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Monogyny in *Leptothorax slavonicus* (Hymenoptera: Formicidae)

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Abstract. Monogyny in *Leptothorax slavonicus* Seifert, 1995 (Hymenoptera: Formicidae: Myrmicinae) was studied under field and laboratory conditions. None of 238 colonies from the Czech Republic and Slovakia were polygynous. Experiments based on mixing two monogynous colonies and offering two queens to an orphaned colony showed that this species is capable of forming genetically rather heterogeneous but never polygynous colonies. Fusion of unrelated colonies and the adoption of alien queens occurred, but the workers always regulated number of queens to one. The workers can recognise their nestmates in experimentally mixed colonies.

Ethology, monogyny, fusion of colonies, recognition of nestmates, Hymenoptera, Formicidae, *Leptothorax slavonicus*, Central Europe

INTRODUCTION

This paper presents the results of an experimental study of monogyny in a recently established leptothoracine ant species *Leptothorax* (*Myrafant*) *slavonicus* Seifert, 1995 (Myrmicinae).

The number of queens (see Terminology) present in a colony of eusocial insects markedly affects its genetic composition. About 50% of ant species form **monogynous colonies** (one queen) while the others may form **polygynous colonies** (several queens) (Buschinger 1974). There are **obligatorily monogynous** species, e. g. *Lasius* (*Lasius*) *niger* (Linnaeus, 1758), *Camponotus* (*Camponotus*) *ligniperda* (Latreille, 1802), *Leptothorax* (*Myrafant*) *unifasciatus* (Latreille, 1798); **facultatively polygynous** species which form both monogynous and polygynous colonies, e. g. *Leptothorax* (*Leptothorax*) *acervorum* (Fabricius, 1793), *Leptothorax* (*Leptothorax*) *muscorum* (Nylander, 1846), and **obligatorily polygynous** species, e. g. *Formica* (*Formica*) *polyctena* Förster, 1850 (all cf. Buschinger 1967, 1968, 1974).

Several unusual cases have been described in *Leptothorax* Mayr, 1855. The **functionally monogynous** colony contains several inseminated females only one of which is the queen and lays fertilised eggs in a facultatively polygynous species *Leptothorax* (*Leptothorax*) *gredleri* Mayr, 1855 (cf. Buschinger 1967, 1968, 1974, Heinze & Buschinger 1988) and some North American species of *Leptothorax* s. str. (cf. Heinze & Buschinger 1986, 1988). **Regular monogyny** is a switch of monogynous colonies to polygyny by fusing colonies (usually observed in polygynous species, cf. Hölldobler & Wilson 1990) when suitable nest sites are scarce; this phenomenon was observed in the usually monogynous species *Leptothorax* (*Myrafant*) *nylanderi* (Förster, 1850) (cf. Buschinger 1967, 1968, 1974). Fusion of colonies in this species was observed also by Foitzik & Heinze (1998, 2000); however, polygyny is only temporary and results in intraspecific slavery (Foitzik & Heinze 1998, 2000) – one of the queens is subsequently eliminated, and workers of her colony serve in the alien colony.

Study of the above phenomene is important for understanding the role of kin-selection and other factors shaping the evolution and maintenance of eusociality.

The existence of monogynous/polygynous strategies in *Leptothorax* (*Myrafant*) *slavonicus*, a species only recently (Seifert 1995) separated from *L.* (*M.*) *nylanderi*, has not been studied. Our investigations began with a study of populations of "*L.* (*M.*) *nylanderi*" from Bohemia and Slovakia. As preliminary observations (Kašpárek unpubl.) suggested, and subsequent field and laboratory studies confirmed (Tichá 1992) these populations are less tolerant of several queens in a colony than West-European populations (Donisthorpe 1927, Chauvin 1947, Buschinger 1967, 1968). Seifert (1995, 1996) studied the morphology of East-European populations of "*L. nylanderi*", and concluded (supported by genetic research carried out at the University of Lund-Douwes pers. comm. in Seifert 1995) that the populations on the eastern side of the line Schwerin–Magdeburg–Leipzig–Döbeln (Germany) belong to an unrecognised parapatric species, *Leptothorax slavonicus*. It was first assigned subspecific rank, *Leptothorax nylanderi slavonicus* in 1995, and that of a distinct species in 1996. The populations we studied belong to this species.

