Patterns of reproduction in slave-making ants

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Sex ratios in slave-making ants have been posed as important test cases for the hypothesis that eusociality evolved via kin selection in insects. Trivers & Hare proposed that sex ratios in slave-makers should reflect the queen's interests whereas sex ratios in free-living host ants should reflect the workers' interests. We analyse patterns of allocation to males versus females, as well as allocation to growth versus reproduction for slave-making ants in the tribe Formicoxenini. We find little support for the hypothesis of exclusive queen control; instead, our results implicate queen-worker conflict in slave-making ants, both over male allocation ratios and over allocation to growth versus reproduction.

Keywords: eusocial; kin selection; slave-makers; ants; social insects; Hymenoptera

1. INTRODUCTION

Problems of reproductive allocation among social insect groups have become pivotal test cases for evolutionary theory (Crozier & Pamilo 1996). According to the kin-selection paradigm developed by Hamilton (1964), and refined by Trivers & Hare (1976), colonies of ants, bees and wasps comprise one to several subgroups, each with distinct genetic interests. For the simplest case of a colony headed by a single, once-mated queen, the queen prefers that 50% of the colony's reproductive energy be allocated to males, whereas workers prefer that only 25% be allocated to males. Thus, differing genetic interests can lead to parent-offspring conflict over allocation to males versus females in the sexual brood (Trivers & Hare 1976). Examination of male allocation ratios, the proportion of reproductive energy allocated to males, has become a central problem in kin selection theory (Crozier & Pamilo 1996).

Trivers & Hare (1976) proposed several comparative approaches to test their idea of queen-worker conflict over male allocation ratios. They suggested that a particularly powerful test would compare allocation ratios of free-living species to those produced by their social parasites, whose juveniles are reared by heterospecific parasitized hosts. Social parasitism in insects covers a variety of syndromes, including brood parasites, temporary social parasites, dulosis (the slave-making habit) and permanently parasitic inquilines (reviewed by Wilson 1971). Within the Hymenoptera, the taxonomic distribution of social parasitism is uneven (Buschinger 1986; Hölldobler & Wilson 1990), and in this paper we concentrate on the obligatory slave-making ants, which have received considerable attention from previous authors (Trivers & Hare 1976; Bourke 1988a,b, 1989; Bourke *et al.* 1988), and for which predictions are reasonably precise (Bourke &

Franks 1995). Further, we restrict our attention to species that have both queens and workers, ignoring those that have lost the worker caste (cf. Buschinger 1989).

The life history of obligatory slave-makers is highly specialized. These ant species initiate new colonies when a queen enters and subjugates established nests of the host species (Buschinger *et al.* 1980; Franks & Bourke 1988). The slave-maker queen commences to lay eggs, and any workers that ultimately eclose are behaviourally limited. While nest maintenance and brood care are performed by the slaves, slave-maker worker activity is usually restricted to periodic raids on nearby host nests to replenish their slave population (Stuart & Alloway 1985). Most importantly, slave-maker workers have little direct contact with the developing brood. Thus, heterospecific slave nurses and not slave-maker workers have proximate control over the sex ratio of reproductives that emerge.

The highly specialized life history of slave-making species led Trivers & Hare (1976) to predict that queens have primary influence over sex allocation patterns, owing to genetic indifference of slaves and behavioural impotence of slave-maker workers. The prediction that queen-worker conflict should occur in unparasitized host colonies but not in slave-makers led to a cornerstone prediction of female bias in reproductive broods of host species but unbiased broods in their parasites (Trivers & Hare 1976). This clever prediction makes assumptions about the genetic structure of both kinds of colonies that may not be warranted (Bourke & Franks 1995). Even so, the tendency for slave-maker colonies to invest equally in the sexes appears to be upheld by the available small database (Nonacs 1986; Bourke 1989).

We question the above line of reasoning, however. First, the assumption that slave-maker workers are impotent requires examination. In slave-making species, workers have different genetic interests from their mother queen, just as in other hymenopteran societies. All else being equal, selection pressures on slave-maker workers to bias the reproductive brood towards their evolutionary optimum are therefore similar to pressures in free-living species. In addition, dulotic species have evolved from

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free-living counterparts, and thus should have had a long evolutionary history of queen–worker conflict. There is no compelling reason to suppose this conflict dissolves with the evolution of slave-making habits. Furthermore, slave-maker workers do indeed have behavioural opportunities to affect brood development (Wilson 1975; Bourke 1989; Heinze 1996) and should not be assumed to be powerless in matters of reproductive allocation. Thus, we examine our data for evidence of conflict between the slave-maker queen and her workers.

Second, we question the assertion that enslaved ants have no evolutionary stake in the sex ratios of their parasites (Trivers & Hare 1976; Gladstone 1981). Like any other host–parasite interaction, coevolution between slave-maker and slave species is undoubtedly ongoing: host species recognize their parasites as enemies (Alloway 1990), and species subjected to slave raids have altered their life histories in response to that selection pressure (Savolainen *et al.* 1996). Slaves, who are unrelated to the brood they nurse, can behave differently from their conspecifics in free-living nests (Alloway 1982) and therefore have a potential to bias reproduction in their parasites. Thus, there are three parties with potentially different evolutionary optima: the slave-maker queen, the slave-maker workers, and the slaves themselves. The behavioural evidence strongly suggests that the balance of power is held by the slave-maker (Buschinger 1986; Le Moli & Mori 1987; Franks & Bourke 1988; Alloway & Hare 1989; Pollock & Rissing 1989), but aggression of slaves towards their parasites has been observed (Alloway & Del Rio Pesado 1983; Wilson 1975; J. M. Herbers and R. J. Stuart, personal observations). The possibility of slave counter-evolution therefore deserves exploration.

