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Sex allocation and queen-worker conflict in polygynous ants

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Summary. Sex allocation theory is developed for polygynous eusocial Hymenoptera in which nests recruit their own daughters as new reproductive queens. Such restricted dispersal of females leads to the expectation of male-biased investment ratios. The expectation depends on the parameter q telling what proportion of the total contribution in the gene pool by all new queens is due to those dispersing. Under queen control the expected sex allocation, expressed as the proportion of resources invested in males, is $IM = 1/(1+q)$. Under worker control, IM depends on the relatedness of old queens, on the number of males they have mated with, and on the proportion of males produced by workers. With single mating and no worker reproduction, the approximate predictions for IM are $1/(1+q)$ when the nests have many highly related queens, $1/(1+2q)$ when the old queens are as related as average worker nest mates, and $1/(1+3q)$ when the old queens are not related to each other at all. The observed investment ratios in polygynous ants would, on average, match values of the parameter q between 0.4 and 0.5. Values of q have not been estimated in nature. If q is smaller than 0.4, which may well be true, the observed sex allocation in polygynous ants is in fact more female-biased than predicted by the theory. This indicates that the female bias found in monogynous ants may not be exceptional and could be due to factors other than worker control of sex allocation. Because the value of q is likely to vary among species, testing the predictions of the theory requires thorough single-species studies.

Introduction

The theory of sex allocation in social Hymenoptera (ants, bees, wasps) has been well established since first presented by Trivers and Hare (1976). Much of that theory can be synthesized using an inclusive fitness formulation (Taylor 1988; Pamilo 1990). The basic significance of the theory centers on the prediction of the queen-worker conflict over resource allocation. Because of unequal relatednesses between colony members, queen-worker conflicts can be expected concerning both sex ratios (Trivers and Hare 1976) and allocation of resources between sexual production and colony maintenance (Pamilo 1990). One major gap in the theory still is that the present formulations do not cover the situation where polygynous nests (nests with multiple queens) recruit some of their own daughters back as new reproductives.

Generally, workers should favor more female-biased sex ratios than do queens. Data from monogynous ants seem to agree with this prediction, and it has been concluded that the queen-worker conflict has been resolved in favor of the workers (Trivers and Hare 1976; Nonacs 1986; Boomsma 1989). This could be possible because the workers take care of the brood and feed the developing larvae. That allows them to influence both the ratio of diploid (females) to haploid (males) offspring and the caste ratio (queens to workers) within the diploid offspring.

Trivers and Hare (1976) further realized that when nests recruit their own daughters as new reproductives, these daughter queens require a share of the nest's workers (which should be counted as an investment in females), leading to the expectation of male-biased sex ratios when only sexual offspring are counted. This suggestion has not gained much popularity, probably because it has not been formalized. It has been considered as a weak argument (Crozier 1979), and it has been shown that the sex ratios tend to approach the 1:1 value under both queen and worker control in polygynous colonies when the reproductive queens are closely related and all sexual offspring disperse (Benford 1978). I here develop a theory for polygynous nests that recruit their own daughters as new reproductives. A reanalysis of published data suggests that sex allocation in polygynous ants may be more female biased than predicted by this theory. This finding makes the earlier conclusions – that a female bias in monogynous ants is exceptional and results from worker control of sex allocation – less convincing.

Model

I define the investment ratio on the basis of resource allocation in sexual offspring. When the resources in a nest are divided: x in new queens, y in males, and w in workers ($x+y+w=1$), the sex allocation is here expressed as the proportional investment in males:

$$IM=\frac{y}{x+y}. \tag{1}$$

I use this measure, which does not depend on w, because it is difficult in practice to estimate what fraction of workers is maintaining the old queens and what fraction supports the new queens recruited by the colony. It should be noted that x and y refer only to those sexuals that disperse from the natal colony. Note also that many authors (e.g., Benford 1978) have used the ratio instead of the proportion of investments. The expectation depends: on whether the queen or workers control allocation, on the genetic heterogeneity of colonies, and on the relative successes of the new queens that either disperse or stay in the natal nest after having mated.

All females disperse

When all females disperse, the sex allocation is predicted by:

$$IM=\frac{g_m v_m}{g_m v_m+g_f v_f} \tag{2}$$

where g_m and g_f are the genetic relatednesses of the male and female offspring to the individual controlling allocation, and v_m and v_f are the sex-specific reproductive values of males and females (Taylor 1988; Pamilo 1990). When the workers do not produce males, $v_f/v_m=2$. Under queen control, the predicted investment ratio is therefore $IM=0.5$.

