarate and Peco, 2003), these keystone species influence the vegetation by depleting and dispersing seeds (e.g., Pacini, 1990; MacMahon et al., 2000) to an extent disproportionate to their numbers or biomass (Hölldobler and Wilson, 1990). Despite their ecological impact, little is known about the life history of Central European *Messor* ants. Their societies are reported to be facultatively polygynous (Buschinger, 1974) and to contain usually less than 1000 workers (Baroni Urbani, 1987), although the demarcation of single nests is sometimes difficult due to the dispersed nest entrances. Pronounced aggression was reported between colonies of the same population (Heller, 1971). Alate gynes and males have been observed within nests from early spring to late autumn, with nuptial flight in spring and possibly a second nuptial flight in autumn (Mayr, 1855; Andrasfalvy, 1961; Heller, 1971; Seifert, 1996).

Here we present bionomical information on Central European harvester ants, particularly on their colony organisation and reproductive strategy: queen number per colony, colony delimitation, development of sexuals, and mode of mating and dispersal. Life history traits were revealed by a combination of non-molecular methods including gyne and male dissections, behavioural assays, a new method of standardised brood photography and laboratory rearing of brood. All Central European populations of the harvester ant genus *Messor* are currently considered to constitute a single species (Seifert, 1996), *Messor structor* (Latreille, 1798). Preliminary mtDNA data, however, suggest the existence of more than one *Messor* species in Central Europe (B.C.

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Schlick-Steiner et al., unpubl.). We therefore term the studied population *Messor* cf. *structor*.

We questioned literature data, which suggested polygyny, multicoloniality and one to two nuptial flights (spring and potentially autumn). With respect to voltinism of sexuals, we tested two competing hypotheses: (a) Sexuals develop exclusively from hibernated larvae (slow brood, Hölldobler and Wilson, 1990) and become adult over a prolonged period, from mid-summer to autumn. (b) Sexuals develop from hibernated slow brood and become adult in summer; an additional brood develops from eggs laid in spring (fast brood, Hölldobler and Wilson, 1990) and becomes adult in autumn. This life history trait would entail two more or less separate periods in which sexuals appear.

Materials and methods

The study was performed on a Central European harvester ant, *Messor* cf. *structor*. We have verified monospecificity of our material based on mtDNA and microsatellite data (Arthofer et al., in press). Field work was carried out in an agricultural area of 90 km² near Retz (15°57'E/48°45'N, Austria) which contained 51 habitat islands of c. 500–200,000 m² with at least one nest of *Messor* cf. *structor*. Habitats comprised near-natural dry grassland with interspersed bare rocks and dry-stone walls. A total of 245 nests were studied on 67 field days between 4 April and 2 November 2004. Nests were recovered by marking nest entrances with plastic nails and using GPS.

Queen number per colony and ovary status

Frequently, more than one dealate gyne per colony were found in spring. From nine such colonies we collected 13 dealate gynes, leaving at least one unharmed in each colony. One to four per colony were dissected. Using a high-resolution stereomicroscope (Nikon SMZ1500; 50–360×), we determined fertility, insemination, egg-laying status and the approximate age by inspecting the ovarioles, the oocytes, the corpora lutea, the spermathecae and the gastral fatty tissue, following Buschinger (1968) and Alloway et al. (1982).

Colony delimitation

Behavioural assays were performed to determine the delimitation of colonies. In preliminary tests we paired (1) single workers, and (2) groups of 50 workers from nest entrances which we supposed to belong to different nests (distance 5 m) in glass tubes for 5 h. Since no aggression was observed, in subsequent tests we used workers from nest entrances at least 30 m apart. For the final assays workers of six *Messor* colonies (two from each of three habitats which were 2–11 km apart) were transferred to plastic boxes, kept at 21 °C, fed and watered. Behavioural assays were performed the following day.

