

Life history of the parasitic ant, *Epimyrma bernardi* Espadaler, 1982

(Insecta, Hymenoptera, Formicidae)

By Alfred Buschinger

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The ant genus *Epimyrma* comprises both actively dulotic species and “degenerate” slave-makers with reduced worker number, or lacking this caste completely. The sexuals of some species conduct mating flights, directly followed by colony foundation of the young queens, others mate inside the mother nests, the females hibernate there, and invade new host colonies in spring. The latter species usually produce rapid brood sexuals within the year of colony foundation. *Epimyrma bernardi* exhibits a novel blend of life history features: Sexuals mate in the nest where they remain until colony foundation in the following spring, but the first adult offspring emerges only after the next hibernation. It then comprises both sexuals and workers. Worker numbers are highly variably, suggesting that slave raids, though observed in the laboratory, are rare in the field and probably not obligatory. In contrast to the first report on this species (Espadaler 1982) the newly collected colonies of 1992 contained no dealate regular queens of the host species *Leptothorax gredosi*.

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Introduction

The ant genus *Epimyrma* is distributed around the Mediterranean with about ten species. They are social parasites of various *Leptothorax* (Myrafant) species, one (*E. kraussei*) coexists with *L. (Temnothorax) recedens*. Their life histories represent an unusually wide range of variation including the evolutionary transition from active slavery to a “degenerate” dulosis, and finally the loss of the *Epimyrma* worker caste (for a review see Buschinger 1989a). Young mated queens of all species singly penetrate colonies of the respective host species, and eliminate the host queen(s) by slowly throttling them to death. They are accepted by the host colony workers.

This may happen in summer or fall, immediately after a mating flight (*E. ravouxi*, *E. stumperi*), or mating and dealation take place during fall within the mother colony, which the young queens then leave in early spring, after hibernation, searching for new host colonies to invade (*E. adlerzi*, *E. algeriana*, *E. corsica*, *E. kraussei*). If an *Epimyrma* queen is successful, the host workers may rear her eggs and larvae to become *Epimyrma* workers in comparatively high numbers (*E. ravouxi*, *E. stumperi*), during the first and following years after colony foundation. The *Epimyrma* workers then conduct slave raids on neighboring, independent host colonies, thus replenishing the slave stock in the *Epimyrma* colony. *Epimyrma* sexuals appear from the second or third year on and for up to 8–10 years.

In the degenerate slave-makers, the first sexuals, sometimes together with a few workers (*E. kraussei*), emerge from rapid brood already in the year of colony foundation, and again in the second year, after which most colonies decline due to slave depletion. Workerless species (*E. adlerzi*, *E. corsica*, an undescribed species from Tenerife) have a comparable life history. *E. algeriana* is exceptional in that it combines intranidal mating with active slavery, and a marked polygyny.

For *Epimyrma bernardi*, Espadaler (1982) claims the unusual feature of coexistence of host and parasite queens, derived from a census of four field-collected colonies. Its as yet only known host species is *Leptothorax (Myrafant) gredosi* Espadaler & Collingwood, 1982. Buschinger (1989a) briefly reports that sexuals of *E. bernardi* mate in the mother colonies, and that colony foundation occurs after hibernation, with *Epimyrma* queens throttling and eliminating the functional host queens in the usual way. *E. bernardi* produces workers which in laboratory experiments were able to conduct normal slave raids. These data were obtained from three colonies collected by X. Espadaler in 1982 and handed over to the author alive.

Due to the very low number of available colonies, however, it was as yet impossible to assess whether slave raiding in this species is obligatory. *Epimyrma* workers were few or none in the first seven colonies collected in the field (Table 1). In September 1992 we collected another 12 colonies in the type locality of *E. bernardi*, Sierra de Gredos (Avila, Spain), the only loacality from which this species is known as yet. Dissectioning of *Epimyrma* and host species dealate females, and laboratory rearing of some colonies revealed that this species exhibits a particular blend of life history features not yet found in the other species investigated.

