

UCLA

UCLA Previously Published Works

Title

Selfish Larvae: Development and the Evolution of Parasitic Behavior in the Hymenoptera

Permalink

<https://escholarship.org/uc/item/0k34p64t>

Journal

Evolution, 46(6)

ISSN

0014-3820

Authors

Nonacs, Peter

Tobin, John E

Publication Date

1992-12-01

DOI

10.2307/2410019

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY
THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. 46

December, 1992

No. 6

Evolution, 46(6), 1992, pp. 1605–1620

SELFISH LARVAE: DEVELOPMENT AND THE EVOLUTION OF PARASITIC BEHAVIOR IN THE HYMENOPTERA

PETER NONACS^{1,2} AND JOHN E. TOBIN

Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138 USA

Abstract.—Queens of hymenopteran social parasites manipulate the workers of other social species into raising their offspring. However, nonconspecific brood care may also allow the parasite larvae to control their own development to a greater extent than possible in nonparasitic species. An evolutionary consequence of this may be the loss of the parasite's worker caste if the larvae can increase their fitness by developing into sexuals rather than workers. We argue that this loss is particularly likely in species in which there is little inclusive fitness benefit in working. Retention of a worker caste correlates with characteristics that increase the fitness of working relative to becoming a sexual, such as worker-production of males, high intracolony relatedness, and seasonal environments where the hosts of potential parasite queens are not always available. Further evidence strongly suggests that when the worker caste is evolutionarily lost in perennial species like ants, it disappears rapidly and through a reduction in caste threshold and queen size, so that parasite larvae become queens with less food than required to produce host workers. This evolutionary process, however, appears to lower overall population fitness, resulting in workerless parasite species having small populations and being geographically restricted. Conversely, in annual species like bees and wasps, workerless social parasitism evolves with no size reduction in queens, which is consistent with an expected lower level of queen/offspring conflict.

Key words.—Ants, dulosis, eusocial evolution, Hymenoptera, inquilinism, larvae, social parasitism.

Received July 29, 1991. Accepted March 7, 1992.

Social Hymenoptera provide a unique opportunity to study the interplay of competition and cooperation in group-living species. One such example is sex investment ratios where queens and their workers can have markedly different optima. The consensus is that workers generally control sex ratios because of their control over brood care (Trivers and Hare, 1976; Nonacs, 1986; Boomsma, 1989). This makes socially parasitic species, which have nonconspecific brood care, important for comparisons of

reproductive strategies because queens can theoretically manipulate workers of the host species to invest at their preferred optima (Trivers and Hare, 1976; Bourke et al., 1988; Bourke, 1989). Parasitized workers seem unable to resist such manipulation giving the appearance that the parasitizing queen controls all aspects of reproductive strategy. In this paper we challenge the notion of exclusive control and suggest that a queen's larvae may also be capable of manipulating their unrelated tenders. We ask under what conditions a larva would prefer to grow up to be a worker, if she also had an opportunity to grow up to be a potential queen. We propose that there is often a conflict between the parasite queen and her daugh-

¹ Present address: Department of Zoology, University of California, Davis, CA 95616 USA.

² The order of authorship reflects PN calling tails at the flip of a coin.

ters over their developmental future and that this conflict constrains the evolution of certain traits in parasites with a worker caste. In addition, we explore how and why the parasite worker caste may be lost.

In the Hymenoptera there are three types of social parasites in which the brood are raised by host workers: temporary social parasites, slave-makers (dulotics), and inquilines or permanent social parasites. The queens of temporary social parasites invade the host colony and kill or cause the demise of the host queens. The invading queen then becomes the egg-layer and the host workers raise her brood. Eventually all the host workers die off and are replaced by the new queen's offspring. Slave-makers raid the colonies of other species and carry large numbers of brood back to their own colonies. When adult, the abducted brood function as workers in the slave-making colony. Slave-making workers are often so specialized for raiding that they are unable to care for brood or carry out other routine chores, and are entirely dependent on workers of the slave species for colony work. Inquilines, considered by some the most derived stage in the evolution of socially parasitic behavior (Hölldobler and Wilson, 1990; but see Buschinger, 1990; Bourke and Franks, 1991), have an ineffectual worker caste or none at all, and often do not kill the host queens but live alongside them and simply introduce their own eggs into the brood production line of the host colony (Sudd and Franks, 1987).

Although we use the terminology of Wilson (1971), Wcislo (1987), and Hölldobler and Wilson (1990), there are alternative systems of classifying social parasites. Bourke and Franks (1991) restrict the use of the term 'inquiline' to species which tolerate the host queen, and distinguish them from 'queen-intolerant workerless parasites' which the previous authors also call inquilines. Buschinger (1990) refers to inquilines as 'permanent parasites without dulosis', and also emphasizes the evolutionary importance of whether or not the host queen is killed. Although Wilson (1971) and Wcislo (1987) refer to many bee and wasp social parasites as inquilines, these do not live alongside the queen but generally kill her upon entering the colony; some consider

them to be more like temporary social parasites than inquilines (A. Buschinger, pers. comm.).

Social parasitism has been reported most commonly in ants and dulosis has only been found in ants (Wilson, 1971). Thus, the literature is heavily skewed towards the Formicidae and the examples we will discuss will be from ants unless otherwise noted. However, unlike ants, many bee and wasp species have annual life cycles, which may change the conflict between parasite queens and their daughters over developmental fates. We will show that this difference has at least one important evolutionary consequence.