This discovery may account for the differences in behaviour of Czech, Moravian and Slovak populations of the above species, and have stimulated other ethological and sociobiological studies of *L. slavonicus*, a species not previously studied in this way (except the seminar study of Tichá 1992).

MATERIAL AND METHODS

1. Terminology (see the Introduction as well)

Queen – dealate, fully fertile, egg-laying female, parent of next generations of females, strongly attractive for her nestmates, dominant in the colony (in *Leptothorax slavonicus* the queen is located in a centre of the colony on a heap of brood, and does not take part in the labour);

worker (in *L. slavonicus*) – wingless female; if egg-laying, then producing non-fertilised eggs only; co-operating with nestmates and performing basic tasks necessary for the well-being of the colony and maintenance of the nest;

brood – juvenile stages;

orphaned colony – colony lacking a queen;

regulation towards monogyny – reduction in the number of queens in a colony resulting in monogyny;

recruitment – increased motor activity of some individuals, which touch the other ants with their antennae and legs, leading to their mobilisation;

tugging – mutual pulling in opposite directions by two (or more) workers, or pulling the queen by a group (groups) of workers;

accepted queen – the female chosen as a queen after fusion of colonies and fully satisfying the above criteria of a queen;

neutral formicarium – clean formicarium uninhabited before the experiment.

2. Origin of the colonies used in this study

Leptothorax slavonicus – 238 colonies were collected in June to September over the period 1989–2000.

Czech Republic – 176 colonies: Mělník env. (14° 32' E, 50° 28' N, Nat. grid No 5553 [after Pruner & Míka 1996]); Praha (14° 22' E, 50° 03' N, No 5952); Mohelno env. (16° 11' E, 49° 07' N, No. 6863), Znojmo env. (15° 54' E, 48° 59' N, No. 7061). Slovakia – 62 colonies: Piešťany env. (18° 53'E, 48° 18' N, No. 7769) (Fig. 1).

Colonies of this small ant usually contain only several dozen individuals, and inhabit small cavities, mainly hollow, dead tree twigs and acorns. They were collected mainly in deciduous (*Quercus*, *Carpinus*), mixed and pine woods. Complete colonies, mostly still in their nest-sites, were placed into plastic bags (when this was not possible, the ants were collected in vials by using an aspirator), and then transferred to the laboratory.

3. Cultures

Number of individuals (queens, alate females, workers, males, brood) in each colony was counted, and the ants were then transferred into tripartite plastic formicaria. Here they were bred (according to Buschinger 1967) and manipulated. Dimensions of the formicaria: cylindrical nest-site, r – 75 mm, l – 135 mm; three types of arenas – 120×80×30 mm, 170×90×70 mm, 270×90×70 mm – each type was used for ten experiments of Series 1 (see

below) and a 170×90×70 type was used in the Series 3 experiments. For the Series 2 experiments an arena sized 120×80×30 mm was used; the flat glass chambers (dimensions 20×20×3 mm) with a millimetre grid were used as the nest-site - this arrangement facilitated observation of ant movements.

4. Marking ants

All the queens in Series 1 were marked by amputation of the last tarsal segment of some of the legs, the queens and the workers used in the Series 2 experiments were marked with acetone nail varnish applied to the thorax or abdomen (manipulation during marking ants as described by Heinze 1993, 1996).

5. Experiments

SERIES 1. Two monogynous colonies (usually of different size) were placed in the arena of a neutral formicarium. Behaviour of the ants was monitored visually, continuously for the first 4 hours, over the next 10 hours at 15 minutes intervals, and than at intervals of 6 hours up to the termination of the experiment. This experiment was replicated 30 times and each lasted 6 weeks. **Questions addressed**: When nest-sites are scarce do colonies of *Leptothorax slavonicus* fuse (as described for *L. nylanderi* by Buschinger 1967, 1968 and Foitzik & Heinze 1998, 2000)? If they do, does queen regulation occur?

