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## QUEEN POLYMORPHISM AND FUNCTIONAL MONOGYNY IN THE ANT, *LEPTOTHORAX SPHAGNICOLUS* FRANCOEUR

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### INTRODUCTION

Queen polymorphism, the occurrence of morphologically different, mated and egg-laying females in one species of ants, has been demonstrated until recently mainly in social parasites. Particularly among the myrmicine tribe Leptothoracini, intermorphic and nearly workerlike queens and fully alate or dealate gynomorphic queens have been found in guest ants such as *Formicoxenus nitidulus* (Buschinger and Winter, 1976), *F. provancheri* (Buschinger et al., 1980), and *F. diversipilosus* (Buschinger, 1979 – erroneously named *F. hirticornis*). Apparently this feature is characteristic of the entire genus (Francoeur et al., 1985). In the slave-making ant, *Harpagoxenus sublaevis*, a genetic mechanism determining queen polymorphism has been detected (Buschinger and Winter, 1986). Queen polymorphism in leptothoracines, however, is not restricted to parasitic species. Recently it has been found in an as yet undetermined, independent *Leptothorax* sp. A from Québec (Heinze and Buschinger, 1987). A genetic mechanism similar to that in *H. sublaevis* is responsible for the queen polymorphism in this species, too (Heinze and Buschinger, 1989). Finally, we report here on queen polymorphism in the recently described *Leptothorax sphagnicolus* Francoeur 1986, another free-living species from Québec.

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In addition we provide evidence for functional monogyny in *L. sphagnicolus*, another feature rarely found in ants. In functionally monogynous ants, a colony normally contains but one inseminated and egg-laying queen, and often alongside her one or several other females may be present which are inseminated but do not develop fertility. Among ants, this phenomenon was first observed in *Leptothorax gredleri* from Europe (Buschinger, 1968), which is an independent ant with exclusively gynomorphic queens. Functional monogyny, however, is characteristic for most of, or perhaps all, the guest ants of the genus *Formicoxenus* (Francoeur et al., 1985), and also for *Leptothorax* sp. A (Heinze and Buschinger, 1987).

Heinze and Lipski (1990) found that a dominance hierarchy among the mated females of this species is responsible for the sterility of all females except the one in  $\alpha$ -position. Ito (1990) described functional monogyny in *Leptothorax acervorum* from North Japan, a species which in Europe is facultatively polygynous (both colonies with one and several queens occur in a population, Buschinger, 1968). All reproductive females, however, are uniformly gynomorphic.

*Leptothorax sphagnicolus* is, therefore, the second example of an independent ant exhibiting both queen polymorphism and functional monogyny.

#### MATERIAL AND METHODS

Considerable numbers of *L. sphagnicolus* were collected previously in 1972/1973 during a study on ecological succession of spruce bog (Francoeur and Pépin, 1975, 1978), in five sites around Chicoutimi/Québec. The sites and the characteristics of these bogs are described in detail in Francoeur and Pépin (1975). We used this material for an evaluation of the proportions of gynomorphs, intermorphs and ergatomorphs in the various localities (Tab. I).

Additional colonies of *L. sphagnicolus* were collected by A.F. between 1980 and 1986 in a spruce bog near Saint-Ambroise. This material comprises the type series of the species. Together with material from the same locality (SA in tab. I) which had been extracted from *Sphagnum* hummocks containing nests of *Formica dakotensis*, we analyzed these samples more closely in order to demonstrate the morphological variability among the intermorphs (Tab. II). Finally, colonies of *L. sphagnicolus* were collected by

A.B on 15 and 19 June, 1983, again in the spruce bog near St.-Ambroise, and on 3 July, 1983, near L'Ascension, in the Saguenay-Lac-St.-Jean area, Québec. The ants there were found in the upper parts of *Sphagnum* hummocks, usually in places where just a few *Polytrichum* stems were growing, but where the *Sphagnum* surface was still fully exposed to insolation. The sac-like nesting chambers can be detected when the *Sphagnum* is gently opened. They reach a depth of 3–5 cm and are coated inside with a layer of apparently chewed *Sphagnum* leaflets (Fig. 1). The ants were aspirated, but due to the spongy structure of the substratum it is difficult to collect complete colonies, a few specimens usually escape.

