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Research article

Social organization, reproductive behavior and ecology of *Leptothorax acervorum* (Hymenoptera, Formicidae) from the Sierra de Albarracin in central Spain

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Summary. *Leptothorax acervorum*, an ant species with holarctic range, occurs in an isolated population in the Spanish Sierra de Albarracin. Dissection of dealate females and laboratory observations revealed that in contrast to other European populations, the colonies are monogynous, with one reproductive queen each and a variable number of virgin or mated dealate but not laying females. Most of the latter probably just hibernate in the mother nests, leaving them in the following spring, but a few remain there for longer time, without reproducing. Such colonies then are functionally monogynous. Alate females exhibit a stationary sexual calling, and mating behavior could be studied in the laboratory. Mated females return to the mother nest where they soon shed wings. When developing fertility before or after hibernation they are evicted from the nests; in nature they probably form daughter colonies. Patchy habitat and rough climatic conditions in the Sierra de Albarracin may be responsible for the particular reproductive behavior of *L. acervorum* in this area. The generally small size difference between queens and workers in the subgenus *Leptothorax* entails high costs of dispersal and colony foundation by single queens who have to forage for their first brood. Some kind of dependent colony foundation therefore is frequently met with in the subgenus. Notwithstanding the marked biological and a few slight morphological differences between central European *L. acervorum* and the Spanish population its taxonomic status as yet is unsettled. We refer to this population provisionally as “*L. acervorum* Albarracin”.

Key words: Leptothorax acervorum, functional monogyny, mating behavior, intranidal mated offspring hibernation, ecology.

Introduction

Queen number, the number of inseminated, reproductive females in social insect colonies, and its regulation, have become major subjects of sociobiological research in the past two decades. Colonies may be monogynous (have a single queen), polygynous (have two or more reproductive queens), or functionally monogynous (one queen is accompanied by mated but non-laying potential queens, usually her daughters). In field populations often facultative polygyny is observed, meaning that the colonies of a given species may be either monogynous or polygynous. The number of reproductives contributing to the formation of workers and sexual offspring affects various features of colony structure, such as relatedness among workers, or between workers and young sexuals. Conflicts of interest within colonies may result mainly from polygyny (cf. Bourke and Heinze, 1994). Because ants of the genus *Leptothorax* have small colonies, are easily collected and maintained in the laboratory, and exhibit a wide range of social structures, they are favored model organisms to test the various hypotheses.

The inconspicuous myrmicine ant *Leptothorax* (*Leptothorax*) *acervorum* (F.) is widespread over vast areas of Eurasia and North America where it mainly inhabits boreal and alpine coniferous forests. Populations of central, western and northern Europe are known to be facultatively polygynous (Buschinger, 1968a; Douwes et al., 1987; Stille et al., 1991; Stille and Stille, 1993; Chan and Bourke, 1994). In the majority of the colonies two or more reproductive queens are found which lay eggs simultaneously and at similar rates. Recently, Heinze et al. (1995b) suggested a cyclical switch from monogyny to polygyny and back in a population from southern Germany. In contrast, a population of *L. acervorum* from northern Japan has a functionally monogynous colony structure with one primary egg-laying queen and a number of inseminated females which, if at all, lay eggs only at a very low rate (Ito, 1990). In another population of *L. acervorum* from shrub tundra habitats in Denali National Park, Alaska, Heinze and Ortius (1991) found monogynous and polygynous colonies, but aggressive interactions in multiple-female colonies were interpreted as indicating functional monogyny. Finally, Seppä et al. (1995) reported on electrophoretic data suggesting functional monogyny also in populations from Finland.

During a visit at the Spanish Sierra de Albarracin in 1992, one of the authors (A.B.) collected a couple of *L. acervorum* colonies. Laboratory observations and the dissectioning of some dealate females seemed to indicate a functionally monogynous colony structure. Here we report on colony composition and mating behavior of this population. Morphologically, the Spanish specimens cannot be reliably distinguished from central European *L. acervorum*, though the females have a somewhat less sculptured cuticle and darker wings. Heinze et al. (1995a) found no differences between our material from Spain and central European *L. acervorum* in a couple of diagnostic isozymes. There was also a close similarity between this population and ordinary, facultatively polygynous *L. acervorum* from the Pyrenees in a cytochrome b DNA sequence analyzed by Baur et al. (1995), though a central European and even more a Japanese population (Ito, 1990) differed markedly. As long as it remains uncertain whether the population from central Spain really belongs to *L. acervorum*, or perhaps represents a subspecies of the latter, it shall be provisionally named "*L. acervorum* Albarracin". Further isozyme studies and also crossmating experiments with central European populations are in progress in order to assess the relationships among them.

