

The life history of Epimyrma algeriana, a
slave-making ant with facultative polygyny (Hymenoptera, Sonderdruck aus:
Formicidae)

Zoologische Beiträge

Herausgegeben von

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Neue Folge. Band 33. Erstes Heft



DUNCKER & HUMBLLOT / BERLIN 1990

The Life History of *Epimyrma algeriana*, a Slave-Making Ant with Facultative Polygyny (Hymenoptera, Formicidae)

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Received November 16, 1989

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Summary

Epimyrma algeriana, a parasitic ant species widely distributed in northern Algeria and Morocco, is an active slavemaker which is able to form colonies with numerous *Epimyrma* workers. The host species are several *Leptothorax*: *L. spinosus* (the most frequent), *L. tebessae gentilis*, *L. monjauei*, and *L. curtulus*. In most populations studied the colonies are polygynous. Monogynous and functionally monogynous colonies occur as well. The young sexuals mate inside the mother nests. Young queens may remain there, or leave the nests for founding their own colonies, in fall, winter, or in spring, thus over an unusually protracted period and at comparatively low temperatures. Agonistic behavior between the parasite queens in polygynous colonies has been observed. It may be responsible for the decision of young queens either to leave or to remain in the mother nest.

The invasion of host colonies by *Epimyrma algeriana* queens is achieved in the usual way, in that the *Epimyrma* queen throttles the host colony queen to death, stings a few host workers, and is adopted by the remaining ones. Such monogynous colonies established with queens from the population of the Forêt d'Akfadou (Algeria, Kabylie), produced a rapid brood of a few *Epimyrma* workers in the first year, and more workers and numerous sexuals from hibernated brood in the second and the following years. Polygynous or functionally monogynous colonies which regularly retain some new queens are potentially immortal. In favorable and stable forest environment they may be able to exploit very effectively, due to high worker numbers, the large neighboring host species colonies. *E. algeriana* apparently represents a distinct life history and host population exploitation strategy as compared to the two others yet recognized in the genus: (I) Mating flights with immediate dispersal of queens on the wing, host colony infestation through single queens, and slave raiding (*E. ravouxi*, *E. stumperi*), and (II) reduction of *Epimyrma* worker number and slave raids, intranidal mating, hibernation of queens in the mother nests, and local dispersal of all young queens on foot for infestation of neighboring host nests (*E. krausseii*, *E. corsica*, *E. adlerzi*).

Résumé

Histoire naturelle d'*Epimyrma algeriana*, fourmi esclavagiste à polygynie facultative (Hymenoptera, Formicidae)

Epimyrma algeriana, fourmi parasite largement répandu dans le Nord de l'Algérie et au Maroc, est une esclavagiste active qui peut former de grosses colonies où les ouvrières d'*Epimyrma* sont nombreuses. Les espèces-hôtes sont divers *Leptothorax*: *L. spinosus* (le plus fréquent), *L. tebessae gentilis*, *L. monjauxi* et *L. curtulus*. Dans la plupart des populations étudiées, les sociétés sont polygynes mais l'on rencontre aussi des sociétés monogynes ou fonctionnellement monogynes. Les jeunes sexués s'accouplent dans le nid-mère. Les jeunes reines peuvent soit rester dans leur colonie d'origine, soit la quitter pour fonder leur propre société, à l'automne, pendant l'hiver ou au printemps suivant. La période des fondations est donc relativement étendue et se déroule sous des températures basses par comparaison à d'autres espèces d'*Epimyrma*. Des comportements agressifs ont été observés entre les reines parasites dans les sociétés polygynes; ils pourraient être à l'origine du départ ou du maintien dans le nid-mère des jeunes femelles d'*Epimyrma*.

Chez *E. algeriana* l'intrusion dans les colonies-hôtes se déroule selon le processus habituel, c'est-à-dire que la reine d'*Epimyrma* étrangle la reine de *Leptothorax* jusqu'à ce que mort s'en suive, tue avec son aiguillon quelques ouvrières hôtes et se fait adopter par les survivantes.

Des élevages réalisés en colonies monogynes, avec du matériel provenant de la population de la forêt d'Akfadou (Algérie, Kabylie) montrent qu'après la fondation, au cours de la première année, un couvain rapide produit quelques ouvrières d'*Epimyrma*; de nombreux sexués ailés et d'autres ouvrières apparaissent depuis le couvain hivernant, la seconde année et les suivantes.

Les colonies polygynes ou les colonies fonctionnellement monogynes d'*Epimyrma algeriana* sont potentiellement immortelles car elles peuvent remplacer leurs reines à partir des nouvelles formées. Lorsque l'environnement forestier est stable et favorable, elles peuvent contenir un nombre important d'ouvrières et sont alors capables d'exploiter très efficacement par des raids esclavagistes, les grosses colonies voisines des espèces-hôtes. *E. algeriana* présente apparemment un cycle biologique et une stratégie d'exploitation des populations-hôtes, distincts des deux types déjà connus dans le genre:

1. Vol nuptial et dispersion immédiate des reines au vol, infestation de la colonie-hôte par une seule femelle, raids esclavagistes actifs (type réalisé chez *E. ravouxi* et *E. stumperi*).
2. Réduction du nombre d'ouvrières, raids esclavagistes rares ou nuls, accouplements et hivernage dans le nid-mère puis dispersion locale de toutes les jeunes reines par la voie terrestre pour attaquer les colonies-hôtes voisines (type: *E. kraussei*, *E. corsica*, *E. adlerzi*).

1. Introduction

In the leptothoracine ant genus *Epimyrma* an evolutionary transition from active slavery to a degenerate dulosis and, finally, workerlessness has been documented (BUSCHINGER & WINTER 1982, BUSCHINGER 1989, DOUWES et

al. 1988). Some species, *E. ravouxi*, *E. bernardi* and *E. stumperi* are slavemakers, having a considerable number of *Epimyrma* workers in their nests. In *E. krausseii* the worker number is more or less reduced, depending upon the population, and slave raids occur rarely, if ever. Finally, *E. corsica* and *E. adlerzi* are completely workerless. All species, however, share a particular colony foundation behaviour in that the young *Epimyrma* queen, after having penetrated a host nest, throttles the host colony queen(s) slowly to death.

A second, parallel evolutionary trend in this genus refers to sexual behavior in that the active slave-makers *E. ravouxi* and *E. stumperi* make ordinary mating flights, whereas in *E. bernardi*, *E. krausseii*, *E. corsica* and *E. adlerzi* the sexuals mate inside their mother nests, and thus engage in a continuous inbreeding. The colonies of these species are always monogynous.

E. algeriana Cagniant 1968 appeared to represent an extraordinary species. It was assumed to infest already orphaned host colonies, to produce a number of sexuals there in the first, and only very few workers in the second year, and then to decline. The sexuals were observed to mate in the mother nests (CAGNIANT 1968 a).

Recent studies, however, of material collected in Algeria and in Morocco revealed that *E. algeriana* is an actively dulotic species producing high numbers of workers, and that the queens kill the host colony queens in the usual way. Nevertheless, *E. algeriana* exhibits an unusual trait: In most populations a considerable degree of polygyny was found. This is as yet unique in the genus.

2. Material and Methods

During two collecting trips to Algeria (1.4. - 17.4.1986) and Morocco (4.5. - 24.5.1987) a total of 51 colonies of *Epimyrma algeriana* were collected. Tables I and II reveal the collecting sites and data, in the map (Fig. 1) the new sites and the already known localities (CAGNIANT 1968 b, 1969) are presented. Nests were found in rock crevices, beneath small rocks, or within the moss layer covering larger rocks. The colonies were aspirated as completely as possible. Most *Epimyrma* colonies and a number of host species colonies were brought alive to Germany, and kept for up to three years in formicaries, as described by BUSCHINGER (1974). Honey diluted 1:1 with water, and insect pices (*Tenebrio* pupae, cockroaches) were supplied three times a week. Artificial daily and annual temperature cycles were applied in analogy to those which had proved effective in rearing other leptothoracine species from various Mediterranean to alpine areas in Europe (cf. BUSCHINGER et al. 1988). Most important is a long hibernation of at least 5 months at temperatures of about 10°C, as is usually appropriate for leptothoracines of the subgenus *Myrafant* and their parasites. The annual cycle in the laboratory, thus, roughly corresponds to that in nature. It can be shortened down to about 10 months.