THE WORKER/QUEEN DEVELOPMENTAL DICHOTOMY

We begin with the assumption that the parasite species' workers are obligately sterile and can never lay male eggs. Therefore, the fitness of a female larva that becomes a worker is:

$$(P_{n+1} - P_n) \cdot s_w \cdot r, \quad (1)$$

where P_{n+1} and P_n are the number of sexuals the colony produces with or without that larva assuming a worker role. This increase in productivity is weighted by the probability that a worker survives long enough to make a contribution (s_w) and the average relatedness (r) of the sexuals to the worker. This assumes that females and males are produced in equal numbers (i.e., $r = [r_f + r_m]/2$), which appears often to be the case in parasitic species with worker castes (Bourke, 1989). The fitness of a larva that becomes a queen would be:

$$P_n \cdot s_q \cdot r, \quad (2)$$

where s_q is the probability of successful colony foundation and survival long enough to produce P_n sexuals; s_q must be substantially less than s_w .

When queens mate only once (monandry) and colonies have only one queen (monogyny), then the average relatedness of the brood, consisting of either brothers and sisters (1) or sons and daughters (2), is equal and r cancels out. Therefore, working is the fitter option when:

$$s_q/s_w < (P_{n+1}/P_n) - 1. \quad (3)$$

If s_w is close to 1, this relationship can be stated thus: a larva should become a worker when the probability of succeeding as a queen is less than the expected proportion of sexual production gained due to her working.

If, however, workers can and do lay eggs such that all males are worker-produced, then the average relatednesses of brood produced via the two options are not equal. A queen will raise daughters and grandsons (because her daughters will also produce the males), giving an average relatedness of $(0.5 + 0.25)/2 = 0.375$. An average worker will raise more sisters, plus a few of her own sons. The average relatedness of the sexuals for this incremental gain in colony sexual production is $(0.75 + 0.5)/2 = 0.625$. The overall effect of this is to multiply the right-hand side of (3) by a factor of 5/3. In other words, when larvae of a parasite can grow to be reproductive workers, that option (relative to becoming a queen) is almost twice as attractive as when nonreproductive.

The incremental gain of each additional worker ($n + 1$) is a function with diminishing returns: colony productivity increases more slowly with each additional worker. At some given colony size there must be a reversal in fitness such that becoming a queen results in higher fitness than becoming the next worker (Fig. 1). The threshold of increased colony productivity at which working becomes the less attractive option occurs at a greater colony size with egg-laying workers (L) than with nonlaying workers (NL). Note that in Figure 1 the hypothetical productivity curve shows diminishing returns, but other relationships are also possible. For example, in dulotic species a minimum number of workers may be required to successfully carry out slave raids. Therefore, their productivity curves would probably be parabolic in shape, such that becoming a queen would be relatively more favorable in very small or very large colonies. Of course, if growing up to be a queen always results in greater fitness than becoming a worker, then the worker caste becomes unstable and a workerless state should have a high probability of evolving. However, egg-laying by workers should not be assumed to preclude the evolution of workerless inquilinism. If the queen option has

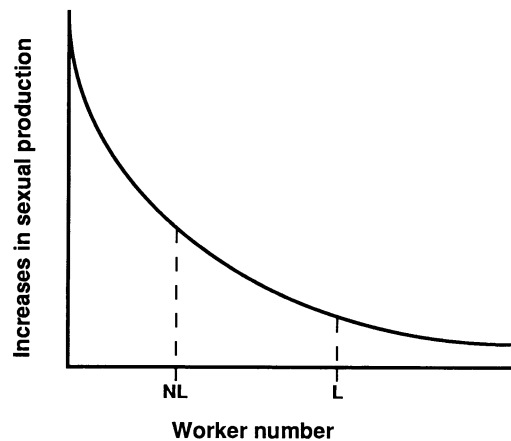


FIG. 1. Hypothetical curve depicting how much each new worker increases colony sexual production as a function of worker number. Colony size with egg-laying (L) rather than nonlaying (NL) workers can get larger before the increase in production declines to the point that developing as a queen has a higher fitness than developing as a worker.

a relatively high success rate, even a facultatively-reproductive worker caste may be evolutionarily unstable.

An evolutionary tug-of-war over male parentage is predicted between nonparasitic queens and their daughter workers, with both sides gaining if they control reproduction (Trivers and Hare, 1976; Charnov, 1978; Ratnieks, 1988; Nonacs, 1992). The situation is no different for parasitic or slave-making species (Bourke, 1988a; Franks et al., 1990). However, parasitic queens may gain long-term benefits by ceding male production in order to maintain a worker caste. Assume that a queen can control both male and female parentage at the expense of losing the worker caste, or cede male production and retain the worker caste. Giving up male production is favored when:

$$P_- \cdot r_- < P_+ \cdot r_+ \quad (4)$$

where P_- and P_+ are the total number of sexuals produced in a colony without and with a worker caste present. Substituting the appropriate relatedness values (daughters and sons in r_- versus daughters and grandsons in r_+) and rearranging gives:

$$4/3 < P_+/P_-.$$

Therefore, if having a worker caste allows the production of one-third more sexuals,

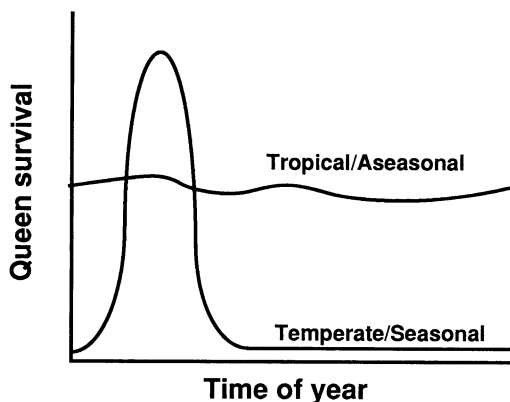


FIG. 2. The survival rate of parasitic queens as a function of the time of year. Survival rates are predicted to be relatively constant across time in aseasonal environments, but to have great variance in seasonal environments.

giving up male production by queens can be favored. Note also that there is an asymmetry between queens and workers as concerns male production. Queens only have to gain $4/3$ in productivity to abandon male production while workers would have to gain $5/3$ to favor obligate sterility.