Aggression tests were modified from Holway et al. (1998) and Roulston et al. (2003). For each replicate, 2 randomly selected workers from the same or different colonies were placed in a 2-cm-diameter glass cylinder for 5 minutes. The wall was flouon-coated to restrict ant activity to the bottom of the vial. Workers of *Messor* species have an atrophied sting and smear opponents with stinking faeces (Maschwitz, 1975). To assess the range of reactions, we initially observed confrontations between *Messor* cf. *structor* and *Formica pratensis* Retzius, 1783, *Lasius alienus* (Förster, 1850), *L. flavus* (Fabricius, 1782) and *Myrmica speciosus* Bondroit, 1918 from the study area. *Messor* cf. *structor* workers' behaviour was scored as 0 = ignore, 1 = touch, 2 = avoid, 3 = aggression (opened mandibles, but no attack), 4 = anal secretion, and 5 = fight (bit-

ing). Subsequently, every possible pairing of the six *Messor* colonies, including intracolony confrontations, was performed in 5 replicates, resulting in a total of 105 tests.

Tolerance tests (Astruc et al., 2001) were conducted to assess whether colonies were closed or open (sensu Le Masne, 1952). Workers from different colonies were marked with paint markers (Edding 751). Glass vials containing 20 nestmate workers were placed in an arena at the same distance from a food source, and then were opened. 24 h later the numbers and identities of dead and living, injured and intact, and fighting workers were recorded, as were their positions in the different vials and in the arena. We collocated the two colonies of a given habitat (3 tests) and three colonies of three different habitats (2 tests).

Development of sexuals

We developed a field method of standardised brood photography (adapted from Buschinger, 1973) to assess brood development. Representative samples of brood were taken from the nest and arranged on a 5 × 5 cm piece of mm-scaled cardboard, photographed (Fig. 1) and returned to the nests. 48 such documentations were made, on 15 dates between 25 May and 7 October, at intervals of 4–14 d. In cool and rainy as well as in hot and dry periods, no brood was found near the surface. In hot periods we searched between 5 a.m. and 9 p.m. in order to test whether the positioning of the brood varied with time of day, but we never found brood near the surface.

To determine the reproductive maturity of males we dissected testes and vasa deferentia of 151 males between 4 September and 2 November. The state of the testes (from sperm-producing to atrophied) and the amount of sperm in the vas deferens (from empty to filled) were determined. Atrophied testes and filled vasa deferentia indicate sexual maturity (Glancey, 1976; Ball and Vinson, 1984; Hölldobler and Wilson, 1990).

On 5 May we transferred 20 workers plus 56 larvae to the laboratory. This colony fragment was kept at a daily temperature regime of 23 °C for 12 h and 18 °C for 12 h and was fed with diluted honey, insects and seeds. We recorded the development of larvae and of prepupae to pupae and adults.

Mating and dispersal strategy

The presence of alate sexuals within nests was documented during the whole field season, from 4 April to 2 November 2004. To observe possible extranidal mating and nuptial flight or the increased activity of workers and sexuals preceding such events, we inspected the nest areas and nests every day from 4 April to 5 May and at least every other day from 26 August to 2 November. Since only few alates come near the surface below 15 °C, we no longer visited the colonies on cool days, but we carefully screened the surface on every field day and searched, from 4 September to 2 November, beneath 100 stones in three to six habitats for wandering or hiding sexuals. This search strategy should also detect signs for mating during very early or late hours of the day.

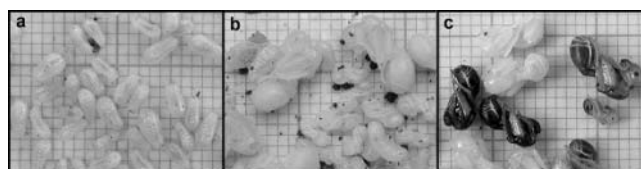


Fig. 1. Examples of standardised brood photography of *Messor* cf. *structor* (1.5 × 2.0 cm of the originally 5.0 × 5.0 cm shown); (a) 25 May 2004: hibernated larvae; workers and sexuals not distinguishable, (b) 12 July 2004: larvae and early-stage worker and gyne pupae, (c) 7 October 2004: various stages of worker, gyne and male pupae.