For studying slave raiding behavior we used subdivided arenas according to WINTER (1979a) or BUSCHINGER et al. (1980). An *Epimyrma* nest and a nest with a slave species colony are placed each in one of the two separate parts of the arena, and after at least 3 days, when the two colonies have explored their territories, a hole in the separating wall is opened. It is important to wait until *Epimyrma* workers ("scouts") spontaneously begin to search around in their arena compartment. Slave raids were observed in natural sunshine or under a strong artificial light source (200 W) above the arena, and at temperatures of 22 - 28°C.

Colony foundation was studied under a variety of conditions. Since dealate *Epimyrma* ♀♀ left their mother nests during hibernation (constant 10°C, 8/10°C and 7/8°C), in 10/20°C spring temperature rhythm and also in higher temperatures (15/25°C, always 12/12 h) we set up experiments in different temperature conditions, and at different times in the annual cycle, in late fall, during the winter, and in spring.

Apart from the "normal" type of colony foundation where one *Epimyrma* queen, or several simultaneously, are placed into a formicary with a complete, queenright host species colony, we also established new colonies with one *Epimyrma* queen each and a few slaves from their mother nests. Host worker pupae from foreign nests were then added to build up a sufficient workforce ("passive" colony foundation). In order to reduce losses of *Epimyrma* ♀♀ due to the defense of the host colonies, we often split a host colony, put the *Epimyrma*-♀ to a small part of it (queen and 3 - 5 ♂♂), and after the *Epimyrma* had begun to throttle the host queen the remaining host workers and brood were successively added. This procedure appears justified because natural nests in moss or in the soil beneath pebbles are much more structured than our artificial nests. The *Epimyrma* queen, thus, has more opportunities to retreat or to hide somewhere when attacked by the host workers, and she is not immediately confronted with all the colony.

Dissectioning of *Epimyrma* ♀♀ and ♂♂ was done as described by BUSCHINGER & ALLOWAY (1978a). *E. algeriana* in this respect is more difficult than most other lepto-thoracines, because the ovaries even in egg-laying queens are relatively small, and the corpora lutea are not as brightly yellow as usual. Newly mated ♀♀ begin ovarian maturation while still remaining in the mother nests. During hibernation, when no yolk is deposited in growing oocytes, it is sometimes difficult to distinguish between old queens (having quite inconspicuous c. lutea in the bases of their ovarioles) and young ones with already somewhat enlarged ovaries. In "summer" conditions, when large numbers of eggs are present in the nests, some ♀♀ have growing and mature oocytes (with white yolk deposition), and others have not. The latter either are somehow inhibited, as the non egg-laying supernumerary ♀♀ in functionally monogynous ant species (BUSCHINGER 1968), or they represent young ♀♀ who are still in the process of developing fertility. A few specimens had, in the summer, ovaries without growing oocytes, but with small corpora lutea present. Presumably they were old queens which had stopped egg production.

3. Results

3.1. Field data: Collecting sites, size and composition of colonies and populations

As revealed by tables I and II, and the map (Fig. 1), *E. algeriana* is fairly widespread in the Atlas and Rif mountains of N'Algeria and Morocco. The

species is locally common, e.g. in the Forêt d'Akfadou (Algeria), around Azrou and in the Rif (Morocco) where we easily could have collected much more colonies. We observed, however, that *E. algeriana* is strictly bound to comparatively old, little disturbed forest stands, both of deciduous (oaks) and coniferous (cedar) trees.

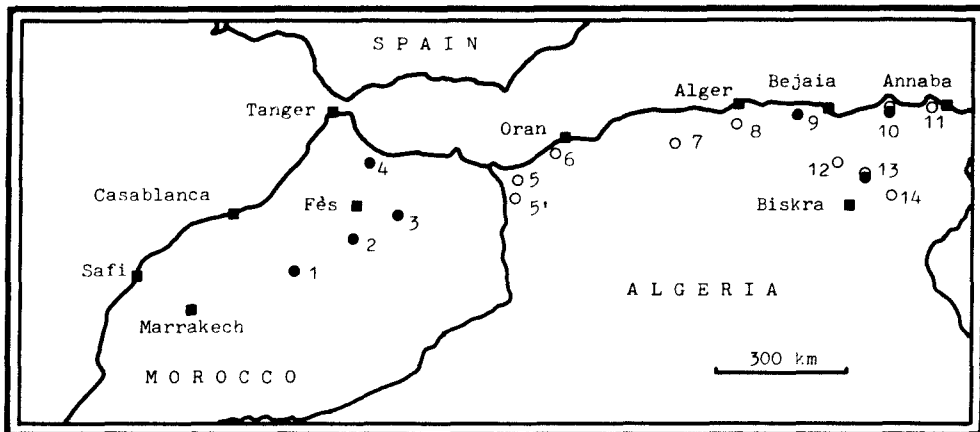


Fig. 1. The known range of *Epimyrma algeriana*. Darkened circles: Sites in Morocco and Algeria from which the ant material for this study was taken; open circles: other Algerian sites from CAGNIANT (1968b, 1969). 1: Tizi-n-Ifar (NE Beni Mellal); 2: Cèdre Gouraud, Djebel Hébri, Tizi-n-Tretten (Region of Azrou); 3: Region of Bou Iblane; 4: Bab Besen (Rif); 5: Forêt d'Hafir and Kerrouch (Region of Tlemcen); 6: Forêt de M'Sila (Oran); 7: Teniet el Haad (Ouarsenis); 8: Chréa (Atlas de Blida); 9: Forêts de Yakouren and Akfadou (Kabylie); 10: Melab, Zitouna and Cap Bougaroun (Collo); 11: Massif de l'Edough (Region of Annaba); 12: Djebel Bou Taleb (Region of Sétif); 13: Djebel Belezma, Dj. Titougelt (Region of Batna); 14: Dj. Chélia, Dj. Pharaon (Aurès de Khenchela).

The host species in most of the populations checked is *Leptothorax spinosus* (Forel), a monogynous typical species of the subgenus *Myrafant*. In two localities close to the Mediterranean coast of Algeria (Collo, Zitouna, near Cap Bougaroun), however, we found different host species, at Collo *Leptothorax tebessae gentilis* (Santschi) (cf. CAGNIANT 1968b), and at Zitouna *L. monjauszei* Cagniant, which is a new host for *E. algeriana*. Since these samples comprise but two and one colonies, respectively, we will refer to them only incidentally. The *Epimyrma* female from Zitouna in addition is morphologically somewhat different from the usual *E. algeriana*, and it may represent a different species or subspecies. Both localities near Collo, as some others along the coast indicated by CAGNIANT (1968b), where *E. algeriana* had been found with *L. tebessae*, are situated in much lower elevations (400 - 700 m, our sample of Collo nearly at sea level) than all the other populations of Tab. I and II which were found in 1200 - 2100 m.

At Tizi-n'Tiskrine (near Dj. Bou Iblane, 1450 m, in a stand of Green Oak), X. ESPADALER (pers. comm.) has collected an *E. algeriana* female with workers of *Leptothorax curtulus* Santschi.

A number of *E. algeriana* colonies were censused either immediately after collecting, or soon after the return to Darmstadt. The various populations from Algeria and Morocco are quite similar with respect to the numbers of slaves and slave-maker ♀♀ (see Tab. I and II). In the population Dj. Belezma a mean number of *L. spinosus* ♀♀ of 128.2 (range 40 - 369, n = 9) was found, in the Forêt d'Akfadou these figures are 128.4 (range 16 - 485, n = 15), in the Moroccan saples 116 (range 32 - 276, n = 15 col. censused). These numbers are similar to the worker numbers in colonies of other dulotic *Epimyrma* species, e.g. *E. ravouxi* (mean 137.9 slaves, range 4 - 514, n = 56 col.; BUSCHINGER & WINTER 1983).

The numbers of *Epimyrma* workers also are comparatively high in *E. algeriana*, the mean and maximum values even exceeding those found in *E. ravouxi*. In the population Dj. Belezma we found a mean of 25.9 *E. a.* ♀♀ (range 6 - 64, n = 7 col., two incipient colonies omitted) in the Forêt d'Akfadou: mean 69.7 (range 6 - 222, n = 15), in Morocco: mean 45.5 (range 1 - 110, n = 15 col. censused). In *E. ravouxi* these figures are: mean 24.9 (range 1 - 77, n = 52, incipient colonies omitted) (BUSCHINGER & WINTER 1983).