SERIES 2. Ten workers and their queens were marked and used instead of the colonies in experiment identical with Series 1 experiments. There were 5 replicates of this experiments. Timing of the observations was as in Series 1. Duration of each experiment was 6 weeks. **Questions addressed**: Does the original nestmates continue to recognise one another, and does any hierarchy develop in the mixture?

SERIES 3. Two foreign queens were added to an orphaned colony. This was repeated ten times. Observations were as in Series 1 and 2. Duration of each experiment was six weeks. **Questions addressed**: What is the behavioural response of orphaned colonies to foreign queens and is there any regulation towards monogyny when foreign queens were adopted?

6. Statistical assessment of results

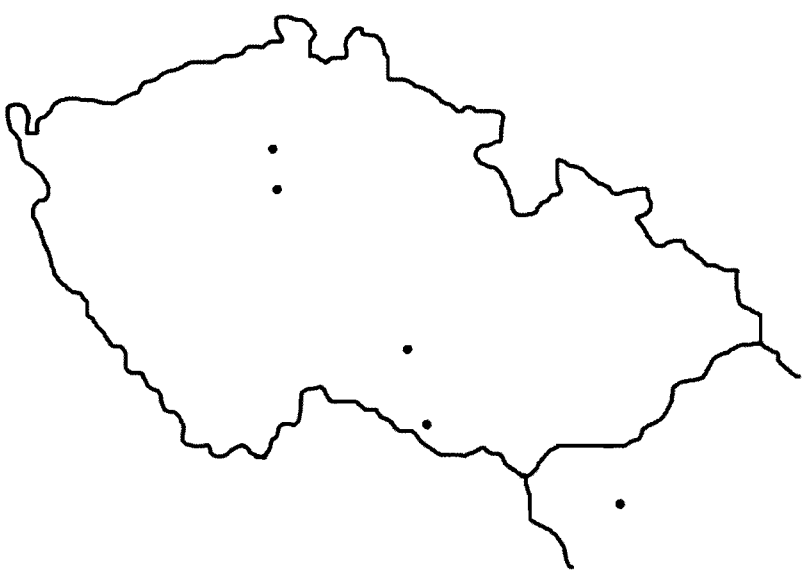

Fig. 1. Localities in the Czech Republic (CZ) and Slovakia (SK) where the colonies of *Leptothorax slavonicus* Seifert used in the experiments were collected.

Tab. 1. Summary of experimental results. Explanations: N – number of experiments, NRM – number of regulations to monogyny (= elimination of supernumerary queens), NF – number of fusions of two monogyous colonies, N2M – number of originations of two monogynous colonies, N0 – number of experiments resulting in orphancy of the colony, NAQ – number of adoptions of an alien queen; * – adoption before orphancy, ** – adoption of a winning by workers from the colony of the eliminated queen after the fusion

design	N = 100%	NRM	NF	N2M	NO	NAQ
series 1	30	24	24	6	1*	24**
series 2	5	0	0	5	0	0
series 3	10	6	0	0	4	6

Fisher exact test from Statistica 93 was used in the statistical evaluation of the choice of a queen.

RESULTS

1. Monogyny of *Leptothorax slavonicus* in the field

All of the 238 colonies examined (100%) had only one queen.

2. Experiments (Tab. 1, Fig. 2)

SERIES 1. The mixing of two monogynous colonies (30 experiments) resulted in the colonies fusing to form one colony, and the workers reducing the number of queens to one in 24 cases (monogynous colonies formed in all cases except one, in which the accepted queen died before the termination of the experiment, and an orphaned colony resulted). The colonies separated and formed two monogynous colonies, each in a different part of the formicarium in 6 cases. A digynous colony was never formed.

SERIES 2. The mixing of two marked groups of ants (5 experiments) resulted in the ants of the different colonies living in one formicarium, but as two autonomous and distinct fractions. No case of fusion was observed.