Material and methods

In September 1995 and in May 1996 altogether 83 mostly complete colonies of "*Leptothorax acervorum* Albarracin" were collected. The ants were aspirated from their nests in rotting pine and oak wood and censused as soon as possible. After transfer to the laboratory 61 colonies were kept alive in 3-chambered formicaries, in daily temperature rhythms and artificially shortened annual cycles as described by Buschinger (1974a). During a hibernation period of eight weeks or a few more a daily temperature cycle of 10 °C (12 h) and 0 °C (12 h) was applied. "Spring" conditions were simulated with two weeks at temperatures of 20 °C (12 h) with light during the warm hours, and 10 °C (12 h) at night. A "summer" period of 12 weeks or more with temperatures of 25 °C (14 h) and 15 °C (10 h) followed. Before entering the next hibernation the colonies were kept for another two weeks or more in the "spring" conditions as described above.

All 246 dealate females of 32 randomly selected colonies were dissected directly after collecting to determine their reproductive status. In other colonies the females were dissected after a more or less prolonged period of maintenance under laboratory conditions. The dissections were carried out as described by Buschinger and Alloway (1978) and Alloway et al. (1982). The ovaries were exposed by removing the subgenital plate with a pair of pointed forceps under a dissecting microscope at 32×. The size and content of the ovarioles, the receptacula seminis and the presence of corpora lutea were checked. Additionally, the thorax was opened in order to see if a female was young or of older age. In female ants after dealation the wing muscles are replaced by fat body. The colour of the fat body usually changes from white in younger females to yellow in older ones. In "*L. acervorum* Albarracin", however, the thoracic and gastral fat bodies remain white or become only slightly yellowish. Six types of dealate females can be distinguished. The following functional classification is based on a system as described by Buschinger (1968a), Alloway et al. (1982) and Heinze and Buschinger (1988).

A-females:	Inseminated, fertile queens. The ovarioles when uncoiled are longer than the ants' body, corpora lutea are clearly visible, and during the egg-laying period in summer the ovarioles each contain several white, growing oocytes.
a-females:	Inseminated, older females, not laying. No corpora lutea present, ovarioles are short, wing muscles replaced by yellowish fat body.
b-females:	Inseminated young females, not laying. Corpora lutea are absent and the ovarioles are short as in virgin females. Flight muscles intact or later degenerating.
b → A-females:	Inseminated but not yet laying females. Eggs begin to develop, the ovarioles are somewhat elongated, but no corpora lutea are visible as yet.
c-females :	Virgin, not egg-laying females.
C-females:	Virgin females laying haploid eggs (not found in "*L. acervorum* Albarracin" or any other *L. acervorum* population).
d-females:	Virgin alate females.

Only in field-collected A-females of "*L. acervorum* Albarracin" the fat body is distinctly yellow, whereas it is more or less whitish in individuals of the other types. Therefore we were not able in this species to distinguish clearly between young b-females (having mated in the previous season) and the a-females which have spent one or more years in the colonies without becoming reproductive (Buschinger, 1968a; Heinze and Buschinger, 1988). Consequently, "b-females" in this paper include all mated females except for those developing fertility (b → A) and the A-queens. Egg-laying C-females as described in Heinze and Buschinger (1988) lack in this population, as is generally the case in *L. acervorum,* whereas non-laying c-females are quite common.

Mating experiments with sexuals of "*L. acervorum* Albarracin" were performed in flight cages with dimensions of 15 × 20 × 30 cm under daylight conditions. The flight cages were heated either by sunlight or by a 100 W bulb. Formicaries with alate females were put into the flight cages after the temperature there had reached 25 °C. Males were added when most of the females exhibited sexual calling behavior.