Most striking for an *Epimyrma* species, however, is the fact that multiple-female nests of *E. algeriana* were found in all Algerian and Moroccan populations except that of Dj. Belezma (and also the 3 colonies of near Collo were monogynous). The numbers of dealate *Epimyrma* females in the Forêt d'Akfadou were: mean 14.2 (range 1 - 49, n = 15), in Morocco (all populations together): mean 10.6 (range 1 - 35, n = 15 censused).

In all the other *Epimyrma* species with intranidal mating the young ♀♀ shed their wings and remain in the mother nests over all or part of the winter. For the population of the Forêt d'Akfadou which was collected in the first half of April we first assumed that the multiple females there also represented a queen and her offspring in each colony, and that in the Dj. Belezma the young queens had already left the mother colonies, perhaps due to warmer climate. In Morocco, however, multiple-female nests were collected during May, evidently too late for such an interpretation to be right. Thus, dealate ♀♀ were dissected in order to determine their reproductive condition (see below).

A final aspect to be treated here is the number of incipient colonies found in the field samples. For the slave-making *E. ravouxi* a proportion of about 9% incipient colonies was determined, corresponding to an estimated lifetime of about 10 years for an established colony (BUSCHINGER & WINTER 1983). Such incipient colonies contain one *Epimyrma* queen, no *Epimyrma*-

♀♀ and a variable number of host species ♀♀. In the second year the colonies have a few (usually 3 - 5) *Epimyrmica*-♀♀.

In the *E. algeriana* population of Dj. Belezma two incipient colonies among 9 collected were found (Tab. I). This roughly corresponds to the proportion found in *E. ravouxi*, taking into account that the sample was small. In the Forêt d'Akfadou among 15 colonies none without *Epimyrmica* ♀♀, and only one with a single *Epimyrmica* queen (but with already 22 ♀♀) were found. In the 24 colonies from Morocco there were two with a single *Epimyrmica* queen each, and lacking *Epimyrmica*-♀♀, one with an *Epimyrmica* queen and one ♀, and one with 2 *Epimyrmica*-♀♀ and without *Epimyrmica*-♀♀. We conclude that in the populations with multiple-female nests of *E. algeriana* colony foundation by single young queens in the usual way may be rare.

3.2. Results of dissections: Facultative polygyny in *E. algeriana*

In the nest-mating *Epimyrmica adlerzi*, *corsica*, and *kraussei*, the inseminated, dealate young queens remain in the mother nests over winter, and leave in March or April in search of host nests for colony founding. Young queens still found in the old nests in March, or those just engaged in throttling their host colony queens, have comparatively short ovarioles containing transparent oocytes without visible yolk deposition, and they lack the corpora lutea.

For *E. algeriana* it was therefore of interest whether the numerous queens found in the colonies were young, still staying in the monogynous mother nests, or whether they were reproductive queens of polygynous colonies. The collecting dates suggested the latter to be true, and dissections of numerous such females in fact revealed that most *E. algeriana* populations exhibit a true polygyny.

Queens from Moroccan colonies were dissected soon after collecting, on 28 May 1987, and then in intervals on 21 June, 1st and 19 July, and after one laboratory brood production and hibernation, in March and April 1988. In some colonies, e.g. 13106, 13115, 13117, 13122, 13131, 13156, females were dissected successively, in order to see whether the remaining ones, after the removal of a first group, would perhaps replace them and also become reproductive. The results (Tab. III) clearly reveal that in most nests polygyny is realized.

However, by far not all dealate and inseminated ♀♀ were egg-layers. Some colonies contained only one reproductive queen and a number of not (yet?) laying ♀♀ and thus were "functionally monogynous". In other colonies young ♀♀ apparently were just about to develop fertility (b → A), and

Table I: Sites and data of *Epimyrmica algeriana* colonies collected in Algeria, 1986

Dates	Localities	col. no. ¹	Ep. ♀♀	Ep. ♂♂	host ♂♂	remarks
7. 4. 86	Dj. Belezma (Cedar forest)	12 523	1	—	79	host <i>L. spinosus</i> , incipient col.
		12 524	1	10	124	host <i>L. spinosus</i>
		12 525	—	12	40	host <i>L. spinosus</i>
		12 526	1	6	47	host <i>L. spinosus</i>
		12 532	1	—	55	host <i>L. spinosus</i> , incipient
8. 4. 86		12 542	1	45	100	host <i>L. spinosus</i>
		12 543	—	13	77	host <i>L. spinosus</i>
		12 544	—	64	396	host <i>L. spinosus</i>
		12 549	1	31	236	host <i>L. spinosus</i>
sub-total	Dj. Belezma	9 col.	6	181	1154	
mean				25.9 ²	128.2	
12. 4. 86	Forêt d'Akfadou (Deciduous oak forest)	12 605	28	154	232	host <i>L. spinosus</i>
		12 606	8	6	74	host <i>L. spinosus</i>
		12 607	17	27	91	host <i>L. spinosus</i>
		12 608	10	75	57	host <i>L. spinosus</i>
		12 609	11	33	88	host <i>L. spinosus</i>
		12 610	12	45	48	host <i>L. spinosus</i>
		12 611	17	116	84	host <i>L. spinosus</i>
		12 612	8	116	75	host <i>L. spinosus</i>
		12 616	14	23	164	host <i>L. spinosus</i>
		12 621	7	9	16	host <i>L. spinosus</i>
		12 622	19	222	485	host <i>L. spinosus</i>
		12 623	1	22	57	host <i>L. spinosus</i>
		12 624	49	80	71	host <i>L. spinosus</i>
		12 625	8	39	140	host <i>L. spinosus</i>
		12 626	18	78	244	host <i>L. spinosus</i>
sub-total	Forêt	15 col.	227	1048	1926	
Mean	d'Akfadou		14.2	69.7	128.4	
10. 4. 86	Collo (Cork oak forest)	12 558	1	—	4	host <i>L. tebessae</i> <i>gentilis</i> , incipient colonies
		12 567	1	—	56	
	Zitouna	12 574	1	5	23	host <i>L. monjauei</i>
Total		27 col.	236	1234	3163	
Mean			—	53.6 ²	117.1	

¹ In order to facilitate a future identification we use the numbers of the colonies in the collection and card file of A.B.² Means of *Epimyrmica* worker numbers are calculated from colonies having workers, incipient colonies are excluded.

Table II: Sites and data of *Epimyrma algeriana* colonies collected in Morocco, 1987. The host species was always *Leptothorax spinosus*, except for the colony from Tizi-n'Tiskrine (coll. X. ESPADALER) which had *L. curtulus* as host species

Dates	Localities	col. no. ³	Ep. ♀♀	Ep. ♂♂	host ♂♂	remarks
13. 5. 87	Tizi-n-Ifar	13 105*	7	45	194	
		13 106*	31	31	107	
14. 5. 87	Azrou: Dj. Hebri	13 115*	13	71	66	incipient col.
		13 116*	1	—	49	
		13 117*	17	87	205	
		13 118*	7	45	42	
14. 5. 87	Azrou: 5 km E	13 119*	2	4	59	
		13 120*	5	68	32	
		13 121*	35	87	188	
		13 122*	12	110	276	
		13 123*	9	8	53	
15. 5. 87	Azrou: Cèdre Gouraud	13 125	2	+	+	not censused
		13 126	ca. 40	+	+	not censused
16. 5. 87	Azrou: Dj. Hebri	13 131	6	+	+	not censused
		13 132*	5	27	ca. 150	not censused
		13 133	2	—	+	not censused, incipient?
17. 5. 87	Azrou: Tizi-n-Tretten	13 138	2	+	+	not censused
18. 5. 87	Dj. Bou Iblane	coll. H. C. *	1	1	ca. 80	not censused, incipient?
	Tizi-n-'Tiskrine	coll. X. E.	1	—	+	
20. 5. 87	Bab Besen (Rif)	13 154*	12	75	ca. 200	not censused large colony
		13 155	3	+	+	
		13 156	4	+	+	
		13 157	ca. 40	+	+	
		13 158*	2	24	40	
Total of 15 col. censused*		24 col.	159	683	ca. 1740	
Mean			10.6	45.5	ca. 116	

³ Numbers of colonies in the collection and card-file of A.B.

a few queens ("old A") had evidently stopped egg production, perhaps because of old age (or "dominance" of other, more fertile queens?). It is remarkable that in these field colonies non-inseminated females were very rare (col. 13117). On the contrary, among the young ♀♀ leaving from the mother nests (Tab. V) many were not inseminated.

