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J. J. Boomsma; A. Grafen

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## INTRASPECIFIC VARIATION IN ANT SEX RATIOS AND THE TRIVERS-HARE HYPOTHESIS

J. J. BOOMSMA<sup>1</sup>

*Department of Population Biology and Evolution, University of Utrecht, Utrecht, THE NETHERLANDS and Department of Zoology, University of Oxford, Oxford, U.K.*

AND

A. GRAFEN<sup>2</sup>

*Department of Zoology, University of Oxford, Oxford, U.K.*

*Abstract.*—We consider worker-controlled sex investments in eusocial Hymenoptera (ants in particular) and assume that relatedness asymmetry is variable among colonies and that workers are able to assess the relatedness asymmetry in their own colony. We predict that such “assessing” workers should maximize their inclusive fitness by specializing in the production of the sex to which they are relatively most related, i.e., colonies whose workers have a relatedness asymmetry below the population average should specialize in males, whereas colonies whose workers have a higher than average relatedness asymmetry should specialize in making females.

Our argument yields the expectation that colony sex ratios will be bimodally distributed in ant populations where relatedness asymmetry is variable owing to multiple mating, worker reproduction, and/or polygyny. No such bimodality is expected, however, in ant species where relatedness asymmetry is known to be constant, or in cases where relatedness asymmetry is supposed to be irrelevant due to allospecific brood rearing under queen control, as in the slave-making ants.

Comparative data on colony sex ratios in ants are reviewed to test the predictions. The data partly support our contentions, but are as yet insufficient to be considered as decisive evidence.

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The sex ratio of eusocial Hymenoptera is one of the foremost test cases of modern evolutionary biology. In a remarkable paper, Trivers and Hare (1976) constructed predictions about the female-bias in these sex ratios from a combination of sex ratio theory (Fisher, 1958), inclusive fitness theory (Hamilton, 1964, 1972), and parent-offspring conflict (Trivers, 1974). Trivers and Hare's theory began thriving literature on the sex ratio in eusocial Hymenoptera, and on the distinct but connected question of the role of relatedness asymmetries in the evolutionary origins of eusociality.

While there is little room for doubt about the lasting value of their theory, Trivers and Hare's analysis and interpretation of the empirical data, particularly those on ant sex ratios, have met with much scepticism. Alexander and Sherman (1977) were first on the attack, and they and later authors dwelt on problems such as the unreliability

of the field data, uncertainty over the measurement of investment, and the possibility that other hypotheses could better explain the detailed patterns in the data set. The balance of evidence now seems to be on Trivers and Hare's side (Nonacs, 1986; Boomsma, 1989), but much of the variation in ant sex ratios, especially the colony level variation, has so far remained unexplained.

The present paper concentrates on the optimal investment decisions of individual colonies and introduces a new line of argument, together with some relevant evidence, on the central themes of Trivers and Hare: that workers control sex allocation and consequently the species' sex ratio is female-biased (throughout this paper we will use the word female or gyne for reproductive offspring females and the word queen for a colony-mother). The idea is that, if the evolutionary forces posited by Trivers and Hare are responsible for the pattern between species, we should be able to detect signs of their operation in the pattern of sex ratios within species as well. As we will argue, only one additional assumption on colony-level assessment of relatedness asymmetry suffices to predict that colony sex ratios should

<sup>1</sup> Present address: Institute of Ecology and Genetics, University of Aarhus, Ny Munkegade, DK-8000 Aarhus C, DENMARK.

<sup>2</sup> Present address: Department of Plant Sciences, University of Oxford, Oxford OX1 3RA, UK.

be bimodally distributed in all those species where relatedness asymmetry is variable owing to multiple mating, worker reproduction, and polygyny.