A related question is the more general life history problem of allocation to growth (new workers) versus reproduction (sexuals). For hymenopteran social insects, the reproductive allocation ratio (proportion of energy allocated to reproduction rather than to growth) can also be the focus of queen–worker conflict (Pamilo 1991). Very few studies have addressed reproductive allocation ratios in insect societies (Backus 1995; Sundström 1995; Bansbach & Herbers 1996; Herbers & Stuart 1996), and none has provided empirical data on this issue for slave-making species.

In this paper, we explore patterns of allocation among three slave-making species in the ant tribe Formicoxenini (cf. Bolton 1994), and compare their reproductive biology to that of their hosts living in the same habitat. This paper thereby augments the available database for slave-making ant species, provides a test of the Trivers–Hare predictions, and gives the first analysis of growth versus reproduction in a socially parasitic species.

2. MATERIALS AND METHODS

Data for three obligate slave-makers in the ant tribe Formicoxenini and their hosts were collected. *Protomognathus* (= *Harpagoxenus*) *americanus* (Emery) parasitizes three species of North American *Leptothorax* in the Myrmecini group. In both parasite and host species, colonies can be polydomous, consisting of two or more discrete nests (Alloway *et al.* 1982; Del Rio Pesado & Alloway 1983). *Leptothorax duloticus* (Wesson)

uses the same hosts as *P. americanus*, and data for a Michigan population of this slave-maker and its host *Leptothorax curvispinosus* (Mayr) were summarized by Talbot (1957); here we analyse her raw data. The population structure of *L. duloticus* is not well understood, but the queenless condition appears to occur through both orphaning and colony fractionation (Talbot 1957; Alloway 1979). *Harpagoxenus canadensis* (M. R. Smith) parasitizes nests of species in the *Leptothorax muscorum* (Nylander) complex (Stuart 1978; Buschinger & Alloway 1979). Nests without queens are fairly common, but whether they arise via orphaning or colony budding is not known. However, since its European congener has monodomous colonies (Bourke 1988a), we assume here that nests without queens represent orphaned colonies for *H. canadensis*.

We analysed census information (numbers of workers and slaves) via parametric statistics on log-transformed data when appropriate or via non-parametric statistics if we could not normalize the data. Male allocation ratios were computed as proportional dry mass investment in males. For *P. americanus* and *H. canadensis*, alate sexuals were collected as adults, dried to constant mass, and individually weighed to the nearest 0.01 mg. We computed an index of sexual dimorphism from the ratio of average female dry mass to average male dry mass. This ratio was corrected according to the formula of Boomsma (1989) to give the energetic cost ratio (Bourke & Franks 1995; $ECR = (\text{average female weight} / \text{average male weight})^{0.7}$). Finally, male allocation ratios were computed as $(\text{number of males}) / (\text{number of males} + (ECR \times \text{number of females}))$. All allocation ratios were arcsin-transformed prior to statistical analysis.

Population male allocation ratios were computed as the proportional allocation to males for data pooled over an entire sample. We computed the expected number of males and females in these samples for two hypotheses: (A) equal investment in males and females, and (B) three times as much investment in females as in males. These expected numbers were generated according to the following equations:

hypothesis A:	hypothesis B:
male investment = 0.5	male investment = 0.25
$0.5 = M / (M + C(B - M))$	$0.25 = M / (M + C(B - M))$
$M = BC / (1 + C)$	$M = BC / (3 + C)$
$F = B - M$	$F = B - M$

where M = expected number of males, F = expected number of females, C = energetic cost ratio, B = observed (number of males + number of females). These expected numbers of males and females were then compared with the observed numbers in the entire population via χ^2 -tests with 1 d.f. each.

Information on the numbers of worker pupae is needed to examine allocation to growth versus reproduction, but was available only for *L. duloticus* and *P. americanus*. We had no data on the weights of newly eclosed workers for any species. Therefore, we used simple counts of pupae, and only included those nests in which worker pupae had not started to eclose. The reproductive allocation ratios reported below refer to the proportion of all broods that are sexuals.

We used two general approaches to examine reproduction in slave-makers. First, we compiled all information on the slave-making species and compared patterns across species and samples within species. Second, we compared patterns of reproduction in *P. americanus* and *L. duloticus* with populations of their respective hosts, *L. longispinosus* and *L. curvispinosus*, collected in the same locales and in the same years.

Table 1. *Nest demography for the eleven data sets used in the analysis*

(Nests of *P. americanus* were collected in West Virginia (Watoga State Park, Pocahontas County), New York (E. N. Huyck Preserve, Albany County) and Vermont (Mallett's Bay State Park, Chittenden County). Data for the *L. duloticus* nests were collected in 1954 and 1955 by Mary Talbot on the E. S. George Reserve in Michigan. *H. canadensis* colonies were collected near Rouyn, Quebec, in 1976 and 1981 by R. J. Stuart, and in 1987 by T. M. Alloway.)