Results

Range and habitat specification

"*Leptothorax acervorum* Albarracin" as yet has been recorded only from a mountain range in east central Spain, the Sierra de Albarracin, about 170 km east of Madrid. In this area approximately 120 km^2 are covered nearly completely with an autochthonous pine forest. The highest region is the Sierra Alta (1856 m), however, *L. acervorum* could only be found at elevations of 1500 to 1700 m. The species is patchily distributed within the pine forest, where it could be localized at only five sites as yet. The typical habitat where the species was regularly met with is characterized as old *Pinus sylvestris* forest with an understory of oaks (*Quercus pubescens*). At such sites the colonies inhabit rotting pine sticks lying on the ground. A dense cover of lichens growing on the pines' bark and twigs indicates a humid and rather cool climate all over the year, or at least sufficient dewfall in the night during dry weather. Pubescent Oaks are absent in most parts of the Sierra, and "*L. acervorum* Albarracin" apparently lacks in habitats without an understory of such oaks. This is probably the reason for their patchy distribution in the Sierra de Albarracin with only a few isolated sites. The patches where "*L. acervorum* Albarracin" could be found have a diameter of approximately 100 to several hundred m, and they are between one and five km apart from each other. In the drier parts of the area *L. acervorum* is replaced by *Leptothorax unifasciatus* and *L. nylanderi*. Especially the latter occurs in high population densities of up to three mature colonies per m^2.

Colony- and population structure

Among the 83 samples collected in 1995 and 1996, and also among the nine of 1992, there was no incipient colony without workers. 58 colonies were censused directly after collecting. In May the colonies comprised up to 200 workers (mean: 68.9 ± 54.3) and up to 43 dealate females (mean 11.2 ± 11.3). In September the figures were somewhat higher for females (15.4 ± 10.8) but lower for workers (58.3 ± 40.5), though the differences are not significant (Table 1). Only very few winged sexuals could be detected in the colonies in September 1995. The dealate females of 32 "*L. acervorum* Albarracin" colonies were dissected in order to determine their reproductive status. 15 of the colonies had been collected in late summer 1995 (Table 2), 17 others in May 1996 (Table 3). None of the colonies contained more than one fertile female (reproductive status A), the resident queen. An A-queen was not found in 11 out of the 32 colonies. Females with developing ovaries (status b → A) occurred exclusively in colonies lacking a reproductive queen, with a single exception (# 4 in Table 3).

In queenright as well as in colonies without a reproductive queen variable numbers of b- and c-females were present, on average 8.3 (range 0–20) in late summer, and 5.1 (range 0–23) in the spring sample. The number of inseminated b- (or a-) females in a nest usually exceeds that of the unmated c-females. In late summer the number of b-females in queenright colonies is 8.5 on average, the number of c-females only 1.5. In spring, both these values were lower, the number of b-females being 5.2, and that of c-females 0.85. b-females found in May have mated in the previous summer, or earlier, and have spent all the winter and spring in the nests, since the hibernated larvae which would yield the new sexuals had not even reached the prepupal instar.

The population densities were comparatively low, with about one colony per 10 m^2. The nearest distance between two nests was 1 m, but distances of 3 to 4 m are more usual. In contrast, *L. acervorum* in Germany may reach 17 colonies per 100 m^2, and locally up to 4 per 1 m^2 (Buschinger, 1968 b).

Table 1. Composition of 58 colonies of "*L. acervorum* Albarracin" in fall and spring which were censused immediately after collecting. All colonies comprised at least one dealate female

	(1)	(2)	(3)
September 1995	58.3 ± 40.5	24 of 27	15.4 ±10.8
May 1996	68.9 ± 54.3	26 of 31	11.2 ± 11.3

(1) mean number of workers ± SD per colony.
(2) number of colonies with more than one dealate female.
(3) mean number of dealate females ± SD per colony.

