6 | The *Pallens* Morph of the Ant *Leptothorax nylanderi*: Description, Formal Genetics, and Study of Populations

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Abstract: The *pallens* male morph differs from the *nylanderi* type by its thorax which is lightened to a russet or testaceous colouring; the extreme *euxanthus* form has a pale testaceous yellow thorax and the rest of its body is a pale yellowish brown. The *pallens* queen and the *pallens* worker have an abdominal band which is a yellowish-grey or yellowish grey-brown instead of black-brown in the typical *nylanderi*; this dark band disappears nearly completely in the extreme *euxanthus* form of worker. The *pallens* morph is determined by a recessive gene which shows itself directly in males because they are all hemizygotes; *pallens* females are recessive homozygotes. The *pallens* gene has been observed in 5·5% of colonies studied in the Paris region; it is present in these colonies at a mean frequency of 32·5%; which gives a frequency of 1·8% in the population. Genetics of populations having the *pallens* gene confirms two presumptions: (1) the great majority of males come from worker eggs; (2) one queen can mate with 1 to 10 males.

INTRODUCTION

One generation of ants, from mother queen to daughter queen, often lasts several years. Social polymorphism, which is not genetically determined, produces larger variations than genetical variations. Consequently works

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on morphological genetics of ants, apart from those of Buschinger (1975, 1978) on the alate or ergatoid queens of *Harpagoxenus*, are rare.

The temperature at pupation can modify the coloration of several species of *Leptothorax* (Plateaux, 1970), so I have hesitated to identify genetical morphological polymorphism in *Leptothorax nylanderi*, concentrating initially on phenetic variation. By rearing ants in stable conditions and maintaining well-known stocks for more than ten years, experiments in formal genetics have provided evidence for polychromatism in *Leptothorax nylanderi*.

DESCRIPTION OF THE *PALLENS* PHENOTYPE AND VARIATIONS (Fig. 1)

Males

The thorax of males is russet or of a testaceous yellow colouring, instead of brown or black; head and abdomen are more or less dark-brown. This pale form is named *pallens*, *n.f.* Some individuals are paler: the thorax is of a pale testaceous yellow, like the base of the abdomen; the head and most part of the gaster are of a yellowish brown, sometimes pale. I have designated this extreme form *euxanthus n. f.*, in contrast with the form *pseudoxanthus* which is modified by a parasite (Plateaux, 1972).

Workers

Typical *nylanderi* workers have a wide transverse black or dark-brown band on the abdomen; this band is so characteristic that Schenck (1852) named the species *cingulata*. The *pallens* form has the same band; however, it is much paler with a yellowish grey-brown colouring and is clearly delimited posteriorly by a dark brown line. This band is often lighter anteriorly and appears hazy at its anterior limit.

On some individuals only the dark posterior line of the abdominal band can be seen distinctly, the rest of the band merging into the yellow base of the gaster. I attribute such individuals to the extreme form *euxanthus*. In contrast, some *pallens* workers have a relatively dark abdominal band. Their *pallens* character can usually be recognized by the posterior line being darker than the rest of the band.

