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FUNCTIONAL MONOGYNY IN THE AMERICAN GUEST ANT *FORMICOXENUS HIRTICORNIS* (EMERY) (= *LEPTOTHORAX HIRTICORNIS*), (HYM., FORM.)

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SUMMARY

12 samples of *Formicoxenus hirticornis* (Emery) were collected from 4 *Formica obscuripes* nests in the Yellowstone Park, Wyoming, in August, 1977. The dealate females and intermorphs, and some workers were dissected. All 16 females and 13 of the 16 intermorphs were inseminated, but only 10 females and 4 intermorphs were egg-laying. It seems that each colony normally contains only one fully fertile specimen, and a few additional, inseminated but sterile females or intermorphs. These results are very similar to our observations on the European guest-ant *Formicoxenus nitidulus* (Nyl.). We conclude that *F. hirticornis* (and maybe the closely related *F. diversipilosus*, too) is functionally monogynous like *F. nitidulus* and *Leptothorax gredleri* Mayr, which means that supernumerary inseminated females and intermorphs are accepted in queenright colonies, but they are kept sterile by a mechanism which is not yet known.

Leptothorax hirticonis Emery and *L. diversipilosus* M.R. Smith in my opinion belong to the genus *Formicoxenus*, since they have, together with *F. nitidulus*, a number of unique, common characters : The males of all three species are wingless and workerlike, they all live as guest ants in the mound nests of *Formica* species, and they have a peculiar female polymorphism with both dealate and intermorphic queens besides normal workers.

ZUSAMMENFASSUNG

Funktionelle Monogynie bei der amerikanischen Gastameise Formicoxenus hirticornis **(Emery)** (= Leptothorax hirticornis), **(Hym., Form.)**

12 Proben von *Formicoxenus hirticornis* (Emery) wurden im August 1977 im Yellowstone Park, Wyoming, aus 4 Nestern von *Formica obscuripes* entnommen. Die entflügelten Weibchen und Intermorphen sowie einige Arbeiterinnen wurden seziert. Alle 16 Weibchen und 13 der Intermorphen waren begattet, doch legten nur 10 Weibchen und 4 Intermorphe Eier. des Volk scheint normalerweise nur ein voll fertiles und daneben einige zusätzliche, begattete, aber sterile Weibchen oder Intermorphe zu

enthalten. Diese Ergebnisse sind unseren Beobachtungen an der europäischen Gastameise *Formicoxenus nitidulus* (Nyl.) sehr ähnlich. Wir schließen daraus, daß *F. hirticornis* (und vielleicht auch der nahe verwandte *F. diversipilosus*) wie *F. nitidulus* und *Leptothorax gredleri* Mayr funktionell monogyn ist, das heißt, daß überzählige begattete Weibchen und Intermorphe in weiselrichtigen Sozietäten zwar akzeptiert, aber durch einen bisher unbekannten Mechanismus steril gehalten werden.

Leptothorax hirticornis Emery und *L. diversipilosus* M.R. Smith gehören meines Erachtens in die Gattung *Formicoxenus*, da sie eine Anzahl einzigartiger Merkmale mit *F. nitidulus* gemeinsam haben: Die Männchen aller drei Arten sind flügellos und arbeiterinähnlich, alle drei leben als Gastameisen in Hügelnestern von *Formica*-Arten, und sie haben einen merkwürdigen Polymorphismus mit entflügelten und intermorphen königinnen neben normalen Arbeiterinnen.

INTRODUCTION

The interesting biology and the irregular polymorphism of the European guest ant *Formixoxenus nitidulus* have been described by various authors (ADLERZ, 1884, DORNISTHORPE, 1927, STAGER, 1925, STUMPER, 1918, 1949, WASMANN, 1915, STITZ, 1939). BUSCHINGER (1976) developed a method for breeding this species in the laboratory. In a field study (BUSCHINGER and WINTER, 1976) we could demonstrate, that most of the dealate and " ergatoid " or intermorphic females of *F. nitidulus* are inseminated, but only a rather small percentage is fertile and lays eggs. Apparently there is always only one fertile " queen " in one colony unit, the supernumerary " potential queens " being kept sterile. This kind of social organisation was named " functional monogyny " when first detected in the ant *Leptothorax gredleri* Mayr (BUSCHINGER 1968), on the analogy of comparable behavioural mechanisms in *Polistine* wasps (PARDI, 1940, GERVET, 1956).