Mating and readoption of newly mated females

Sexuals of "*L. acervorum* Albarracin" mate readily in the laboratory, as is the case with, e.g., central European *L. gredleri* and *L. muscorum* (Buschinger and Alloway, 1979), or the North American *Leptothorax* sp. A (Heinze and Buschinger, 1989). In contrast, *L. acervorum* sexuals from central European populations never mate under laboratory conditions (Buschinger, 1971). Males and females of

Table 2. Reproductive status of females in colonies collected on 9 and 10 September 1995

colony-number	A-females	b → A-females	b-females	c-females
1	1	–	10	7
2	–	1	3	6
3	1	–	18	2
4	1	–	18	2
5	–	–	2	2
6	1	–	–	–
7	1	–	7	–
8	–	7	12	1
9	1	–	11	–
10	–	–	2	–
11	–	–	1	–
12	–	–	1	–
13	–	–	14	1
14	1	–	2	–
15	1	–	2	1
$\sum/\phi$	8/0.53	8/0.53	103/6.86	22/1.46

Table 3. Reproductive status of females in colonies collected between 17 and 21 May 1996

colony-number	A-females	b → A-females	b-females	c-females
1	1	–	–	–
2	1	–	1	–
3	1	–	2	–
4	1	2	19	4
5	1	–	7	–
6	1	–	9	–
7	1	–	17	1
8	1	–	–	–
9	1	–	1	4
10	1	–	6	–
11	1	–	3	2
12	–	1	–	–
13	1	–	1	–
14	–	1	–	–
15	1	–	2	–
16	–	–	3	–
17	–	1	4	1
Σ/ϕ	13/0.76	5/0.29	75/4.41	12/0.7

"*L. acervorum* Albarracin" become active in the incubators about one or two hours after the morning rise in temperature. At this time, after transfer of the formicaries into the flight cages, mating behavior could be studied under natural daylight. When the temperature had reached 25 °C, the winged females left the nest chambers. After a short period of walking around in the arena they usually climb the walls of the flight cage and perform a stationary sexual calling behavior as is known from other formicoxenine ants, the so-called "Locksterzeln" (Buschinger, 1971). Other females exhibit their sexual display already at very short distances from the nest entrance, for example on the edge of the open three-chambered formicary. Flying before the sexual calling could never be observed.

The males are always highly aroused when put into a flight cage with calling females, and usually they try immediately to mount a calling female and to insert the genitals. During the first contact both partners antennate each other intensively. After the insertion of the genitals the male tilts backwards and remains more or less immobile in this position. The female usually sits still during the copulation, the male sometimes grooms its antennae. After 30 to 90 seconds the female turns round and bites into the males' gaster, which typically ends with separation 10 to 20 seconds later. Copulations could be observed until six or seven hours after the morning rise in temperature, i.e. for a daily period of four to five hours, though most copulations took place between one and two hours after the first females began to exhibit sexual calling. After that time all females returned to their nests, though the temperatures of 25 to 30 °C in the flight cage were still high.

Females of "*L. acervorum* Albarracin" mate only once. Newly mated females directly try to return into the nest of their mother colony. After a successful copulation the inseminated females shed wings within one day. Dealate females were never seen performing sexual calling behavior. A few females, however, which after mating had retained their wings showed sexual calling again in the following morning. Dissections of four such females revealed that their receptacles were empty. Evidently the first mating had not been successful. If mating was successful, newly inseminated females reject all males that try to mount them on their way back into the nest. Such a female would press the gaster to the ground, and it would not respond to antennation of a male trying to mount her again. We therefore believe that "*L. acervorum* Albarracin" is monandrous.

Fate of readopted mated females

Newly mated (b-)females returning into their colonies do not elicit aggressive behavior of nestmates. Sometimes returning females were groomed by workers in the nest chamber. Several days later, however, and moreoften after the hibernation of the colonies, some fighting could be observed between newly mated females and workers. In these instances a readopted female would be pulled out of the nest by a few workers and sometimes also by non-laying females, and eventually killed. 15 such expelled females were dissected. They all were mated and had developing ovarioles (reproductive status b → A). b-females with short ovarioles were never attacked, as well as virgin c-females. We did not observe aggression of the laying queen towards mated nonlayers, but the colonies were not specifically monitored for detecting such events.

In the first few colonies collected in September, 1992, a small number of mated females were observed which apparently had spent a longer time in the colonies, alongside an A-queen. The colonies were kept alive, hibernated as indicated in "Material and methods", and most dealate females were dissected in the following first laboratory summer when the colonies had pupae and eggs:

Colony # I had four dealate females. One physogastric female, apparently the A-queen, was left alive. Among the other three females two were developing fertility (b → A), and one was a typical a-female with slightly yellow fat body in the thorax. The dissectioning was done when pupae were present but no sexuals had hatched as yet.