Materials and methods

For this paper all extant material of *E. bernardi* has been used and evaluated:
 4 colonies collected on 22/23 July 1979 (Espadaler 1982);
 3 colonies collected on 14 August 1982 (leg. Espadaler), handed over to the author in September 1982;
 12 colonies collected on 20 September 1992 (leg. Buschinger and Douwes).

Tab. 1. Composition of field colonies of *Epimyrma bernardi*. #1-4: Data from Espadaler (1982); #5-7: Composition on 18 Sept. 1982 when the colonies were handed over to the author.

Col.#	<i>Epimyrma</i> adults				<i>Leptothorax gredosi</i>			date of coll.	collectors
	deal.	alate	♂♂	♀♀	♀♀	♀♀	♂♂		
	♀♀	♀♀							
1	–	–	–	2	many al.	many	–	22/23 July 79	Espadaler
2	1	–	–	–	1 deal.	many	–	22/23 July 79	Espadaler
3	3	–	–	4	“queens”	many	+	22/23 July 79	Espadaler
4	–	–	–	3	–	many	–	22/23 July 79	Espadaler
5	1	ca25	2	–	–	60	–	14 Aug 82	Espadaler
6	1	–	–	–	–	87	–	14 Aug 82	Espadaler
7	1	–	–	–	2 deal.	100	–	14 Aug 82	Espadaler
8	2	–	2	4	–	40	–	20 Sept 92	Buschinger & Douwes
9	1	–	–	–	–	74	–	20 Sept 92	Buschinger & Douwes
10	6	13	4	22	3*	273	–	20 Sept 92	Buschinger & Douwes
11	1	–	–	–	–	208	–	20 Sept 92	Buschinger & Douwes
12	–	–	–	15	–	111	–	20 Sept 92	Buschinger & Douwes
13	1	–	–	–	–	51	–	20 Sept 92	Buschinger & Douwes
14	1	–	–	–	–	199	–	20 Sept 92	Buschinger & Douwes
15	1	–	–	–	–	128	–	20 Sept 92	Buschinger & Douwes
16	7	12	3	24	–	148	–	20 Sept 92	Buschinger & Douwes
17	2	4	15	2	–	88	–	20 Sept 92	Buschinger & Douwes
18	1	–	–	–	–	382	–	20 Sept 92	Buschinger & Douwes
19	1	–	–	–	1**	ca300	–	20 Sept 92	Buschinger & Douwes

* 3 microgynes of *L. gredosi*
 ** mixture of an *Epimyrma*- and a free-living *L. gredosi* colony.



Fig. 1. Microgyne (top) and normal-sized macrogyne of *Leptothorax gredosi*, host species of *Epimyrma bernardi*. The size difference is not only due to the distended gaster of the macrogyne. The microgyne thorax is dorsally more vaulted, the mesonotum less prominent above the pronotum. Division of scale: 1 mm.

All colonies were aspirated as completely as possible, however, certain losses were inevitable because the nests are located beneath rocks in leaf litter and partially in the soil. Host colony density is locally high, sometimes two or even three discrete nests and colonies share one covering rock of 30-50 cm diameter. At least in one instance in 1992 an *Epimyrma* colony by chance was mixed with a neighboring but not parasitized host colony, and in one colony (not included in Table 1) an *Epimyrma* queen was seen in the field, but later lacked in the sample. Living colonies were reared according to Buschinger (1974) in 3-chambered plastic formicaries with a plaster floor, and in artificial nests made from a plastic frame between two microscopic slides. Food (honey and water 1:1, insect pieces) was provided ad libitum three times a week. Colonies were hibernated for 4-5 months in constant 10 °C. Spring was simulated during 2 weeks in a temperature rhythm of 10/20 °C (12:12 h), summer for about 4 months in 15/25 °C (10:14 h) with weak illumination during the warm hours. When the development of new pupae decreases the colonies go through another 2 weeks at 10/20 °C (12:12 h) into the next hibernation.

Dissectioning of females was done as described in Buschinger (1968) and Alloway et al. (1982). "A" denotes a fully fertile queen with long ovarioles and corpora lutea in their bases, and with a receptacle containing sperm; "b" is a newly mated young gyne with still short ovarioles and lacking corpora lutea; "d" are dealate or alate, not inseminated young gynes ("c" would be older, dealate but not inseminated specimens).