	number of nests				data on worker pupae?	median worker:slave ratio	
	without queens	with queens		total		without queens	with queens
		without workers (newly founded)	with workers				
<i>P. americanus</i>							
West Virginia 1983	10	1	5	16		0.08	0.33
West Virginia 1988	4	11	5	20	yes	0.14	0.27
New York 1987	13	13	15	41	yes	0.14	0.08
New York 1992	5	1	3	9	yes	0.09	0.06
New York 1993	4	2	8	14		0.07	0.12
Vermont 1986	19	3	5	27	yes	0.14	0.09
<i>L. duloticus</i>							
1954	14	0	8	22	yes	0.11	0.15
1955	112	4	66	182	yes	0.16	0.25
<i>H. canadensis</i>							
1976	10	1	12	23		1.00	0.41
1981	7	1	19	27		1.08	0.86
1987	9	0	8	17		0.70	0.43

3. RESULTS

(a) *Patterns among slave-maker species*

(i) *Nest demography*

We compiled 11 data sets for slave-makers with sufficient sample sizes for analysis (table 1). In all, there were six data sets for three populations of *P. americanus*, two for a single population of *L. duloticus*, and three for a single population of *H. canadensis*. All samples included nests without queens; furthermore, totals of five *P. americanus* nests and three *L. duloticus* nests contained more than one morphological queen. Because polygynous nests were rare and we were uncertain whether all queens were in fact fertile, we pooled them together with monogynous nests to form the category of nests with queens.

Most samples included nests that contained a slave-maker queen but no workers (table 1). These apparent newly founded nests were rare, except in two samples of *P. americanus* (11 nests in WV88 and 13 nests in NY87). Annual fluctuations in the frequency of such newly founded nests presumably reflect varying rates of recruitment by slave-makers in the previous year. For most analyses below, we exclude these incipient nests.

Details of nest demography for our slave-maker samples are shown in figure 1; there was no significant variation among years for any of the demographic variables, and thus we report data pooled across all years in a given population. Nests of *P. americanus* typically contained fewer than ten workers, whereas more slave-maker workers resided in nests of *L. duloticus* and *H. canadensis* (figure 1a). In each data set, nests with queens had more workers than did nests without queens, and the difference was significant for four of these (ANOVAs on log-transformed data; $p < 0.05$ for

P. americanus in Vermont and *H. canadensis*; $p < 0.0001$ for *P. americanus* in New York and *L. duloticus*). Therefore, we must be careful to separate worker effects from queen presence or absence.

The numbers of slaves (figure 1b) showed considerable variation across the data sets as well. Overall, nests of *H. canadensis* had the fewest slaves, while the other two species had higher slave numbers. Comparisons among nests with and without queens (figure 1b) showed for four data sets that nests with queens had more slaves than nests without queens, but no difference was found for *P. americanus* in West Virginia (ANOVAs, all other p -values less than 0.01). Thus slave number potentially confounds any comparisons based on queen presence or absence.

We also examined the ratio of slave-maker workers to slaves (table 1). In all our samples, the vast majority of nests had fewer slave-makers than slaves, yielding ratios of less than 1.0, and the *H. canadensis* nests had more slave-makers per slave than the other two species, on average. We compared worker-to-slave ratios between nests with and without queens. There was no general pattern across the data sets (table 1), and a significant effect of queen presence was found only for *L. duloticus* in 1955 (Kruskal-Wallis tests, with Bonferroni sequential corrections, $p < 0.01$). Thus, queen presence or absence had no consistent effects on the ratios of slave-maker workers to slaves.

(ii) *Reproduction and male allocation ratios*

Rates of reproduction in the slave-maker species (figure 2) are given for data pooled across populations and years, as there were no significant differences among data sets within a species (G -tests, $p > 0.05$). For *P. americanus* and

Figure 1. Nest demography for the populations studied. (a) Number of slave-maker workers per nest. (b) Number of slaves per nest. Means + 1 s.e. are shown. Key to abbreviations: P.a. = *P. americanus*; L.d. = *L. duloticus*; H.c. = *H. canadensis*; WV = West Virginia; NY = New York; VT = Vermont. Open bars represent nests without queens, filled bars are nests with queens.

L. duloticus, a significantly greater fraction of the nests without queens reared at least one sexual than did nests with queens (*G*-tests with 1 d.f., $p < 0.01$ for both) but there was no difference for *H. canadensis* ($p > 0.05$). That is, the two species with polydomous colonies showed a difference in reproduction rates dependent on queen number but the species with single-nest colonies did not. There were no differences in worker number between producers and non-producers for any of the data sets, nor were there differences in slave number for *L. duloticus* or *H. canadensis* (two-way ANOVA with queen and producer class as main effects, all $p > 0.05$). However, nests of *P. americanus* that reared sexuals had more slaves than those that failed ($p < 0.001$). Thus, nest demography could have important effects on reproductive success or failure, but the details varied across our three species. We return to the issue of nest demography below.

Data on the dry masses of sexuals are given in table 2. The extent of sexual dimorphism was pronounced for *P. americanus*, and we found no evidence of geographical variation in the relative sizes of males versus females. Sexual dimorphism was less pronounced for *L. duloticus* and *H. canadensis*. When we applied the Boomsma (1989) correction to give energetic cost ratios, we found that, on

Figure 2. Patterns of reproduction in slave-makers. Non-producers (open areas) failed to rear any sexuals, whereas producers (filled areas) reared at least one fertile adult.

average, slave-maker females are 1.8 times more costly to produce than slave-maker males.