Queens

Typical queens are coloured like workers, but their dark abdominal band

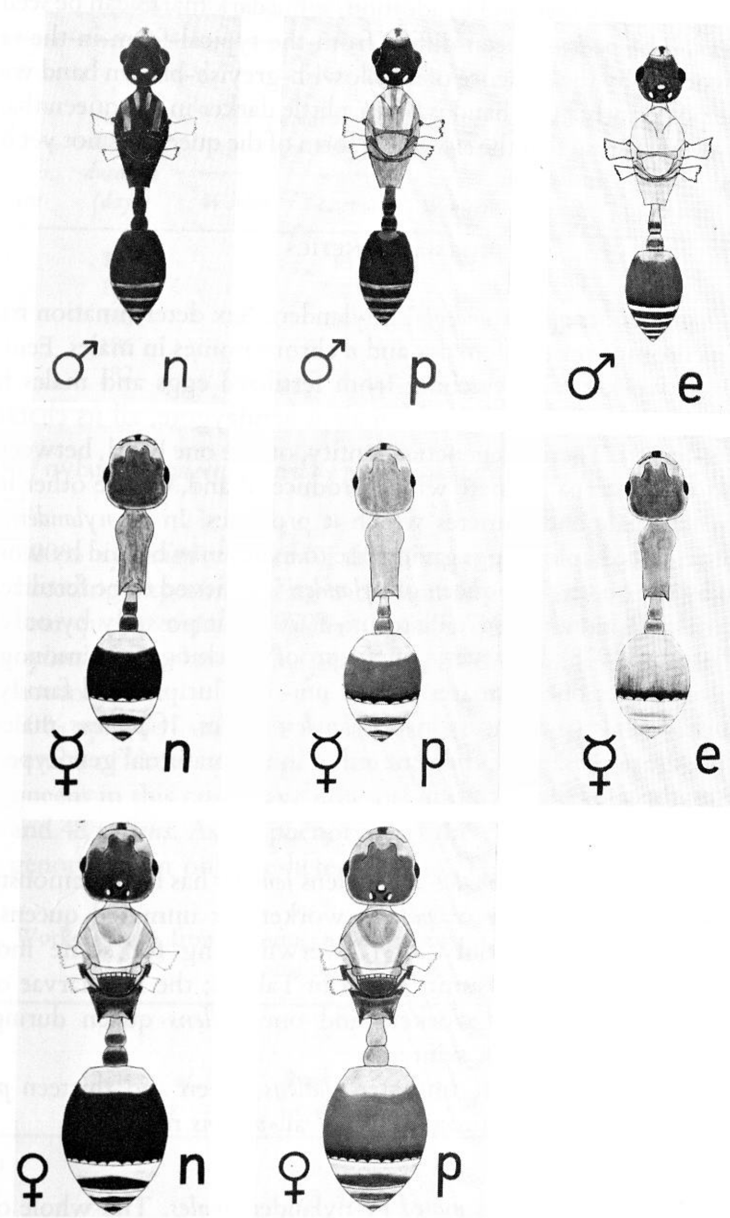

Fig. 1. Typical *nylanderi* forms (n) compared with *pallens* forms (p) of the male, queen and worker, and with *euxanthus* forms (e) of the male and worker.

is often somewhat wider, and in addition, some dark marks can be seen on the thorax. The *pallens* queen differs from the typical form in the same way as workers by the presence of a yellowish-greyish-brown band with a dark line posteriorly. This band is often a little darker in the queen than in the *pallens* worker, so that the *euxanthus* form of the queen has not yet been observed.

FORMAL GENETICS

Genetic characteristics of ants and of L. nylanderi. Sex determination results from 2 *n* chromosomes in females and *n* chromosomes in males. Females, queens and workers always come from fertilized eggs and males from haploid eggs. Thus, genetically the male is hemizygote, all its characters being sex-linked. There is a genetic identity, on the one hand, between the male and the maternal gamete which produces it and, on the other hand, between the male and gametes which it produces. In *L. nylanderi*, and many other ants, haploid eggs giving rise to males may be laid by workers and also by the queen. The queen of *nylanderi* is believed to be fertilized by several males (Chauvin, 1947; Plateaux, 1970), but possibly by only one male (Plateaux, 1978); however, genetic proof is lacking. Each monogynic colony constitutes one unimaternal and uni- or pluripaternal family.

A pure *nylanderi* produces only *nylanderi* males. If *pallens* males are produced, the *pallens* gene is present either in the maternal genotype or in the spermatheca of the queen.

Correlation between pallens *males and* pallens *females* has been demonstrated by observing the progeny of *pallens* workers or unmated queens; this progeny becomes adult only after overwintering for some months. Breeding experiments are summarized in Table I; the first larvae of AP were produced by seven workers and one *pallens* queen during the summer preceding the first winter.