For indications of intranidal mating, we dissected alate gynes whenever they were detected within the nests ($n = 202$ from 81 nests; 4 April to 2 November).

To assess the flying capability of sexuals, the thoraces of adult gynes and males were dissected and the condition of the flight muscles evaluated using a Nikon SMZ1500 stereomicroscope (360 \times) and a Zeiss transmitted-light microscope (1000 \times). We examined 5 nest queens (queen status verified by dissection of ovaries), 12 alate gynes and 20 males, sampled between 8 April and 20 May and between 4 September and 2 November.

Results

Queen number per colony and ovary status

The dissection of dealate gynes from the interior of nests revealed that all were old nest queens. Up to eight dealate gynes were observed within single colonies; the queen status of up to four gynes was confirmed by dissection. Queens dissected in April still had not resumed egg-laying activity; the largest oocytes were still transparent. Only after 3 May ovaries contained fully developed, white eggs.

Colony delimitation

All aggression tests yielded 0 = ignore or 1 = contact. The results of intracolony pairings (arithmetic mean \pm 1 SD: 0.47 ± 0.51 , $n = 30$) were nearly identical to those of intercolony pairings from one habitat (0.47 ± 0.52 , $n = 15$) and different habitats (0.50 ± 0.50 , $n = 60$).

In the tolerance tests, no case of aggressive behaviour was observed. After 24 h all workers were alive, intact and peaceful. Workers of different colonies – in within-habitat as well as in between-habitat combinations – were always found mixed (Table 1), frequently aggregated in one spot.

Development of sexuals

The standardised brood photography revealed parallel developments of gynes and males and of brood in the different habitats. On 25 May, larvae measured 4–5 mm (Fig. 1a). First sexual prepupae were detected on 22 June, first sexual pupae (eyes already dark) on 12 July (Fig. 1b). First adult gynes and males were found on 13 August. On 7 October, still very young pupae of gynes and males were detected, along with dark pupae that were ready to hatch (Fig. 1c). After this date no brood was observed due to a temperature decline and increasing precipitation.

The colony fragment transferred to the laboratory yielded numerous workers, and a total of four males developed from hibernated larvae. The pupal stage lasted 40–60 d, and the first male became adult on 20 October. Workers laid eggs in summer, but no young larvae were observed, as workers obviously ate the eggs.

Based on dissection, the first sexually mature male (testes atrophied, vasa deferentia filled with sperm) was detected on 16 September in a field nest. Subsequently, the proportion of mature males steadily increased up to early November, although even at that time some males were immature (testes still intact and producing sperm).

Mating and dispersal strategy

Numerous alate sexuals appeared within the nests in early spring. Until 20 April no inseminated gyne was found; their ovaries were small and immature. In the afternoons of 20–24 April, males and alate gynes emerged from the nests in various habitats, climbed low vegetation close to the nest entrances, but neither copulated nor flew. No inseminated gynes were detected among these individuals. After 24 April, dissection of alate gynes from inside the nests revealed insemination in

Table 1. Tolerance tests following Astruc et al. (2002) between 20 workers each from two *Messor* cf. *structor* colonies (1, 2) from three habitats each (A, B, C): Localization of workers after 24 h. All workers were alive, intact and peaceful.