We examined population-wide patterns of allocation to males (table 3). We first computed a male allocation ratio by pooling sexuals over all nests. These pooled values are highly sensitive to variation in productivity among nests, and so we also computed a back-transformed mean male allocation ratio. To compute this mean, we excluded nests that reared fewer than five sexuals, as these ratios are sensitive to brood size (cf. Herbers 1984). The median numbers of sexuals reared by these species were 5 (*P. americanus*), 8 (*L. duloticus*) and 6.5 (*H. canadensis*), which meant that the mean ratios reported in table 3 are based on only 60% of all nests that reproduced. We found that the two measures of population central tendency (one from pooling data and the second by computing a mean from a subset of the population) were strongly correlated (Kendall's τ , $p < 0.001$), although for some samples the numbers were quite different (notably New York 1992). The pooled data are most inclusive and representative of the population at large, and so we proceed to interpret the pooled population allocation ratios.

Samples taken from the same population in different years show considerable annual variation in male allocation ratios. For example, *H. canadensis* shifted from an unbiased male allocation ratio of 0.458 in 1976 to a strongly male-biased allocation ratio of 0.843 in 1987. By contrast, *P. americanus* in New York had relatively constant male allocation ratios in three different years. Differences among populations are evident for the *P. americanus* data as well: the most southern population in West Virginia had female-biased allocation ratios, whereas the most northerly

Table 2. *Investment in reproductives for the slave-making species studied*

	average dry weight mean $\pm$ s.e. in mg (<i>N</i>)		weight ratio	energetic cost ratio
	females	males		
<i>P. americanus</i>				
West Virginia	0.44 $\pm$ 0.028 (22)	0.14 $\pm$ 0.006 (5)	3.14	2.23
New York	0.58 $\pm$ 0.033 (60)	0.19 $\pm$ 0.005 (120)	3.07	2.19
Vermont	0.39 $\pm$ 0.026 (15)	0.12 $\pm$ 0.011 (70)	3.28	2.30
<i>L. duloticus</i> ^a	0.20	0.10	2.00	1.62
<i>H. canadensis</i>				
1981	0.50	0.38	1.30	1.20
1987 ^b	0.61 $\pm$ 0.028 (10)	0.38 $\pm$ 0.087 (74)	1.59	1.38

^aM. Talbot (unpublished data), as reported by Trivers & Hare (1976).^bT. M. Alloway (unpublished data).Table 3. *Pooled reproductive data across the data sets*

(We compared the population-level male allocation ratios to those expected under pure queen control (0.50) and pure worker control (0.75).)

	total number of males	total number of females	pooled allocation to males	mean male allocation ratio	deviation from 0.50 ^a	deviation from 0.25 ^a
<i>P. americanus</i>						
West Virginia 1983	38	37	0.315	0.338	***	n.s.
West Virginia 1988	16	25	0.223	0.247	***	n.s.
New York 1987	133	90	0.403	0.282	**	***
New York 1992	29	19	0.411	0.882	n.s.	* ^b
New York 1993	20	10	0.477	0.614	n.s.	**
Vermont 1986	186	34	0.704	0.888	***	***
<i>L. duloticus</i>						
1954	121	104	0.418	0.415	* ^b	***
1955	1349	544	0.605	0.769	**	***
<i>H. canadensis</i>						
1976	48	44	0.458	0.415	n.s.	***
1981	185	154	0.500	0.554	n.s.	***
1987	74	10	0.843	0.882	***	***

^aSignificance levels: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$; n.s., $p > 0.05$.^bNot significant after sequential Bonferroni table-wide testing.

population in Vermont had a strongly male-biased ratio. Thus, variation between years within a population as well as variation between populations characterize the slave-maker allocation ratios, just as they do in their hosts (Herbers 1990; Herbers & Stuart 1996).

The median over all 11 pooled population estimates in table 3 was 0.458, and the (back-transformed) mean was 0.489, with a 95% confidence interval of [0.432, 0.612]. The central tendency across all these data sets therefore shows unbiased male allocation ratios. In table 3, we compare the observed male allocation ratios to those expected under pure queen control (0.50) and pure worker control (0.25). Of the 11 data sets, six deviated significantly from equal investment in males, and eight deviated significantly from female-biased investment. Thus, the mean across all data sets is consistent with pure queen control, but the individual point estimates fail to support either hypothesis strongly.

We examined data pooled across nests without queens and across nests with queens within a sample (figure 3). For some samples (e.g. WV83 for *P. americanus* and 1981 for *H. canadensis*), the male allocation ratios did not differ strongly between nests with and without queens, but for others there was a considerable disparity (e.g. VT86 for *P. americanus* and 1955 for *L. duloticus*). For four data sets, the differences between nests with and without queens were significant; furthermore, nine out of ten data sets showed that nests without queens invested more in males than did nests with queens (binomial test, $p = 0.011$). The mean male allocation ratios were 0.769 and 0.429, respectively, with 95% confidence intervals of [0.500, 0.954] for nests without queens and [0.329, 0.542] for nests with queens. From the population-level data, then, an overall pattern emerged for nests without queens to produce male-biased broods relative to nests that contained queens.

Figure 3. Male allocation ratios for data pooled over nests with queens (filled bars) and without queens (open bars). Asterisks indicate significant differences between nests with and without queens ($p < 0.05$).

We also examined male allocation ratios produced by individual nests (figure 4). Again, we restricted our analysis to nests that reared at least five sexuals. Figure 4 shows that the frequency distributions of male allocation ratios were bimodal for *P. americanus*, unimodal for *L. duloticus* and near-uniform for *H. canadensis*. Although the data suggest that nests without queens had distributions more male-biased than nests with queens for each species (figure 4), our reduced sample sizes lowered statistical power such that the effect of queen number was significant only for *L. duloticus* (G -test, $p < 0.05$).