After an inspection of the population of each nest, 21 of them were selected for dissection of all or of representative samples of the ergatomorphs, intermorphs and dealates present. Other colonies were kept alive in order to study their offspring. Dissections were made according to Buschinger and Winter (1976) and Buschinger and Alloway (1978). Living colonies were kept in formicaries and in daily changing temperatures as described by Buschinger (1974).



Fig. 1: Nest of *Leptothorax sphagnicolus* within a *Sphagnum* hummock, seen from above. The nesting chamber of about 3×1 cm is visible in the center, where the *Sphagnum* was pulled apart.

## RESULTS

a) In table I we present the proportions of gynomorphs, intermorphs and ergatomorphs in the 1972/1973 samples, from five different spruce bogs. The samples "SA" from the *F. dakotensis*-inhabited *Sphagnum* hummocks are included. It appears that the ratios of intermorphs and ergatomorphs vary considerably between the sites (13.1 to 40.2% intermorphs, which are potential queens, as is shown below!), and that gynomorphs are very rare (.7% of the total female population). Table II reveals a certain morphological variation among the intermorphs. The proportions of inferior, intermediate and superior intermorphs again vary widely between the samples from different localities.

b) In table III the composition of 38 individually collected colonies (= inhabitants of one nest) is analyzed. The colonies evidently are very small in comparison with other *Leptothorax* species where a nest may contain up to several hundred adults. In *L. sphagnicolus* we found a mean number of  $7.5 \pm 9.8$  (median 4.5) specimens, with maxima of 42 and 49 individuals in the largest nests. A size of more than 15 adults is apparently rarely reached.

c) Already during collecting in the field we observed that never more than one specimen in each colony had a largely extended gaster. In 23 colonies out of the 38 of table III we could identify a female reproductive, and in all these instances it was an intermorph, even when gynomorphs also were present (no. 29, 30, 37). By dissecting the gynomorphs, intermorphs and representative numbers of ergatomorphs of several colonies we could demonstrate that in fact each colony contains only one mated and egg-laying specimen. However, where more than one intermorphic and/or gynomorphic specimen were found together, all of them were inseminated. They had ovaries with  $2 \times 3$  ovarioles, the usual number in *Leptothorax* queens, and a receptacle, whereas the ergatomorphs have only  $2 \times 1$  ovarioles, and lack a spermatheca. In the following some results of dissecting shall be detailed.

1. Samples without intermorphs and gynomorphs always contained only ergatomorphs with two ovarioles each, without a spermatheca, and not egg-laying (table III, no. 1, 2, 5, 31, 34). We interpret these samples to be colony fragments where the queen most probably was lost during collecting.

Table I. Proportions of gynomorphs, intermorphs and ergatomorphs in samples of *Leptothorax sphagnicolus* from five spruce bogs in Québec. The material was collected in 1972/1973 during a study on ecological succession of spruce bog (Francoeur and Pépin, 1975, 1978). The samples do not necessarily represent individual, complete colonies. Localities: AM = Saint-Ambroise; SA = Saint-Ambroise, colonies extracted from *Sphagnum* hummocks containing nests of *Formica dakotensis*; BA = Bagotville; LA = Laterrière; LE = Saint-Léon; TC = Notre-Dame-du-Rosaire.

Locality	n samples	n gyno-morphs	n inter-morphs	n ergato-morphs	total n females	% gyn.	int. of females	erg.	n males and male pupae
AM	27	4	134	255	393	1.0	34.1	64.9	60
SA	13	4	156	228	388	1.0	40.2	58.8	1
BA	6	0	5	23	28	0.0	17.9	82.1	-
LA	1	0	3	12	15	0.0	20.0	80.0	1
LE	11	0	16	106	122	0.0	13.1	86.9	1
TC	27	0	57	163	220	0.0	25.9	74.1	5
TOTAL	85	8	371	787	1166	(0.7)	(31.8)	(67.5)*	67

\* Figures in parentheses refer to the average percentage of all female specimens.