SERIES 3. When two foreign queens were offered to an orphaned colony (10 experiments) one queen was adopted, the other eliminated in 6 cases, and both queens eliminated, i. e. the colonies remained without queen, in 4 cases.

3. Behaviour of ants during experiments

3. 1. Experimental Series 1

The ants first explored the arena and nest-site, which was accompanied by aggressive interactions between the workers and attacks on both queens, then formed a cluster around each queen, and either retained this separation up to the termination of the experiment, or the clusters inhabited the nest-site, formed a fused colony, and regulated the number of queens to one. Six successive behavioural phases (unless stated otherwise) were identified in nearly all the experiments : a-b-c-d-e-f, or a-b-c-d-g-h.

(a) **Exploration.** During this phase the ants became acquainted with the new situation, arena and strangers. This was associated with increased **mobility** with **exploratory behaviour** prevailing over other activities. **Ritualised attacks** in which the mandibles were opened wide against strangers, but there was no body contact, were common. **Grooming of the queens by workers** lasted until one of the queens was eliminated. Duration of this phase was about 15 minutes.

(b) **Aggregation of workers around the alien queen** during which the workers seized the legs, antennae, head of the queen and **dragged** it across the arena or **transported** it by holding it by its petiole and **attacked** it with their mandibles. **The queens** characteristically remained **passive** and **rigid** during transportation. At the same time the workers **explored the nest-site** and **transported**

the brood, first into heaps near the shaded part of the arena and later into the nest-site, and transported their queens to the heaps of brood. **Trophallaxis** among workers was observed until the experiment was terminated. Both queens were fed prior to regulation, when only the accepted one was fed. In cases when the colonies separated, feeding of both queens continued. **Recruitment** occurred in 18 experiments. **Individual conflicts** took the form of **tugging** (27 experiments) and **fighting** (24 experiments); **group conflicts** also involved **tugging** (15 experiments) and **fighting** (7 experiments), but rarely **stinging** (3 experiments). In two cases both the queens used their sting in mutual fights that lasted 20 or 40 seconds (no evident relation with any other factor). Duration of this phases was 10 minutes to 2.5 hours.

(c) **Formation of two monogynous colonies** occurred when the brood was divided into two heaps, each of which was occupied by one of the two queens accompanied by a group of workers. This was followed by the subdivision of the remaining workers in two groups. Duration of this phase was 10 minutes to 2.5 hours.

(d) **Decreased activity** occurred when the ants in both groups remained immobile for 25 minutes to 24 hours.

The next two successive phases occurred in one of the two variants.

VARIANT I (e, f)

(e) **Occupation of the nest-site by both the colonies.** This was accomplished by **the movement of individual ants**, or their passive **transport** in the supine position (head or the petiole held by other ants) along with the transfer of both the queens. The resulting colony was **seemingly digynous**, however egg-laying by the queens was never observed. This took 23 hours to 22 days to complete.

(f) **Return to monogyny by the elimination of one of the queens** at the periphery of the arena occurred in 24 of 30 experiments, usually within 23 days of the start of the experiment. This was

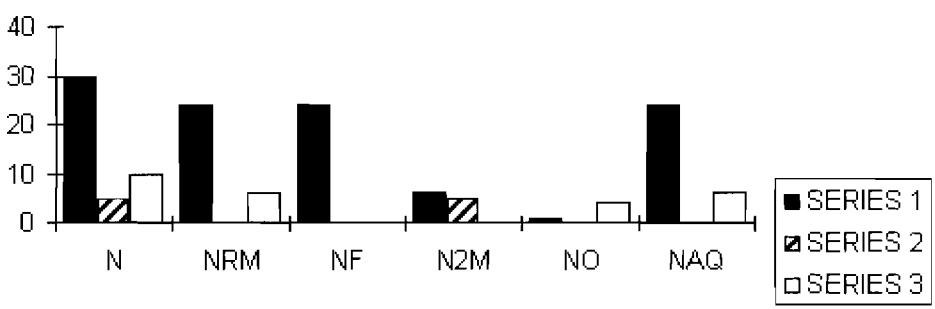

Fig. 2. Results of experiments series 1–3. Explanations: N – number of experiments, NRM – number of regulations to monogyny (= eleimination of supernumerary queens), NF – numbers of fusions of two monogynous colonies, N2M – number of originations of two monogynous colonies, N0 – number of experiments resulting in orphancy of the colony, NAQ – number of adoptions of an alien queen.