From the colonies collected in Algeria only a very small sample of ♀♀ was immediately dissected. Ten ♀♀ from a multiple-female nest (col. 12605) from the Forêt d'Akfadou all proved inseminated. Two were apparently "A", having corpora lutea, in six others the c. lutea were only faintly visible, and two ♀♀ appeared just newly inseminated and very young ("b").

During the following weeks in higher temperatures (15/25°C, later 17/28°C) only a few ♀♀ (one or two per colony) left the nests, most remained inside and became physogastric.

Dissections of females from multiple-female laboratory-reared colonies confirmed that true polygyny is characteristic also for the Algerian population of the Forêt d'Akfadou. Young ♀♀, after having mated in the mother nest in summer or fall may become reproductive alongside the mother queens, in the following spring, or when the mother queen has died meanwhile; and when several ♀♀ together have invaded a host colony they also may simultaneously develop fertility (Tab. IV).

It is obvious, however, that both in the field samples from Morocco and in the laboratory colonies originating from Algerian stock not all inseminated ♀♀ are equal. Usually several in a nest are fully reproductive, others apparently are somehow inhibited. We conclude that in most populations of *E. algeriana* which we investigated, true polygyny exists, but in colonies with many ♀♀ remaining not all of them develop fertility, and sometimes even only one is reproductive (functional monogyny) (e.g. col. 13121, 13156 in Tab. III).

3.3. Ethological observations: Agonistic behavior of queens in multiple-female nests

Direct observations of females in the nests strongly corroborated the assumption of differing reproductive roles. The colonies were checked once a week for brood production and general development. During these checks which usually last for a few minutes for each colony, we regularly recorded that multiple females were sitting in close vicinity inside the colony. Nevertheless, in the newly collected colonies both from Algeria and Morocco, we saw a lot of agonistic behavior in the first weeks. In 8 out of 17 multiple-female nests from Morocco (collected 13.5. - 20.5.87) between 28 May and 18 June, 1987, in laboratory culture such "fights" were recorded, sometimes of two or three pairs of ♀♀ simultaneously.

Table III: Results of dissectioning of *Epimyrma algeriana* females from multiple-female field colonies (Morocco). The queens of the first 4 colonies were dissected soon after collecting. Others were dissected later in the same year, or after a sexual production and hibernation, in the following year

Col. no.	Population	dissect. date	n ♀♀ present	n ♀♀ dissected	reproductive status of ♀♀ ⁴	status of colony
13 118	Azrou	28. 5. 87	7	7	7b → A	incomplete? A lacking
13 119	Azrou	28. 5. 87	2	2	2A	polygynous
13 120	Azrou	28. 5. 87	5	4	2A, 2a	polygynous
13 158	Bab Besen	28. 5. 87	2	2	1A, 1b → A	monogynous, becoming polygynous
13 105	T.-n-Ifar	21. 6. 87	7	4	4A	polygynous
13 125	Azrou	1. 7. 87	2	2	2A	polygynous
13 132	Azrou	19. 7. 87	5	5	2A, 3b → A	polygynous
13 154	Bab Besen	1. 7. 87	11	9	6A, 1a → A, 2 old A	polygynous
13 156	Bab Besen	1. 7. 87	4	4	1A, 1a → A, 2a	functionally monogynous developing polygyny?
13 106	T.-n-Ifar	19. 4. 88	5	5	5A	polygynous
13 115	Azrou	2. 3. 88 19. 4. 88	15 2	13 2	9A, 4b → A 2A	polygynous
13 117	Azrou	2. 3. 88 19. 4. 88	14 4	10 4	2A, 6b, 2c 4A	polygynous
13 121	Azrou	28. 4. 88	2	2	1A, 1a	functionally monogynous
13 122	Azrou	2. 3. 88 19. 4. 88	16 3	11 3	5A, 6b 2A, 1 old A (?)	polygynous, 2 ♀♀ died
13 126	Azrou	28. 4. 88	4	4	4A	polygynous
13 131	Azrou	2. 3. 88 19. 4. 88	31 6	25 6	3A, 22b 1A, 5a	polygynous, later: functionally monogynous
13 155	Bab Besen	28. 4. 88	3	3	3A	polygynous

⁴ A = inseminated fully reproductive queen with corpora lutea (in *E. algeriana* often only faintly visible!)
old A = inseminated, c. lutea present, ovarioles elongate as in A, but no yolk deposition in the oocytes.
a = inseminated, ovaries not fully developed, no growing oocytes and no c. lutea
b = newly inseminated, young, no developing oocytes
c = not inseminated, ovaries undeveloped
C = not inseminated, long ovaries with developing oocytes; reproductive
(A detailed description is found in ALLOWAY et al. 1982)

Table IV: Results of dissectioning of *Epimyrma algeriana* females from multiple-female laboratory colonies (population Forêt d'Akfadou, Algeria)

Col. no	n ♀♀ in the nest	n ♀♀ insemi- nated	n ♀♀ with (nearly) mature eggs	reproductive status of ♀♀ ⁹	status of colony
12 605 ⁵	8	8	8	1A, 7b → A	becoming polygynous
Je 27a ⁶	4	4	3	3A, b	polygynous
Je 27b ⁶	3	3	3	3A	polygynous
Je 27f ⁶	4	4	3	3A, b → A	polygynous
Je 27h ⁷	3	3	2	2A, b	polygynous
Je 27i ⁷	2	2	2	2A	polygynous
Je 27k ⁷	3	3	3	3A	polygynous
Je 77a ⁸	3	1	2	A, c → C, C	see ⁹
Je 77b ⁸	3	2	2	2A, c → C	polygynous
Je 77c ⁸	3	2	3	2A, C	polygynous

⁵ Field colony. In the spring, 1986, all ♀♀ except one (a presumptively functional queen) were removed, and then all the ♀ offspring of 1986. From the offspring 1987 some young ♀♀ remained in the nest. All 8 ♀♀ still present were dissected in May, 1988, when numerous eggs appeared in the nest. A is presumably the old queen of 1986.

⁶ Laboratory-founded colonies with one queen each, in the spring, 1986. The multiple females comprise this queen and her daughters of 1987, dissected in the summer, 1988, after spring egg-production had ceased.

⁷ Laboratory-founded colonies, in the spring, 1986, with one queen each. These queens have died, the dissected ♀♀ are their 1987 offspring, dissected in the spring, 1988, during high egg-production.

⁸ Pleometrotic laboratory colonies, founded in the winter, 1987/1988. The ♀♀ were dissected in the spring, 1988, when egg-laying had begun.

⁹ cf. ⁴. In leptothoracine ants not inseminated but nevertheless fertile females (C-♀♀) occur in a few species (ALLOWAY et al. 1982).

In one colony (no. 13 121, with 35 ♀♀) fights were recorded on 31.5., 10.6., and 18.6., twice two pairs and once three pairs of ♀♀. The "fighting" behavior was a rapid antennation and mutual biting attempts. However, casualties were never observed. In colony no. 13 132, with 5 dealate ♀♀, two pairs of fighting females were observed on 1.6.87. When all the ♀♀ were dissected on 19.7.87, two fertile queens (A) and three inseminated ♀♀ in process of developing fertility (b → A) were found. Similar observations, including also throttling attempts between *Epimyrma*-♀♀, were made in colonies from Algeria (pop. Forêt d'Akfadou).

Such agonistic behavior might be responsible for the different reproductive conditions of multiple females, and might be involved in the decision of whether or not a female will stay in the nest.