Two closely related guest ants are known from North America, *Leptothorax hirticornis* Emery (1895), and *Leptothorax diversipilosus* M.R. Smith (1939). Both species live together with *Formica obscuripes* Forel and related subspecies, building their small nests in cavities in the *Formica* mounds. ALPERT and AKRE (1973) studied in detail the distribution, polymorphism, and behaviour of *L. diversipilosus*. As already SMITH (1956) had pointed out, the polymorphism as well as the biology of *diversipilosus* are very similar to that of *Formicoxenus nitidulus*. The same holds true for *Leptothorax hirticornis*, whose females and ergatoid males were described by SNELLING, 1965, together with some notes on its biology. The only major difference between the North American species and *F. nitidulus* is the presence of a lamellate process beneath the petiole and a spine beneath the postpetiole in the latter. All three species differ from normal *Leptothorax* by several unique, common characters: The wingless, ergatoid males, a peculiar female polymorphism with both alate and numerous intermorphic

queens, and their biology as obligatory guests in *Formica* mounds. Because of these characters both North American species in my opinion belong to the genus *Formicoxenus*. SMITH (1956) hesitated to propose this taxonomic correction only because in his opinion it should better be accomplished together with a complete revision of the tribe *Leptothoracini*.

Since up till now nothing was known about the functions of the " ergatoid females " in both *Formicoxenus diversipilosus* and *F. hirticornis*, it seemed desirable to make a similar study as in *F. nitidulus* (BUSCHINGER and WINTER, 1976) on either of the two species.

During a travel through the Rocky Mountains in August, 1977, which was in part devoted to the study of ants, I had the opportunity to collect some colonies or samples of *F. hirticonis*. The dissection of the material showed that this species in all probability is functionally monogynous like *F. nitidulus*.

METHODS AND MATERIALS

The ants were collected the 12th of August, 1977, near the Midway Geyser Basin in Yellowstone Park, Wyoming. 12 samples of *F. hirticornis* containing more or less complete colonies could be obtained from four thatchwork mounds of *Formica obscuripes* (the host species seems to be *F. obscuripes ravida* Wheeler). The colonies were found in small crevices and tunnels in the tree stump which mostly constitutes the center of the *Formica* nests in this area. Parts of these stumps were removed, and after shaking off most of the *Formica*, the wood was carefully cut in pieces. All *Formicoxenus* who seemed to belong to the same system of brood chambers and tunnels were sucked up with an aspirator, sealed in a vial, and kept separate from other such samples. Since it was a very hot day, and both the host ants and the guests quite active, I was not able to decide with certainty whether I always collected only ants belonging to one guest society or mixed up the members of two or more colonies. The samples also never contain a complete colony.

The very evening the guest ants were counted, and all females and " ergatoid females " as well as some workers were dissected. The method is described by BUSCHINGER and WINTER (1976).

RESULTS

In the following account the first number indicates the *Formica*-colony, the second numbers mark the different samples of *Formicoxenus* from one host nest.

I/1 : One dealate *F. hirticornis* female, alone with 3 larvae in a small chamber.

Dissection : Female with 6 rather short ovarioles, one developing egg, small corpora lutea present, spermatheca filled with sperm.
Apparently and incipient colony.

2 : 3 dealate females, 4 intermorphs, 43 workers, 2 ergatoid males, larvae and worker pupae.

Dissection: One female with 6 long ovarioles (about the length of the whole body), with ample corpora lutea and developing eggs, functional queen. — Second female: 6 short ovarioles without developing eggs, no corpora lutea, spermatheca filled with sperm, wing muscles replaced by fat body. This indicates that the female was not just newly inseminated, but may have lived in the colony for several months, if not since the last year. — Third female: 6 short ovarioles, with developing eggs, inseminated. Since one antenna was cut off, presumably by workers of the colony, this female might have been a colony founding queen which was by chance aspirated together with the neighbouring colony. — 4 workerlike intermorphs with 6 short ovarioles each, but inseminated.

3 : 2 intermorphs, 1 worker.

Dissection: First intermorph with 3 ocelli, thoracic sutures like the "queenlike ergatoid female" described by SMITH (1939), 6 ovarioles of intermediate length (half the length of the body), with developing eggs and corpora lutea, inseminated. — Second intermorph: same external characters, ovary nearly of the same length, with corpora lutea, but no developing eggs, inseminated. — Worker: 3 short ovarioles, no spermatheca.
This sample seems to be a mixture of parts of two small colonies with ergatoid queens. The queens of most of the colonies had only a few white eggs in their ovaries, which means that yolk material was still deposited in the growing oocytes. Some highly fertile queens had already stopped the incorporation of yolk, which signals the end of the summer egg laying period. The oocytes then look transparent like the nutritive cell groups. Thus the second intermorph may already have stopped egg laying in this season, which doesn't mean that she was less fertile than the first intermorph in this sample.