(iii) Allocation to growth versus reproduction

To examine allocation to growth versus reproduction, we used count data on the numbers of worker pupae, male pupae, and queen pupae reared by nests. Table 4 gives the pooled data across all nests for which reliable numbers of worker pupae were available. The reproductive allocation ratios in table 4 show that, in general, slave-makers reared more sexuals than workers. The most extreme reproductive allocation ratio in our database was from *P. americanus* collected in West Virginia; in that sample, one nest reared a single worker. This population, then, appears to devote the majority of its energy to reproduction rather than to growth.

By pooling data across all nests with and without queens, we computed population-level reproductive allocation ratios for nests with and without queens (figure 5). These data show that, over all six data sets, nests without queens produced broods with more sexuals than nests with queens (binomial test, $p = 0.016$). Further, the differences were significant for four of the individual data sets. It appears, then, that these two classes of nests have distinctly different life history strategies.

We also examined the reproductive allocation ratios produced by individual nests (figure 6). To avoid biases associated with small brood sizes, we restricted our analysis to those nests that reared at least five pupae. The distribution of the reproductive allocation ratios was uniform for *P. americanus*, but strongly bimodal for *L. duloticus*. Further, the bimodality in *L. duloticus* derives from strong differences between nests with and without queens. Queenless nests showed distributions shifted towards sexual reproduction, whereas nests with queens were much more likely to rear only workers (G -test, $p < 0.01$). By contrast, there were no differences between *P. americanus* nests with or without queens (figure 6) in their relative investments in growth versus reproduction.

(iv) Alternative reproductive strategies

Two classes of nests provide insight into alternative reproductive strategies of both host and slaves (table 5). The first group contained no adults of the slave-maker species (neither queen nor workers), and were initially classified as free-living nests of the host species. Inspection of the brood, however, showed that these nests contained sexual pupae of their slave-maker parasites that were reared to adulthood (table 5a). Such nests were rare (only 12 out of a total of 398 nests in our database), and they reared both new queens and new males of the slave-maker. A second class of nests contained adult slave-makers, but reared sexuals of the enslaved species (table 5b). These nests also were quite rare (9 nests out of a total of 398), and all but one included slave-maker workers (table 5a), which suggests they were mature. That none of these nests rearing host sexuals also reared slave-maker sexuals suggests that

Figure 4. Distributions of male allocation ratios produced by individual nests of slave-makers; data are given only for those nests that reared at least five sexuals. (a) *P. americanus*; (b) *L. duloticus*; (c) *H. canadensis*. Open bars represent nests without queens, filled bars are nests with queens.

slaves were able to circumvent total control by their parasites.

(v) Nest demography reconsidered

Finally, we examined the combined impacts of variation in queen, worker, and slave numbers for patterns of reproduction. Table 6 shows the results of partial correlation analysis for five measures of reproduction (biomass of males reared, biomass of females reared, male allocation ratio, number of worker pupae reared and reproductive allocation ratio). Queen presence or absence was found to have significant effects in four of the 21 analyses; worker number in three; and slave number in five. Of all these, however, only two retained significance after we conducted

a table-wide Bonferroni correction. We also examined the signs of partial correlation coefficients for comparable tests (e.g. effect of slave number of male allocation ratio, compared across five data sets). Only three were consistently positive (or consistently negative): slave number always had a negative effect on male allocation ratio; worker number always had a positive effect on number of new workers reared; and queen number had consistently negative effects on reproductive allocation ratios.

(b) Slave-makers in sympatry with their hosts

We were able to compile seven data sets that included information on a slave-maker species as well as its free-living hosts collected from the same geographical location in the same year. Six are for *P. americanus* and its host *L. longispinosus*. The data for *L. longispinosus* have been analysed in detail elsewhere (Herbers 1984, 1990; Herbers & Stuart 1996) and they show considerable complexity, with allocation ratios varying among nests, years and populations. We therefore pooled data across samples for this species only if there were no significant differences among subsamples. The seventh comparison is for *L. duloticus* and *L. curvispinosus*, drawn from information published by Talbot (1957).

Comparisons of rates of reproduction between slave-makers and their hosts showed no significant differences among any of the samples for *P. americanus* and *L. longispinosus* (figure 7; *G*-tests, all $p > 0.05$). That is, the proportions of *P. americanus* nests that reared at least one sexual within a given year reflected similar proportions in their hosts (cf. Herbers 1990). The data from Talbot (1957), however, showed that the *L. duloticus* nests had a significantly higher rate of reproduction than did their hosts *L. curvispinosus* (*G*-test, $p < 0.001$).

Population-level, male allocation ratios for slave-makers and their hosts are shown in figure 8. There was a very strong correlation between the allocation ratios produced by free-living *L. longispinosus* and those produced by *P. americanus* ($r = 0.89$, $p < 0.01$). The exception to the tight correlation between parasite and host male allocation ratios was *L. duloticus*, which reared brood more male-biased than its host *L. curvispinosus*; including this data point weakened the overall correlation to non-significance ($r = 0.69$, $p > 0.05$). Furthermore, the positive correlation was strongly affected by the data point from Vermont, and until we have more data from northern populations we must interpret the relationship with caution. Even so, only four out of seven data points fit the Trivers–Hare prediction that allocation ratios are more male-biased in the slave-maker than in their hosts (binomial distribution, $p > 0.05$). We conclude that male allocation ratios in the parasite tend to track those of their hosts.