achieved by workers **attacking** one of the queens with their mandibles, never with their stings. The eliminated "queen" died while being transported (3 out of 24) or immediately after (13 out of 24), or was kept in isolation at the periphery of the arena, without grooming and trophallaxis (8 out of 24). The workers action was co-ordinated, with no mutual conflicts, and the rejected "queen" remained passive. The accepted queen was adopted by the workers and monogyny persisted until the termination of the experiment. This phase took between 10 minutes to 8 hours to complete.

VARIANT 2 (g, h)
(g) **Occupation of the nest-site by one colony** while the other remained in the arena, which was accepted as a "nest-site" on 6 occasions. This phase lasted for between 10 minutes and 4 hours.
(h) **Return to monogyny.** The two colonies functioned independently and behaved as two distinct monogynous colonies until the termination of the experiment.

Choice of queen
There was a relation between the actual sizes of the experimental colonies and choice of accepted queen (Fig. 3). After fusion of the colonies in the experiments of Series 1 (24 occasions) the queen of the larger colony was chosen in 18 cases, and that of the smaller colony in 6 cases ($c^2 = 6$, $p = 0.0143$, $df = 1$).

3. 2. Experimental Series 2
The behaviour of ants was very similar to that in Series 1, but both the colonies retained their autonomy and never fused. Conflicts only occurred between members of different colonies, and the ants were always able to recognise their nestmates (interactions: allogrooming, trophallaxis, etc.) from non-nestmates (interactions: both ritualised and true attacks). The recognition was not impaired even immediately after marking the ants with nail varnish, the odour of which probably interfered with nest scents. The resulting two monogynous colonies were formed exclusively from the original nestmates in all five experiments.

3. 3. Experimental Series 3
These experiments resulted either in adoption of one of the queens or elimination of both, never in digyny. Even in these experiments 5 successive behavioural phases were regularly observed either in sequence a-b-c-d-e, or a-b-c-d-f.
(a) **Identification of the queen.** Workers approached a queen, touched it with their antennae, departed, etc. This phase lasted about 30 minutes.
(b) **Aggregation of workers around queens.** Workers formed clusters around quite **passive queens, seized them, transported and attacked them with their mandibles** etc., as in the previous experiments, including the same kind of conflicts between the workers (sting never used), i.e. ritualised attacks (6 out of 10 experiments), tugging (4 out of 10) and fighting (3 out of 10 experiments), and group tugging (1 out of 10) involving maximally 4 individuals. Duration of this phase was 30 minutes to 3 hours.
(c) **Decreased activity.** The majority of the workers joined one of the groups around the queens, and remained stationary. This phase lasted far from 55 minutes to 8 hours.
(d) **Intermediate phase with two "queens".** Formation of a **seemingly digynous** colony in the nest-site, but the queens did not lay eggs. Duration of this phase was from 5 hours to 6 days.

VARIANT 1
(e) **The establishment** (6 experiments out of 10) **of monogyny.** One of the two "queens" in the colony was attacked in the nest-site and **transferred to the periphery and eliminated.** This queen died in 4 cases (out of 6) or was kept in isolation at the periphery of arena without grooming and

trophallaxis until the termination of the experiment in 2 cases (out of 6 cases) . This occurred not later than 7 days after the start of the experiment. Duration of this phase was from 30 minutes to 6 hours. The remaining queen was adopted and the colony functioned as a monogynous colony until the end of the experiment.

VARIANT 2

(f) **Elimination of both "queens" and return to orphancy** (4 experiments out of 10). Within 6 days both "queens" were attacked, eliminated and died. This phase lasted far from 3 hours to 2 days. The orphaned colony remained in this state up to the end of the experiment.