In colony # II, again with four dealate females in the first laboratory summer, also one physogastric female was left alive (probably an a- or b → A-female), whereas among the three which were dissected, one was the A-queen, one was in status b → A, and one was an a-female, though with white fat body.

Colony # III in the first laboratory summer comprised a physogastric female (probably the A-queen, which was not dissected) and two a-females with yellowish fat body.

The latter colony was devided into two in the fifth laboratory summer (in artificially shortened annual cycles!). Alates had been produced in every summer, and several dealate females remained in the nests. After another four laboratory cycles all dealate females of the two colonies were dissected:

Colony III A comprised 14 females, among them 1A-, 5 a-, 3 b-, 4 c- and 1 d-female; in colony III B a total of 27 dealate females were found, among them 1 A-, 15 a-, 6 b-, 4 c- and 1 d-female.

These observations suggest that a fraction of mated female offspring is expelled from the colonies soon after readoption, a larger fraction remains there for hibernation until dispersal in spring, and some may coexist with the A-queen for longer time. Such colonies then are functionally monogynous according to the definition (Buschinger, 1968 a). Together with the composition of field-collected colonies in fall and spring these results indicate that a control behavior in "*L. acervorum* Albarracin" prevents the transition to polygyny and ensures a permanent monogyny. The behavior of the colonies towards mated and readopted young females, however, appears highly flexible.

Discussion

*"*L. acervorum *Albarracin": Polygyny, functional monogyny, or something else?*

For the discussion of a social organization as observed in the Spanish *L. acervorum* population we strongly emphasize that terms like functional monogyny, polygyny, queen etc. must be strictly applied according to unambiguous definitions. We here apply a functional definition of these terms (cf. Buschinger, 1987 a; Bourke and Franks, 1995). Any more liberal use of such terms, or a blending of functional and morphological caste definitions will give rise to confusion and misconception (cf. Buschinger, 1974 c, 1987 a; Buschinger and Crozier, 1987). Thus, we do not understand functional monogyny as an instance of "variation in queen number" (e.g., Seppä et al., 1995 for the functionally monogynous *Leptothorax sp.* A). It also cannot be viewed as a form of polygyny (cf. Lipski et al. 1994; Stille, 1996), since the latter is defined as coexistence of several mated and fully reproductive females in a colony. Monogyny means that only one mated female, the queen, is reproductive in a society, which may or may not comprise virgin or mated non-laying females in addition.

Our results clearly reveal that *L. acervorum* from the Spanish Sierra de Albarracin is monogynous, never having more than one reproductive (A-)queen in a nest. The monogynous colony structure in this population was also confirmed by Heinze et al. (1995 a): Their isozyme data revealed a nestmate worker relatedness of r = 0.72 ± 0.142 for "*L.acervorum* Albarracin", which closely matches the theoretical value of 0.75 for monogynous colonies with monandrous queens.

A fraction of field-collected colonies (Tables 2, 3) without an A-queen but containing a-, b- or b → A-females may represent newly formed daughter colonies due to budding, though in a few instances the A-queen may have recently died or was lost during collecting. Most queenright colonies, both in the fall and in the spring samples, also comprise a variable number of dealate females, some of which are not inseminated (c-♀♀), but most are inseminated (b- or a-♀♀). Behavioral observations have demonstrated that females with growing ovarioles and oocytes (b → A-♀♀) in queenright colonies may be attacked by workers and/or c-females, and eventually are evicted from the nest. Presumably it is a laboratory artifact when such females are killed; in the field they most probably emigrate and try to establish own colonies.

However, not all the b-females of "*L. acervorum* Albarracin" develop fertility immediately after mating, or after a first hibernation in the mother colony. A few females were found having the flight muscles replaced by slightly yellowish fat body, and thus corresponding to status "a", or having survived in laboratory colonies for more than just one hibernation. Such potential queens regularly occur in colonies of, e.g., European *L. gredleri* (Buschinger, 1968 a) and *Formicoxenus nitidulus* (Buschinger and Winter, 1976), and of the North American *Leptothorax* sp. A. (Heinze and Buschinger, 1988). The permanent coexistence of "replacement" or "supernumerary potential queens" alongside the A-queen is characteristic of functional monogyny (Buschinger, 1968 a; Bourke and Franks, 1995). Thus, functional monogyny according to the definition does occur in "*Leptothorax acervorum* Abarracin".