4. DISCUSSION

In the 20 years since Trivers & Hare (1976) incorporated sex ratio theory into inclusive fitness theory, a large body of empirical work has shown that queen–worker conflict is important under a range of ecological conditions (Queller & Strassmann 1998). However, a test of Trivers & Hare's prediction of queen control in slave-makers has rested upon a very slim body of data (Bourke

Table 4. *Population-level data on allocation to growth versus reproduction*

(The reproductive allocation ratio is the proportion of all broods that were sexuals.)

data set	number of nests	total number of males	total number of females	total number of worker pupae	reproductive allocation ratio
<i>P. americanus</i>					
WV88	13	9	19	1	0.966
NY87	25	66	97	88	0.649
NY92	9	29	19	44	0.522
VT86	20	112	10	53	0.697
<i>L. duloticus</i>					
LD54	22	121	104	115	0.662
LD55	63	646	189	337	0.712

Figure 5. Reproductive allocation ratios for data pooled over nests with queens (filled bars) and without queens (open bars). Asterisks indicate significant differences between nests with and without queens ($p < 0.01$).

1989). Here we have more than doubled the available data needed to examine this fundamental question. Even so, our study has severe limitations as well. A complete analysis of reproductive allocation in hymenopteran social insects must incorporate such factors as relatedness asymmetry, multiple mating, local mate competition, worker egg-laying and a host of other complications (cf. Herbers 1990; Crozier & Pamilo 1996). Because we had only census data from which to draw inferences, we cannot gauge the impact of most of these factors; rather, we point out below how they might influence our conclusions.

The population male allocation ratios across 11 slave-maker data sets did centre on 0.50, as Trivers & Hare (1976) predicted if queens are in control in slave-maker colonies. However, the large variation around the median, together with our result that 6 of the 11 deviate significantly from 0.50, shows that exclusive queen control cannot explain slave-maker sex ratio data. Rather, we must sort out the variation to understand how allocation decisions are made by these ants.

Populations can differ in their overall allocation to males versus females, which undoubtedly reflects an underlying shift in background ecological variables. Second, within any given population, the ratios vary from year to year, which is characteristic of other ant species (Elmes 1987; Herbers 1990). Finally, within any sample, different nests produced male allocation ratios over the entire possible range (figure 4). Nonacs (1986) first pointed out that, for ant species, this variation typically shows a bimodal pattern, which is consistent with queen-worker conflict and strong worker control; the bimodality reflects a 'tug of war' between colonies whose relatedness asymmetries fall below and above the population average (Boomsma & Grafen 1990; Sundström 1994; Sundström *et al.* 1996) or between those with and without queens (Herbers 1984; Snyder & Herbers 1991; Backus 1995; Banschbach & Herbers 1996). Inspection of the allocation ratios produced by individual nests (figure 4) shows 'split sex ratios' in *P. americanus*, a unimodal distribution in *L. duloticus*, and a uniform distribution in *H. canadensis*. Thus, the hypothesis of queen-worker conflict and/or

Figure 6. Reproductive allocation ratios produced by individual nests of slave-makers; data are given only for those nests that reared at least six pupae. (a) *P. americanus*; (b) *L. duloticus*. Open bars represent nests without queens, filled bars are nests with queens.

worker control in slave-maker species has limited support from these data.

Many of our analyses focused on differences in queen numbers among nests. Nests without queens appear to arise exclusively by orphaning in *H. canadensis*, which is known to have important effects for male allocation ratios in its European congener *H. sublaevis* (Bourke 1988a; Bourke *et al.* 1988). Under these conditions, colonies with queens should overproduce females to compensate for overproduction of males from worker-laid eggs in orphaned colonies, a phenomenon known as sex ratio compensation (Forsythe 1981; Taylor 1981). Indeed, queenless nests of this species reared broods more male-biased than their counterpart nests with queens (figure 3), which is consistent with overproduction of worker-laid haploid eggs in orphaned colonies and female overproduction in colonies with queens. Orphaning also has strong implications for allocation to growth versus reproduction—we would expect orphaned colonies to invest exclusively in sexual reproduction—but, unfortunately, we have no data on this effect for *H. canadensis*.

Queenless nests of *P. americanus* and *L. duloticus* have mixed ontogeny. Some of them are undoubtedly orphans, but a sizeable fraction also represent subunits of larger polydomous colonies (Del Rio Pesado & Alloway 1983).

Table 5. Anomalous reproduction by nests of (a) the host species and (b) the slave-maker

(a) Nests containing no adult slave-makers, yet which reared slave-maker sexuals

species	site/year	number of slaves	male sexuals	female sexuals
<i>P. americanus</i>	WV83	60	0	5
		17	4	3
<i>L. duloticus</i>	1955	50	0	1
		15	25	6
		30	1	0
		14	21	0
		2	3	0
		14	14	0
		3	10	0
		6	37	0
		1	11	0
		14	2	0

(b) Nests containing adult slave-makers and rearing sexuals of the enslaved species

species	site/year	queens	workers	slaves	host males reared	host females reared
<i>P. americanus</i>	VT86	0	2	37	1	0
		0	2	17	0	1
		0	1	29	2	1
<i>L. duloticus</i>	1955	1	26	37	3	0
		0	16	29	3	0
		0	13	12	2	0
		0	4	28	1	0
		0	8	1	1	0
		1	0	10	10	0

Unfortunately, we have no way of disentangling these two groups in our database. Workers of nests without queens are known to lay haploid eggs that mature to become males in *P. americanus* (Franks & Scovell 1983; Bourke 1988b), and we assume they do in *L. duloticus* as well. It is interesting to note that nests without queens have a higher rate of reproduction in both polydomous slave-maker species (figure 2), which may reflect workers exerting more influence over reproduction when physically disjunct from their mother queen.