### *The Theoretical Argument*

The core-parameter in this paper is the asymmetry in relatedness of females and males towards the workers that raise them (relatedness asymmetry =  $r_{fw}/r_{mw}$ ). In the original theory (Trivers and Hare, 1976; Oster and Wilson, 1978), a population of eusocial Hymenoptera is assumed to be infinite and uniform in all relevant characters (including relatedness asymmetry), and so there should be no intra-specific pattern of the sex ratio. In a later extension by Benford (1978), relatedness asymmetry is allowed to vary between colonies, but—as workers are (implicitly) assumed not to be able to measure the relatedness in their own colony—the overall sex ratio optimum is still the same for all colonies. The first attempt to explain bimodal sex ratio variation in ants was made by Taylor (1981), who modeled the situation where orphaned colonies produce only males, whereas the queenright colonies compensate for (half of) this bias by overproducing females. We note, however, that the “males-only” output of orphaned colonies is not a response to natural selection on the sex ratio itself and that the sex ratio compensation by queenright colonies still depends only on population-wide frequency dependent selection.

More recently, it was shown by Grafen (1986) that active selection for different sex ratios can occur at the level of separate colonies, if the cost of producing an individual of either sex differs between colonies, and provided that the workers are able to detect cost-related cues in the environment. This argument runs parallel to other cases of facultative sex ratio manipulation—e.g., host-size discrimination by ovipositing hymenopteran parasitoids—where investing females evaluate external cues to infer the future reproductive success of young (Trivers and Willard, 1973; Charnov, 1982).

Hymenopteran workers have yet another possible cue to infer the extent to which sexual investments will transfer their genes to future generations, i.e., the intra-colony relatedness asymmetry itself. Sufficient

variability in colony-to-colony relatednesses occurs in many species of ants (and other eusocial Hymenoptera), because of multiple mating (Page, 1986), partial worker reproduction (Bourke, 1988) and variable polygyny. A tentative argument as to how workers in facultatively polygynous populations might adjust their colony-level sex ratios was given by Nonacs (1986). Below we will develop this argument in more general terms and specify the necessary assumption.

The response of workers to differential relatednesses depends critically on the information available to them. If workers have no way of assessing which type of colony they belong to, then they must produce a sex ratio corresponding to the average, population-level relatednesses of the gyne and male offspring to workers (Benford, 1978). If, at the other extreme, workers can identify the exact relatedness of each individual, then they are selected to rear only their own full sibs, and so sharing a colony with less related individuals will not affect the sex ratio.

For our argument, we are going to assume that the workers have an intermediate level of information, and can detect, e.g., whether they are among full sibs or part of a mixture of full sibs and half sibs, but cannot discriminate between the individuals. Recent studies on kin recognition have indicated that workers of highly eusocial insects can discriminate between differently related nestmates, as long as the number or contributing genomes (e.g., patriline) is limited (Breed and Bennett, 1987; Carlin et al., 1987; Hogendoorn and Velthuis, 1988). However, in most cases where kin-correlated differences in behaviour are statistically significant, only a limited amount of the variance in altruistic or aggressive behaviour towards other individuals is actually explained. We note that the overall level of recognition-efficiency suggested by these studies is likely to be sufficient for the largely qualitative “kin awareness”, which our assumption requires.

Applying this assumption, it follows that workers in different classes of relatedness asymmetry will still have distinct and different optimal sex ratios, even after the overall equilibrium sex ratio in the population has been reached. This contrasts with the original theory, which implies that—at

equilibrium—workers are either indifferent towards their colony sex ratio (in infinite populations) or prefer to produce the same sex ratio as the overall equilibrium (in finite populations). In our alternative scenario, however, workers remain under selection to capitalize on relatedness asymmetry and should tend to specialize in the sex to which they are relatively most related.

The direction in which workers should deviate from the overall equilibrium sex ratio depends on whether their colony-level relatedness asymmetry is higher or lower than the average relatedness asymmetry in the population. Those colonies with a relatively low relatedness to females should specialize on males, while those with a relatively high relatedness to females should make mostly gynes.