Functional monogyny has been claimed for other populations of *L. acervorum* already, e.g., for *L. acervorum* from Hokkaido (Ito, 1990): A fraction of the colonies which were collected between May and October, contained one reproductive queen each and several mated but not laying dealate females in addition. Though it is not exactly indicated which colonies were collected at what season, it seems that mated non-layers (a-♀♀) are present all over the year. Some colonies had one or two mated "supplementary egg-layers" alongside a fully reproductive queen. From the description we conclude that they correspond to our type b → A. Heinze and Ortius (1991) have studied a facultatively polygynous *L. acervorum* population from Alaska, however, in the lab they recorded "aggressive interactions similar to those observed in functionally monogynous nests of *Leptothorax* sp. A and *L. gredleri*". According to our observations in "*L. acervorum* Albarracin" such aggression may be observed not only between a- and A-females, but may be directed towards young females in the process of developing fertility, prior to their emigration or eviction from the colony. Seppä et al. (1995) inferred from electrophoretic data a monogynous reproductive system for populations of *L. acervorum* from Finland. Additional dealate females from their colonies were not dissected, however, thus functional monogyny, as suggested in this paper, was not proven.

Functional monogyny in "*L. acervorum* Albarracin" is combined with a kind of "extended brood care" (Rosengren et al., 1993), the intranidal hibernation of mated young females. Such a behavior had been unknown when functional monogyny was defined for ants (Buschinger, 1968 a). Intranidal hibernation of mated female offspring, but not functional monogyny, is common in several (parasitic) *Epimyrma* species (Buschinger, 1989), and it occurs in the Spanish *Leptothorax* (*Myrafant*) *gredosi* (Buschinger, 1995).

We conclude that functional monogyny according to the definition for ants (Buschinger, 1968 a) may occur in the Japanese and the Alaskan populations of *L. acervorum* as well. The presence of numerous mated females alone, however, which leave the nests, or are forced to leave them after hibernation, should not be confused with functional monogyny, where a-females stay with the mother colony sometimes for years. The *L. acervorum* populations considered here seem to employ a mixed strategy of both functional monogyny and intranidal hibernation with spring dispersal of the majority of young mated females.

Ecological correlates of functional monogyny and intranidal mated offspring hibernation

"*Leptothorax acervorum* Albarracin" is the first European population of *L. acervorum* in which functional monogyny in accord with the definition has been established, though Seppä et al. (1995) found high nestmate worker relatedness also in Finnish populations with "multiple females". The dealate females, however, had not been dissected, the colonies thus may have been monogynous with additional virgin females (= pseudopolygynous), as is common in *L. acervorum* (Buschinger, 1967, 1968 a, 1974 c).

It is remarkable that the two other populations for which functional monogyny has been claimed, from northern Japan and from Alaska, are living at the northern boundaries of the species' range. In contrast, "*L. acervorum* Albarracin" represents the southernmost known population in Europe, living close to 40^0 latitude. It seems to be isolated from the next ordinary (i.e. facultatively polygynous) *L. acervorum* population in the Pyrenees by more than 200 km.

Are there ecological conditions which might explain the reproductive strategies of "*L. a.* Albarracin"? According to Heinze (1992) and Bourke and Heinze (1994), functionally monogynous ants occur predominantly in isolated, patchy habitats. Both facultative polygyny and functional monogyny are expected to develop when dispersal risk is high for the young queens, and when solitary colony foundation becomes difficult, e.g. due to competition, queen predation and nest site limitation.

In the case of "*L. a.* Albarracin" there is little evidence of the latter. We always had to check numerous seemingly suitable twigs for eventually finding a colony. Internest distances were high enough to exclude also competition. Queen predation in the Sierra de Albarracin is probably not different from central European habitats of facultatively polygynous *L. acervorum*. The rareness and restricted size of suitable habitat patches, however, seems to be an important ecological constraint which could select for philopatry and hence stationary sexual behavior of the females. A second constraint may be a comparatively short summer season, similar to boreal or alpine regions: Despite the low latitude of the Sierra de Albarracin, within the Mediterranean zone, the climate at 1500–1800 m is evidently harsh with winter conditions from the end of September until May. In extended boreal forests it is believed that such conditions favor the development of (facultative) polygyny, as is the case with "typical" *L. acervorum*. Combined with habitat patchiness the ecological constraints for *"L. acervorum* Albarracin" are comparable to those for *Leptothorax* sp. A (Heinze, 1992), which is functionally monogynous, too.