Results

1. The composition of field colonies of *Epimyrma bernardi*

Most colonies were censused soon after collecting (Table 1). Eleven out of the 16 colonies containing *Epimyrma* gynes at all had but one female, and none of these single-queen samples comprised *Epimyrma* workers, though one colony (# 5) had produced a high number of alates already. Most colonies having *Epimyrma* workers also contained alate young sexuals and/or multiple dealate gynes (# 3, 8, 10, 16, 17). Dissectioning of a representative sample of gynes (Table 2) revealed that the sole dealate females of colonies lacking both workers and young sexuals (# 9, 11, 18, 19) were inseminated and had long, well-developed ovaries containing corpora lutea in their bases. The ovaries appeared inactive and lacked white, growing oocytes, indicating that oviposition at the time of dissectioning (1st October 1992) had

ceased already, the queens preparing for hibernation. Rearing of these colonies after hibernation (see section 2) revealed that their brood had comprised *Epimyrma* larvae.

Most probably these queens had penetrated their host colonies in the spring, 1992, and had laid eggs during the summer, but no workers or sexuals had developed until the fall of this year.

Colonies with multiple dealate gynes (# 8, 10, 16) contained both inseminated young females with short, inactive ovarioles ("b") and young virgins with ovaries in the same condition ("d"). In col. # 8 and # 10 the original queen ("A") either was lost during collecting, or had died before. The dealate, inseminated gynes suggest that intranidal mating had occurred, and that these gynes prepared to stay with the mother colonies until the following spring. Since males were still present in the colonies with alate and/or dealate d-females these virgins probably would have mated also before the winter.

Colony # 10 in addition to mated and virgin *Epimyrma* gynes contained three microgynes of the host species, *Leptothorax gredosi* (Fig. 1). Dissectioning revealed that these specimens were newly inseminated ("b"). Microgynes are sometimes produced in low number in *L. gredosi* nests, and apparently most or all gynes of this species, too, mate inside or in close vicinity of the nest, but later leave for independent colony foundation; functionally the *gredosi* colonies thus are monogynous.

Colony # 19, evidently a mixture of an *Epimyrma* and a free-living *L. gredosi* colony, contained a fully reproductive host species queen. The workers soon executed the *Epimyrma* queen, but reared its brood (see section 2). Functional host species queens thus were not found in normal *E. bernardi* colonies, though dealate *L. gredosi* females had been recorded in the colonies # 2, 3, and 7. Unfortunately they were not dissected, and I assume they were not reproductive.

Host worker numbers in the *E. bernardi* colonies varied considerably, as in other *Epimyrma* species (Buschinger & Winter, 1983). There was, however, no evidence of higher slave numbers in colonies containing *Epimyrma* workers (mean host workers: 132; range 40-273, n = 5) as compared to the newly founded ones without *Epimyrma* workers (mean host workers: 143; range 51-382, n = 9 colonies, # 19 excluded). Slave raiding, if it occurs at all, apparently does not markedly increase the slave number.

2. Production of workers and sexuals in *Epimyrma bernardi* colonies

The production of colonies with a sole *Epimyrma* queen was particularly interesting: Were *Epimyrma* larvae in their brood? What would be reared from these once-hibernated, first larvae of the queens?

All colonies produced males, gynes and workers (Table 3) except for colony # 13 which reared only workers and one male but no gynes. Probably the lack of gyne production in this nest was due to its low number of only 51 host workers.

Colonies having an *Epimyrma* queen yielded *Epimyrma* workers in numbers which would be sufficient for slave raiding (mean 37.6; range 13-54, n = 3 colonies), and also some males and gynes. Three colonies whose queens had been scarified for dissectioning or (# 15) had died before the hibernation, produced gynes and males in comparable numbers, whereas only few workers were reared (males: 2-5; gynes: 5-27; workers: 4-5). These specimens evidently originated from hibernated larvae, whereas in the queenright colonies additional workers probably developed as rapid brood from eggs laid after the hibernation. Colony # 19 (the mixture of an *Epimyrma*- and a queenright *L. gredosi* colony) during brood rearing still contained the host species queen, whereas the *E. bernardi* queen had been executed before

Tab. 2. Results of dissectioning of dealate *Epimyrma bernardi* females. Colony numbers as in table 1.

