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RENE-ANTOINE FERCHAVLT

Ecvyer Seignevr DE RÉAVMVR DES ANGLES et DE LA BERMONDIÈRE

> COMMANDANT ET INTENDANT DE L'ORDRE ROYAL MILITAIRE DE SAINT-LOVIS MEMBRE DE L'ACADÉMIE DES SCIENCES DE FRANCE DE PRVSSE, DE RVSSIE, DE SVÈDE, DE LA SOCIÉTÉ ROYALE DE GRANDE-BRETAGNE ET DE L'INSTITUT DE BOLOGNE

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QUEEN POLYMORPHISM IN ANTS.

A. BUSCHINGER

Fachbereich Biologie, Institut für Zoologie, der Technischen Hochschule Darmstadt, FRG.

Introduction

The ordinary queen of ants is the well-known alate female, with 3 ocelli on the head, with a thorax with clearly separate pro-, meso-, meta- and epinotum and as well clearly distinguishable lateral sclerites. After mating she sheds off her wings. On the other hand an ordinary ant worker has a much smaller thorax, without wings, and the sclerites more or less fused.

However, in a variety of ant genera, it is more difficult to distinguish between "queen" and "worker", since the ordinary queen may be replaced in part or completely by more or less workerlike individuals. Sometimes we find a number of distinct stages, or even a continuous intergradation between the ordinary queen and the ordinary worker.

To make things even more complicate, queens and such intermediate forms bear a variety of, sometimes ill-defined, names like : ergatoid female, ergatoid queen, microgyne, gynecoid worker, full queen, dealate queen, gyne, etc...

In order to have a solid base for discussion, I tried in some of my recent papers (e.g. BUSCHINGER and WINTER, 1976), to propose a set of well defined terms, the meaning of which should be obvious as far as possible. Starting point of my considerations is, that we need a clear definition of the term "caste".

WILSON (1953) defined "caste" as "a differentiated morphological form with a specialised function". He uses this same definition in his 1971 book "The insect societies".

However, this definition is sufficient only as long as form and function are really corresponding. And this is not the case in a good deal of our ant species. MICHENER in his 1974 book "The social behavior of the bees" gives a much better definition : "Castes in bees are physiologically, behaviorally, and sometimes morphologically different forms (not age groups) of females occurring together in a colony". I would prefer to follow this definition, and to define "caste" exclusively by the function.

In order to preserve the widespread and generally accepted terms I would propose that "queen" should be reserved for functional, inseminated, egg-laying females, and "worker" for individuals who really have this function. However, these terms should be used without regarding the morphological aspect of the individuals in question.

The morphological appearance could easily be indicated by the following terms : "Gynomorph" - with the aspect of an ordinary winged or dealate female. This term is essentially synonymous with "gyne" of several English authors. However, "gyne" is often used only in the sense of "unfertilized, young queen", and "gynomorph" includes the fertile, ordinary queen, too.

"Ergatomorphs" would be individuals with a generally workerlike habitus, and "intermorph" could describe all morphologically intergrading stages between gynomorph and ergatomorph.

Such a clear distinction between functional castes and morphologically determined morphs is, in my opinion, highly important to avoid further confusion about whether an "intercaste", a "gyne", a "female", a "queen" is considered merely in a morphological sense or comprises as well their function. From the morphological aspect it is often impossible to decide,

whether all "gynomorphs" in a seemingly polygynous colony are true queens or not, and whether among the "ergatomorphs" -formely "workers" - of a species with "ergatoid queens" there is a truly fertile "ergatomorphic queen" - as I would now say. Gynomorphs, intermorphs and ergatomorphs may act both as queens or workers, depending from their being inseminated and fertile or not.

Determining the function of a given individual is rather easy by dissection, as we have shown in a variety of ant species (BUSCHINGER and WINTER, 1978), and if this investigation cannot be done, then a neutral designation only indicating the morphological aspect is much better then a designation in the usual style, which may lead to misinterpretations.

Examples of queen polymorphism among ants

After this statement, we should now have a look at several cases of queen polymorphism in ants, well understood as polymorphism of queen caste, polymorphism of inseminated, egg-laying females in a given species. Such kind of polymorphism has been established in certain

Ponerines, so in several Australian species of the genus Rhytidoponera, e.g.

R. metallica, following HASKINS and WHELDEN (1965). Their paper has the significant title "Queenlessness, worker sibship etc... in the genus Rhytidoponera". In fact, in these species there exist queens, of course, but ergatomorphic ones. And in this paper, and in a later one of HOLLDOBLER and HASKINS (1977) they describe mating of males with such ergatomorphic females. "True queens", or in our sense better "gynomorphs" occur in several species of Ponerines, but in highly variable amounts. Some species seem to lack this form completely.