3.4. Colony foundation in *Epimyrma algeriana*

As CAGNIANT (1968a) had already observed, the young sexuals of *E. algeriana* mate inside their natal nests. This is indicated by the presence of many inseminated young ♀♀ in our field-collected colonies, and in origi-

nally monogynous colonies founded in the laboratory, after a first brood of sexual offspring had been reared. Occasionally we directly observed mating in the laboratory nests. As in other nest-mating *Epimyrma* species (DOUWES et al. 1988, WINTER & BUSCHINGER 1983) light appears to stimulate courtship behavior of males, e.g., when the transparent red plastic lid covering the laboratory nests is removed. Mating attempts of the males begin soon after the sexuals have hatched. Sexual behavior continues for about 2 weeks, and ♀♀ not having mated during this time apparently are not inseminated later. Like mated ♀♀, however, they usually shed their wings after a while.

According to our observations mainly of *E. algeriana* from the Forêt d'Ak-fadou, the ♀♀ having mated in June, all remain in the nests until September. During these 3 months they usually form a cluster, whereas the old queens move around in the nest. The clusters then slowly break up. In laboratory culture the nests are placed in a temperature rhythm of 10/20°C (12/12 h) during September, which simulates fall conditions. After 4 weeks in these conditions the first ♀♀ were seen to leave the nests. An increase in temperature, e.g. when the colonies were checked in the warm laboratory, often stimulated some more ♀♀ to leave. They crawl around in the formicaries, usually return into the nests later, but when given the opportunity they walk away over several meters. If this happens in the field they presumably will not find back to their natal nests.

Females leaving the nests were observed also later, during the artificial hibernation at a constant 10°C, or in rhythms of 8/10°C and 7/8°C (and successful colony foundation was recorded in these temperature conditions, too). Finally, a number of ♀♀ having spent all the winter in the mother nests, left them not before the colonies were brought into spring conditions of 10/20°C, and others remained without ever leaving the nests.

Only the population of Dj. Belezma exhibited a somewhat different behavior in that all young ♀♀ left the mother nests during late fall and winter at temperatures of 10/20°C or 8/10°C. This is consistent with the observation that no young queens occurred in the field colonies collected in April, 1986.

Thus, in *E. algeriana* the period of colony foundation may be much more extended, through fall, winter, and early spring, than in the other *Epimyrma* species we have studied.

A number of ♀♀ were taken out of the nests after the mating period, or were dissected when they spontaneously had left the nests, in order to determine the condition of their reproductive system (Tab. V). Apparently the development of the first oocytes begins soon after mating, and in queenless colonies (Tab. V, line 2) some ♀♀ may quickly become fertile. In queenright colonies, on the contrary, ovarian development stops and the condition of

the ovaries does not change between fall and spring. Thus, ovarian development probably is not responsible for the spontaneous outset of ♀♀ for colony foundation. In a couple of instances the ovaries of ♀♀ leaving the nest in winter or spring even gave the impression of some secondary reduction of previously already more advanced egg formation. This parallels our observations in the field-collected, naturally hibernated ♀♀ from the Forêt d'Akfadou.

Table V: Ovarian development in young *Epimyrma algeriana* females staying in the mother nests, or leaving them for colony foundation during fall, winter, and early spring (all from population Forêt d'Akfadou)

Origin of the ♀♀	n ♀♀ dissected inseminated/ not insem.	Ovaries of inseminated ♀♀ with			Ovaries of not inseminated ♀♀ with		
		empty ovarioles	develop. eggs	mature eggs	empty ovarioles	develop. eggs	mature eggs
removed from queenright mother nest after mating period	7/ 4	0	7	0	3	1	0
removed from orphaned natal nest, 4 weeks after mating period	9/ 2	0	7	2	0	0	2
dealate ♀♀ which left the nests at 10/20°C, in fall	48/21	15	33	0	15	6	0
same time, alate ♀♀	0/25	—	—	—	22	3	0
dealate ♀♀ which left the nests at 8/10°C, in winter	13/11	1	12	0	4	6	1
same, at 7/8°C, in late winter	17/ 7	11	6	0	2	5	0
same, at 10/20°C, in early spring	34/ 4	3	31	0	3	1	0

The colony foundation behavior of *E. algeriana* was studied with ♀♀ who deliberately had left their mother colonies in fall, winter, or spring. They were placed either singly, or in groups of up to 3 simultaneously, into formicaries containing queenright host species nests. Tab. VI provides a survey of the experiments.

A number of experiments failed in that the *Epimyrmica*-♀♀ were attacked and killed by the host colony workers. Where possible these ♀♀ were dissected, and quite often they were not inseminated. Thus, in the experiments with ♀♀ from Dj. Belezma (Tab. VI, lines 4 and 5), among a total of 15 ♀♀ which all failed, 7 were not inseminated, the remaining 8 were too much

Table VI: Survey of colony foundation experiments with *Epimyrmica algeriana* from Algerian populations ("active" colony foundation, ♀♀ placed to queenright host colonies)

Type of experiment, origin of <i>E.</i> -♀♀ and host colonies	<i>n</i> exp.	<i>n</i> exp. failed ¹⁰	<i>n</i> experiments where we observed ¹¹		
			throttling of host ♀	paralyzation of host ♀	paralyzation of host ♂♂
1-Single <i>E.</i> -♀, host <i>L. spinosus</i> , both Forêt d'Akfadou	18	8	10	10	10
2-Several <i>E.</i> -♀♀, host <i>L. spinosus</i> , both Forêt d'Akfadou	8	2	3	6	6
3-Single <i>E.</i> -♀, both Forêt d'Akfadou, host <i>L. monjauezi</i> from Collo	3	0	1	3	3
4-Single <i>E.</i> -♀, Dj. Belezma, host <i>L. spinosus</i> , Forêt d'Akfadou	1	1	—	—	1
5-Several <i>E.</i> -♀♀, host <i>L. spinosus</i> , both Dj. Belezma	5	5	1	1	2
6-Single <i>E.</i> -♀, host <i>L. monjauezi</i> , both Zitouna	2	0	2	2	1

¹⁰ In these experiments the *Epimyrmica* females were killed by host colony workers.

¹¹ The colonies were not continuously surveyed. Thus, throttling in some instances may have been overlooked. Paralyzation of ♀♀ and ♂♂ lasts for days, so certainly all of them have been recorded.

decomposed for evaluating their status. However, other ♀♀ of this population who had left their nests have been inseminated.

In all experiments which eventually succeeded, the host species queen was killed by an *Epimyrma* ♀ through throttling, as is known for all other species yet studied (Fig. 2).

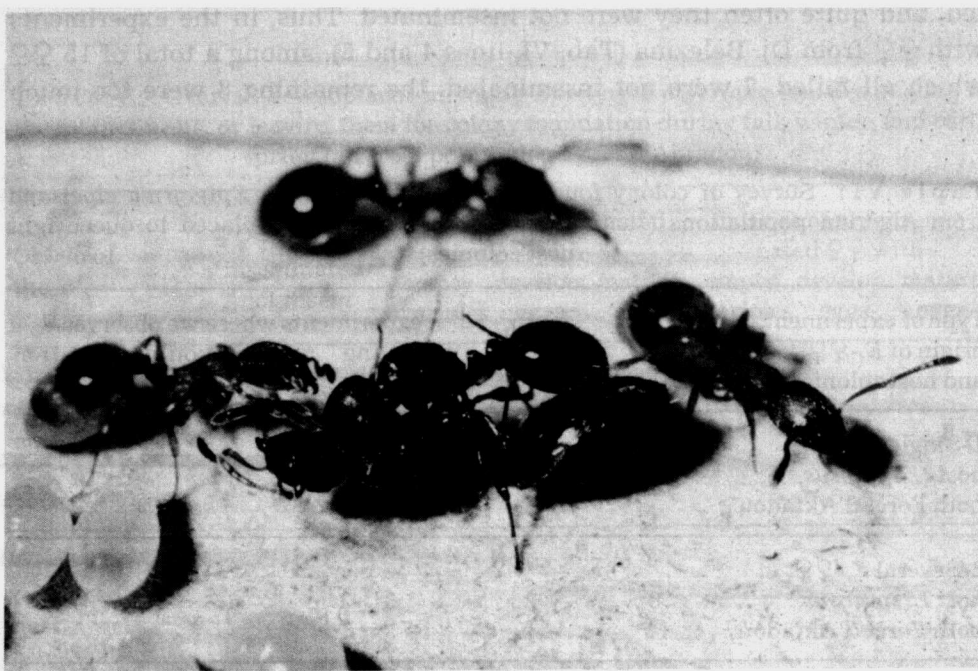


Fig. 2. *Epimyrma algeriana* queen throttling the much larger queen of a *Leptothorax spinosus* nest (Photo W. EHRHARDT).