within habitat									
pairing localization	A1 vs. A2			B1 vs. B2			C1 vs. C2		
	vial of A1	vial of A2	arena	vial of B1	vial of B2	arena	vial of C1	vial of C2	arena
number of workers	4 (A1)	0 (A1)	16 (A1)	19 (B1)	0 (B1)	1 (B1)	9 (C1)	8 (C1)	3 (C1)
(colony identity)	0 (A2)	0 (A2)	20 (A2)	20 (B2)	0 (B2)	0 (B2)	1 (C2)	17 (C2)	2 (C2)
between habitats									
pairing localization	A1 vs. B1 vs. C1				A2 vs. B2 vs. C2				
	vial of A1	vial of B1	vial of C1	arena	vial of A2	vial of B2	vial of C2	arena	
number of workers	0 (A1)	0 (A1)	0 (A1)	20 (A1)	0 (A2)	0 (A2)	19 (A2)	1 (A2)	
(colony identity)	0 (B1)	0 (B1)	0 (B1)	20 (B1)	0 (B2)	0 (B2)	17 (B2)	3 (B2)	
	0 (C1)	0 (C1)	0 (C1)	20 (C1)	0 (C2)	0 (C2)	19 (C2)	1 (C2)	

all cases. From 6 May on, inseminated gynes had single, big, opaque eggs filled with yolk, but most of their oocytes were still small and transparent, and the number of alate gynes and males within the nests decreased. No males were found after 30 April, no alate gynes after 25 May.

From the first detection of newly developed alates on 13 August until the end of the field season (2 November), dissection of alate gynes never revealed insemination. Ovaries always were small and immature. We never found flying sexuals or hiding or founding queens. Also, no dead males were found, neither within nor outside nests.

Flight muscles were intact in all males and alate gynes in spring and autumn. Nest queens, on the other hand, had atrophied flight muscles with interspersed tracheoles and fatty tissue.

Discussion

In agreement with previous findings (Buschinger, 1974), the dissection of nest queens suggests that the investigated *Messor* ants live in polygynous colonies. The questions whether polygyny is facultative or obligate and whether the degree of polygyny varies between habitats requires further investigation. The colonies represent open societies *sensu* Le Masne (1952). Lack of agonistic behaviour in aggression- and tolerance tests indicates that the inhabitants of all nests are members of a unicolonial population. The level of intraspecific, intercolonial aggression is known to be positively correlated with the degree of intracolony relatedness (Crozier and Pamilo, 1996; Pirk et al., 2001). In unicolonial ant species, clear colony boundaries are absent, inhabitants of the single nests intermingle (Bourke and Franks, 1995) and the degree of relatedness within nests is low. In such species, lack or very low degree of intraspecific aggression was repeatedly detected (e.g., Giraud et al., 2002; Suarez et al., 2002; Steiner et al., 2003, 2004; Chapuisat et al., 2005). To our knowledge, unicoloniality has never been verified for *Messor* ants. Though Heller (1971) reported on pronounced fighting between neighbouring nests of *Messor structor* from Germany (vicinity of Mainz), this behaviour was not observed in the studied *M. cf. structor*.

The observed egg-laying by *M. cf. structor* workers agrees with the results of Goetsch and Eisner (1930) for *M. structor* from South Europe, also concerning the obvious consumption of all eggs by the workers.

Sexual brood of the investigated *Messor cf. structor* develops slowly (Fig. 2). With standardised brood photography we determined that the minimum duration of the pupal stage of sexuals was 30 d. In the laboratory colony fragment, kept at a lower mean temperature than in the field, the pupal stage of males lasted 40–60 d, thus corroborating the slow development. Given that nest queens started egg-laying as late as May and that first sexual adults appeared as early as early August, fast brood, i.e. the development of sexuals from this year's eggs, seems improbable. Rather, sexuals develop from hibernated larvae, i.e. slow brood (Fig. 2). Our 2004 results agree with hypothesis (a) on the annual cycle of sexuals: one