There are several factors which the model does not address directly, but which could affect the evolutionary stability of the worker caste. For example, Franks et al. (1990), in a model based on the life history of the dulotic species *Harpagoxenus sublaevis*, found facultative worker reproduction to be very advantageous for both queens and workers if queens are short-lived and sexual production is possible in orphaned colonies. However, other conflicts over reproduction between queens and workers, and within the worker caste, remain, producing possible outcomes such as egg-laying by social parasite workers because of their inability to female-bias sex investment ratios (Bourke, 1988a).

Multiple queens per colony (polygyny) or multiple mating by individual queens (polyandry) would decrease the stability of the worker caste. Both polygyny and polyandry decrease the average relatedness of workers to their sibs (the r in equation 1), but do not affect mother/offspring relatedness, thus decreasing the attractiveness of working relative to colony founding. Therefore, neither should be common in parasitic species with worker castes.

Social parasites can also be divided into those that kill their host queen and those that do not, which may have implications on how social parasitism initially evolves and whether one type of parasitic life history can be evolutionarily derived from another (see Buschinger, 1990 and Bourke and Franks, 1991 for a discussion). This distinction, however, has little effect on the arguments presented here, except that host queen survival may insure a source for future workers and therefore becoming a worker will be less likely to increase colony productivity enough to satisfy the inequality in (3) for a parasite larva. Therefore, host queen survival should decrease the likelihood of maintaining an effective parasite worker caste.

Another important factor affecting the relative fitness of the developmental pathways is a larva's expected success rate as a queen. This may not always be a constant over time for parasitic species because of their dependence on host availability. In temperate and seasonal environments, host colonies suitable to be successfully parasitized may be available at only a certain time of the year, resulting in long periods of time where becoming a sexual would be nearly futile. On the other hand, because seasonality also forces potential hosts into predictable cycles of brood maturation or colony founding, larvae that synchronize their maturation into sexuals with these cycles could expect to find hosts relatively readily (Wcislo, 1987; Franks and Bourke, 1988). Furthermore, cold periods in temperate climates may make potential host colonies sluggish and diminish nestmate recognition abilities, thus facilitating the initial invasion by a parasitic queen (Wilson, 1971; Hölldobler and Wilson, 1990). Therefore, success rates in temperate areas may be quite variable across the year: very low at most times, but with at least one peak of greatly increased potential success. However, in tropical and aseasonal environments success rates may be much more constant and never prohibitively low, but also without a period of high host availability (Fig. 2). Seasonal environments, by providing host predictability, may favor the initial evolution of parasitism (Wcislo, 1987; Franks and Bourke, 1988), and by their constraints may

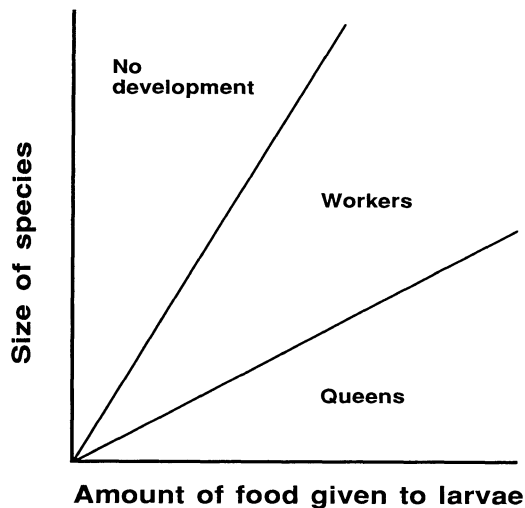


FIG. 3. The relationship between larval nutrition, the physical size of the species, and caste determination. It is assumed that the caste threshold is closely correlated with the size of the species. Below a certain amount, a larva is not adequately fed, development fails, and the larva dies. If the amount fed to the larva causes it to cross its caste threshold, then a queen is produced; otherwise, a worker will result. In general, the amount of food that will produce a worker in a large species may suffice to produce a queen in a smaller species.

prevent the disappearance of the worker caste because only those larvae maturing at the right time of the year should favor becoming queens rather than workers. This could, however, also lead to a segregation between when workers and sexuals mature (i.e., all or the great majority of larvae maturing during the window of opportunity would become sexuals, and all larvae maturing at other times would be workers, so that generally sexuals and workers do not reach adulthood simultaneously). Conversely, in aseasonal environments the initial evolution of a parasitic life history may be less favored and, once evolved, the existence of the worker caste may become unstable because all cohorts of larvae mature during times when hosts are available.