With single mating, the relatednesses of the offspring to the workers in the nest are $g_f=\{3+(n-1)G\}/(4n)$ and $g_m=\{1+(n-1)G\}/(2n)$, where n is the number of coexisting old queens and G is the relatedness among them. The investment ratio under worker control is then:

$$IM=\frac{1+(n-1)G}{4+2(n-1)G}. \tag{3}$$

When the queens are not related ($G=0$), the sex ratio is expected to be $IM=0.25$ (Frank 1987). If the queens are highly related to each other ($G \gg 1/n$), the sex ratio should approach 0.5 with increasing n (Trivers and Hare 1976; Benford 1978). When the relatedness of the queens is an inverse of the number of them, IM from Eq. (3) is approximately 0.33. These predictions, however, do not hold any more when some of the new queens are recruited back to their natal nest. Positive G must result from previous recruitment of related queens or from relatedness of primary foundresses. The latter alternative is not supported by the existing data (Hagen et al. 1988).

Colonies recruit daughters

When daughters are recruited back, optimal allocation depends on the relative successes of the dispersing and staying queens. I next analyse such a situation. The investments x and y now refer to the dispersing offspring, and I assume that no local mate competition or local resource competition occurs among related same-sex offspring.

Let the probability of an old nest surviving to the following year be S, and let the overall reproductive value of such a nest be v_o. This reproductive value is proportional to the probability that a randomly picked gene in a future generation originated from this nest. Assume further that the dispersing daughters establish new nests, the reproductive value of each nest being $v_n = c_v v_o$. If, on average, c_n new nests will be established when a nest produces only daughters (i.e., $x=1$), the combined success of new nests is xcv_o, where $c=c_v c_n$. The proportional representation in the population of nests is therefore $cxv_o/(cXv_o+Sv_o)$, where X is the mean investment in females in the whole population. The contribution to the inclusive fitness (Pamilo 1990) of the old colony members through dispersing daughters is thus:

$$g_f v_f \frac{cx}{cX+S}. \tag{4a}$$

Males contribute to future generations by inseminating either dispersing queens or queens that stay in their natal colony as new reproductives. Let p be the proportion of such new recruits among queens of an old colony. The relative contribution of new queens in the whole population is $(cXv_o+pSv_o)/(cXv_o+Sv_o)$. The contribution in the inclusive fitness through sons in a colony allocating a proportion of y of its resources in sons is:

$$g_m v_m \frac{cX+pS}{cX+S}\frac{y}{Y} \tag{4b}$$

where Y is the mean investment in males in the whole population.

We can combine the parameters c, p, and S as a single one:

$$q=\frac{cX}{cX+pS} \tag{5}$$

where the numerator and denominator give the contributions by new queens in the gene pool; the numerator gives that by dispersing queens and the denominator that by all new queens. The equilibrial sex ratio can be found by taking derivatives of (4a) and (4b) with respect to x and y. Making these equal gives:

$$Y=\frac{g_m v_m(cX+pS)}{g_f v_f c}$$

and

$$IM=\frac{Y}{Y+X}=\frac{g_m v_m}{g_m v_m+q g_f v_f} \tag{6}$$

as the expected equilibria. When $q=1, IM$ from (6) equals that given by (2), and when $q=0, IM=1$. This latter result means that when dispersing females are unsuccessful, nests should only produce a small number of new queens (which are all recruited back) and use remaining resources in producing workers and males.

When a proportion ψ of all males is produced by workers, the ratio of the sex-specific reproductive values is $v_f/v_m=2-\psi$ (Pamilo 1990). We can now solve the expected investment ratios separately under queen control and under worker control.

The relatednesses of the offspring to a random queen in a polygynous nest are $g_f=\{1+(n-1)G\}/(2n)$ and $g_m=(2-\psi)\{1+(n-1)G\}/(2n)$. Inserting these in (6) gives, under queen control,

$$IM=\frac{1}{1+q} \tag{7}$$

independently of ψ.