Table II: Polymorphism of females in individual samples of *Leptothorax sphagnicolus* from Saint-Ambroise. The individuals are rated in a series from 1 = ergatomorph, 2-8 = intermorphs, to 9 = gynomorph. Inferior intermorphs (2, 3) have 1 or 2 tiny ocelli and traces of thoracic sutures, intermediate intermorphs (4-6) with 2 or 3 small ocelli and clearly visible thoracic sutures, superior intermorphs (7, 8) have always 3 ocelli and thoracic sutures nearly as complete as in the gynomorphs, but lack the wings or wing stumps.

Sample no.	n individuals belonging to class									
	1	2	3	4	5	6	7	8	9	
9526	58	5	2	9	6	7	16	19	11	
10166	28	-	-	-	2	3	6	1	-	
10399	20	-	-	1	-	-	-	-	-	
10446	40	2	2	2	1	5	12	17	-	
12335	23	2	-	1	-	6	4	-	1	
Subtotal	169	9	4	13	9	21	38	37	12	312
%	54.2	2.9	1.3	4.2	2.9	6.7	12.2	11.9	3.8	
SA 05	2	-	-	-	-	-	-	-	-	
SA 12	6	5	6	-	-	-	-	-	-	
SA 16	56	6	12	2	-	3	4	-	-	
SA 18	2	-	-	-	-	-	1	-	-	
SA 22	13	-	1	-	-	-	-	-	2	
SA 24	31	9	15	-	2	3	2	1	-	
SA 25	10	3	6	1	1	1	1	-	-	
SA 26	10	3	6	2	1	-	-	1	-	
SA 27	5	1	-	-	-	-	-	-	1	
SA 29	10	3	8	2	2	-	4	1	-	
SA 32	5	2	-	-	1	-	1	-	-	
SA 33	44	9	12	1	2	1	1	2	-	
SA 35	34	2	1	-	-	-	2	-	1	
Subtotal	228	43	67	8	9	8	16	5	4	388
%	58.8	11.1	17.3	2.1	2.3	2.1	4.1	1.3	1.0	
TOTAL	397	52	71	21	18	29	54	42	16	700
%	56.7	7.4	10.1	3.0	2.6	4.1	7.7	6.0	2.3	

Table III: Composition of 38 samples of *Leptothorax sphagnicolus* collected on 15 and 19 June, 1983, at St.-Ambroise (SA), and on 3 July, 1983, near L'Ascension (AN). "Fragment" means that presumably only part of the colony was collected. Only specimens found with larvae and within nests were included in this table, not single foragers. The queens were identified by dissection.