THE EVOLUTION OF WORKERLESS INQUILINISM

In the Hymenoptera, female caste determination depends in large part on the amount and quality of food the larvae receive during development (Wheeler, 1986). A limited amount of food will produce a

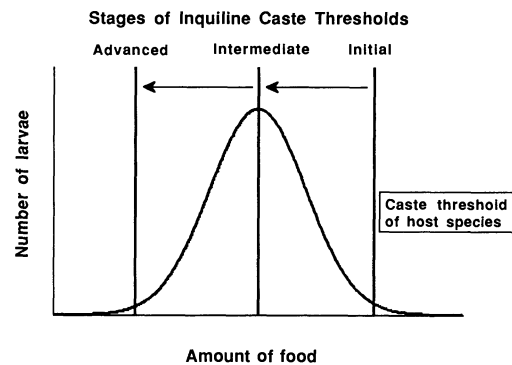


FIG. 4. The number of larvae that get a given level of food. At the initial stage in the evolution of the host/inquiline relationship, the caste thresholds (above which, more food produces a queen) of the parasite and host are similar, if not identical. In the intermediate stage, as the inquiline becomes miniaturized and the caste threshold shifts to the left relative to that of the host, fewer and fewer inquiline workers are produced. At an advanced stage in the evolution of the relationship, the inquiline's caste threshold may have shifted so far to the left that no workers are produced under normal conditions, although the ability to produce them may remain unaltered.

worker. More food may push a larva over a species-specific caste threshold, in which case development will take a different course and the larva will become a queen. Caste threshold is likely an increasing function of size of the species, such that the amount of food required to produce a queen of a small species may only suffice to produce a worker of a larger species (Fig. 3). Therefore, a parasitic larva may become a queen rather than a worker in one of two ways. One is to direct the host workers to feed her more than host larvae in the colony are routinely fed. There is, however, no evidence that larvae manipulate tenders into excessively feeding them. The second way is to have a lower caste threshold than the host species (Tobin, 1990), such that for a given amount of feeding, more parasite brood become queens and fewer become workers (Fig. 4). Evolutionarily, miniaturization would be favored until the amount of food needed to produce an inquiline queen is less than that required for a host worker. Thus small size, one of the most distinctive traits of formicid inquilines, may have been selected not for its own sake, but rather as a mechanism to insure that larvae become queens. Inquilines with low caste thresholds should produce

mostly or exclusively reproductives and inquiline queens that are larger than their host workers should still produce workers.

Bourke and Franks (1991) argue that small size may have evolved by larvae avoiding gyne (queen) suppression, where workers destroy larvae that are large and may develop into queens. However, smaller females may not be able to start colonies on their own and therefore may have no choice except to parasitize existing colonies. Eventually, new, small inquiline species evolve. Although the mechanism we suggest may act in concert with gyne suppression, our explanation for the small size of inquilines adds quantitative predictions about the relative sizes of inquiline queens and host workers, and about the scarcity or absence of inquiline workers.

The conflict between the queen and her larvae decreases once larvae start to sexualize themselves routinely (i.e., win the conflict). At this point, queens gain little by having a few, ineffectual workers, resulting in a rapid loss of the worker caste because all parties (queens and larvae) favor increasingly higher sexual/worker ratios. Note that this runaway selection, although increasing individual fitness of the larvae, could markedly reduce the average population fitness, resulting in inquiline species almost always being rare.

Finally, queen and larval developmental optima would be much more similar in annual species (bees and wasps) where having workers is of lesser benefit to queens because the colony has no future beyond the end of the season, regardless of investment strategies. When an inquiline queen takes over an annual host species' colony, it is usually close to the time when sexuals must start being raised. Therefore, it is in the interest of both the parasite queen and her offspring that they all grow up to be sexuals. Moreover, the host workers are also at this point in the colony cycle predisposed to feed all larvae enough to make them sexuals, and would not need to be directed into feeding parasitic larvae at higher than normal rates. Therefore, with little or no queen/offspring conflict, inquiline queen size should reflect ecological considerations. Given that bee and wasp inquilines always kill or physically dominate their host queens (Wilson, 1971),

large size rather than miniaturization may be more advantageous.

PREDICTIONS OF THE SELFISH LARVAE HYPOTHESIS

Larvae of social parasites are capable of, and predisposed to, controlling their own sexualization under conditions where becoming a worker is unlikely to have high payoffs. Winter and Buschinger (1986) raised *Harpagoxenus sublaevis* larvae in colonies with a living host queen, but without an *H. sublaevis* queen or adult workers. Such colonies, from the *H. sublaevis* larvae point of view, have no long-term future and the parasite larvae develop into potential queens at a very high rate (76–88% of all larvae become queens in the host colonies as compared to 19–60% in colonies with a conspecific queen). Furthermore, larvae vary in their genetic predisposition to develop as queens within intact *H. sublaevis* colonies. Brood homozygous for the recessive e-allele are significantly more likely to develop into queens than are brood with the E-allele (Winter and Buschinger, 1986). The existence of such genetic variation suggests that if conditions are unfavorable to maturing as a worker, the caste may be in danger of being evolutionarily lost. Therefore, we believe it is possible to make a set of predictions about the characteristics of social parasites with and without workers.

Prediction 1: Worker Reproduction and Evolutionary Stability of the Worker Caste.—Facultative reproduction by workers should increase the evolutionary stability of the worker caste in a parasitic species, although workerless parasitism can still evolve. However, workerless inquilinism is the only parasitic syndrome that is likely to be stable if a parasite's free-living ancestors had obligately sterile workers.