The extent to which the population sex ratio is affected by a class of colonies specializing in the production of one sex depends on the relative abundance of that class, i.e., the frequency of a specializing class determines whether its workers should produce exclusively one sex or some mixed but still rather biased sex ratio. For instance, it is only advantageous for workers in a two-father colony to produce exclusively males as long as the overall population sex ratio remains more female biased than 2:1. This will be the case only if the proportion of two-father colonies is relatively small compared to a “standard” 3:1 relatedness-asymmetry class (the one-father colonies) which sets the overall sex ratio.

If such frequency-distribution of relatedness-asymmetry classes is stable through evolutionary time, the majority class is under frequency dependent selection to balance the bias introduced by any rare “one-sex-only” class, such that overall the population sex ratio will reflect the relatedness asymmetry of that majority class. If there are more than two relatedness-asymmetry classes the argument remains the same: at most one class is selected to produce an intermediate sex ratio, but the other classes should specialize on unisexual broods. Thus, our argument does not imply that workers are selected to produce exclusively one sex in all circumstances. It does imply, however, that their optimal sex-investment is often more extreme than the average relat-

edness asymmetry in the population or even the relatedness asymmetry in their own colony. Elsewhere we will present a formal inclusive fitness model to quantify these predictions. It will also be shown there that as long as populations are large and workers are sterile, the sex ratio compensation by the “balancing” relatedness-asymmetry class will generally be close to 100% and that a 50% sex ratio compensation (Taylor, 1981) is to be expected only in the special case where a “non-balancing” class produces males from worker-laid eggs. Thus, in the general case of a random mating infinite population, the population-wide sex ratio equilibrium will reflect the relatedness asymmetry of the balancing class, the only class whose colonies are indifferent between female and male production once the equilibrium is reached.

#### *Empirical Evidence*

*Predictions for Natural Populations.*— Translating the relatedness-asymmetry classes into less abstract categories we can make the following predictions. In nature, the male-making colonies should be those with doubly inseminated queens in populations with a mixture of single and double matings, and those with worker-produced males in populations where other colonies have sterile workers. In facultatively polygynous ant species where queens in the same colony tend to be related, male production should predominate in the polygynous colonies, whereas the monogynous colonies are expected to concentrate on gynes. Note that when the queens are unrelated, the relatednesses of the females and males towards the investing workers dilute equally with each additional queen so that their ratio (the relatedness asymmetry) remains the same. Accordingly, in polygynous species with a relatively constant number of queens, the colonies with related queens should produce males and those with unrelated queens should produce females.

Obviously, the realized distribution patterns in natural populations will not be as precise as the predictions based on our sex ratio optimization argument. Local population sex ratios are likely to vary and will normally not be exactly at equilibrium. As workers are unlikely to be able to track either

the local population sex ratio or the frequency of relatedness-asymmetry classes in their population, both the direction and the vigor of selection for extreme colony sex ratios will vary between local populations.

Accordingly, the sex ratio optimum of a relatedness-asymmetry class varies among local populations, and this frequency dependent variation is expected to increase even more when the number of relatedness-asymmetry classes also differs between those local populations. To give an extreme example, in a sub-population where triple mating occurs regularly, workers in two-father colonies are selected to produce mostly gynes, whereas they should specialize in males in other localities where triple mating is rare. Such unpredictability of the breeding population is likely to induce a certain amount of evolutionary bet-hedging (Seger and Brockmann, 1987), which will tend to reduce the frequency of colonies producing exclusively one sex. On the other hand, the possibility exists that patterns of sex ratio variation are additionally affected by cost-differences in the way hypothesized by Grafen (1986), which should then increase the frequency of extreme sex ratios (but not in correlation with relatedness-asymmetry).

Finally, evaluating workers may suffer from occasional erroneous assessments of relatedness asymmetry. This may be due, for instance, to chance genetic similarity between the odor cues of half sibs, or phenotypic differences between full sibs due to environmental effects. It should be noted, however, that the type of assessment needed for our argument to work is likely to be based on cumulative information from a massive number of individual encounters. Therefore, as long as sufficient odor-cue diversity is available, the qualitative relatedness-asymmetry assessment by workers may well be quite accurate, even if the error-rates in individual kin-recognition are high.