no.	loc.	Gynom.	Interm.	Ergatom.	Total n	Remarks
1	SA	—	—	1	1	fragment
2	AN	—	—	1	1	fragment
3	SA	—	1	—	1	incipient col.?
4	SA	1	—	—	1	incipient col.?
5	AN	—	—	2	2	fragment
6	AN	—	1	1	2	intermorph = queen
7	AN	—	1	1	2	fragment
8	AN	—	1	1	2	fragment
9	AN	—	1	1	2	fragment
10	AN	1	—	1	2	fragment/branch?
11	AN	—	2	—	2	fragment? 1 int. = queen
12	AN	—	1	2	3	intermorph = queen
13	AN	—	1	2	3	intermorph = queen
14	SA	—	—	4	4	fragment
15	SA	—	—	4	4	fragment
16	SA	—	1	3	4	intermorph = queen
17	SA	—	1	3	4	intermorph = queen
18	SA	—	1	3	4	intermorph = queen
19	SA	—	1	3	4	intermorph = queen
20	SA	—	1	4	5	intermorph = queen
21	SA	—	1	4	5	intermorph = queen
22	SA	—	1	4	5	intermorph = queen
23	AN	—	1	4	5	intermorph = queen
24	SA	—	1	6	7	intermorph = queen
25	SA	—	1	7	8	fragment/branch?
26	AN	—	2	6	8	1 int. = queen
27	SA	—	1	8	9	intermorph = queen
28	SA	—	3	6	9	1 int. = queen
29	AN	1	2	6	9	1 int. = queen
30	SA	3	1	5	9	intermorph = queen
31	SA	—	—	10	10	fragment
32	AN	—	1	9	10	intermorph = queen
33	AN	1	1	8	10	fragment/branch?
34	SA	—	—	11	11	fragment
35	SA	—	1	11	12	intermorph = queen
36	AN	—	3	12	15	1 int. = queen
37	AN	15	1	26	42	intermorph = queen
38	AN	5	1	43	49	fragment, no queen
TOTAL		27	36	223	286	
%		9.4	12.6	78.0		

Mean individuals per nest:  $7.5 \pm 9.8$ ; median: 4.5

2. Several samples contained workers and intermorphs and/or gynomorphs, but no reproductive queen. Thus, the dealate gynomorph of no. 10 was inseminated, and was found with one worker and a brood. However, this female had never laid eggs, her ovarioles were short and translucent as in virgin females, and no corpora lutea were present. Similarly, sample no. 25 contained an inseminated, not laying intermorph with workers, and no. 33 a gynomorph and an intermorph, both inseminated but not egg-laying. These samples may represent colony fragments having lost the single reproductive during collecting, or perhaps have recently separated from a "mother colony" (budding, see discussion).
3. The samples no. 26, 28, and 36 comprised 2–3 intermorphs. One of them in each colony was the reproductive queen, the others were inseminated but not laying.
4. In three colonies (no. 29, 30, 37) an egg-laying intermorph was found alongside 1, 3, and 15 gynomorphs, respectively, which were all mated but not laying.
5. Samples no. 3 and 4 consisted of only one intermorph respectively gynomorph, both mated and not laying, perhaps in the process of independent colony foundation. At least the dealate gynomorph of no. 4 had a few visible oocytes in the ovaries with beginning yolk deposition.
6. Usually the inseminated, non-laying intermorphs and gynomorphs had a whitish fat body, indicating that they were not too old, perhaps living in the colonies only since the swarming period of the preceding year. However, the 5 gynomorphs and one intermorph in colony no. 38 had yellow fat bodies. Such a coloration usually appears in *Lepthorax* species after more than one year of adult life.

From these dissection results we may conclude that *L. sphagnicolus* is monogynous, having only one fully reproductive queen per nest. This queen in most cases is an intermorphic specimen. In a sizeable fraction of the colonies, a number of mated, but non-laying intermorphs and/or gynomorphs are living alongside the queen. In our samples these supernumerary potential queens must have been with their colonies for at least one year, since the colonies contained just eggs, larvae, and a few prepupae, but not yet young



adult sexuals of the current year. Pupae and adult males were found in colonies collected later in July and in August.

d) Laboratory rearing of *L. sphagnicolus* was by far not as successful as is usual with other leptothoracine species. The colonies collected in June/July 1983 contained larvae and prepupae. They were kept in artificial summer conditions (Buschinger, 1974) until mid-August, at which time they produced a reasonably high number of males, gynomorphs, intermorphs and ergatomorphs. After an artificial hibernation until mid-November for three months (which is sufficient for many related *Leptothorax* species) most colonies had lost much brood and workers, and only a few males and female forms appeared in the following artificial summer. In a third laboratory summer only one colony still produced four intermorphs. In part, the difficulties with laboratory rearing were due to the fact that the colonies had to be kept quite humid, in order to simulate the conditions in their natural habitat. This however, led to serious growth of mold in the nest chambers.

