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Queen Polyandry and the Evolution of Parasite Virulence

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Abstract

Eusocial queen polyandry increases genetic diversity within colonies, and genetically diverse colonies presumably suffer less from omnipresent parasites than genetically homogeneous colonies. So eusocial queen polyandry may have evolved in response to parasite load. Ewald's theory of the evolution of virulence specifies conditions favoring the evolution of virulent, damaging parasites.

Applying these ideas to parasites of ants, it is inferred that parasites are more virulent, and hence queen-polyandry is more often expected, when colonies are larger, when colonies are founded dependently, and when colonies are mobile or nomadic. An analysis of an ant-database supports these predictions. Further analyses, preferably using a generally accepted database, seem valuable.

Keywords: Parasites; Evolution of virulence; Polyandry; Ant database

Introduction

Single queens and single mating

The classic image of an eusocial colony such as an ant nest is that of many sterile individuals ('workers') and only one reproducing female, the 'queen'. For a variety of reasons [1,2] workers refrain from producing offspring of their own and instead help a reproductive female, often their mother.

Indeed, colonies of eusocial species indeed contain workers who are often, but not always, sterile. And in many, but certainly not all cases there is only one queen (monogyny) who, as in contrast to females of most solitary insects [3], usually mates with only one male [4], 'monandry'. This arrangement results in a higher degree of relatedness between workers than if the queen were to mate with multiple males (polyandry) or if there were multiple queens in one colony (polygyny).

Darwinian and 'Hamiltonian' [5] biologists accept the idea that natural selection tends to favor an association between degree of relatedness and cooperation [6], so one singly mated queen promotes cooperation within a colony better than multiple mating or multiple queens. Workers are more closely related amongst themselves when all have the same father and the same mother.

Monogyny seems conductive to colony cohesiveness when colonies frequently move, as in the group-hunting and migratory army ants. Likewise, with a bounty around valuable enough to compete for, such as fungus-gardens, a limited supply of decaying wood or a store of honey, a monogynous breeding system effectively puts a limit to internal competition for these resources.

Polygyny on the other hand may result from queens and their lineages having little to compete for amongst themselves, while due to ecological pressures such as nest site limitation or high risks associated with independent nest founding [7] it is in each one's interest to use the same protective nest [8].

As noted, females of most solitary insects mate with multiple males. This increases genetic diversity of offspring and therefore seems adaptive, since these females usually should not be concerned about cooperation between their offspring. But such cooperation between offspring is an essential feature in eusocial species, so why do some eusocial queens nevertheless mate with multiple males?

Rough sex suggesting important causes

Multiple queen-mating seems important in some species. Queens often take considerable risks while trying to get mated by multiple males, and copulations tend to be short and 'business-like'. As in contrast to male termites, hymenopterian males die shortly after copulation, usually on the same day and often instantly after copulation. *Pogonomyrmex occidentalis* queens mate on average with 6.3 different males [9]. According to Nonacs "males are often found with severe wounds on the gaster attributable to females gnawing at them to terminate copulations". Nonacs writes on the same page about *P. barbatus*, *P. desertorum*, *P. maricopa*, and *P. rugosus*, (all of which are also monogynous, polyandrous species): "males compete intensively between themselves for access to females and remain in copulation until the females bite their gaster. Females are frequently found with male copulatory organs attached. (....) *Formica pergandei* chew the abdomen and sometimes the head off of males after copulating" [10]. Army ants and honey bees are known to be extremely polyandrous. While army ant gynes (= unmated queens) are wingless and mated by incoming males, honeybee queens mate on the wing, and every extra copulation means more exposure to predation, so they are under time pressure. Wilson writes "The mating is quick and violent; the male literally explodes his internal genitalia into the genital chamber of the queen and quickly dies. The queen makes as many as 3 flights a day for a total of up to 12 flights or more, and on each flight she mates with a different male" [11].

Since a single male is usually capable of providing a sufficient amount of sperm [12] then why would natural selection result in queens of some species, but not all, spending extra time and energy, and risking more predation, in order to get additional copulations?

Polyandry and parasite loa

Denny et al. report exceptionally high levels of multiple queen mating in the army ant *Eciton burchellii*. After evaluating various

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explanations, they propose that multiple mating evolved in *E. burchellii* to increase genetic diversity, in order to co-evolve in the arms-race with parasites. They also remark that *E. burchellii* is more susceptible to parasites than other ant species because of their nomadism and predatory lifestyle, and because reproduction by fission (also called dependent founding) prevents parasites from being shed in the way that solitary founding queens might do [13,14] Like *E. burchelli*, honeybees reproduce by colony fission, have high parasite loads and high levels of multiple mating [15]. So although polyandry compromises the (genetic and social) unity in an eusocial colony, it may nevertheless be favored by natural selection because genetic diversity is an adaptation to parasite load [16,17]. If this idea is correct, then polyandry should vary with parasite-load in monogynous eusocial species, since the number of males mating with the queen directly varies with genetic diversity in monogynous species. (In polygynous species genetic diversity also varies with the number of queens).