4 : 2 dealate females, 4 intermorphs, 19 workers, 3 males, numerous larvae and worker pupae.

Dissection: Female one with 6 long ovarioles, ample corpora lutea, inseminated, transparent oocytes, queen of this colony. — Second female with 6 short ovarioles, no corpora lutea, but inseminated. Wing muscles replaced by little fat body and inflated tracheae. — Two "workerlike", and one "queenlike ergatoid females" (in the sense of SMITH, 1939), with 3 ocelli, all with 6 short ovarioles, without corpora lutea, the spermathecae filled with sperm. — Fourth intermorph with 6 short ovarioles, but spermatheca empty.
A rather complete colony with a composition like many *F. nitidulus* colonies!

5 : 2 dealate females, 1 intermorph, 45 workers, numerous eggs, larvae and worker pupae.

Dissection: Both females had long ovarioles, ample corpora lutea, and were inseminated. The oocytes in both queens were already transparent. — The intermorph, a "workerlike ergatoid female", had 6 short ovarioles, the spermatheca was empty. — 3 workers had 2 short ovarioles each and no spermatheca.
In this case two queenright colonies may have been mixed together. I prefer this interpretation instead of supposing a polygyny. The latter would not explain the presence of old, inseminated, but sterile females in so many colonies.

6 : 1 dealate female, 1 intermorph, 5 workers, larvae.

Dissection: Female with 6 short ovarioles, no corpora lutea, but inseminated. Wing muscles replaced by fat body. — Intermorph: workerlike except the 3 ocelli, 6 long ovarioles with corpora lutea, inseminated, but oocytes already transparent, functional queen! An apparently complete society. Like in *F. nitidulus* a colony may have an ergatoid queen and one or several inseminated, but sterile, dealate "potential queens".

II/1 : 1 dealate female, alone in a small chamber.
Dissection : 6 short ovarioles, but with developing eggs, spermatheca filled with sperm. Incipient colony.

2 : 1 dealate female, 1 workerlike intermorph, some larvae.
Both the female and the intermorph had 6 short ovarioles, were inseminated but sterile. Apparently a small part of a colony.

3 : 1 dealate female, 3 workers, some larvae and worker pupae.
The female had 6 short ovarioles, was inseminated, but sterile. The wing muscles were replaced by fat body. Again apparently a part of a colony.

4 : 1 dealate female, 6 workers, some larvae and worker pupae.
The female was a functional queen.
Small, but rather complete society.

III/1 : 2 dealate females, 2 intermorphs, some larvae.
One female was a functionnal queen with developing eggs, the second female had only short ovarioles without developing eggs, but was inseminated. Wing muscles replaced by fat body. — One " queenlike " intermorph with 6 short ovarioles, inseminated. — The second " workerlike " intermorph with 6 short ovarioles, spermatheca empty. Since workers lack in this sample it should be only a part of a colony.

IV/1 : 1 dealate female, 1 intermorph, 8 workers, 1 male, some larvae.
The female was a functional queen with 6 ovarioles of about the length of her body, corpora lutea, developing eggs and the spermatheca filled with sperm. The workerlike intermorph was as well inseminated, but had 6 ovarioles of only about half the length of her body, with corpora lutea.
Since the intermorph seems to be younger than the dealate female, I suppose that in this sample a complete colony (with the dealate queen) was mixed with an incipient colony, newly founded by the intermorph.
The results are compiled in the following table I.

Table I. — Composition of 12 samples (colonies or parts of colonies) of *Formicoxenus hirticornis*.

Tabelle I. — Zusammensetzung von 12 Proben (Kolonien oder Teilvölker) von *Formicoxenus hirticornis*.