Another example is given with *Ponera eduardi* from southern France. In detailed studies, LE MASNE (1953, 1956) found out, that there exist colonies who produce normal, alate gynomorphs, and alate males, and other colonies who never produce alates. The latter comprise two kinds of "workers", however, the so-called "major workers" are in fact a kind of intermorphs who may be inseminated, fertile "ergatomorphic" or "intermorphic queens". In these colonies the males are as well wingless, ergatoid, and there seems to be no genetic connection between the two kinds of colonies in the populations which were studied.

Among the Formicines, polymorphism of a similar kind is observed mainly in a few social parasitic species, such as *Polyergus rufescens* (STITZ, 1939). Besides normal, alate gynomorphs and gynomorphic queens there exist intermorphic queens, or, may be, only fertile intermorphs. Once I had the opportunity to dissect two such individuals living alongside the true, gynomorphic queen, in a colony. Both intermorphs were egg-laying, but lacked a spermatheca and thus could not be inseminated.

Egg-laying, fertile ergatomorphs and intermorphs occur, alongside an inseminated, fertile queen, rather often in ant colonies. Incidentally, I would hesitate to consider such egg-laying "workers" as equivalent to true queens, even when their eggs develop into males and are not merely eaten as trophic eggs. Among several reasons the most persuasive one is the observation, that such individuals may live alongside the normal queen even in strongly monogynous species, e.g. *Harpagoxenus sublaevis*, *H. americanus* and *H. canadensis*, who never would tolerate a second, inseminated female in a colony.

Other examples of queen polymorphism among Formicines are known from the inquiline Aporomyrmex ampeloni (FABER, 1969), a workeless social parasite of *Plagiolepis*. There the intermorphic queens are rather similar to gynomorphic ones, lacking only the wing stumps because they already eclose without wings. They also have a somewhat smaller mesonotum compared with the alate gynomorph.

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A rather spectacular case of queen polymorphism seemed to be the so-called -and -females of *Acanthomyops latipes*. However, WING (1968) could prove that this was a misinterpretation, the -females being the true gynomorphs of *latipes*, and the -females being hybrides of *latipes* and *A. claviger*.

Changing to Myrmicines we have, again, a number of examples among social parasitic species.

So several guest ants, tiny species living in colonies of Formica or Myrmica - species, show complete intergradations between the ordinary ergatomorph and the fully alate gynomorph. This is the case with Formicoxenus nitidulus from Europe, and with Leptothorax hirticornis and L. diversipilosus from North America, both belonging to the genus Formicoxenus in my opinion, too.

In these species, most of the gynomorphs are inseminated (BUSCHINGER and WINTER, 1976). In each colony unit only one of these females is fertile, this may be a gynomorphic or an intermorphic one. Gynomorphs and intermorphs who are not inseminated, and ergatomorphs who ordinarily lack a spermatheca, act as workers. The function of the supernumerary potential queens, the gynomorphs and intermorphs who are inseminated but sterile, still remains uncertain.

Up till now we have no idea about the significance of queen polymorphism in all the examples I have mentioned.

The genetically mediated queen polymorphism in Harpagoxenus sublaevis

Working on the biology and polymorphism of the slavemaker ant, Harpagozenus sublaevis, since many years, we could just recently develop a hypothesis about the significance of the queen polymorphism which we can observe in this species.

It is known, since a long time, that most colonies of *H. sublaevis* have an ergatomorphic, or slightly intermorphic, queen. Only a very low percentage of the colonies in the open have a dealate, gynomorphic queen. In one population, near Nuremberg, W-Germany, we collected during 15 years a total of 600 queenright colonies of this species. Only 6 of them, or 1 %, contained a gynomorphic queen all the others had ergatomorphic queens.

241 colonies with ergatomorphic queens were kept in the laboratory until they had produced at least 2 or 3 sexual broods, so that we could determine whether they yielded gynomorphs or only ergatomorphs. We also observed

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the offspring of all the 6 colonies with gynomorphic queens. The results are shown in table I :

Table I

Numbers and offspring of colonies with gynomorphic or ergatomorphic queen.

Type of queen	n colonies	n colonies producing			
	total	ergatomorphs only	gynomorphs and ergatomorphs		
gynomor- phic	6 (100 %)	3 (50 %)	3 (50 %)		
ergato- morphic	241 (100 %)	222 (92,1 %)	19 (7,9 %)		

Percentages calculated for the complete population of 600 colonies (= 100 %)

Type of	% colonies	% colonies producing		
queen	total	ergatomorphs only	gynomorphs and ergatomorphs	
gynomor- phic	1 %	0,5 %	0,5 %	
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ergatomor- phic	99 %	91,2 %	7,8 %	

Half of the colonies with gynomorphic queen had gynomorphic offspring, but only a small percentage of colonies with ergatomorphic queen produced this morph. In the second part of table I the ratios of the different kinds of colonies are calculated for the complete population.