On an ecological time scale, these complicating factors will not change the average direction of sex-ratio selection for workers. We should therefore expect: 1) to find bimodal sex ratio variation in many natural populations of eusocial Hymenoptera whose workers control the sexual investments; 2) the actual proportion of extreme sex ratios

to be correlated with the known or inferred variation in relatedness asymmetry in the particular species or populations.

*Comparative Evidence Across Ant Species.*—Several authors recently have presented or reviewed data showing that colony-level sex ratios in ants tend to be generally bimodal as extreme investment ratios are much more common than intermediate ratios. Pamilo and Rosengren (1983) presented frequency distributions of samples of colony-investments for 12 species of *Formica* ants, showing a more or less bimodal pattern to occur throughout this ant genus. The large majority of these species are known to be at least partly polygynous, and the number of functional queens per colony is variable between colonies of the same breeding population. Also, the egg laying queens that share the same nest are known to be related in some populations (Pamilo, 1981, 1982a) and/or to be multiply inseminated in part (Pamilo, 1982b). Relatedness asymmetry must therefore have been variable among colonies in many of these *Formica* populations. Our theoretical argument predicts extreme colony sex ratios to prevail in this case, provided that workers are able to measure their colony relatedness-asymmetry to some extent.

In a review paper, Nonacs (1986) gives similar frequency distributions of colony sex ratios for 29 other ant species. Although the overall proportional investment in gynes across species seems to fit the population-level predictions of Trivers and Hare (1976) (but see Boomsma, 1989), colony-level sex allocation is shown to be clearly bimodal throughout both the monogynous and the polygynous ants. Acknowledging that both worker reproduction (Bourke, 1988) and multiple mating (Page, 1986) are common throughout the ants, this pattern is again consistent with the theoretical argument presented above.

A complication in the analysis of colony sex-ratio distributions is that colonies producing only a few sexuals are much more likely to be unisexual by chance than colonies producing many sexuals. In the data presented by Nonacs (1986) all colony-outputs are weighted equally, and the overall extent of bimodality is overestimated accordingly. This problem can be avoided

TABLE 1. Comparative data on extreme colony sex-ratios in different categories of ants.  $N$  is the number of colonies, the figure in brackets referring to the number remaining after excluding the known worker-reproductive, non-monogynous (in the slave makers and the monogynous ants) and queenless (in the polygynous ants) colonies.  $Q$  is the mean number of mother-queens per colony.  $M_E$  and  $G_E$  are the proportion of males and gynes that came from colonies producing a unisexual batch of offspring.  $M_{Eq}$  and  $G_{Eq}$  are the same proportions for colonies for which  $N$  is given in brackets.