During five broods, one unmated *pallens* queen and thirteen *pallens* workers produced a total progeny of 27 all-*pallens* males.

Progeny of nylanderi *queens mated by* nylanderi *males*. The whole of this progeny is constituted of *nylanderi* workers. This result was confirmed by more than one hundred homozygote or possibly heterozygote queens fertilized by *nylanderi* males, which produced some thousands of workers.

Table I. Rearing of *pallens* males by *pallens* females.

Experiment	Winter duration (days)	Population overwintering: Workers	Population overwintering: Larvae	Population at end of summer: Workers	Population at end of summer: Pallens males	Population at end of summer: Old larvae	Population at end of summer: Young larvae
AP 1	121	7	13	5	8	2	31
AP 2	113	3	7	1	3	2	3
AQ 1	113	6	20	5	10	2	15
AP 3	186	1	4	1	4		1
AQ 2	182	1	4	1	2	1	

Progeny of nylanderi *queens mated by* pallens *males*. Two different results are observed.

(1) 100% *nylanderi* workers. Table II summarizes the results of these breeding experiments, after the annual cycle of rank *n*. Twenty-four queens mated by *pallens* males produced 414 individuals, all *nylanderi* workers. The genotype of these queens is dominant homozygote.

(2) 50% *nylanderi* and 50% *pallens* workers. Table III summarizes the results of these crossings, after the annual cycle of rank *n*. The 4 queens in this table have now produced 94 workers: 46 *nylanderi* and 48 *pallens*. As the phenotype of these queens is *nylanderi*, their genotype can only be heterozygote. The queen D8A51CE had

Table II. Workers born from crossing *nylanderi* queens and *pallens* males, after the seasonal cycle of rank *n*.

Brood series	Number of colonies	Rank of cycle	Total production of nylanderi workers	No. of pallens workers
D85A180	2	3	46	0
D99L110	11	3	286	0
D213B	3	3	22	0
D213C	7	2	43	0
D213D	1	3	17	0

Table III. Workers born from crossing *nylanderi* queens and *pallens* males, after the seasonal cycle of rank *n*.

Colonies	*Rank of cycle*	*Total production of workers (or young queens)*		
		Nylanderi	Pallens	*Total*
D85A4b	7	40	37	77
D213CB	3	2	4	6
D85A1CA	1	4	2	6
D85A1CE	1	0	5	5

only one chance in 32 (3%) of producing five *pallens* workers. Multiplying by the number of observed colonies, the probability of this result rises to 12%.

Two other heterozygote queens were mated by *pallens* males, but possibly partly by *nylanderi* males too (see Table VIII, D85A1b), D99L21).

Progeny of pallens *queens mated by* pallens *males.* Table IV gives the first results of successful experiments after the first annual cycle. Five *pallens* queens have now produced 16 workers, 15 typically *pallens* and one with a pale band without a dark posterior line; the latter could be classified as a pale *nylanderi* rather than a *pallens*.

Table IV. Workers born from crossing *pallens* queens and *pallens* males, after one seasonal cycle.

Colony	*Number of workers produced*			
	Pallens	*Pale* nylanderi	*Typical* nylanderi	*Total*
D85A1BA	2	1	0	3
D85A1BD	3	0	0	3
D85A1CC	4	0	0	4
D85A1DA	2	0	0	2
D85A1DB	4	0	0	4

Recessivity of the pallens *genotype.* These observations confirm that the *pallens* genotype is recessive. However, the variability of the *pallens* phenotype in invariable ecological conditions suggests the existence of other genes acting upon the coloration and makes it sometimes difficult to identify even the *pallens* female phenotype.

NATURAL FREQUENCY OF *PALLENS* INDIVIDUALS

Of 163 colonies of *nylanderi* collected in the Paris region and observed in laboratory cultures 9 produced *pallens* males; only one also produced *pallens* females. Therefore 5·5% of colonies have the *pallens* gene; the only colony producing *pallens* females accounts for 0·6% of the observations and has a heterozygote queen mated by both types of males. No colony with a *pallens* queen has been collected.