There is a general relationship between reproductive workers and the occurrence of social parasitism (Choe, 1988). Specifically, egg-laying by workers has been found in parasitic species of the genera *Chalepoxenus*, *Epimyrmica*, *Harpagoxenus*, *Leptothorax*, *Myrmoxenus*, *Protomognathus*, *Formica*, and *Polyergus*. Egg-laying has not been looked for in parasitic species of the genera *Aphaenogaster*, *Myrmica*, *Tetraponera*, *Bothriomyrmex*, *Acanthomyops*,

Camponotus, *Lasius*, and *Rossomyrmex*, but nonparasitic species in the same genus or in the closest related genus have been shown to have fertile workers (Table 1B).

The proportion of all males which are worker-produced in the above genera is unknown. There is considerable evidence that workers will readily produce males in queenless colonies (Otto, 1960; Hung, 1973; Pamilo and Rosengren, 1983; Bourke, 1988a, 1988b; A. Buschinger, pers. comm.), and queenless colonies can account for up to 22% of the males in populations of *H. sublaevis* (Bourke et al., 1988). Fertile workers are demonstrably present in colonies with queens as well, but the extent to which workers contribute to male production is difficult to ascertain and the evidence to date is equivocal (Pamilo and Varvio-Aho, 1979; Smeeton, 1981; Pamilo, 1982b; Bourke et al., 1988). Winter and Buschinger (1983) estimate that about half the males in the dulotic *E. ravouxi* are worker-produced, based on inferences of queen egg-laying capacity and observed population male production.

Reproductive workers appear to strongly influence social behavior in *H. sublaevis*. Workers form dominance hierarchies where rank correlates with ovarian development and those with well-developed ovaries tend to avoid dangerous activities like raiding (Bourke, 1988a). In total, much of the behavior of *H. sublaevis* workers seems geared to produce individual rather than colony-level benefits (Bourke et al., 1988; Franks et al., 1990).

Contradictions to the prediction of worker castes only in parasitic species with reproductive workers may be *Pheidole inquilina* and the genera *Oxyepoecus* and *Strongylognathus*, which have evolved from genera or species where workers have degenerate ovaries and are therefore obligately sterile. However, worker number in *P. inquilina* colonies is always low (Hölldobler and Wilson, 1990), suggestive of an ongoing evolutionary transition to a workerless state. The behavior of species in *Oxyepoecus* has been poorly studied in the field and it is by no means certain that they are true inquilines and do not care for their own brood (S. P. Cover, pers. comm.). *Strongylognathus* species are most definitely dulotic and

have evolved from obligately sterile *Tetramorium caespitum*, but workers of this genus have not, to our knowledge, been systematically examined for functional ovaries. Buschinger (pers. comm.) has dissected two *S. testaceus* workers that had no traces of ovarioles, but this species is also the only inquiline in the genus. Clearly, in relation to this prediction, more such data are eagerly awaited.

Workerless inquilinism has evolved in species with both obligately and facultatively sterile workers (Table 1A). Particularly striking is evolution of inquilinism in or from those genera with obligate worker sterility. In these groups there are no examples of any stable intermediate parasitic syndromes having robust worker classes (e.g., *Crematogaster*, *Monomorium*, *Pheidole*, *Pogonomyrmex*, and *Solenopsis*).

In summary, the prediction that workerless inquilinism can evolve in both obligately and facultatively sterile taxa seems well supported and the prediction of a correlation between worker fertility and a robust worker caste is also supported, with the possible exception of *Strongylognathus*.

Prediction 2: Worker Number and Sexual Production.—Parasite worker number should positively correlate with both colony-level production of sexuals and the likelihood of worker reproduction in dulotic species with obligate brood care by non-conspecific slaves.

Herbers and Pamilo (unpubl. data), through the use of path analysis on eight species of slave-making ants, found that colonies raising sexuals had significantly more parasite workers than colonies that failed to produce sexuals (the analysis controls for the effect of slave number). Further analysis of only sexual-producing colonies showed that parasite worker number had a significant positive effect on investment in female sexuals. The effect of male production, however, was not similarly consistent across species. The presence of fertile, slave-maker workers does not appear to reduce colony productivity in *H. sublaevis*, and the proportion of workers with developed ovaries increases with colony size (Buschinger and Winter, 1978; Bourke et al., 1988). In total, the above results suggest that parasite larvae can substantially increase their fitness by

TABLE 1A. Workerless inquiline species and their nearest related genus. Worker sterility in the nearest genus is either facultative (F), obligate (O), or unknown (?). Parasite species, taxonomic relations and evidence of worker reproductive status are from Choe (1988), Hölldobler and Wilson (1990) and A. Buschinger (pers. comm.).