	$N$	Males	Gynes	$Q$	$M_E$	$G_E$	$M_{Eq}$	$G_{Eq}$	Notes
<b>Polygynous ants</b>									
<i>Formica obscuripes</i> "Area I"	13	960	371	—	0.379	0.016	—	—	(1)
<i>F. obscuripes</i> "Area III"	30	5,076	4,700	—	0.422	0	—	—	(1)
<i>F. pallidefulva incerta</i>	12 (5)	346	427	4.0	0.853	0.475	0.894	0.704	(1)
<i>Myrmica rubra</i>	11 (0)	3,490	417	18.7	0.849	0	—	—	(1)
<i>M. sabuleti</i>	126 (56)	10,106	2,344	2.4	0.567	0.017	0.652	0.012	(1)
<i>M. scabrinodis</i>	12 (2)	147	145	0.8	0.333	0	—	—	(1)
<i>M. sulcinodis</i> "Stoborough"	45 (15)	851	673	3.5	0.360	0.297	0.108	0.279	(2)
<i>M. sulcinodis</i> "Winfrith"	38 (15)	1,039	188	3.2	0.850	0.154	0.995	0	(2)
<i>M. sulcinodis</i> "Tulloch"	22 (7)	596	518	1.6	0.639	0.035	0.423	0	(2)
Mean (overall; $n = 5-9$ )				4.9	0.584	0.110	0.615	0.199	
Mean (complete records; $n = 5$ )				2.9	0.654	0.196	0.615	0.199	
<b>Monogynous ants</b>									
<i>Aphaenogaster rudis</i>	14 (9)	305	56	1.1	0.502	0	0.402	0	(1)
<i>A. treatae</i>	12 (10)	1,171	794	0.8	0.061	0	0.035	0	(1)
<i>Formica fusca</i>	18	283	112	—	0.693	0.152	—	—	(1)
<i>F. pallidefulva nitidiventris</i>	19 (19)	352	1,153	1	—	—	0.864	0.631	(1)
<i>Lasius flavus</i>	10 (9)	1,232	486	0.9	0.172	0	0.159	0	(1)
<i>L. niger</i> "Strandvlakte"	125 (123)	59,045	19,925	1.0	0.098	0.027	0.002	0.027	(3)
<i>L. niger</i> "Kobbeduinen"	50 (49)	23,642	2,072	1.0	0.183	0.056	0.097	0.056	(3)
<i>L. niger</i> "Kooiuiden"	26 (26)	6,966	2,032	1	—	—	0.004	0	(3)
<i>Leptothorax curvispinosus</i>	10 (6)	221	138	0.6	0.566	0.268	0.969	0.037	(1)
<i>L. longispinosus</i>	13 (4)	80	127	0.5	0.213	0.008	0.250	0	(1)
<i>Myrmica ruginodis</i> (macrogyne)	32 (9)	3,877	4,568	0.4	0.293	0.011	0.233	0	(1)
<i>M. schencki</i>	10 (7)	187	608	0.9	0.016	0.071	0	0.066	(1)
<i>Pogonomyrmex montanus</i>	39 (33)	5,998	5,733	0.9	0	0.096	0	0.126	(1)
<i>Prenolepis imparis</i>	12 (7)	1,780	229	0.9	0.091	0.066	0.191	0.104	(1)
<i>Stenamma diecki</i>	10 (4)	267	212	1.1	0.371	0.113	0.900	0	(1)
<i>Tetramorium caespitum</i> "Ditch"	35 (35)	7,588	10,027	1	—	—	0	0	(4)
<i>T. caespitum</i> "Knoll"	39 (39)	14,028	8,908	1	—	—	0	0	(4)
Mean (overall; $n = 13-16$ )				0.9	0.251	0.067	0.257	0.065	
Mean (complete records; $n = 12$ )				0.8	0.214	0.060	0.270	0.035	

TABLE 1. Continued.

	N	Males	Gynes	Q	M <sub>E</sub>	G <sub>E</sub>	M <sub>Eq</sub>	G <sub>Eq</sub>	Notes
Slave-making ants									
<i>Epimyrma ravouxi</i>	30 (15)	1,915	1,257	0.6	0.213	0.001	0.006	0.001	(5)
<i>E. kraussel</i>	18 (13)	71	224	0.7	0.014	0.013	0.014	0.013	(5)
<i>Harpagoxenus sublaevis</i> "Sweden"	37 (25)	961	753	0.7	0.057	0.019	0.009	0.021	(6)
<i>H. sublaevis</i> "Germany"	33 (33)	774	885	1	—	—	0.003	0.095	(7)
<i>H. americanus</i>	16 (5)	343	158	0.3	0.260	0.063	0	0.024	(1)
Mean (overall; n = 4-5)				0.7	0.136	0.024	0.006	0.031	
Mean (complete records; n = 4)				0.6	0.136	0.024	0.007	0.015	