I have to add, that, whenever a colony yielded gynomorphs in a first brood period in the laboratory, such individuals were produced in all following brood periods as well. And colonies which were listed as yielding only ergatomorphs could by no means be induced to produce gynomorphs later on.

We were able to breed this ant, and to prove by crossbreeding experiments, that a simple genetic mechanism mediates this kind of queen polymorphism (BUSCHINGER, 1978).

Following our terminology, an allele "E", which dominates "e",

prevents the development of larvae into alate females. Only such larvae, who are homozygous for "e", are capable to develop into gynomorphs, provided that the ordinary determining conditions are favourable.

All kinds of larvae, ee, eE and EE, may be determined to become true workers, this means ergatomorphs who lack a spermatheca. Heterozygous (eE) larvae, and those who are homozygous for E, may be determined to become potential queens, with a spermatheca, however morphologically only in the form of ergatomorphs or worker like intermorphs. From these experiments we know, that colonies with gynomorphic queens, who yield gynomorphs again, must have an eequeen who had mated with an e-male. The queens mate only once.

Those gynomorphic queens who do not yield gynomorphs, must have mated with an E-male. Both types of colonies represent only 0.5 % of the total population either. 7,8 % are colonies with ergatomorphic queens who yield gynomorphs. We suggest that these colonies have a heterozygous queen (eE), who mated with an e-male. Since ergatomorphic ee-queens are only very rarely produced in our laboratory colonies, most of the gynomorph-producing colonies should belong to the type eE x e.

91.2 % of all colonies in the open have ergatomorphic queens, and produce ergatomorphs only. Unfortunately this big group comprises three types, colonies with EE-queens mated with E- or e-males, and eE-queens mated with Emales. And we cannot distinguish the homozygous and heterozygous ergatomorphic queens by morphological characters.

Notwithstanding we can try to estimate the frequencies of the alleles E and e in the field population with the aid of the HARDY-WEINBERG formula. The result is quite puzzling (table II).

We may calculate these frequencies on the base of the known ratio of gynomorphic queens, on the base of gynomorphic queens who have mated with an e- or E-male (because of the very low number of examples this is the least significant value !), and on the base of the number of ergatomorphic queens producing alate offspring, this is the number of heterozygous queens who mated with an e-male. All the 3 calculations lead to results which are quite different from the observed ratios in our natural population.

We conclude, that this population is far from an equilibrium which could be described with the HARDY-WEINBERG formula. Several reasons could be responsable for that.

We may exclude the influence of genetic drift, the population of Nuremberg comprises more than 1 million colonies, and thus is big enough to suppress this effect. We have arguments against the assumption of an immigration of for example alate females, too. There is also little reason to believe in a very rapid evolution leading for example towards the extinction of the allele e. And an evolution with ordinary speed could never cause such conspicuous deviations from the equilibrium conditions as we can observe.

Our conclusion is, that strong selective pressures must keep the gene frequencies in an artificial relation, which is newly adjusted in each generation.

Consequently we tried to find out whether one or the other of the possible gene combinations would have a clear selective advantage or disadvantage compared with the others. This work is mainly done by my student, U. WINTER, and the following hypotheses and results of her work are not yet published.

Table II

Calculation of gene-frequencies on the basis of a) percentage of ee-queens among all queens ; b) percentage of e- and E- males who mated with an ee-queen ; c) percentage of heterozygous queens who mated with e-males.

	ee x e	ee x E	eExe	eE x E + EE x e + EE x E
Observed population	0,5 %	0,5 %	7,8 %	91,2 %
Population calculated on the basis of 1 % ee-queens (p _e = 0,1 ; q _E = 0,9)	0,1 %	0,9 %	1,8 %	16,2 % + 8,1 % + 72,9 % 97,2 %
Population calculated on the basis of 50 % e-males (50 % of ee- \$? mated with e-males) (p _e = 0,5 ; q _E = 0,5)	12,5 %	12,5 %	25,0 %	25,0 % + 12,5 % + 12,5 % 50,0 %
Population calculated on the basis of 7,8 % eE x e-colonies (p _e = 0,225 ; q _E = 0,775)	1,1 %	3,9 %	7,8 %	27,0 % + 13,5 % + 46,6 %

The significance of queen polymorphism in Harpagoxenus sublaevis - a hypothesis

We can imagine many possibilities how the two alleles could affect the fitness of their bearers. They could influence the sexual behaviour of males or females, the behaviour and success of queens during colony foundation, the behaviour of workers during slave raids and so on.