We also found a strong effect of queen presence or absence on allocation to growth versus reproduction for these two species, which suggests queen-worker conflict over these life history decisions, as Pamilo (1991) has predicted. Because workers have shorter lifetime expectancies than their mother queens, they prefer to invest in reproduction rather than growth, whereas their mothers prefer the longer-term fitness benefits of first investing in growth (Pamilo 1991). Indeed, in both species, nests without queens invested more in reproduction than did nests with queens (figure 5). Further, we consistently found that the number of slave-maker workers in a nest had positive effects on the number of new workers reared, whereas queen presence had consistently negative effects

Table 6. *Effects of nest demography on reproduction in three species of slave-makers*(Entries are the partial correlation coefficients^a.)

on	effect of queen presence	worker number	slave number
<i>P. americanus</i> in WV			
male biomass	-0.130	-0.225	0.667*
female biomass	0.226	0.259	-0.357
male allocation ratio	0.394	0.007	-0.313
<i>P. americanus</i> in NY			
male biomass	0.051	0.229	-0.154
female biomass	0.117	0.187	-0.066
male allocation ratio	-0.005	0.134	0.034
worker pupae	0.008	0.177	0.245
sexual allocation ratio	-0.033	0.182	-0.346
<i>P. americanus</i> in VT			
male biomass	-0.403	0.630*	0.040
female biomass	0.305	0.096	-0.088
male allocation ratio	0.149	-0.146	0.105
worker pupae	0.332	0.580**	-0.121
sexual allocation ratio	-0.597**	-0.132	0.516**
<i>L. duloticus</i>			
male biomass	-0.212**	0.009	0.091
female biomass	0.127	0.078	-0.083
male allocation ratio	0.077	-0.038	-0.158*
worker pupae	0.349** ^b	0.064	0.149
sexual allocation ratio	-0.346** ^b	-0.104	-0.090
<i>H. canadensis</i>			
male biomass	0.007	-0.054	0.341*
female biomass	-0.164	0.405*	0.146
male allocation ratio	-0.293	0.256	-0.361*

^aSignificance levels: *, 0.01 < *p* < 0.05; **, 0.001 < *p* < 0.01.^bSignificant after table-wide Bonferroni testing.

on reproductive allocation ratios (table 6). Thus, the data on allocation to growth versus reproduction provided additional support for the hypothesis of queen-worker conflict in slave-maker species.

Overall, our data show that slave-maker species tend to invest roughly equally in growth versus reproduction (table 4). However, the exception to this inference is particularly telling. The West Virginia population of *P. americanus* is close to the edge of this species' and its hosts' ranges. The density of the primary host *L. longispinosus* is low there (Herbers & Stuart 1996), and undoubtedly acts as a limiting resource for the parasite. Under such conditions, the slave-maker might exhaust all host resources within its foraging range (Savolainen & Deslippe 1996a), with the consequence that colonies should invest primarily in sexuals that can disperse to new locales rather than in growth that cannot be supported by the local environment. By contrast, more northerly populations of this species and its host have densities that are tenfold greater than those in West Virginia (Herbers & Stuart 1996), allowing for increased investment in growth by slave-maker colonies in the richer environment. We infer from Dr Talbot's collection records that densities of the *L. duloticus* slave-maker and its host *L. curvispinosus* in Michigan compare favourably to the densities of *P. americanus* in New York and Vermont. Certainly, the balance between allocation to growth and

reproduction in that species (table 4) is consistent with a reasonably dense host population for *L. duloticus*.

The partial correlation analyses showed only weak effects of demography on reproductive parameters (table 6). Thus, decomposing variation in reproduction within a data set for these parasitic species appears to be as difficult as it has proven to be in their hosts (Herbers 1990; Backus 1995). We were particularly surprised to find only weak effects of slave number on reproduction in the parasite. Slaves are essential for long-term health in these obligate social parasites (Buschinger 1986), and a recent study shows that addition of slaves enhanced reproduction in their hosts (Savolainen & Deslippe 1996b). Our analysis, however, shows that reproduction in slave-makers is more dependent on the numbers of slave-maker queens and workers than on their slaves.

The presence of anomalous reproductive patterns in some nests provided insight into host and parasite options. The presence of nests that contained no adult slave-makers but which reared slave-maker sexuals suggests that slaves are powerless to change reproductive allocation patterns in their parasite. However, we have no data on the frequency of similar nests that did shift allocation after release from the parasite. That is, we cannot tell the difference between queenless nests of the host that have always been free-living and those in which all slave-maker adults have recently died. Only direct experimentation will allow us to

Figure 7. Rates of reproduction in slave-makers and sympatric populations of their hosts. The numbers of nests in each sample are indicated at the base of the respective bars. Open bars represent data for the slave-makers, filled bars show data for the hosts.

Figure 8. Male allocation ratios produced by populations of slave-makers and sympatric populations of their hosts; the dashed line indicates equality of ratios between host and parasite. Squares represent the relationship for *P. americanus* and *L. longispinosus*, whereas the circle represents the relationship between *L. duloticus* and *L. curvispinosus*. Data for *L. longispinosus* were reported by Herbers (1990) and Herbers & Stuart (1996); data for *L. curvispinosus* were reported by Talbot (1957).

understand the slaves' options when released from parasitism.