NOTES: Reviews on other aspects of these sex ratio data are given by Trivers and Hare (1976), Nonacs (1986), Boomsma (1989) and Bourke (1989). Sources indicated by (1) are given in detail by Nonacs (1986) and are omitted here to save space. For the present analysis, data sets as reviewed by Nonacs were included only if they contained at least 10 sexually productive colonies. M<sub>Eq</sub> and G<sub>Eq</sub> were calculated only if at least four colonies belonged to this category. Larger data sets, containing colony sex-ratios from more than one area, were analyzed at the level of the separate populations. (2) The three populations of *Myrmica sucinoidis* are Tulloch Moor (Elmes, 1974), Stoborough Heath and Winifrid Heath (Elmes 1987a, 1987b). Data on the latter two populations are the same as those referred to by Nonacs (1986) and cover the years 1979-1983 in Elmes (1987a, 1987b). In contrast to Nonacs (1986) and Boomsma (1989) *Myrmica sucinoidis* is here categorized as a polygynous species, on the basis of its mean number of queens in the reproducing colonies. (3) The three populations of *Lasius niger* are the same as those in Boomsma et al. (1982). Boomsma and Isaaks (1985) and Van der Have et al. (1988). (4) The data on *Tetramorium caespitum* were analyzed following the "Ditch/Knoll" habitat-dichotomy given by Brian (1979). The data on slave-making ants were interpreted following the recommendations by Bourke (1989). Four of these references were not considered by Nonacs (1986) and are therefore given in full: (5) Winter and Buschinger (1983), (6) Bourke et al. (1988), (7) Buschinger et al. (1975). The data on *Formica obscuripes* refer only to the source paper by Herbers (1979).

through weighting each colony sex ratio by its relative contribution to the mating swarm (see Boomsma, 1988), and determining what proportion of the total amount of gynes and males collected was produced in a unisexual colony.

We have compiled a comparative data set using the same references as Nonacs (1986) and some additional data on slave-making ants (cf. Bourke, 1989), to test whether the frequency of extreme sex ratios does indeed increase with the inferred variation in relatedness asymmetry. The ant species were categorized as either polygynous, monogynous, or slave-making. As in previous reviews (Trivers and Hare, 1976; Nonacs, 1986), the monogynous group is slightly heterogeneous, containing also species that have more than one queen in some of the colonies.

In slave-making ants the allocation of resources to the sexual brood is done by non-related allospecific workers and supposedly controlled by the queen (suggested on theoretical grounds by Trivers and Hare, 1976; confirmed empirically for *Harpagoxenus sublaevis* by Bourke et al., 1988). The only possible source of sex ratio bimodality connected with relatedness is the fact that males can be produced from worker-laid eggs, particularly in queenless colonies (Bourke, 1989).

In the monogynous ants, worker control is likely to be effective (Trivers and Hare, 1976; Nonacs, 1986; Boomsma, 1989) and both partial worker reproduction and multiple mating can induce variation in relatedness asymmetry between colonies, on which the workers may capitalize by producing an extreme sex ratio. Note, however, that the number of relatedness-asymmetry classes is likely to be limited in many monogynous populations and that relatedness asymmetry will vary only in the range of 3:1 to 2:1, unless mating-frequencies higher than two occur. Accordingly, many populations in this category will have only two or three relatedness-asymmetry classes, and we may therefore not see both male-specialist and gyne-specialist colonies in the same population.

In polygynous ants the variability of relatedness asymmetry is potentially enormous. Many such species periodically adopt

new queens into the nests, which may either be related or not (Pamilo, 1981, 1982*a*; Elmes 1987*a*, 1987*b*). Consequently, the relatednesses of gynes and males to workers are likely to be temporarily variable and may well drop to values around zero at times. If the males are normally produced from worker-laid eggs, as seems to be the case in some species of *Myrmica* ants (Brian, 1969; Elmes and Wardlaw, 1981), the workers may even be temporarily more related to males than to gynes. Accordingly, both across and within species, polygynous ants have about the maximum possible range of variation in relatedness asymmetry. Because there will be normally many different relatedness-asymmetry classes in a population of polygynous ants, the frequency of the separate relatedness-asymmetry classes will tend to be low. We thus expect to find the highest incidence of extreme colony sex ratios in this group.