This throttling behavior was seen in *Epimyrma*-♀♀ from populations Dj. Belezma, Forêt d'Akfadou, and Zitouna (Tab. VI). *Epimyrma*-♀♀ from the Forêt d'Akfadou which had *L. spinosus* as host species also attacked and killed the queens of *L. monjauezi* colonies from Collo (Tab. VI, line 3).

Typically, the *Epimyrma*-♀ when placed into a formicary with a host colony soon, sometimes within a few hours, but also up to 3 - 4 days later, tries to penetrate the nest. If not attacked too much, by several host workers who try to sting or dismember her, the *Epimyrma*-♀ begins to palpate and then to throttle the host queen. As in other *Epimyrma* species, the *E. algeriana* ♀ during the phases of biting into the host queens' neck or throat also brushes her with the forelegs, and then wipes over her own body, presumably transferring cuticular secretions and colony odor onto herself. She also often rigorously licks the surface of the host queen.

The host colony queens were paralyzed usually during the first day of repeated throttling, and they were dead after about 10 to 24 days, in one instance after 7 weeks. In multiply infested host colonies usually only one *Epimyrma*-♀ was throttling at a time, and presumably this was not always the same specimen. Two *Epimyrma*-♀♀ throttling simultaneously a host queen were recorded in one experiment. In the multiply infested colonies we also rarely observed an *Epimyrma*-♀ attacking and briefly throttling one of the other *Epimyrma*-♀♀, but without causing her death. Instead, in several experiments two or three *Epimyrma*-♀♀ became fully fertile after the host queen was eliminated.

As in other *Epimyrma* species a number of host workers are stung by the *E. algeriana* ♀♀. They then are lying in the nest or the formicary, are paralyzed, and finally die. This is somewhat different from what we observed, e.g., in *E. kraussei*. There a much higher number of host ♂♂, often nearly all in a nest, are stung, but most of them eventually recover. Stinging of host species workers, however, was also seen in older *E. algeriana* colonies where several *Epimyrma*-♀♀ and ♂♂ were already present. It was most conspicuous in such colonies where agonistic behavior between *Epimyrma*-♀♀ was recorded (see above). Apparently, young queens who stay in the mother colony nevertheless exhibit part of their usual colony foundation behavior, redirecting their aggression against defending host colony workers towards the slaves already present.

It is somewhat surprising that all this colony foundation behavior in *E. algeriana* could be studied in the low temperatures of 7/8°C, 8/10°C, but also in 10/20°C and 15/25°C.

In a few instances we placed *E. algeriana* queens into queenless host colonies. These experiments, as the "passive" colony foundations, were usually successful in that female offspring was produced. CAGNIANT (1968a) had already reported such experiments with *E. algeriana* from Chr  a (Atlas de Blida) in host colonies with workers and larvae only, and also at the low temperature of 12°C.

3.5. Brood production in field and laboratory-founded colonies of *Epimyrma algeriana*

A number of *E. algeriana* colonies collected in the spring, 1986 (Dj. Belezma and For  t d'Akfadou, Algeria) and 1987 (Morocco), were kept in the laboratory, and their production of sexual and, partially, also worker progeny was recorded over up to three years. When collected in the spring the colonies contained hibernated larvae. Thus, from the Algerian populations the production of the summers of 1986, 1987, and 1988 was obtained, from the Moroccan material only that of 1987 and 1988. Tab. VIIa, b, c reveals the

results, separately for each population because they were treated in somewhat different ways.

Most colonies with functional queens produced a reasonable number of *Epimyrma* workers, including the colonies from Morocco, where this production was not censused. The sexual production in all populations was markedly queen-biased, as is usual in *Epimyrma* species with intranidal mating. We counted a total of 405 ♂♂ and 1846 ♀♀ produced in field (Tab. VIIa, b, c) and laboratory-founded (Tab. VIII) colonies, the numerical sex ratio thus being 0.22 ♂/♀. If the ♂♂ and ♀♀ are subtracted which arose from colonies producing but one gender these figures are 286 ♂♂/1824 ♀♀, sex ratio 0.16 ♂/♀. Since mating takes place inside the nests, and males will rarely, if ever, get into a foreign nest for mating, the latter sex ratio appears more realistic.

The production of the colonies from Dj. Belezma (Tab. VIIa) in the first season is exceptional in that only two ♀♀ were reared, in one among 9 colonies. This obviously does not reflect the natural conditions, and we suspect that the particularly long transportation of these colonies was somehow detrimental to the brood from which the first offspring was reared. Thus, workers may have developed from originally queen-destined larvae.

Table VII a: Brood production of field-collected colonies of *Epimyrma algeriana*. Population Dj. Belezma: Monogynous colonies, two incipient, three collected without queen (queenless)

Col. no.	1st season 1986			2nd season 1987			3rd season 1988			remarks
	♂♂	♀♀	♀♀	♂♂	♀♀	♀♀	♂♂	♀♀	♀♀	
12 523	5	—	35	7	19	—	—	—	—	incipient, ♀ died May 1986
12 524	3	—	4	4	19	5	5	38	14	
12 525	(18)	—	—	(12)	—	—	(20)	—	—	queenless
12 526	2	—	4	—	—	1	—	—	1	
12 532	2	—	24	—	7	5	5	33	3	incipient
12 542	1	—	12	4	15	2	13	30	9	
12 543	1	—	32	(45)	—	—	(24)	—	—	queenless
12 544	—	—	3	1	—	—	—	—	—	queenless, col. died 1987
12 549	1	2	—	4	2	1	—	—	—	♀ died in the winter 1986/87
Σ	33	2	114	77	62	14	67	101	27	

Sex ratio ♂/♀, all colonies: 1.24 (1987); 0.66 (1988).

Sex ratio ♂/♀ except the only ♂-producing colonies (): 0.31 (1987); 0.23 (1988).

The comparatively very high sexual production of the Moroccan colonies (Tab. VIIc) perhaps was due to the presence of multiple queens in most colonies. The monogynous, laboratory-founded colonies from Forêt d'Akfadou (Tab. VIII) produced only a few ♀♀ in the first season after colony foundation. For the "passively" founded colonies this was the summer of 1986, the adult ♀♀ having hibernated in the field, whereas the "active" colony foundations originated from laboratory-reared ♀♀ which penetrated their host colonies in the fall, 1986, hibernated, and produced the ♀♀ in 1987. In both groups these first ♀♀ were reared as "rapid brood" from non-hibernated larvae. In the second season, after the colonies had hibernated with *Epimyrmma* larvae, high numbers of ♀♀ and sexuals were produced in both groups.

Table VII b: Brood production of field-collected colonies of *Epimyrmma algeriana*. Population Forêt d'Akfadou: Multiple-female colonies. All ♀♀ except one per colony (a presumptive A-♀) were removed in the spring, 1986, and all young sexuals in the summer, 1986. The 1987 production, thus, is offspring of one queen per colony

Col. no.	1st season (1986)			2nd season (1987)		
	♂♂	♀♀	♀♀	♂♂	♀♀	♀♀
12 605	2	8	13	14	28	—
12 608	1	9	11	1	5	8
12 609	2	30	20	6	2	1
12 610	2	4	17	1	23	—
12 616	1	8	29	27	20	6
12 624	1	16	10	—	—	1
Σ	9	75	100	49	78	16
Mean	1.5	12.5	16.7	8.2	13.0	2.7
Sex ratio ♂/♀	0.12			0.63		

All the colonies of Tab. VIII were founded by single *Epimyrmma*-♀♀. The results demonstrate that a single queen may have a comparatively high number of descendants (e.g. col. Je 35e with 3 ♂♂, 107 ♀♀, 60 ♀♀) within one year, polygynous colonies (Tab. VIIc) only rarely producing more. This is also indicated by the fact that the colonies of the Forêt d'Akfadou (Tab. VIIb) in the first season reared the hibernated larvae of multiple queens (cf. Tab. I). In the second season, after all but one queen had been removed in the spring, 1986, they reared an about equal number of ♀♀, but markedly less ♀♀, and more ♂♂.