Table IV reveals the results obtained with rearing of 11 colonies. Due to uncontrolled losses of brood stages and young adults the production values are surely too low; they represent but the minimum numbers observed. In colony no. 4 and 7 the broods of three other, small colonies were added shortly after collecting of the material, in order to obtain a higher production. The total production during one, two or three breeding cycles is added up; however, in the column "remarks" we indicate the numbers of individuals produced in the second or third cycles. The breeding results are not unequivocal with respect to the question whether the queen polymorphism is genetically mediated, or due to environmental influences. Gynomorphs did appear in the offspring of intermorphic queens, alongside of intermorphs, whilst other colonies with intermorphic queens produced only intermorphs. The progeny of gynomorphic queens could not be checked because all colonies had only an intermorphic queen each, even the colonies no. 9 and 19 with dealate gynomorphs (cf. preceding section). In the offspring produced, the percentage of gynomorphs (6.43%) is not much different from that in the original, spring population (6.83% in the colonies reared in the lab, and 9.4% in all colonies of table III). It is, however, much higher than in the field samples of table I (.7%) and table II (2.3%). The percentage of intermorphs

Table IV: Results of laboratory rearing of *Leptothorax sphagnicolus*. The colonies were collected in spring condition, with larvae and a few prepupae. In artificial summer conditions they produced sexuals and workers. Some colonies were producing offspring in a second (2), and one colony in a third (3) breeding cycle.

Col. no.	Original composition:			Production in (1), (2) or (3) summers:			Remarks			
	Gyn.	Int.	Erg.	Total	Gyn.	Int.		Erg.	Total	males
24	-	1	6	7	-	1	13	14	-	(1)
17	-	1	3	4	-	2	6	8	-	(1)
18	-	1	3	4	-	-	1	1	-	(1)
28	-	3	6	9	3	4	9	16	8	larvae added (2:1♂)
19	-	1	3	4	-	3	2	5	-	(1)
22	-	1	4	5	1	3	2	6	-	(2: 2 int.)
27	-	1	8	9	-	3	14	17	4	larvae added (2: 2 int.)
23	-	1	4	5	1	3	4	8	1	(1)
30	3	1	5	9	1	3	6	10	3	(2: 3 erg.)
38	5	1	43	49	3	21	32	56	19	(2: 2♂, 3 int.) (3: 4 int.)
35	-	1	11	12	2	12	16	30	10	(2: 6♂, 2 int., 3 erg.)
Σ 11	8	13	96	116	11	55	105	171	45	
%	6.9	11.2	82.7	(100)	6.4	32.1	61.4	(100)		

produced in laboratory culture (32.2%) is comparatively higher than in the original colonies (11.1% in the colonies reared, and 12.6% in all colonies of table III) it matches, on the other hand, some of the values in table I.

#### DISCUSSION

The social organization and the caste and morph differentiation system of *Leptothorax sphagnicolus* surely deserves to be studied with more material and more intensely. Only in comparison with similar situations in related species are we able to interpret our observations with some reliability. Functional monogyny and queen polymorphism in this species are highly probable, and a genetically mediated morph determination as in *Harpagoxenus sublaevis* (Winter and Buschinger, 1986) and in *Leptothorax* sp. A (Heinze and Buschinger, 1987, 1989) is likely at least. Functional monogyny in *L. gredleri* (Buschinger, 1968) and in several *Formicoxenus* species (Francoeur et al., 1985) is characterized by the presence of inseminated but non-egg-laying females, always together with one fully reproductive queen, in a colony over the entire year. The "supernumerary" females, after one or more years, have a yellow fat body, whereas in young females, during their first year of adult life, the fat body appears white. In *L. sphagnicolus* we found such "supernumerary" females in spring and early summer before the eclosion of new sexuals. Thus, they must have been staying with the colonies for at least one year, since the preceding swarming period. Most of the females, however, had white fat bodies, except those of colony no. 38/table III, which apparently were older.