One way to measure parasite load is to count the *number* of parasite-species associated with certain eusocial species [12,18], and indeed, these authors report that parasite loads correlate with intra-colony genetic variability. However, a drawback of this approach is the theoretical possibility that individuals of a few very virulent parasite-species do more damage than parasites belonging to many different species which are less virulent or even benign. So the number of parasite-*species*, and even the number of parasites itself may not be a reliable measure of parasite load.

Parasites evolve through a process of natural selection like all living creatures do, and potentially malicious parasites are ubiquitous. So it seems vital to understand why some parasites (or 'guests') evolve to be benign while others are malicious and virulent. Ewald's theory of the 'evolution of virulence" (1993) provides exactly such an explanation. Applying this theory to parasites of eusocial colonies results in three predictions about queen-polyandry [19].

The evolution of virulence and three hypotheses

Species of parasites differ in the degree they cause damage to their hosts. The relation between a 'host' and its 'guests' may be parasitic and one-sided, but also mutualistic. For instance, ants 'milk' aphids, cultivate fungus gardens, protect acacia-trees, and so on, apparently to the benefit of both parties.

The empirically well supported theory of Paul Ewald about the 'evolution of virulence' allows an understanding of why relations between hosts and guests are sometimes mutualistic and benign, and at other times parasitic [20,21]. In a nutshell this theory says that in a host-guest (or host-parasite) relation, the parasite is more damaging to its host if it can easily transmit to other hosts, and reproduce independently of the current host. Because if the current host needs not stay healthy and alive for the parasite to reproduce, then the parasite can evolve to deplete its resources while attempting to reproduce maximally and spread to other hosts. In contrast, when the parasite has great difficulty transmitting itself to new hosts, it is in its interest to keep the current host healthy and alive, and mutualistic relations are expected to evolve. So the 'transmissibility' of parasites is the key variable explaining their virulence.

Ewald's theory permits the inference of hypotheses about the virulence of parasites of eusocial species. The easier it is for a parasite to infect a new colony, the more damaging the parasite will be, and so queens tend to be more polyandrous, since polyandry increases genetic diversity. The three hypotheses presented here about the evolution of eusocial polyandry all have to do with conditions facilitating the transmission of parasites from one eusocial colony to another.

Firstly, species with larger (in contrast to smaller) colonies are more easily found and infected by parasites, so parasites are expected to be more virulent [7,22], and queens more polyandrous.

1. In monogynous eusocial species with large colonies, queens tend to be more polyandrous.

Secondly, colonies which are founded dependently (that is, with the help of workers) are more easily infected by parasites than independently founded colonies, because dependent founding "prevents parasites from being shed in the way that solitary founding queens might do" [13].

2. Monogynous eusocial species whose colonies are founded dependently are more often polyandrous than similar species with independent founding.

Finally, parasites are more likely to be contacted and picked up by species with nomadic colonies (as in contrast to permanent or sessile colonies).

3. In monogynous eusocial species with mobile colonies, queens tend to be more polyandrous than queens in species with permanent nests.

Materials and Methods

Data and variables

In this article, polyandry is assumed to have evolved in order to increase genetic diversity within colonies. But polygyny also increases genetic diversity, so in order to test the three hypotheses mentioned above, data about monogynous ant species are needed, including variables measuring the level of polyandry, the mode of colony foundation and the mobility of colonies. One would also wish to control for other possible confounding variables, and furthermore compare relevant correlations with similar correlations in polygynous species. In sum, a large database of ants with many variables covering several key social aspects of ants is needed. More will be said below about establishing such a database.

A database containing information about 458 species of ants has been constructed. The values of variables like colony size, effective mating frequency, monandry/polyandry, monogamy/polygyny, etcetera were collected from the literature, mainly from tables included or attached to publications [7,10,18,23-37].

The key variables

Of the 297 species coded for the variable 'Gyny', 188 (63.3%) are monogynous, 15 (5.1%) are monogynous or polygynous, 71 (23.9%) polygynous, and for 23 species (7.7%) the value is 'unclear/disputed', meaning that authors disagree among themselves.

'Colony-size' was coded in eight values, ranging from 50 workers or less to over 500.000 workers. Information about colony size was available for 297 of the 458 species (64.8%), and this information was coded for 102 species described as clearly monogynous.

'Mode of colony foundation' has three values: independent foundation, independent foundation or dependent foundation and dependent foundation. Information about this variable was available for 179 of the 458 species (39.1%). Of these species, 113 are founded independently, 17 independently or dependently and 49 dependently (63.1%, 9.5% and 27.4 %).