Table VII c: Brood production of field-collected colonies of *Epimyrma algeriana*. Populations from Morocco. Only sexual production was recorded, and only for the second season in laboratory culture (1988). Multiple females had remained in the nests, but most of the production of 1987 had been removed. Where the reproductive status of ♀♀ is indicated, these ♀♀ were dissected in the spring, 1988, during the time the young sexuals were reared (cf. Tab. III)

Col. no.	♂♂	♀♀	reproductive status of ♀♀ present in the nests, in the spring, 1988
13 105	12	41	4 (not dissected)
13 115	10	130	11 A, 4 b → A (polygynous)
13 121	7	65	1A, 1a (funct. monogynous)
13 122	11	72	7A, 6b, 1 old A (?) (polygynous)
13 126	—	15	4A (polygynous)
13 131	30	121	4A, 5a, 22b (polygynous)
13 132	12	35	5 (not dissected, young ♀♀ of 1987)
13 155	13	230	3A (polygynous)
13 156	1	18	3b → A (young ♀♀ of 1987)
13 157	19	111	3 (not dissected)
Σ	115	838	sex ratio ♂/♀ = 0.14

3.6. Slave raids of *Epimyrma algeriana*

Because of the high numbers of *Epimyrma*-♂♂ found in field colonies of *E. algeriana* there was little doubt that this species is an active slave-maker like some of its congeners. In most colonies we observed, during the summer period, that numerous ♂♂ formed clusters, preferably just inside the nest entrance, apparently "waiting" for the invitation of a successful scout to follow her for a raid. In arena experiments up to 15 *Epimyrma*-♂♂ were seen simultaneously crawling around outside the nest, with the typical behavior of scouts, e.g. of *E. ravouxi*.

The group recruitment of *E. algeriana* (Fig. 3) is evidently the same as in *E. ravouxi* (WINTER 1979b), or *Mymoxenus gordiagini* (BUSCHINGER et al. 1983), and as in these species the raiding party of 10 - 40 *Epimyrma*-♂♂ pounces into the host species nest upon arrival at this target. They sting the host workers to death except those which escape, and after a while the captured host brood is carried towards the *Epimyrma* nest.

Slave raids were observed with colonies from the populations Dj. Belezma and Forêt d'Akfadou (Algeria) as well as from Morocco. Since the slave raids were so similar to those already described for other species we refrain from giving details. However, a few remarkable observations shall be reported.

Table VIII: Brood production in monogynous laboratory founded colonies of *Epimyrma algeriana*, population Forêt d'Akfadou. "Passive" colony foundation with young ♀♀ taken from field colonies, May 1986; "active" colony foundations with laboratory reared ♀♀ who left the nests in the fall, 1986. (Part of the 1987 ♀♀ remained and became reproductive in the "Je 27" colonies, cf. Tab. IV)

"passive" Col. no.	1st season (1986)			2nd season (1987)		
	♂♂	♀♀	♂♀	♂♂	♀♀	♂♀
Je 27a	—	—	8	—	37	21
Je 27b	—	—	3	—	53	16
Je 27c	—	—	—	1	47	26
Je 27d	—	—	5	—	6	16
Je 27e	—	—	1	—	34	26
Je 27f	—	—	3	2	34	10
Je 27g	—	—	5	—	65	22
Je 27h	—	—	1	8	35	4
Je 27i	—	—	1	15	56	9
Je 27j	—	—	—	—	3	—
Je 27k	—	—	1	15	14	3
sub-total (11)	0	0	28	41	384	153
"active" Col. no.	1st season (1987)			2nd season (1988)		
	♂♂	♀♀	♂♀	♂♂	♀♀	♂♀
Je 35b	—	—	—	9	89	1
Je 35d	—	—	—	1	1	8
Je 35e	—	—	3	3	107	60
Je 35h	—	—	2	—	40	15
Je 35i	—	—	1	2	69	9
Sub-total (5)	—	—	6	15	306	93
total (16)	0	0	34	56	690	246
sex ratio ♂/♀		—			0.08	

Thus, we repeatedly saw processions of *Epimyrma*-♂♀ leaving from the slave-maker nest apparently spontaneously; this means that no successful scout had been seen re-entering the *Epimyrma* nest before. In some experiments, however, scouting had been seen during the one or two preceding days, not immediately followed by a raid. We believe that an *E. algeriana* scout may remember a target colony it has found, and lead a raiding party towards it another day. A similar delay of raiding recently has been documented for another slave-maker, the amazon ant *Polyergus breviceps* (TOPOFF et al. 1987).

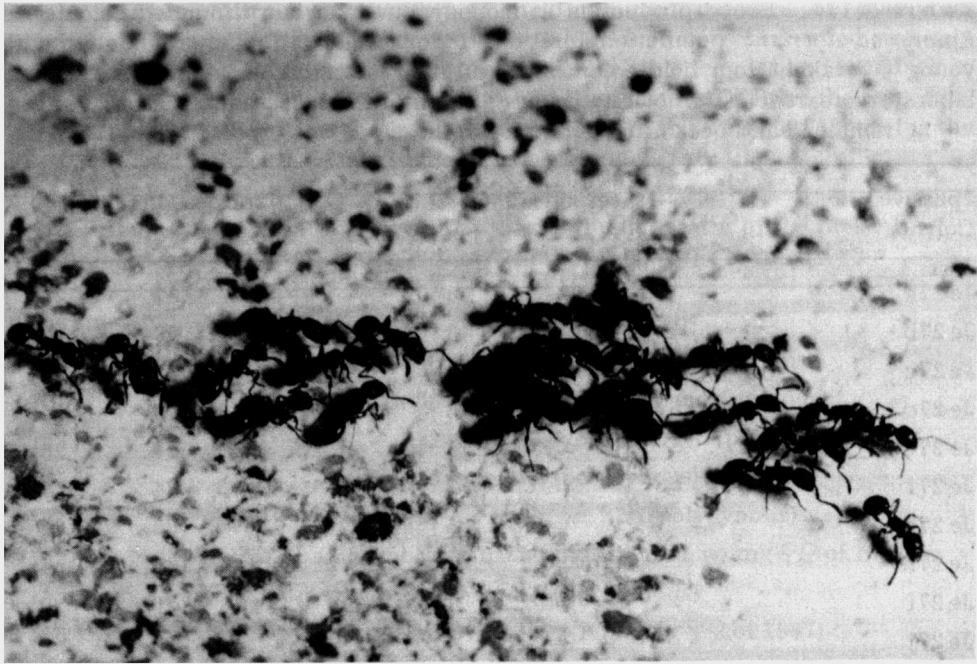


Fig. 3. Raiding party of *Epimyrma algeriana* workers. The "scout" (right) leads nestmates on a pheromone trail towards a *Leptothorax spinosus* nest.

Other observations refer to the behavior of the *E. algeriana*-♀♀ towards the captured brood. Often the ♀ and ♂ pupae of *L. spinosus* are destroyed before the other broods are carried back to the *Epimyrma* nest. Then the *Epimyrma*-♀♀ usually lead slaves towards the raided nest, often in tandem runs but nevertheless evidently laying a pheromone trail in front of the single follower. Only rarely an *Epimyrma*-♀ is carrying broods, most of the transportation is done by the slave workers of the *Epimyrma* colony.

Finally, in one experiment with a colony from Tizi-n-Ifar, Morocco, a *L. spinosus* colony was raided, but some of its brood remained in the nest, together with one *Epimyrma*-♀ and about 8 *spinosus* (presumably slaves from the *Epimyrma* colony.). Within about a week the number of *Epimyrma*-♀♀ in the former *spinosus* nest increased to 15, and also about 12 - 15 *spinosus*-♀♀ were there. Again a week later a total of 9 *Epimyrma*-♀♀ still remained in that nest, one of which was visibly physogastric. This worker was dissected. It had 6 ovarioles (as is usual in *Epimyrma*-♀♀), in 5 of which eggs were developing with marked yolk deposition. No receptacle was present, however. The situation resembles that found in *Harpagoxenus americanus* (BUSCHINGER & ALLOWAY 1978b), where branch colonies with male-producing workers are common. Since we did not find any such colony of *E. algeriana* in the field, however, this event was perhaps a laboratory artifact.