Sample No.	Dealate females		Intermorphs			Workers	Males	Remarks and interpretation
	inseminated		inseminated		n. ins.			
	fertile	sterile	fertile	sterile	sterile			
I/1	1	—	—	—	—	—	—	incipient colony
I/2	2	1	—	4	—	43	2	incip. col. mixed with big colony
I/3	—	—	2	—	—	1	—	mixture of 2 parts of colonies
I/4	1	1	—	3	1	19	3	"normal" colony
I/5	2	—	—	—	1	45	—	mixture of 2 colonies
I/6	—	1	1	—	—	5	—	"normal" colony
II/1	1	—	—	—	—	—	—	incipient colony
II/2	—	1	—	1	—	—	—	small part of a colony
II/3	—	1	—	—	—	3	—	part of a colony
II/4	1	—	—	—	—	6	—	"normal" colony
III/1	1	1	—	1	1	—	—	part of a colony
IV/1	1	—	1	—	—	8	1	incip. col. mixed with normal colony
12	10	6	4	9	3	130	6	

In the following two tables (II and III) our results are compared with the observations of ALPERT and AKRE (1973) on *F. diversipilosus*, and BUSCHINGER and WINTER (1976) on *F. nitidulus*.

Table II. — Numbers and percentages of dealate females, intermorphs, workers and males in collections of *F. hirticornis*, *F. diversipilosus* and *F. nitidulus*.

Tabelle II. — Anteile von entflügelten Weibchen, Intermorphen, Arbeiterinnen und Männchen in Aufsammlungen von *F. hirticornis*, *F. diversipilosus* und *F. nitidulus*.

	F. hirticornis		*F. diversipilosus* (*)	*F. nitidulus*	
	n	%	%	n	%
Dealate females	16	9,5	2,5	26	2,6
Intermorphs	16	9,5	18	203	20,6
Workers	130	77,4	76	757	76,8
Males	6	3,6	2	0	—

(*) Numbers not indicated by ALPERT and AKRE (1973).

Although the collections are not ideally comparable, since *F. hirticornis* was collected in August, *F. diversipilosus* over several years from February to August, and *F. nitidulus* during hibernation (the table comprises only our data from southern Germany), the similarity of the polymorphism in this 3 species is surprising.

In table III a comparison is only possible for *F. hirticornis* and *F. nitidulus*, since the *F. diversipilosus* material was not dissected.

Table III. — Numbers and percentages of inseminated, fertile or sterile dealate females and intermorphs in collections of *F. hirticornis* and *F. nitidulus*.

Tabelle III. — Anteile von begatteten, fertilen oder sterilen entflügelten Weibchen und Intermorphen in Aufsammlungen von *F. hirticornis* und *F. nitidulus*.

		F. hirticornis		*F. nitidulus*	
		n	%	n	%
Dealate females	inseminated, fertile	10	31,2	6	2,6
	inseminated, sterile	6	18,7	19	8,3
	not inseminated	0	0	1	0,4
Intermorphs	inseminated, fertile	4	12,5	22	9,6
	inseminated, sterile	9	28,1	148	64,6
	not inseminated	3	9,4	33	14,4
All " potential queens " together		32	100	229	100

In this table, again, only the results of our study in hibernating *F. nitidulus* from South Germany are considered. There are substantial

differences in the percentages of fertile dealate females and inseminated, but sterile intermorphs, if we compare the two species. But we also can find some striking similarities. So in both species only a small part of the " potential queens ", the dealate and intermorphic females with a spermatheca, remain unmated (9,4 % in *F. hirticornis* and 14,8 % in *F. nitidulus*). And in both species a high percentage of the inseminated, dealate or intermorphic females doesn't become fertile (46,8 and 72,9 % respectively). According to our observations on *F. nitidulus* these females remain for a longer time, more than one year, in colonies with one fertile queen. We suppose that this queen by any mechanism, which we do not yet understand, prevents the growth of the ovarioles and the development of oocytes in the " supernumerary " potential queens.

CONCLUSIONS

The result of our study on *F. hirticornis* is, that this species, like *F. nitidulus*, seems to have a " functional monogyny ". Otherwise the occurrence of a high percentage of inseminated but sterile females and intermorphs in our samples could not be explained ; in colonies of truly polygynous species normally all inseminated females become fertile.

The data of *F. diversipilosus*, given by ALPERT and AKRE (1973), suggest that the same social organisation is realised in this species, too. Functional monogyny might be an ancient, common character of the genus *Formicoxenus*, or it might be an adaption to the special conditions of living and nesting as guest ants in *Formica* nests. Further studies will be necessary to decide which of these alternatives is true. These studies should include *F. diversipilosus* as well as the guest ant of *Myrmica, Letpothorax provancheri* Emery with " numerous ergatoid females " (WHEELER, 1910), and *Symmyrmica chamberlini* WHEELER, with ergatoid males, guest of *Manica mutica.*

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