Lacking detailed information about the mobility of colonies, all species were coded as not mobile, except for 14 army ants and army ant-like species, Monomorium pharaonis and the curious 'migrating ant' Dolichoderus (Diabolus) cuspidatus.

Published data about effective mating frequencies were chosen as the dependent variable 'level of polyandry'. Following Hughes et al. these frequencies were coded in four values: obligate monandry, facultative polyandry (<2 effective mates), moderate polyandry (2-10 effective mates), and extreme polyandry (>10 effective mates). Information about effective mating frequencies was available for 145 (31.7%) of species [7].

Parasitic species were excluded from the database, as were queenless species and species with conflicting or unclear reports about monogyny/polygyny. Species that are both monogynous and polygynous, as well as species with both independent and dependent foundation were also excluded.

Results

Table 1 presents the correlations between the dependent variable 'level of polyandry' and the three independent variables 'colony-size', 'mode of colony foundation' and 'mobility of colonies' for monogynous and polygynous species.

Strong and significant correlations are found in monogynous ant-species between the level of polyandry and the independent variables colony size, mode of foundation and the mobility of colonies. No such correlations were found in the polygynous species. Following Ewald's theory, parasites are expected to be more harmful in colonies that are large, mobile or dependently founded. Polyandry increases genetic diversity in colonies, and genetic diversity is presumed to be an adaptation to parasites. So as expected, polyandry is more often found in large, mobile and dependently founded *monogynous* species.

But since polygyny also increases genetic diversity, no significant correlations between the level of polyandry and the three independent variables were expected in polygynous species, and these were indeed not found.

So by applying Ewald's theory of the evolution of virulence, and without mentioning even a single species of ant-parasites, this study supports the idea that eusocial queen polyandry evolved to counter the effects of parasites. At least fourteen different explanations of eusocial queen polyandry have been proposed [12] and it appears that the role of parasites is a clear favourite. However, the correlations above are based on a database constructed by the same person that used it to test the hypotheses he proposed. This brings me to the issue of concluding remarks.

Discussion. Wanted: A General and Acknowledged Ant Database

Ahead of his time, in 1962 anthropologist George P. Murdock initiated systematic data bases of the best earliest descriptions of hundreds of human societies, for the purpose of testing cross-cultural hypotheses about human behaviour. These data-bases, occasionally corrected and expanded, have been used for that purpose ever since. A similar data-base about ants would be valuable. It should contain the names of thousands of species, and variables with information about the average size of colonies, the mode of colony foundation, monogyny/polygyny, monandry/polyandry, the sex-ratios and much more. Certainly, dozens of myrmecologists have produced tables and databases of ants in order to give overviews, illustrate certain points or test cross-species hypotheses. But there are drawbacks associated with the situation where every researcher produces a database of his or her own. In the first place, in an ideal world the person testing certain theoretical hypotheses should preferentially not be the same as the one who collected the data and constructed the database used to test these hypotheses. Furthermore, after completing his or her own database, the attention of a researcher often shifts to different subjects. Other scientists however, interested in some of the data, face the boring prospect of copying them for their own research. During this process of copying mistakes are inevitably made, then perhaps copied to another table, and so on. More important is perhaps that tables existing today provide information which is in part contradicted in other tables. In other words, empirical reports are often disputed, while not being labelled as such. Let me give one example out of many. *Leptothorax longispinosus* is described in three articles [7,25,31] as polygynous, [5] having "few" effective queens, and in two other articles [34,37] as monogynous. It should be possible to resolve some of these disagreements. The first step would be to draw attention to them, and a general database does just that. Such a database should contain references to the original empirical sources (including page-numbers) and highlight missing data. Its establishment should be a goal in itself. On the one hand, researchers could not ignore it, while on the other hand they might be happy to contribute and correct data. Keller (1998) wrote: "I suggest that students of social insects would greatly benefit if information on colony characteristics, individual phenotypes and behaviour would become available for a larger number of species, perhaps on a database that would be accessible on the web." And: "(…) this information is frequently difficult to retrieve from the literature because it is often mentioned in a cryptic manner in papers dealing primarily with other issues." Such a database would facilitate easy access to numerous data on ant species and elaborate statistical testing of theoretical hypotheses about ants. Finally, it would free both authors and journals from publishing ever longer tables (and lists with references), often largely containing information which had, at least in part, been published before, often many times over, in other tables [38].

	Monogynous species			Polygynous species		
	Kendall's t	Sign	N	Kendall's t	Sign	N
Colony size	.597	.000	57	-.152	.448	20
Mode of Foundation	.416	.002	50	.092	.742	13
Mobility	.448	.000	73	-.167	.338	33

Table 1: The correlations between the dependent variable 'level of polyandry' and the three independent variables 'colony-size', 'mode of colony foundation' and 'mobility of colonies' for monogynous and polygynous species.

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