Species	Nearest genus	Sterile
Myrmeciinae		
<i>Myrmecia inquilina</i>	<i>Myrmecia</i>	F
Pseudomyrmecinae		
<i>Pseudomyrmex leptosus</i>	<i>Pseudomyrmex</i>	F
Myrmicinae		
<i>Anergates atratulus</i>	<i>Tetramorium</i>	O
<i>Cardiocondyla zoserka</i>	<i>Cardiocondyla</i>	?
<i>Chalepoxenus brunneus</i>	<i>Leptothorax</i>	F
<i>Crematogaster atitlanica</i>	<i>Crematogaster</i>	F
<i>C. creightoni</i>	<i>Crematogaster</i>	F
<i>C. kennedyi</i>	<i>Crematogaster</i>	F
<i>Doronomyrmex goesswaldi</i>	<i>Leptothorax</i>	F
<i>D. kutteri</i>	<i>Leptothorax</i>	F
<i>D. pacis</i>	<i>Leptothorax</i>	F
<i>Epimyrma adlerzi</i>	<i>Leptothorax</i>	F
<i>E. corsica</i>	<i>Leptothorax</i>	F
<i>Leptothorax minutissimus</i>	<i>Leptothorax</i>	F
<i>Monomorium hospitum</i>	<i>Monomorium</i>	O
<i>M. inquilinum</i>	<i>Monomorium</i>	O
<i>M. talbotae</i>	<i>Monomorium</i>	O
<i>M. pergandei</i>	<i>Monomorium</i>	O
<i>M. santischii</i>	<i>Monomorium</i>	O
<i>M. effractor</i>	<i>Monomorium</i>	O
<i>Myrmica ereptrix</i>	<i>Myrmica</i>	F
<i>M. faniensis</i>	<i>Myrmica</i>	F
<i>M. hirsuta</i>	<i>Myrmica</i>	F
<i>M. lampra</i>	<i>Myrmica</i>	F
<i>M. lemasnei</i>	<i>Myrmica</i>	F
<i>M. myrmecoxena</i>	<i>Myrmica</i>	F
<i>M. quebecensis</i>	<i>Myrmica</i>	F
<i>M. samnitica</i>	<i>Myrmica</i>	F
<i>M. kabylica</i>	<i>Myrmica</i>	F
<i>M. karavejevi</i>	<i>Myrmica</i>	F
<i>M. winterae</i>	<i>Myrmica</i>	F
<i>M. symbiotica</i>	<i>Myrmica</i>	F
<i>Pheidole lanuginosa</i>	<i>Pheidole</i>	O
<i>P. microgyna</i>	<i>Pheidole</i>	O
<i>P. parasitica</i>	<i>Pheidole</i>	O
<i>P. neokohli</i>	<i>Pheidole</i>	O
<i>P. acutidens</i>	<i>Pheidole</i>	O
<i>P. symbiotica</i>	<i>Pheidole</i>	O
<i>P. argentina</i>	<i>Pheidole</i>	O
<i>P. elecebra</i>	<i>Pheidole</i>	O
<i>Pogonomyrmex anergismus</i>	<i>Pogonomyrmex</i>	O
<i>P. colei</i>	<i>Pogonomyrmex</i>	O
<i>Pseudoatta argentina</i>	<i>Acromyrmex</i>	F
<i>Serrastruma inquilina</i>	<i>Serrastruma</i>	?
<i>Solenopsis acuminata</i>	<i>Solenopsis</i>	O
<i>S. daguerri</i>	<i>Solenopsis</i>	O
<i>S. solenopsidis</i>	<i>Solenopsis</i>	O
<i>Strumigenys xenos</i>	<i>Strumigenys</i>	?
<i>Teleutomyrmex schneideri</i>	<i>Tetramorium</i>	O
<i>Tetramorium microgyna</i>	<i>Tetramorium</i>	O? ¹
<i>T. parasiticum</i>	<i>Tetramorium</i>	O? ¹
Formicinae		
<i>Anoplolepis nuptialis</i>	<i>Anoplolepis</i>	?
<i>Formica dirksi</i>	<i>Formica</i>	F

TABLE 1A. Continued.

Species	Nearest genus	Sterile
<i>F. talbotae</i>	<i>Formica</i>	F
<i>Paratrechina</i> spp.	<i>Paratrechina</i>	?
<i>Plagiolepis ampeloni</i>	<i>Plagiolepis</i>	F
<i>P. grassei</i> ²	<i>Plagiolepis</i>	F
<i>P. regis</i>	<i>Plagiolepis</i>	F
<i>P. xene</i>	<i>Plagiolepis</i>	F

¹ The host species of these parasites do not belong to the *T. caespitum* species group and therefore sterility cannot be assumed.

² Colonies can have a few workers.

becoming workers: either indirectly through increasing overall sexual production, or directly by increasing their probability of producing sons as parasite worker number increases.

Prediction 3: High Within-Colony Relatedness.—Colony relatedness will be high in parasites with a worker caste and social modifications that reduce intracolony relatedness (polyandry and polygyny) will be rare.

Colonies of *Harpagoxenus* species rarely if ever have more than one queen and females cease trying to attract males after their first mating, indicating species monandry (Buschinger and Alloway, 1979; A. Buschinger, pers. comm.). Indeed, genetic colony-level relatedness in *H. sublaevis* of $r = 0.74$ confirms both monogyny and monandry (Bourke et al., 1988).

All dulotic species of the genus *Epimyrma* are probably monandrous and all, except one, are strictly monogynous. The exception, *E. algeriana*, has intranidal sib mating which may keep relatedness high in spite of having multiple queens (Buschinger, 1989).

Allozyme studies of temporary social parasites and facultative slave-makers in the genus *Formica* indicate multiple-mating by queens, but mating frequency ranges from close to 1.0 in *F. exsecta* to about 1.5 in *F. sanguinea* (Pamilo, 1982a; Pamilo and Rosengren, 1984). Such low-level polyandry may not greatly affect queen-worker interactions (Nonacs, 1992) and may be further attenuated by the fact that sperm use tends to be biased towards one male (Pamilo, 1982a). Multiple mating by females has been observed in the field for several parasitic species (e.g., *F. pergandei*, *F. rufa*, and *Polyergus lucidus*; see Page, 1986 for references), but these data must be considered with cau-

tion. For example, *Iridomyrmex humilis* females mate multiply, but only the first male successfully transfers sperm (Keller et al., 1992). In apparent contradiction to the prediction, many *Formica* colonies have many queens, which reduces intracolony relatedness to almost zero in some species (Pamilo, 1982b; Pamilo and Rosengren, 1984; Rosengren et al., 1993). However, colonies with low relatedness appear to occur exclusively in conjunction with a polydomous (a single colony occupies multiple nest sites) life history where colony founding is almost always by fissioning the original colony. Therefore, nonconspecific brood care may never occur, or occur once across many generations (Rosengren et al., 1993). Temporarily parasitic colony founding is probably the rule in monodomous populations. Monodomy is particularly prevalent in the species *F. rufa* and *F. pratensis*, and they have within-colony genetic mean relatedness values of 0.69–0.87. In species like *F. exsecta*, where populations differ in life histories, mean relatedness is uniformly high when monodomous ($r \geq 0.62$) and low when polydomous ($r \leq 0.10$) (see Rosengren et al., 1993 for a summary of relatedness measures in *Formica*).