The relatednesses of the sexual offspring to a random worker also depend on the number of matings, i.e., on how many patrilines each queen produces. Let k be the effective number of patrilines (Starr 1984; Pamilo 1990) among the offspring of a single queen. The relevant relatednesses are $g_f=\{(k+2)/k+(n-1)G\}/(4n)$ and $g_m=\{2-\psi+2\psi/k+(2-\psi)(n-1)G\}/(4n)$. Inserting these in (6) gives, under worker control,

$$IM=\frac{1+2/k+(n-1)G-(4/k)(1-\psi)/(2-\psi)}{(1+q)\{1+2/k+(n-1)G\}-(4/k)(1-\psi)/(2-\psi)} \tag{8a}$$

If we set $q=1$ in (8a) we get a prediction under worker control for the case when no daughters are recruited, i.e., all new queens disperse. If we set both $q=1$ and $k=1$ (i.e., monandry), Eq. (8a) equals the formula derived by Benford (1987: Eq. 29).

The real aim of the present model, however, is to extend the theory to cases when some of the daughter queens are recruited back, i.e., $q<1$. When the workers produce all of the males ($\psi=1$) or the number of matings is large, Eq. (8a) reduces into:

$$IM=\frac{1}{1+q} \tag{8b}$$

independently of n and G.

When the queens produce all of the sexual offspring ($\psi=0$), the expected investment ratio under worker control depends on the relatedness among the old queens and can be written $IM=1/(1+aq)$ where $a=1+2/\{k(1+(n-1)G)\}$. When the relatedness is high ($G \gg 1/n$), the investment ratio is approximately $1/(1+q)$ as given in (8b). If the relatedness is approximately an inverse of the number of queens, for example $G=1/(n-1)$,

$$IM=\frac{1}{1+(1+1/k)\,q}. \tag{8c}$$

This would be the expectation when the nests generally recruit their own daughters back as new reproductives. Namely, when there is no reproductive dominance, the expectation is (Pamilo and Varvio-Aho 1979) $G=3/(3n+1)$. Finally, if the queens are not related at all ($G=0$),

$$IM=\frac{1}{1+(1+2/k)\,q}. \tag{8d}$$

With single mating, the predictions from (8c) and (8d) are $1/(1+2q)$ and $1/(1+3q)$. The predictions are simple. Unfortunately, we lack information on the values of the parameter q in nature. The higher the proportion of successfully dispersing new queens (high q), the closer the expected ratio from (6) is to that given by (2). When dispersing is risky, a high proportion of new queens will be recruited back to old nests. In that situation (small q), it is profitable to produce both workers maintaining old nests and males inseminating the queens recruited, but it does not pay to produce extraneous females if their fate is to perish when dispersing.

Data

Sex ratio data are available from 42 monogynous and 27 polygynous ant species (Table 1). From further analysis I omit the species in which no estimates of the weight of the sexuals could be found. This leaves 40 monogynous and 25 polygynous species. It should be pointed out that it is not always evident how to classify a species when some nests are monogynous and some polygynous.

The sex allocation IM is calculated as $r/\{r+(1-r)E\}$ where r is the numerical proportion of males and E is the ratio of the energetic expenses of producing a queen to that producing a male. E is approximated from the ratio of individual dry weights, D, according to the formula suggested by Boomsma (1989) as $E=D^{0.7}$. In *Pheidole pallidula*, IM is based on fresh weights of the sexuals. In some species no weight data were available and an estimate from related species is used (see footnote, Table 1).

I have pooled the data from different populations of the same species as a single sex ratio estimate. When several dry weight estimates exist, I have used that given in the same study where the sex ratio data come from; otherwise I have used the estimates of Boomsma (1989). There is a significant difference in the average sex allocation between monogynous and polygynous ants ($IM=0.37$ in 40 monogynous and $IM=0.56$ in 25 polygynous species, $t=3.6$, $P<0.001$; t test done from arcsine transformed values).

The investment ratios in monogynous species are, on average, female-biased, as detected earlier (Trivers and Hare 1976; Nonacs 1986; Boomsma 1989). In the polygynous species they range from extremely male biased to highly female-biased. The extremely male-biased ratios characterize species that form large polydomous colonies of interconnected nests and commonly produce new nests by budding. Such species include *Formica exsecta*, *F. pressilabris*, and *Iridomyrmex humilis*. In many other polygynous species in Table 1, new nests are commonly established by budding.