Col.#	n deal. ♀♀	n diss. ♀♀	status of ♀♀	Comments
8	2	2	b, d	Queen (A) lacks
9	1	1	A	Ovaries of queen inactive, with corpora lutea
10	6	6	2b, 4d	Queen (A) lacks, 2 newly inseminated females
11	1	1	A	Queen (A) as in col. 9
16	7	7	A, 3b, 3d	Queen (A) with mated und unmated daughters
18	1	1	A	Queen (A) as in col. 9
19	1	1	A	Queen (A) as in col. 9

the hibernation. The colony reared five males and gynes each, and 25 workers from the *Epimyrma* brood, and numerous sexuals and workers of the host species. Probably the *L. gredosi* queen had an influence on caste formation of the *Epimyrma* brood, causing worker development of most of the female larvae. Most of the about 50 *L. gredosi* gynes in this colony were inseminated when a sample of them was dissected at the end of the rearing season.

Sexual production in the *Epimyrma* colonies was markedly gyne-biased, as far as can be deduced from the comparatively small number of colonies (0.36 ♂ / ♀, n = 7 colonies).

Little can be said as yet on the production of *E. bernardi* colonies in their third and following years. Rearing of colony # 5 and # 7, and of a number of laboratory-founded colonies with mated gynes from colony # 5, was not very successful despite host worker pupae were regularly added. The *Epimyrma* queens died in the first, second or third "summer". A few males, gynes and workers appeared in these colonies up to the summer following the queen's death, i. e. up to the fourth year.

Discussion

The parasitic ant genus *Epimyrma* with about ten species distributed around the Mediterranean, exhibits a stunning variety of life histories. Among the most interesting features is a reduction of worker number, combined with a transition from the original slave-making to a derived, completely workerless condition, though the parasite queens still eliminate the host colony queens by throttling them to death (Buschinger 1989a). A second variable feature is mating behavior, which may be a mating flight (in most of the actively dulotic species), or intranidal mating and hence adelphogamy among the progeny of the usually only one mother queen. One slave-raiding species, *E. algeriana*, combines intranidal mating with polygyny (Buschinger et al. 1990).

Epimyrma bernardi Espadaler, 1982 exhibits an as yet unknown blend of features. The sexuals mate during summer and fall within their mother colonies, which contain but one *Epimyrma* queen (monogyny). The markedly gyne-biased numerical sex ratio (0.36 ♂ / ♀) corroborates the observations. It corresponds to sex ratios in other adelphogamous *Epimyrma* species (*E. adlerzi*: 0.19; *E. algeriana*: 0.16-0.22; *E. corsica*: 0.08; *E. kraussei*: 0.3), whereas in the swarming *E. ravouxi* it is 1.5 ♂ / ♀ (Buschinger 1989a).

Dealate mated females most probably spend the winter within the mother colonies which they leave on foot in early spring, in search of suitable host colonies to invade: In the fall, 1992, we had found mated young gynes within the *Epimyrma* colonies, but no young queen just taking over a host colony. This process usually lasts for several weeks so that the chance is high in the right season to find a *Epimyrma* queen throttling the host colony queen in her nest. The observations on *E. bernardi* correspond well to those on other "degenerate slave-makers" of the genus which also invade host colonies after the hibernation (*E. adlerzi*, *E. corsica*, *E. kraussei*). Having penetrated a *L. gredosi* colony the

Tab. 3. Production of presumably newly founded *Epimyrma bernardi* colonies lacking *Epimyrma* workers. Three colonies contained an *Epimyrma* queen, in four colonies the queen was absent during brood rearing.