Prediction 4: Environmental Seasonality.—Temporarily parasitic and dulotic species should be primarily found in environmentally seasonal habitats and individual brood cohorts should tend to be either mostly sexuals or mostly workers. However, inquilinism will not be as severely restricted by seasonality.

Because temperate climates have received far more intensive attention than the tropics, the seasonality prediction is vulnerable to the possibility that the tropics contain many, as yet undescribed, socially parasitic species. This may be particularly

TABLE 1B. Parasites with a worker caste, their nearest taxonomic nonparasitic genus, the type of parasitism involved, and the sterility of the parasite workers (a question mark after an F or O indicates that data for the parasitic species are not available, but that data are available for the nearest genus).

Species	Nearest genus	Parasitism	Sterile
Pseudomyrmecinae			
<i>Tetraponera ledouxi</i>	<i>Tetraponera</i>	Temporary	F?
Myrmicinae			
<i>Antichthonidris bidentatus</i>	<i>Antichthonidris</i>	Dulosis?	?
<i>Aphaenogaster tennesseensis</i>	<i>Aphaenogaster</i>	Temporary	F?
<i>Chalepoxenus insubricus</i>	<i>Leptothorax</i>	Dulosis	F
<i>C. kutteri</i>	<i>Leptothorax</i>	Dulosis	F
<i>C. muellerianus</i>	<i>Leptothorax</i>	Dulosis	F
<i>C. siciliensis</i>	<i>Leptothorax</i>	Dulosis	F
<i>C. tramieri</i>	<i>Leptothorax</i>	Dulosis	F
<i>Epimyrma algeriana</i>	<i>Leptothorax</i>	Dulosis	F
<i>E. bernardi</i>	<i>Leptothorax</i>	Dulosis	F
<i>E. kraussei</i>	<i>Leptothorax</i>	Dulosis	F
<i>E. ravouxi</i>	<i>Leptothorax</i>	Dulosis	F
<i>E. stumperi</i>	<i>Leptothorax</i>	Dulosis	F
<i>E. tamarae</i>	<i>Leptothorax</i>	Dulosis	F ³
<i>E. zaleskyi</i>	<i>Leptothorax</i>	Dulosis	F ³
<i>Harpagoxenus canadensis</i>	<i>Leptothorax</i>	Dulosis	F
<i>H. sublaevis</i>	<i>Leptothorax</i>	Dulosis	F
<i>H. zaisanicus</i>	<i>Leptothorax</i>	Dulosis?	F ⁴
<i>Kyidris media</i>	<i>Smithistruma</i> ?	Inquiline	?
<i>K. yaleogyna</i>	<i>Smithistruma</i> ?	Inquiline	?
<i>Leptothorax faberi</i>	<i>Leptothorax</i>	Inquiline	F
<i>L. duloticus</i>	<i>Leptothorax</i>	Dulosis	F?
<i>Manica parasitica</i>	<i>Manica</i>	Inquiline	?
<i>Myrmica bibikoffi</i>	<i>Myrmica</i>	Inquiline	F?
<i>M. colax</i>	<i>Myrmica</i>	Temporary	F?
<i>Myrmoxenus gordiagini</i>	<i>Leptothorax</i>	Dulosis	F
<i>Oxyepoecus bruchi</i>	<i>Solenopsis</i>	Inquiline?	O?
<i>O. daguerri</i>	<i>Solenopsis</i>	Inquiline?	O?
<i>O. inquilina</i>	<i>Solenopsis</i>	Inquiline?	O?
<i>O. minuta</i>	<i>Solenopsis</i>	Inquiline?	O?
<i>Pheidole inquilina</i>	<i>Pheidole</i>	Inquiline ⁵	O?
<i>Protomognathus americanus</i>	<i>Leptothorax</i>	Dulosis	F
<i>Strongylognathus</i> 23 spp.	<i>Tetramorium</i>	Dulosis	O?
<i>S. testaceus</i>	<i>Tetramorium</i>	Inquiline	O
Dolichoderinae			
<i>Bothriomyrmex</i> 34 spp.	<i>Tapinoma</i>	Temporary	F?
<i>Conomyrma medeis</i>	<i>Conomyrma</i>	Temporary	?
<i>C. reginacula</i>	<i>Conomyrma</i>	Temporary	?
Formicinae			
<i>Acanthomyops latipes</i>	<i>Lasius</i>	Temporary	F?
<i>A. murphyi</i>	<i>Lasius</i>	Temporary	F?
<i>Camponotus universitatis</i>	<i>Camponotus</i>	Inquiline	F?
<i>Formica</i> (11 spp. <i>exsecta</i>)	<i>Formica</i>	Temporary	F
<i>Formica</i> (14 spp. <i>microgyna</i>)	<i>Formica</i>	Temporary	F?
<i>Formica</i> (8 spp. <i>rufa</i>)	<i>Formica</i>	Temporary	F
<i>Formica</i> (12 spp. <i>sanguinea</i>)	<i>Formica</i>	Dulosis	F
<i>Lasius</i> (11 spp. <i>umbratus</i>)	<i>Lasius</i>	Temporary	F?
<i>L. reginae</i>	<i>Lasius</i>	Temporary	F?
<i>Polyergus breviceps</i>	<i>Formica</i>	Dulosis	F
<i>P. lucidus</i>	<i>Formica</i>	Dulosis	F?
<i>P. nigerrimus</i>	<i>Formica</i>	Dulosis	F?
<i>P. rufescens</i>	<i>Formica</i>	Dulosis	F
<i>P. samurai</i>	<i>Formica</i>	Dulosis	F?
<i>Rossomyrmex minuchae</i>	<i>Formica</i>	Dulosis	F?
<i>R. proformicarum</i>	<i>Formica</i>	Dulosis	F?