What U. WINTER found out up till now was, that the alleles e and E have no measurable effect on most of the items mentioned above. Only during colony foundations, the heterozygous females seem to be more successful than both homozygous types. However, much more conspicuous is an influence of e and E on caste determination : Apart from their influence on queen morphology, they affect the ratios of workers and potential queens, ergatomorphic as well as alate ones, who are produced in a given colony. E not only prevents completely the formation of winged females, it also lowers the rate of ergatomorphic young queens in the brood, and increases the number of larvae developing into true workers. On the other hand, colonies, whose larvae bear the allele e, produce an up to 10 times higher amount of alate or ergatomorphic females, an rather little workers.

To evaluate the potential meaning of this mechanism in terms of population genetics, we have to consider, that :

1st : a colony of *H. sublaevis* has, if successfully founded, an average lifetime of about 10 years.

2nd : during the first 2 or 3 years the colony has to grow, this means to produce a sufficient number of workers, who have to conduct successful raids on host colonies in order to get enough slaves.

3rd : later on a colony should produce sexuals and workers in reasonable proportions, to ensure both reproduction and further growth or sustaining of the colony by raiding slaves.

4th : in bigger colonies a few workers become fertile alongside the queen, their offspring will be males. And after the death of the queen the colony will produce even more males as offspring of workers during 2 or 3 years.

So, our hypothesis, including this four suppositions and the presumed effects of e and E on caste determination, predicts the following development for colonies of the 6 possible genetic types :

a) colonies with an ee-queen, mated with an e-male, should have a rather low fitness. They produce only few workers, who surely make less efficient slave raids. Thus the colonies should not grow to a sufficient number of slaves to breed many sexuals. Supposedly many colonies of this type will die out after a few years.

- b) Colonies with an EE-queen, mated with an E-male, should yield many workers, make many successful raids, grow to a considerable size, but, genetically mediated, produce rather little ergatomorphic young queens. However, the fertile "workers" will produce E-males in high numbers, especially after the death of the queen.
- c) Colonies with eE x e-, ee x E, and EE x e-queens may have an average fitness, yielding eE-workers in more or less sufficient numbers, and also some sexuals.
- d) Colonies with a heterozygous (eE) queen, mated with an E-male, should have the highest fitness : the colonies produce two kinds of larvae. The homozygous EE-larvae would preferably develop into workers, thus ensuring that the colonies will have a reasonably high number of workers under all circumstances, and that slave raids may be conducted with sufficient success. The heterozygous larvae will preferably develop into ergatomorphic young queens. Many, preferably E-males will as well be produced by such colonies, as offspring of EE-workers.

So, if we remember that in the open field population, only 1 % of the colonies have a dealate, gynomorphic queen (ee x e and ee x E together), we may suppose that most of the colonies belong to the type eE x E, producing high numbers of heterozygous ergatomorphic queens. Colonies of the type EE x E, producing preferably E-males in high numbers, may also be rather common. Thus the system could be self-perpetuating. The occurrence of colonies with gynomorphic queen, and of alate gynomorphs at all, could then be a mere by-product with little significance for population genetics.

This is, of course, a hypothesis, and we will presumably never be able to prove it in all details. However, we have some experimental evidence which supports this construction :

For example, in our laboratory experiments, all colonies instead of raiding on slave nests, are provided during every summer season with equal numbers of slave pupae. The determining influences on larvae, such as food, glandular secretions from slave workers, and so on, thus should be comparable. Under these conditions we found, that colonies of the type ee x e began to rear female sexuals already in the first year after colony foundation, and yielded up to 10 times more young queens than colonies of the type EE x E during the first 5 breeding seasons. Colonies of type eE x E produced about 50 % workers, and 50 % ergatomorphic young queens, in their 3rd and 4th brood period, and so on. Thus we are rather hopeful that we will be able to prove at least some of the major assumptions of our hypothesis.

Unfortunately, up till now *H. sublaevis* is the only example where it was possible to undertake an experimental investigation of queen polymorphism. For both the related species *H. canadensis* and *H. americanus*, a similar queen polymorphism was reported in the literature (CREIGHTON, 1950). However, I could find out that both species have an essentially normal polymorphism, with gynomorphic queens, ergatomorphic workers, and only a rather high number of intermorphs.

The latter, however, do not possess a spermatheca, and thus never act as queens.

Nevertheless the significance of our observations in H. sublaevis is, that perhaps other known cases of queen polymorphism could be explained by similar mechanisms, that we not only may speculate about direct advantages or disadvantages of the presence of such a queen polymorphism. Instead, such a polymorphism may be a mere by product of a much more important mechanism which enhances the overall fitness of a given population, or improves its adaptation to given environmental factors.

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