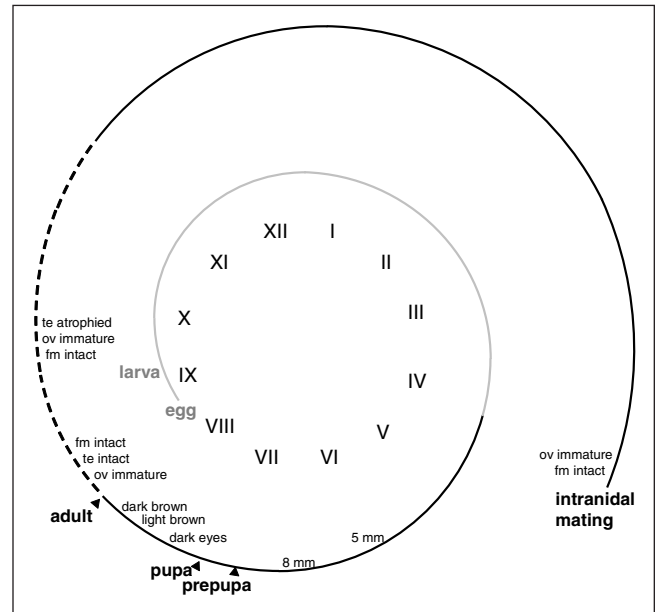


Fig. 2. Annual cycle of *Messor cf. structor* sexuals in 2004: I–XII = months, black line = substantiated, grey line = supposed, broken line = co-occurrence of pupal and adult sexuals within the nests, triangles = first occurrence of a life stage, coinciding in gynes and males; fm = flight muscles, ov = ovaries, te = testes.

sexual brood per year, developing from hibernated larvae. The long period in summer and autumn in which adult and pupal sexuals co-occur inside the nest also corroborates this hypothesis. No support was found for hypothesis (b), a bi-phasic production of sexuals due to both a slow and a fast brood. With respect to mating and dispersal strategy, neither nuptial flight nor extranidal mating was detected. The lack of nuptial flight in spring remains unexplained: the flight muscles were intact, in contrast to the atrophied flight muscles of nest queens which we found. In autumn, the lack of mating despite the presence of mature males and gynes may be due to the asynchronous development of sexuals. It remains open whether extranidal mating takes place in the studied populations in other years. A possible permanent lack of extranidal mating might either be a lineage-specific character of the studied *Messor* species, or a response of a Central European population to the regional climate.

Development of sexuals from slow brood is likewise known for other ants, such as *Myrmica ruginodis* Nylander, 1846 (reviewed by Hölldobler and Wilson, 1990) and numerous *Leptothorax* and *Temnothorax* species (Buschinger, 1973). The annual cycle of sexuals in the studied *Messor* population is similar to that of *Camponotus herculeanus* (Linnaeus, 1758) (summarized by Hölldobler and Wilson, 1990), with the difference that *C. herculeanus* sexuals undertake a nuptial flight in spring. Our detected lack of nuptial flight or extranidal mating in 2004 is in contrast to reports on nuptial flights of Central European *Messor structor* (Mayr, 1855; Andrasfalvy, 1961; Heller, 1971; Seifert, 1996). Literature data, however, should be discussed with

caution, since conspecificity with our species cannot be verified. Moreover, previous authors partly contented themselves with indications of nuptial flight, such as the emergence of alates or the mere presence of alates within nests (G. Heller, pers. comm.). Like in our *M. cf. structor* population, in *Tetramorium moravicum* Kratochvil, 1941 asynchronous development of sexuals was found and was suspected to constitute a precondition for intranidal mating (Schlick-Steiner et al., 2005). Atrophied flight muscles of nest queens like found by us in *M. cf. structor* had repeatedly been observed by, e.g., Janet (1906), Baroni Urbani (1968), Petersen-Braun and Buschinger (1975). Similar to our observations, the appearance of alate sexuals on the soil surface close to the nest entrances for several consecutive days in spring without nuptial flight was reported for *M. structor* (Finzi, 1929), although from South Europe.

The combination of non-molecular methods yielded new bionomical details of a Central European *Messor* population. The discovered life history traits provide testable hypotheses for our future molecular analyses of the social structure and the gene flow properties of that population.

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