DISCUSSION

Both field observations and laboratory experiments have shown that *Leptothorax slavonicus* is an **obligatory monogynous species**, as are many other species of the subgenus *Myrafant* Smith, 1950. The regulatory mechanisms restor monogyny reliably in cases when in a colony occur two queens. Monogynous colonies may fuse, regulate number of queens and form genetically heterogeneous colonies. This occurs in *Leptothorax nylanderi* (cf. Foitzik & Heinze 1998, 2000) where it is regarded as intraspecific slavery.

Frequent finds of wood cavities resembling empty nest-sites of *L. slavonicus* in winter (Kašpárek & Tichá unpubl.) may suggest colony fusion occurs in this species under natural conditions. Hence we cannot exclude existence of intraspecific slavery in this species. Moreover, our experiments indicate that nest-site limitation plays a role in the fusion of colonies of *L. slavonicus* (as in *L. nylanderi*) – first the two colonies attempt to live independently, but after some time elapses they occasionally fuse.

However, *L. slavonicus* seems less tolerant than *L. nylanderi* of even the temporary presence of several queens in a colony. This is supported by a faster reduction in the number of queens than in the latter species. Foitzik & Heinze (1998) recorded the survival of several "queens" in one colony of *L. nylanderi* for more than 64 days, while in our experiments on *L. slavonicus* the regulation towards monogyny took place within 23 days.

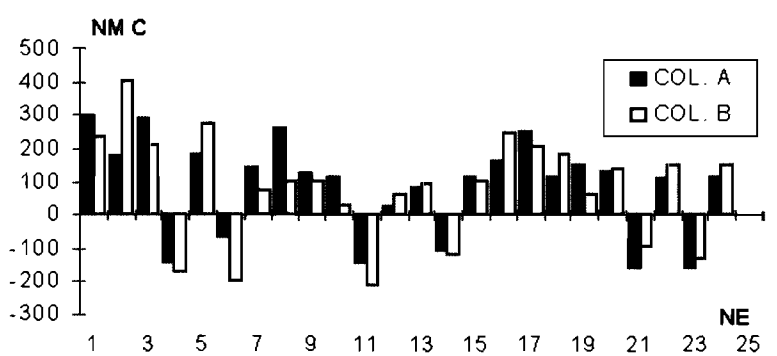

Fig. 3. Choice of the queen. Explanations: NE – number of experimental colonies, NMC – number of members of the colony; negative values = the winning queen from smaller colony.

This difference was observed by Kašpárek (pers. comm.) and Tichá (1992) prior to the taxonomic separation of the two species, and we then hypothesised that "*L. nylanderi*" consists of two or more genetically and ethologically distinct populations. Independently of this hypothesis, this was proved by morphological and genetic studies, which revealed it consisted of two parapatric species. The West European *L. nylanderi* (type locality Aachen, Germany *fide* Radchenko 2000) and the Central and East European *L. slavonicus* (type locality Kr. Görlitz, Schönau-Berzdorf, Hutberg; cf. Seifert 1995, Radchenko 2000). The uncertainty of several authors (Donisthorpe 1927, Chauvin 1947, Buschinger 1967, 1968, Foitzik & Heinze 1997, 1998, 2000, Plateaux, pers. comm.) concerning monogyny/polygyny and monoandry/polyandry of colonies of West European populations of *L. nylanderi* (Chauvin 1947, Plateaux 1970, 1978, 1981, Foitzik et al. 1997) indicate the need for morphological and genetic studies of metapopulations of this species in regions not yet investigated and to re-investigate its ethology.