4. Discussion

Several of the results presented here are of a somewhat preliminary kind, and more data would be desirable in many instances, e.g. for correctly

evaluating sex ratios, the frequency of polygyny, of slave raids, or of colony foundation by single or multiple queens in the field. Such deficiencies, however, are quite common when rare species are investigated, when it is difficult to collect and study more field material, e.g. at various times in the annual cycle, or when the species in question exhibit other features than originally expected. In order to find out as much as possible with the restricted material we sometimes had to change conditions during current experiments, or had to reduce the numbers of replicates in order to set up other experiments with differing aims. Nevertheless we worked out many certainly reliable data on the life history of *E. algeriana*, which also are very different from what was previously published on this species:

- *E. algeriana* is a species with a high number of *Epimyrma*-♂♂, which are able to conduct slave raids in the same way as other actively dulotic *Epimyrma* species.

- Young *E. algeriana* queens, like those of all congeners yet studied, are able to penetrate host species colonies, and to kill the host colony queens through protracted throttling. Stinging of host colony workers also occurs, as in other *Epimyrma* species, during colony foundation.

- The young sexuals are reared from hibernated brood, like in the actively dulotic *E. ravouxi*, but different from the “degenerate slave-makers” *E. kraussei*, *E. corsica*, and *E. adlerzi*, whose first sexual offspring arises as rapid brood in the very of year colony foundation.

- Mating takes place within the mother colonies, as in the “degenerate slave-makers” mentioned above, but different from the actively dulotic *E. ravouxi*, *E. stumperi*, and the closely related *Myrmoxenus gordiagini*.

- An as yet unique feature in the genus is the polygyny we observed in most populations of *E. algeriana* except that from Dj. Belezma and perhaps that from Cap Bougaroun.

- Functional monogyny, as is common in several other leptothoracine species (BUSCHINGER 1968, FRANCOEUR et al. 1985, HEINZE & BUSCHINGER 1987), was found in some colonies of the usually polygynous populations.

According to CAGNIANT (1968a), the young queens of *E. algeriana*, after colony foundation, first produced some sexuals and very few workers, and after a few more workers emerged in the following year the colonies were found to decline and die. The marked difference between these earlier and our new observations requires an explanation.

Most of CAGNIANT's (1968a) results were obtained with small colonies (1 queen, ca. 60 host workers) collected in the Atlas de Blida or in the Ouarsenis (Tienet el Haad) in cedar forests. The host species populations consisted of small (presumably young) *L. spinosus* colonies. All the parasite colonies

were monogynous, like our newly collected ones from Dj. Belezma. The habitats in these sites were more or less disturbed, and we suspect that such conditions do not favor large and polygynous *Epimyrma* colonies. Small, monogynous colonies may produce only few *Epimyrma* workers, having difficulties to conduct successful slave raids. Such colonies due to lack of sufficient slaves will soon decline.

On the contrary, the *L. spinosus* colonies in the Forêt d'Akfadou, and in most sites in Morocco, were large, and only few smaller, young colonies were found. This is characteristic for mature ant associations with stable, climax conditions, where the colonies of a given species are often about equal in size, colony turnover is low, and successful foundation of new colonies is rare due to competition of the old ones. Such conditions might be more favorable for long-lived, polygynous *Epimyrma* colonies with large worker forces who are able to overwhelm and raid upon large host species nests.

Even if so, however, one inconsistency in our observations remains to be explained: We assume that the populations from the Forêt d'Akfadou (Algeria), and those from Morocco, are biologically identical in that they all exhibit the same life history traits with respect to colony foundation, *Epimyrma* worker numbers, slave-raiding, and facultative polygyny. In the population of Dj. Belezma, however, no polygynous colonies were found, and no young, inseminated females were present in the nests when collected in early April. The colonies were by no means all incipient ones, since several contained comparatively high numbers of *Epimyrma* workers (Tab. I). They should already have produced sexuals in the foregoing year.

Thus, the *E. algeriana* population of Dj. Belezma might represent a separate, infraspecific taxon, to which also the populations studied by CAGNIANT (1968a) may belong. Further investigations of these populations, as well as that from Cap Bougaroun, will be necessary to clarify the differences observed.

With the characters of slave-raiding and intranidal mating, *E. algeriana* exhibits a particular life history. Two evolutionary trends have been recognized in the genus *Epimyrma*, one being the reduction of *Epimyrma*-♂♂ numbers and slave raiding, up to complete workerlessness as in *E. corsica* and *E. adlerzi*, the other is the transition from mating flights to intranidal mating. Whilst *E. ravouxi* and *E. stumperi* are active slave-makers and conduct mating flights, the "degenerate slave-makers" *E. kraussei* (with few ♂♂) and the workerless species engage in intranidal sib-mating. *E. algeriana* combines the latter with active dulosis, and is therefore perhaps similar to *E. bernardi* from Spain, for which, however, the data base is still small.

BUSCHINGER (1989) points out that intranidal mating, and the subsequent dispersal of young queens on foot, should mean an intraspecific, and even

intrapopulation, competition between the foundation of new colonies, and the raiding of host species nests which leaves less of them for the formation of young colonies. Thus, it sounds logical when *E. krausse*i, *adlerzi*, and *corsica* have reduced their workforce and have abandoned slave-raiding. In *E. algeriana*, however, we find both intranidal mating and active slavery.

The unexpected, frequent polygyny of many *E. algeriana* populations may be a consequence of this dilemma, a third strategy of host population exploitation, which perhaps is particularly adapted to the utilization of large host colonies. Young queens having mated in the mother nest have the option to leave and to found an own colony in a nearby nest of the host species, or to remain in the mother colony and reproduce there, in case of functional monogyny after a certain delay. In truly polygynous, thus potentially immortal, colonies the young queens would share the slaves which a large *Epimyrma* workforce, the combined offspring of themselves, their mothers, and later daughters, can gather from surrounding host species nests. The colony foundation by single *Epimyrma* queens is a risky venture, particularly when host colonies are large. And the small workforce of a young *Epimyrma* colony may have difficulties to overcome a large host colony for raiding. *E. algeriana*, thus, may have evolved polygyny, but has not (yet) lost the capability also to found new colonies through single queens where the host species population and the ecological conditions render this alternative more favorable, e. g. in the population Dj. Belezma (and perhaps in the Atlas de Blida).

Our observations of agonistic behavior between dealate ♀♀ in the nests demonstrate that polygyny in *E. algeriana* is not unrestricted. Certain ♀♀ may be more or less tolerant towards additional ♀♀, and the different reproductive states of the ♀♀ may reflect the variable degrees of mutual tolerance. Presumably the agonistic behavior is a remainder of the strong regulation mechanism ensuring monogyny in the other *Epimyrma* species, and its existence is perhaps indicative of a comparatively recent evolutionary transition to polygyny.

Variable degrees of mutual tolerance, and an individual variation in the ontogenetic development of aggressivity, may also account for the fact that young ♀♀ leave the mother nests successively over an extended period, from fall to spring.

Budding, the formation of daughter colonies, would be a logical consequence of the polygynous colony structure. However, we have no data suggesting its occurrence in nature.

With respect to kin selection theory the polygyny of *E. algeriana* is not problematic, since due to intranidal mating all queens and workers are very closely akin to each other. The species only had to reduce the regulation

mechanisms which in monogynous species prohibit the coexistence even of sister queens. The intranidal mating and the slow dispersal of young queens on foot may have prevented that this perhaps comparatively recent behavioral change has spread already to all *E. algeriana* populations. This might be another reason for the monogyny found in the populations of Dj. Belezma or the Atlas de Blida, but this has to be investigated again.

Acknowledgements

We are grateful to the Deutsche Forschungsgemeinschaft for grants which enabled us to collect in Algeria (A. B., K. J.) and in Morocco (A. B.). JÜRGEN HEINZE (in Algeria and Morocco), XAVIER ESPADALER (in Morocco), and URSULA WINTER (in Algeria) have helped to collect the material. H. CAGNIANT was supported by a grant of the Conseil Scientifique de l'Université P. Sabatier, Toulouse, for a "Study of Moroccan Ants". We acknowledge the helpful comments of three anonymous referees.

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