In a panmictic population conforming to the Hardy–Weinberg rule the frequency of a male hemizygote phenotype is equal to the frequency of the corresponding gene. This should lead to the conclusion that the frequency of the male phenotype is the frequency of the gene. However, within a monogynous colony, this conclusion does not follow directly because it implies that males arise from worker eggs. This is, in fact, so for the majority of them.

Table V gives the frequency of *pallens* males in six natural colonies, for which I have analysed male production for one or more years. The mean of these frequencies is 32·5%. If 5·5% of the natural colonies have 32·5% *pallens* genes, the frequency of this gene in the population is 1·8%, which is not insignificant.

Table V. Frequency of *pallens* males produced by rearing in natural colonies.

Colony	*Number of males*		*Frequency of* pallens *(%)*
	Pallens	*Total*	
D62	4	10	40
D63	13–15	29–30	45–50
D98	22	36	61
D99	13	111	12
D213	45	173	26
D219	4	50	8

PRODUCTION OF MALES AND NUMBER OF MALES MATING ONE QUEEN

It is generally supposed that there is no selection handicapping any one type of male during its development. This seems to be true when the breeding follows a normal cycle with workers less than three years old, as is more common in the field.

Hypothesis That All Males Are Produced by the Queen

Three queen genotypes are possible: nyl/nyl, nyl/pal, pal/pal, producing respectively 100% of *nylanderi* males, 50% of each type of male, and 100% of *pallens* males. Only the less precise natural frequencies (D62 and D63) are consistent with such proportions, the others being less consistent (for D98, $P=6{\cdot}5\%$ (χ^2 test)) or completely inconsistent ($P<1\%$ for D99, D213 and D219). The hypothesis that all males are produced by the queen can thus be excluded.

Hypothesis That All Males Are Produced by Workers

In this hypothesis, the contents of the queen spermatheca intervene, and the number of males which have fertilized the queen complicates the issue by affecting the proportion of *pallens* and *nylanderi* gametes in the spermatheca (assuming that the two types of gametes are equally competitive). The number of males mating one queen during swarming is estimated at one to ten (Plateaux, 1970, 1978). Table VI expresses the percentages of *pallens* males produced by workers only, when the queen is fertilized by all *nylanderi* spermatozoa, all *pallens*, or from 10 to 90%; the genotype of the queen is nyl/nyl or nyl/pal, no *pallens* queen having been

Table VI. Percentages of *pallens* males produced by workers according to the genotype of the queen and the contents of its spermatheca.

Queen genotype	*100%* nylanderi *sperm* *(%)*	*100%* pallens *sperm* *(%)*	*10–90%* pallens *sperm* *(%)*
n//n	0	50	5–45
n//p	25	75	30–70

observed. All the observed natural frequencies fall within the range of this hypothesis.

Discussion

It is known that some foundresses can accidentally produce a few males at the beginning of colony foundation; these males come from eggs laid before the emergency of the first workers, when the foundress is absorbed in nursing activity (Plateaux, 1970). However, the production of males in a colony is usually very low or zero during the first five years. It is only when the population of workers has reached about one hundred that regular male production occurs. The queen shows herself unable to inhibit the egg-laying of workers entirely, and the males develop from these eggs. This leads to the conclusion that the role of queen in the production of males is very low, which is confirmed by the consistency of the natural frequencies with the second hypothesis rather than with the first one.

Genetic proof of the mode of male production is given only by colonies with well-known genotypes which have developed to the stage in which they produce sexual forms regularly. It now seems clear, however, that the great majority of males come from worker eggs.