Queenright colonies				Queenless colonies				
Col.#	production of			Col.#	production of			
	♂ ♂	♀ ♀	♀♀		♂ ♂	♀ ♀	♀♀	
13	1	–	13	9	3	7	4	
14	6	10	54	11	5	27	5	
18	6	24	46	15	2	5	4	
				19	5	5	25	
Σ	13	34	113	Σ	15	44	38	Σ 97

♀ / ♀ ratio queenright: 1:3.32; queenless: 1:0.86

♂ / ♀ ratio queenright: 1:2.6; queenless: 1:2.9

♂ / ♀ ratio total: 1:2.78

E. bernardi queen eliminates the host queen, and begins to lay eggs. In the year of colony foundation, however, no adult *Epimyrma* progeny is reared, which is different from the "degenerate slave-makers" mentioned above. The latter produce a first batch of sexuals as rapid brood until late summer of the very year of colony foundation. *E. bernardi* instead hibernates again with her first brood of larvae, from which adults emerge in the following year, as the rearing experiments have revealed (Table 3).

This first brood comprises both sexuals and a few workers, as is the case with most populations of the "degenerate slave-maker", *E. kraussei* (Buschinger 1989b). Worker numbers in field colonies of *E. bernardi*, however, are rarely sufficient for effective slave-raiding (Table 1). I presume therefore that the higher worker numbers produced in queenright laboratory colonies (Table 3) are an artifact. Due to good laboratory conditions with respect to food and temperature regime a batch of rapid brood workers was reared, whereas in the field, according to our observations in a number of Mediterranean Leptothoracini, brood rearing decreases during the hot and dry summer season.

I suggest that *E. bernardi*, as *E. kraussei*, is a "degenerate slavemaker" which in the field will conduct slave raids only occasionally, if at all. The fact that colonies with *E.* workers have not more slaves than colonies lacking *E.* workers support this assumption. In the "degenerate slavemaker", *E. kraussei*, slave numbers decrease with increasing numbers of *E.* workers, whereas in the actively dulotic *E. ravouxi* colonies with more slavemaker workers usually also have more slaves (Buschinger & Winter 1983).

Another correspondence to *E. kraussei* refers to population structure: Most of the 19 *E. bernardi* colonies, i.e. at least 10, were in their first year, containing no young sexuals or workers when collected between end of July and 20. September (Table 1). Some of the colonies comprising sexuals and workers probably were in their second year, and a few which already lacked the *Epimyrma* queen perhaps were in the third year. Life expectancy of *E. bernardi* colonies thus is low, two or three years, as in the other "degenerate slavemakers" or workerless species (Buschinger 1989a).

A final problem refers to the presence of dealate host species females in some of the *E. bernardi* colonies (Table 1). Espadaler (1982) observed one "dealtated queen" in colony # 2, and "many queens of *Leptothorax*" in colony # 3. He suggested therefore that *E. bernardi* might not kill the host colony queens. Also colony # 7 originally comprised two dealate *L. gredosi* females. All these "queens", however, were not dissected and their reproductive status thus is unknown. Most of the colonies listed in Table 1 contained no dealate or alate host species females, and laboratory observations have revealed that *E. bernardi* is able to throttle and to eliminate the host colony queens as do all other *Epimyrma* species. The host species, *L. gredosi*, however, exhibits a feature which is unusual in other free-living *Leptothorax* (*Myrafant*) species, and which may explain the presence of dealate host females in some of the *Epimyrma* colonies: *L. gredosi* sexuals mate within or near to the mother nest, and at least some of the mated females remain there over winter. In spring they fight each other and try to leave from the colony (unpubl. observations). In four out of six unparasitized *L. gredosi* colonies collected together with the *E. bernardi* colonies in September, 1992, I found several dealate, recently mated *gredosi* females alongside always one fully fertile queen. Also alate females and *gredosi* males were still present. If the *E. bernardi* queen in the year of colony foundation does not completely inhibit the rearing of gynes and males from the remaining host species brood in the nest, some *L. gredosi* sexuals may eclose and mate there in the presence of an *Epimyrma* queen. The throttling behavior of the latter apparently is directed only against fully reproductive host queens. Furthermore, *L. gredosi* colonies sometimes produce microgynes in low numbers, alate females or specimens with reduced wings, which are smaller than ordinary gynes. *Epimyrma* colony # 10 (Table 1) contained three such microgynes which were inseminated but not egg-laying. I presume they would have left the *Epimyrma* colony after the winter. Coexistence of *Epimyrma bernardi* with reproductive host species queens thus appears improbable.

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