An alternative interpretation of the presence of inseminated, yet sterile, females in the colonies would be that they just remain in their mother colonies after having mated in the vicinity, overwinter, and that they leave during the following summer, perhaps together with a few workers, forming daughter colonies. Dominance behavior between inseminated females may be involved, as reported for *Leptothorax* sp. A (Heinze, 1990). Some of our samples (table III, no. 10, 25, 33) could represent such recently formed buds or branch colonies, where the young queen had not yet developed her ovaries to the size of fully reproductive females. The two hypotheses, however, are not mutually exclusive.

Queen polymorphism has been documented for *Harpagoxenus sublaevis* (Winter and Buschinger, 1986), in *Formicoxenus* species (Francoeur et al., 1985), and in *Leptothorax* sp. A (Heinze and Buschinger, 1988, 1989). In these cases, both intermorphic and fully gynomorphic specimens have been found to be the reproductives of field colonies. In *L. sphagnicolus*, all our colonies had intermorphic queens, if any, and gynomorphs were only found as "supernumerary", inseminated but not laying females. Only one gynomorph (Table II, no. 4) perhaps was becoming a functional queen, having slightly developed ovaries. However, she was found alone, with a brood, but without workers. So, more field studies are necessary in order to find, perhaps, colonies with actual reproductive gynomorphs.

The question of a genetic mechanism involved in the production of gynomorphs and intermorphs must be studied with crossbreeding experiments, as in *Harpagoxenus sublaevis* (Buschinger, 1978) and in *Leptothorax* sp. A (Heinze and Buschinger, 1989). Since most of the female reproductives are wingless intermorphs, we may assume that this species exhibits a stationary sexual calling behavior, as *Harpagoxenus sublaevis* and many other leptothoracines (Buschinger and Alloway, 1979), and mating in laboratory colonies already has been observed (Francoeur, 1987). This is a favorable precondition for breeding experiments. The laboratory conditions, temperature regime, humidity, food, were surely different from field conditions, and obviously not optimal. Nevertheless both gynomorphs and intermorphs were produced in fairly high numbers (Tab. IV). This result is consistent with our assumption of a genetic mechanism involved in morph determination also in *L. sphagnicolus*: With an environmental control of morph differentiation we would expect that, under uniform laboratory conditions, only one queen morph is formed.

The adaptive significance of the intermorphic queens in *L. sphagnicolus* may be the same as in *Formicoxenus* and in *L. sp. A*: They all inhabit small, patchily distributed spots in a wide, non-inhabitable environment. These patches are the nests of host species in the case of xenobiotic *Formicoxenus* species (Francoeur et al., 1985), and not very large rock outcrops within dark and often humid forest areas in the case of *L. sp. A* (Heinze and Buschinger, 1987, 1989), each, however, suited to bear a

population of several dozen or more nests. The *Sphagnum* hummocks which are suitable for *L. sphagnicolus* also are quite scattered in the large spruce bogs, with wide areas being too humid or too dry. The species, thus, may use a mixed strategy of colonizing a suitable patch with branch colonies, and intermorphic queens which are unable to fly away, and perhaps spreading to other patches by alate females.

#### SUMMARY

The recently described ant, *Leptothorax sphagnicolus*, is inhabiting *Sphagnum* hummocks in spruce bogs in Québec. Its queens are usually intermorphic, i.e., morphologically between the worker and the alate/dealate female. Gynomorphs are rare, but very probably they also can be queens of colonies. Like a few other, mostly parasitic leptothoracines, *L. sphagnicolus* exhibits a queen polymorphism. Each colony has only one fully fertile queen, but alongside her a number of mated, non-egg-laying females may be present. The colonies are thus functionally monogynous. The supernumerary potential queens, after mating, stay with their mother colony at least until the next summer, perhaps longer. Some of them presumably leave the nest, together with workers, in order to establish own colonies (budding). The adaptive value of combined functional monogyny and queen polymorphism is discussed.

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