In addition to functional monogyny, and even more pronounced, we observed intranidal offspring hibernation, with mated young females joining the mother colonies for some time. Mating in the vicinity of the nests enables these females to return and to remain there at least until they begin to develop fertility, either in the fall or after the hibernation. In the latter case, it is certainly an advantage to stay in the natal nest over winter instead of hibernating alone or with a small first brood: The survival rate of single queens is considerably lower than that of specimens overwintering in clusters of nestmates (Heinze, 1992; Heinze et al., 1996). And even if the young females in spring should not be accompanied by sister workers they would have all the favorable summer season for colony foundation instead of just a few weeks after mating, e.g., in August/September. For "*L. a.* Albarracin", however, we must recall that single founding females as yet were not observed.

Evolutionary aspects

Sexual calling is not uncommon in *Leptothorax* (s.str.) and related parasitic genera. Alate females of central and western European *L. acervorum* are known to land, after more or less extended nuptial flights, and to take up a calling posture, releasing a sexual pheromone from the poison gland for attracting males (Buschinger, 1971; Franks et al., 1991). The behavior of the Spanish population is perhaps derived from that of central European *L. acervorum*, which may have retained the swarming flight as an ancestral trait, or vice versa.

With respect to functional monogyny, Heinze and Ortius (1991) speculate that "polygyny and functional monogyny are not mutually exclusive but rather represent a continuous series of colony structures with varying degrees of queen tolerance, ranging from peaceful coexistence to total incompatibility". Notwithstanding the attractiveness of this hypothesis we can imagine also that functional monogyny is derived from "extended brood care", from intranidal hibernation of mated offspring until the next spring. It seems to be a small step from this condition to developing functional monogyny, where a fraction of the b-females remains in the mother nest for longer time, becoming a-females and "waiting" for a chance to replace the A-queen. Similarly, readoption of mated young females is a prerequisite for developing secondary polygyny. Intranidal mated offspring hibernation as was observed in "*L. a*. Albarracin" thus could represent an evolutionary predecessor both of functional monogyny and secondary polygyny.

Finally, one characteristic of the subgenus *Leptothorax* shall be addressed which as yet has received little attention in discussions on their social structures (cf. Heinze, 1992, and the exhaustive discussion in Bourke and Heinze, 1994), namely the very small size difference between queen and worker. Some data on queen/worker thorax volume ratios in *Leptothorax*- and *Myrafant*-group species can be found in Stille (1996). For size relations of queens, males and workers see also Buschinger (1967, 1974b). *Leptothorax acervorum* queens have to forage during independent colony foundation, which in fact does occur in central European populations of this species (Buschinger, 1968a, 1974b). Non-claustral colony foundation of solitary queens certainly increases their predation risk considerably. Since all species of the *Leptothorax* s. str.-group including their parasitic genera exhibit this small queen-worker size difference, it is probably not a somehow adaptive trait but represents a phylogenetically primitive condition (Buschinger, 1967). Other features, such as comparatively large males with long antennae, and four larval instars (vs. three in the *Myrafant*-group, Buschinger, 1981, 1987b) also seem to represent ancestral conditions in the tribe Formicoxenini. The relatively small size of the queens thus may explain that most species of this group have developed life histories with some kind of dependent colony foundation, be it (facultative) polygyny with subsequent budding, functional monogyny, intranidal mated offspring hibernation, or inquilinism and dulosis. Species of the *Leptothorax* subgenus *Myrafant* on the other hand have much larger queens with wider thorax as compared to workers. The queens are capable of claustral colony foundation (Buschinger, 1974b). Therefore it is not surprising that *L. (M.) unifasciatus* and *L. (M.) nylanderi* can establish strictly monogynous populations in the vicinity of the habitats of "*L. acervorum* Albarracin".

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