The second series of experiments showed that the workers of *L. slavonicus* consistently recognise nestmates from non-nestmates, even under conditions that probably impair recognition of nest scent, in this case the presence of acetone vapours. Nestmate recognition in ants is based on presence of nest-specific odour which may be individually borne or collectively shared and transferred (*Gestalt*) (Crozier & Dix 1979). This odour involves discriminators recognisable by all the members of a colony, e. g. cuticular hydrocarbons (e. g. Bonavita et al. 1996, 1997, Meskali et al. 1995a, b), polar cuticular lipids (Franks et al. 1990), food quality (Jutsum et al. 1979), a nest material (Breed et al. 1995, Heinze et al. 1996) etc. *Leptothorax* (*Myrafant*) *lichtensteini* Bondroit, 1918, a species closely related to *L. slavonicus*, has nestmate recognition probably based on a *Gestalt* type model (Provost 1985, 1989, 1990, Provost et al. 1993). Strong influence has a nest material on colony odour in another related species, *Leptothorax nylanderi* (Heinze et al. 1996). This factor may explain the ease with which colonies of this species fuse (Foitzik & Heinze 1998). The nature of the recognition in *L. slavonicus* is still unknown. However, its ability to recognise nestmates confirms the general opinion (see, e. g., Holldöbler & Wilson 1977) that monogynous species show a higher degree of closeness than polygynous ones.

The marked individuals from different colonies did not mix, probably because of the small number of individuals involved, and hence the large amount of normal space available. Consequently, we could not determine whether nestmate recognition persists for a long period after colony fusion or whether a hierarchy associated with colony origin exists in mixed colonies.

The series of third experiments showed that orphaned workers of *L. slavonicus* readily adopt an alien queen. Although this has previously been recorded by Foitzik & Heinze (1998) in *L. nylanderi*, it is strange, because the presence of a queen in leptothoracine ants usually inhibits the laying of unfertilised eggs by workers, which is rather common in orphaned colonies (Heinze 1997). The situation seems to be in conflict with the basic tenets of kin selection: there should exist a conflict of interests between the workers and the queen concerning maternal origin of males (Hamilton 1964, Trivers & Hare 1976). An important task for future research is to determine whether the inhibition of egg-laying by workers occurs in the presence of an adopted alien queen.

CONCLUSIONS

1. The species *Leptothorax slavonicus* is monogynous; no case of polygyny was found in natural or experimental conditions.
2. The maintenance of monogyny was accomplished by behavioural regulation which resulted in the elimination of supernumerary queens by workers.
3. Recognition of nestmates occurred even under conditions of impaired scent communication.

4. The queen that was accepted was usually that of the larger of the two colonies used in each experiment.
5. Mixing two monogynous colonies usually resulted in their fusion, formation of a mixed colony and reduction in the number of queens (monogyny).
6. Genetically heterogeneous colonies may persist under experimental conditions.
7. In the laboratory orphaned colonies will adopt an alien queen.

ADDENDUM

Leptothorax (*Myrafant*) *slavonicus* is probably a junior subjective synonym of *Leptothorax* (*Myrafant*) *crassispinus* Karawajev, 1926, a species described originally from Russia (Radchenko 2000, Seifert pers. comm., October 2001).

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ERRATA

We apologise for the mistakes which have arisen for technical reasons. The main corrigenda:

Page 154: Table 1. Summary of experimental results. Explanations: N – number of experiments, NRM – number of occasions when monogyny resulted (= supernumerary queens eliminated), NF – number of fusions of two monogynous colonies, N2M – number of formations of two monogynous colonies. N0 – number of experiments that resulted in orphancy of the colony. NAQ – number of alien queens adopted:* adopted before orphancy ** accepted queen adopted by workers from the colony of the eliminated queen after the fusion

Page 155: Figure 2. Results of experiments series 1 – 3. Explanations: N – number of experiments, NRM – number of regulations to monogyny (= supernumerary queens eliminated), NF – number of fusions of two monogynous colonies, N2M – number of formations of two monogynous colonies, N0 – number of experiments that resulted in orphancy of the colony, NAQ – number of alien queens adopted

Page 156, line 17: c^2 substitute by χ^2

Page 157: Figure 3. Choice of the queen. Explanations: NE – number of experimental colonies. NMC – number of individuals in a colony; negative values = the accepted queen was from the smaller colony

Page 158, line 8: Foitzik & Heinze 1997 substitute by Heinze et al. 1997

Page 158, line 35: Heinze 1997 substitute by Heinze et al. 1997.