Table 1. Sex allocation in ants. *C* is the number of nests examined, *N* is the logarithm ($\log_{10}$) of the number of sexual individuals counted (2 for hundreds, 3 for thousands, etc.), *r* is the numerical proportion of males among all sexuals, and *IM* is the proportion of resources invested in males based on the energetic costs. Note that the references Trivers and Hare (1976) and Nonacs (1986) are reviews with no original data

	C	*N*	*r*	*IM*	References
Monogynous species					
Acromyrmex octospinosus	10	3	0.46	0.31	Nonacs (1986)
Aphaenogaster rudis	14	2	0.85	0.48	Nonacs (1986)
A. treatae	12	3	0.61	0.24	Nonacs (1986)
Apterostigma dentigerum	?	2	0.51	0.51	Nonacs (1986)
Atta bisphaerica	5	4	0.76	0.42[a]	Nonacs (1986)
A. laevigata	6	4	0.74	0.39	Nonacs (1986)
A. sexdens	7	5	0.83	0.54	Nonacs (1986)
Camponotus ferrugineus	6	3	0.56	0.26	Nonacs (1986)
C. herculeanus	1	3	0.71	0.44	Nonacs (1986)
C. pennsylvanicus	12	3	0.56	0.27	Fowler and Roberts (1982) Nonacs (1986)
Carebara vidua	7	2	0.30	0.12	Lepage and Darlington (1984)
Formica exsecta	30	3	0.61	0.56	Pamilo and Rosengren (1983)
F. fusca	29	3	0.60	0.55	Pamilo and Rosengren (1983)
F. lugubris	11	3	0.47	0.43	Pamilo and Rosengren (1983)
F. nitidiventris	19	3	0.23	0.17	Nonacs (1986)
F. pratensis	35	3	0.72	0.68	Pamilo and Rosengren (1983)
F. rufa	32	3	0.50	0.46	Rosengren and Pamilo (1986)
F. truncorum	63	3	0.48	0.45	Rosengren et al. (1986)
Iasius alienus	?	5	0.84	0.30	Nonacs (1986)
L. flavus	12	3	0.69	0.17	Nonacs (1986)
L. niger	201	5	0.79	0.37	Nonacs (1986)
Ieptothorax ambiguus	12	2	0.45	0.18	Nonacs (1986)
L. curvispinosus	97	3	0.57	0.31	Nonacs (1986)
L longispinosus	285	3	0.66	0.46	Nonacs (1986)
L provancheri	13	2	0.42	–	Buschinger et al. (1980)
Myrmecina americana	10	2	0.54	0.38	Nonacs (1986)
Myrmica ruginodis	12	3	0.44	0.37	Nonacs (1986)
M. schencki	10	2	0.24	0.16	Nonacs (1986)
Pogonomyrmex montanus	35	4	0.51	0.40	Nonacs (1986)
P. rugosus	4	3	0.73	0.56	Nonacs (1986)
P. subnitidus	7	3	0.70	0.50	Nonacs (1986)
Prenolepis imparis	12	3	0.89	0.45	Nonacs (1986)
Pseudomyrmex belti	1	3	0.55	0.44	Nonacs (1986)
P. ferruginea	1	3	0.31	0.24	Nonacs (1986)
Rhytidoponera confusa	27	3	0.51	0.36	Ward (1983)
R. purpurea	10	3	0.47	0.32	Ward (1983)
Solenopsis invicta	?	5	0.48	0.28	Trivers and Hare (1976)
Stenamma brevicorne	8	2	0.42	0.28	Nonacs (1986)
S. diecki	10	2	0.56	0.35	Nonacs (1986)
Tetramorium caespitum	157	4	0.58	0.41	Nonacs (1986)
Trachymyrmex septentrionalis	8	3	0.32	–	Nonacs (1986)
Veromessor pergandei	8	3	0.35	0.19	Pollock and Rissing (1985)
Polygynous species					
Crematogaster mimosae	?	3	0.92	0.69	Nonacs (1986)
C. nigripes	?	3	0.72	0.48	Nonacs (1986)
Formica aquilonia	116	3	0.28	0.24	Rosengren and Pamilo (1986)
F. cinerea	9	2	0.37	0.32	Pamilo and Rosengren (1983)
F. exsecta	58	3	0.90	0.85	Pamilo and Rosengren (1983)
F. incerta	12	2	0.45	0.35	Nonacs (1986)
F. obscuripes	46	4	0.58	0.52	Nonacs (1986)
F. polyctena	27	3	0.26	0.22[a]	Pamilo and Rosengren (1983)
F. pressilabris	36	3	0.98	0.98	Pamilo and Rosengren (1983)
F. rufibarbis	11	2	0.47	0.42	Pamilo and Rosengren (1983)
F. sanguinea	12	2	0.22	0.19	Pamilo and Rosengren (1983)
F. truncorum	158	3	0.74	0.72	Rosengren et al. (1986)
F. yessensis	26	4	0.73	0.70[a]	Kim and Murakami (1980)
Iridomyrmex humilis	?	?	0.98	0.97	Trivers and Hare (1976)
Leptothorax diversipilosus	9	2	0.55	–	Alpert and Akre (1973)
Monomorium pharaonis	24	4	0.28	–	Peacock (1951)
Myrmica rubra	4	3	0.89	0.82	Nonacs (1986)
M. ruginodis	5	2	0.89	0.89	Nonacs (1986)
M. sabuleti	107	4	0.81	0.71	Nonacs (1986)
M. scabrinodis	?	2	0.50	0.40	Nonacs (1986)
M. sulcinodis	164	3	0.70	0.51	Elmes (1987)
Pheidole desertorum	40	?	–	0.42	Droual (1982)
P. pallidula	23	3	0.86	0.65	Nonacs (1986)
Pseudomyrmex nigrocincta	1	3	0.58	0.46	Nonacs (1986)
P. nigropilosa	1	2	0.64	0.53	Nonacs (1986)
P. venefica	2	3	0.51	0.40[a]	Nonacs (1986)
Tetraponera penzegi	?	2	0.57	0.46	Nonacs (1986)