Number of Males Mating One Foundress

Table VII gives the results of male production in eight natural or experimental colonies which produced a total of more than 30 *pallens* and *nylanderi* males. All the queens of these colonies being of *nylanderi* type, the queen of a colony producing more than 50% of *pallens* males is surely heterozygote; the queen of a colony producing less than 25% of *pallens* males is surely *nylanderi* homozygote. The queens of other colonies are also nearly all *nylanderi* homozygote, because the colonies contain no *pallens* workers; however, the queen of colony D213 may belong to either of the two genotypes, because the existence of *pallens* workers is not implied.

The percentage of *pallens* spermatozoa in the spermatheca of the queen is given in each case and is in parentheses when it is not significantly different from 0 or 100%, so that the corresponding proportions of *pallens* males are not significantly different from 25% (D213) or 50% (D85AA, D85AB, D99LR). In the case of D98, proportions of *pallens* males are not significantly different from either 50% or 75% and the percentage of

Table VII. Production of males in eight natural or experimental colonies and percentages of *pallens* spermatozoa in the spermatheca, according to the genotype of the queen.

Colony	*Number of males*		*Frequency of pallens (%)*	*Genotype of queen*	*Percentage of pallens spermatozoa in spermatheca*
	Pallens	Nylanderi			
D98	22	14	61	n/p	(72)
D99	13	98	11·7	n/n	23·4
D213	45	128	26	n/p	(2)
				n/n	52
D219	4	46	8	n/n	16
D85AA	24	29	45·3	n/n	(90·6)
D85AB	33	49	40·2	n/n	(80·4)
D99LK	83	189	30·5	n/n	61
D99LR	76	91	45·5	n/n	(91)

pallens spermatozoa are not significantly different from either 50% or 100%.

Table VII shows that the contribution of one male to the fertilization of one queen can be as low as 16% of the contents of the spermatheca (D219).

Table VIII summarizes the production of *pallens* homozygote females in three colonies with heterozygote queens. Percentages of *pallens* sperm are in parenthesis when they are not significantly different from 100%, the proportions of *pallens* and *nylanderi* not differing significantly from 50% respectively. The queen D99L21 swarmed with males which were all *nylanderi* except for a few *pallens* (less than 10%); she belongs to a group of nine swarming queens from which six were fully fertilized (and two others

Table VIII. Production of homozygote *pallens* females in three colonies with n/p queens.

Colony	*Number of workers or young queens*		*Percentage of* pallens *females*	*Percentage of* pallens *spermatozoa in spermatheca*
	Pallens	Nylanderi		
D85A1b	109	135	44·7	(89·4)
D85A4b	37	40	48	(96)
D99L21	23	32	41·8	(83·6)

only partly). The probability of this queen meeting with one *pallens* male was less than 10%, or less than 1% with two *pallens* males. This probability, even when multiplied by the number of fully fertilized queens, is low enough to indicate that queen D99L21 was fertilized by one *pallens* male, and perhaps also to a small extent by a *nylanderi* male.

Queens D85A1b and D85A4b swarmed with 44% of *pallens* males. The spermatheca of D85A1b apparently contained 10·6% of *nylanderi* sperm. This number indicated that one male produced 10% of the contents of spermatheca ($P = 90\%$, χ^2 test).

The estimate of one to ten males fertilizing one swarming queen is confirmed by a consideration of population genetics.

CONCLUSIONS

The study of the *pallens* morph in colonies of *L. nylanderi* confirms the hypothesis of male production especially by workers and also supports the conclusion that the number of males mating one queen varies from one to about ten.

The *pallens* phenotype can appear more or less light or dark; other genetic factors could determine the colouring.

The *pallens* queens seem to show a weak resistance to overwintering; the first four fertilized queens died in winter; one unfertilized queen died in the same way, while the *pallens* workers of the same age survived. This possible weakness of *pallens* queens has yet to be confirmed. If it exists, the *pallens* genotype could remain in populations only because of some unknown advantage which balances the effects of such selection.

Some breeding experiments seem to show that the development of male larvae in severe conditions (poor developmental season resulting from poor hibernation or from the excessive old age of nursing workers) would give an advantage to *pallens* males, which would develop more quickly than the others. This has also to be confirmed.

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