This expectation should become less pronounced if workers in polygynous colonies have more difficulties in assessing relatednesses properly. On the other hand, additional bimodality—not correlated with relatedness asymmetry—may be induced if worker control in polygynous ants is less effective than in the monogynous ants. In line with our predictions about bimodal sex ratio optima for workers, relatively queen-controlled colonies should then specialize in males, whereas relatively worker-controlled colonies should make mostly gynes (see Williams, 1979; Pamilo, 1982*c*).

The expectations formulated above are generally confirmed by the calculations presented in Table 1. The proportions of males ( $M_E$ ) and gynes ( $G_E$ ) produced in unisexual batches of colony-offspring are low in the slave-making ants and reduce to the level of overall insignificance if only queenright colonies are considered ( $M_{Eq}$  and  $G_{Eq}$ , respectively). The same proportions are generally higher in monogynous ants and higher still in the polygynous ants. If the comparison is restricted to the respectively monogynous and queenright colonies in the two latter categories, the proportions remain unchanged.

We analyzed this trend statistically by using the method designed by Grafen (1989), which takes into account that the records in

Table 1 are not independent, but part of a taxonomic hierarchy that reflects the phylogeny of the ant species. Our initial “branch lengths” were derived from Figure 2 in Grafen (1989). After adjusting for effects of taxonomic confounding (applying the “subfamily-tribe-genus” hierarchy of Wilson, 1971 and adding “species” and “population” as lower levels), regression of the proportion of males produced in single-sex batches (using  $M_{Eq}$  where available) on the inferred variation in relatedness asymmetry (3 for polygynous ants, 2 for monogynous ants and 1 for slave-makers) appeared to be significant according to expectation (slope 0.245;  $F_{1,13} = 4.11$ ;  $P < 0.05$ ; one-tailed test). Regression of the proportion of gynes produced in single-sex batches ( $G_{Eq}$ , or  $G_E$  if  $G_{Eq}$  was not available) on the same relatedness-asymmetry-variability parameter turned out to be not significant (slope 0.017;  $F_{1,12} = 0.100$ ).

For the separate species we note, first, that the only monogynous ant in this data set whose workers are known to lack ovaries completely, *Tetramorium caespitum* (see Brian, 1979), is exceptional as it produces two sexes in all colonies. This would be in line with the predictions if multiple mating were also absent in this species. Second, relatedness asymmetry is known to be variable in the populations of *Lasius niger* analyzed in Table 1, due to both multiple mating and worker reproduction. The overall means of proportional investment in gynes show a correlation with the average relatedness asymmetry in the separate populations in the way predicted by the Benford (1978) model (Van der Have et al., 1988). More detailed comparison of the two major populations “Strandvlakte” and “Kobbeduinen” showed that the proportion of sexuals produced in single sex batches is relatively low in the former population, where variation in relatedness asymmetry was low, and much higher in the latter population, where substantial levels of double matings and more worker reproduction were found.

#### CONCLUSION

The central features of our argument—that relatedness asymmetry is variable and that colony sex ratios should depend on some qualitative “kin-awareness” in work-



ers—are potentially valid throughout the eusocial Hymenoptera. The predicted extreme sex ratios for classes of colonies with different relatedness asymmetry potentially allow an adaptive explanation for more of the sex ratio pattern in natural, random mating, populations than the population-wide theory of Trivers and Hare and Benford does alone. We note, however, that the support for this idea is so far restricted to ants and largely circumstantial. The overall agreement between observation and prediction does not prove that the theoretically expected selective forces towards more extreme colony sex ratios have effectively caused the patterns described in Pamilo and Rosengren (1983), Nonacs (1986) and Table 1. The predictions do imply, however, that kinship-theory can be tested at the level of single populations of eusocial Hymenoptera, thus avoiding most of the technical complications attached to across-species comparisons (Boomsma, 1989). Direct estimations of relatedness asymmetry (Pamilo and Crozier, 1982) in categories of colonies contributing a different sex ratio to the same mating swarm will be required to test whether sex allocation strategies that are conditional on the colony relatedness asymmetry are as common as the provisional evidence for ants suggests.

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