[a] No weight data available; values estimated from related species

Assuming that the polygynous nests normally recruit their own daughters, as seems plausible based on the relatedness among coexisting queens (Pamilo 1981, 1982; Pearson 1982; Pamilo and Rosengren 1984; Douwes et al. 1987), the expectation of the sex allocation under worker control is given by Eq. (8c). The observed mean investment in the polygynous species, $IM = 0.56$, would match with the parameter value $q = 0.40$. If we omit the three highly polydomous species listed above, the investment in the remaining species is $IM = 0.51$, matching with $q = 0.49$.

Discussion

The conclusion is that the observed investment ratios in polygynous species are too female-biased for queen control (Eq. 7) unless all daughter queens disperse and none are recruited back. The observations agree with the worker control hypothesis if the future contributions to the gene pool by queens that disperse and by queens that are recruited back are about equal. If the contribution by recruited queens is greater ($q \ll 0.5$), the observed investment ratios are, on average, more female-biased than expected. The value $q = 0.5$ roughly equals the situation where the turnover of queens within a nest has the same rate as the turnover of nests in the population.

Values of q have not been estimated in nature, so it is difficult to assess whether worker control can explain the observed sex ratios in polygynous ants. Nevertheless, the present results imply that we should reevaluate the widely acknowledged conclusion that workers control sex allocation in monogynous ants. This conclusion depends largely on the observed difference in sex ratio between monogynous and polygynous species (Trivers and Hare 1976; Boomsma 1989). If q is small, the present theory predicts that such a difference is also expected under queen control. In fact, taking into account partial polyandry, worker reproduction, and budding, all of which should bias sex ratios in favor of males (Pamilo 1990), it may be reasonable to assert that sex allocation in polygynous ants is more female-biased than predicted by the theory. If this is so, we have to conclude that the observed female-biased sex ratios on monogynous ants are not exceptional and may not reflect worker control. It would be more parsimonious to explain the female biases in both groups – monogynous and polygynous ants – with a single hypothesis other than worker control.

One factor that should make the predicted investiment IM smaller, i.e., less male-biased, is the recruitment of unrelated queens in colonies. Above I assumed that only own daughters are recruited, their frequency being p among colony queens. Let us now assume that the colonies recruit both own daughters and unrelated queens, their frequencies being p_1 and p_2, respectively. If p_2 is not insignificant, dispersal becomes more profitable. Using these assumptions, Eq. (6) holds if we redefine the parameter $q = (cX + p_2 S)/(cX + p_1 S + p_2 S)$. Recruitment of unrelated queens also lowers the average relatedness among queens that, under worker control, should further reduce male bias.

The optimal sex ratios depend not only on the genetic diversity within nests but also on ecological factors, such as the parameter q, and we can expect much heterogeneity among sex ratios of different species with similar nest types (cf. Table 1). Since it may be difficult to control this source of variation because (1) the relative powers of queens and workers vary depending on the species, (2) the data points from related species are phylogenetically correlated (Clutton-Brock and Harvey 1984), and (3) the sex ratio varies greatly among colonies, thorough studies of single species (Ward 1983; Herbers 1984; van der Have et al. 1988) can be much more useful than multispecies comparisons for testing the hypotheses concerning the queen-worker conflict over resource allocation. It is a challenge to empirical studies to try to estimate the success of dispersing females (q) and the relatedness of coexisting queens (G) and to apply these data to predict sex ratios.

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