Occasionally, slave-maker nests were observed to rear host broods, which certainly suggests that slaves are not impotent in matters of reproduction. Alloway (1979) had previously observed that *P. americanus* nests reared host

sexuals that were captured during recent raids; he never observed the phenomenon in *L. duloticus*, but Talbot's data clearly show this is possible for that species as well (table 5b). We find it especially suggestive that, in our samples, slave-maker nests that did rear host sexuals failed to rear any slave-maker sexuals; slave revolt, although rare, may nonetheless occur.

It is telling that all our evidence for slave revolt comes from the species that enslave others with polydomous colonies. Polydomy in the host species provides a clear mechanism by which slave revolt might evolve: if ants that have been enslaved can reduce the probability that their sisters in disjunct nest sites are then parasitized, their sister nests would enjoy higher inclusive fitness than enslaved groups that are unable to reduce the fitness of their parasites. The connection between polydomy and slave making has been made previously (Alloway 1980; Pollock & Rissing 1989), and we now suggest that it provides a platform on which the hosts can counter-evolve against their social parasites.

Our comparisons of slave-makers and their hosts in sympatry showed that for *P. americanus* and *L. longispinosus* the same reproduction patterns seen in the host were observed in the slave-maker (figures 7 and 8). A difficulty interpreting this result derives from differences in life history between slave-maker species and their hosts in the Formicoxenini. Bourke & Franks (1995) pointed out that commonly the parasite species is monogynous, whereas the host species is polygynous; because optimal allocation ratios shift considerably and queen-worker conflict eases in polygynous colonies, comparisons between polygynous hosts and monogynous parasites are confounded. Further, the hosts themselves can engage in brood-raiding behaviour (Alloway 1980), which further complicates comparisons. We acknowledge the confounding effect of

life history differences for such comparisons in general, but we can assess it directly with our data on *P. americanus*. The New York and Vermont populations of *L. longispinosus* are indeed polygynous, but the West Virginia population is almost exclusively monogynous (Herbers & Stuart 1996). Therefore, comparisons of the monogynous parasite and its monogynous host in West Virginia are not confounded by differences in life history, and nests there are sufficiently dispersed that brood raiding is not likely for the host (Herbers & Stuart 1996). Thus, the data for West Virginia provide the clearest test of the Trivers–Hare hypothesis available to date. Our finding that allocation ratios in the monogynous parasite were virtually identical to those of their monogynous hosts in West Virginia is entirely inconsistent with any hypothesis of pure queen control in the slave-maker. The tracking between slave-maker and free-living hosts strongly suggests that whatever cues are used by *L. longispinosus* workers to control male allocation in their own nests are also used by their counterparts rearing broods in *P. americanus* nests. Despite that striking pattern for *P. americanus* and its host *L. longispinosus*, we point out that the one comparison available for *L. duloticus* and *L. curvispinosus* pair is an outlier (figure 8). We cannot conclude whether that particular point reflects an underlying difference in the biology of the two slave-maker species or whether Talbot's collections represent an unusual sample.

We found a curious distinction between slave-makers and their hosts in terms of geographic variation in the sizes of reproductives. The indices of sexual dimorphism for *P. americanus* were very similar across all three populations (table 3), which stands in stark contrast to reports that sexual dimorphism in their *L. longispinosus* hosts is strongly different across these same three geographic sites (Herbers 1990; Backus 1993; Herbers & Stuart 1996). Sexual dimorphism in the host shifts across populations because males reared in the southern population are small relative to northern counterparts (Herbers & Stuart 1996). We saw no such geographical shift in their social parasite (table 2). Thus, whatever proximate or ultimate factors influence alate size from Vermont to West Virginia, those factors affect free-living host colonies differently from their slave-maker parasites.

Whether our results implicating queen–worker conflict will be able to be generalized to all slave-making ant species awaits considerably more data. The species studied herein all belong to the tribe Formicoxenini in the subfamily Myrmicinae, which is one of three major groups in which obligatory slavery has evolved (Wilson 1971). By contrast, other slave-makers are less well-studied; reports on male allocation in the formicine *F. sanguinea* (Pamilo & Seppä 1994) and reproduction in *F. subnuda* (Savolainen & Deslippe 1996a) are not directly comparable to ours, as those species are facultatively rather than obligately parasitic (Bourke & Franks 1995). The biology of other obligate slave-makers can differ in many respects from the species we include here (e.g. species of *Epimyrma* studied by Buschinger (1989)), and so general conclusions cannot yet be drawn.

In this paper we have more than doubled the number of available data sets by which male allocation ratios in slave-making ants can be analysed, and we have examined, probably for the first time, allocation to growth

versus reproduction in a slave-making ant species. Although general conclusions about evolution of reproductive biology in slave-makers must await larger data sets, it is clear that their evolutionary dynamics are much more complex than previously envisioned. Reproductive biology in slave-making ants contains a richness that might implicate both queen–worker conflict and parasite–host coevolution.

Trivers & Hare (1976) were certainly correct to single out reproduction in slave-making ants as inherently interesting for studies of reproductive allocation. Their reasoning, while overly simplistic, points the way to examine how reproduction is affected when queen–worker conflict is overlain with host–parasite conflict. Our results strongly suggest that no single party is exclusively in control of reproduction in slave-maker colonies. Rather, we must include the evolutionary interests of more than the slave-maker queen in our models.

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