³ May be synonyms of *E. ravouxi* (A. Buschinger, pers. comm.)

⁴ May be a synonym of *H. sublaevis* (A. Buschinger, pers. comm.)

⁵ Workers present but scarce.

true for inquilines which, because they tend to be rare (see Prediction 5), are usually found only when areas are rigorously searched (see Wcislo, 1987 and Hölldobler and Wilson, 1990 for a discussion). Be that as it may, not one dulotic species has been found in the tropics. Recent surveys of the tropical rain forest indicate that temporary social parasitism as a life history may also be relatively rare. As a comparison, about one third of the 110 ant species of Switzerland are parasitic (Kutter, 1969), while only 2 out of 280 species recently collected in Peruvian rain forest exhibit a potentially parasitic syndrome, with small, shiny queens having narrow thoraxes and saber-like mandibles (S. P. Cover, J. E. Tobin, and E. O. Wilson, unpubl. data). Obligate parasitic behavior is proportionally more common in temperate species of bees and wasps, with a significant positive correlation between latitude and parasitic bee species as a percentage of the total bee fauna (Wcislo, 1987). Host predictability is thought to have a major influence on this pattern.

Separation of broods into sexual or worker cohorts is distinctly present in most temporarily parasitic species of the *Formica rufa* group, but broods overlap in species of the *exsecta* group and the *sanguinea* group (Pamilo and Rosengren, 1983). In *H. sublaevis* there may be an abrupt switch from worker to sexual production as colony size increases, with mixed broods being uncommon (Bourke et al., 1988). This pattern, however, may be far from universal in this species as other populations have mixed broods (Winter and Buschinger, 1986; A. Buschinger, pers. comm.). Similarly, in *Leptothorax duloticus* and *Protomognathus americanus* workers and sexuals are raised concurrently (Wesson, 1939, 1940). In dulotic species of *Epimyrma*, larvae require overwintering to develop into sexuals, in contrast to inquiline *Epimyrma*, which can produce sexuals without the larvae having to overwinter (Buschinger, 1989).

There are situations where parasite larvae have reduced opportunity for controlling sexualization. In species where social parasitism is temporary or in species that are facultative slave-makers (the workers can and do take care of brood if slaves are not available), nonconspecific brood care may

be present for only one or a few cohorts of larvae and perhaps only during a season where queens would have a low survival rate (Fig. 2). Therefore, exceptions to elements of Predictions 2–4 would be most likely in these species. In contrast, exceptions should be very rare in species in which nonconspecific brood care is perpetual and obligate.

Prediction 5: Inquiline Population Size.—The evolution of inquilinism may increase the fitness of individual larvae at the expense of overall colony fitness. Therefore, inquiline species' populations may be much smaller and more geographically restricted than are closely related non-inquiline parasites, and may be subject to higher rates of extinction.

Although inquilines can be geographically widespread, most species have limited distributions and very few achieve high population densities (Hölldobler and Wilson, 1990). In general contrast, parasitic species with worker castes are often common and widespread. The leptothoracine slave-makers (of the genera *Epimyrma*, *Harpagoxenus*, *Leptothorax*, and *Protomognathus*) can be very common and have high colony densities (Wesson, 1939; Buschinger, 1986; Bourke et al., 1988; Herbers and Pamilo, unpubl. data). The formicine slave-makers (*Formica sanguinea* group, *Polyergus*, and *Rossomyrmex*) do not often form high density populations, but species ranges often encompass large regions of Eurasia and North America (Pamilo, 1981; Hölldobler and Wilson, 1990; Topoff, 1990). The formicine temporary parasites (*Acanthomyops*, *Formica rufa* group and *exsecta* group, and *Lasius umbratus* group) are often common and in the case of *Formica* can be the most abundant and dominant species in many boreal forests (Pamilo and Rosengren, 1984; Savolainen and Vepsäläinen, 1988; Hölldobler and Wilson, 1990).

The relationship also holds within phyletic groups. In *Epimyrma*, *E. adlerzi* and *E. corsica* appear to have derived an inquiline life history from dulotic ancestors similar to *E. ravouxi*. The inquilines are rare with geographically small ranges while *E. ravouxi* is widespread in Europe (Douwes et al., 1988; Buschinger, 1989). *Chalepoxenus brunneus* is a workerless inquiline

TABLE 2. Ant workerless inquilines. Comparison of average head width (H.W.) of inquiline queens with that of queens and workers of their host species (all in mm). Whether parasite queens are tolerant of their host queens is indicated, if such data are available. A question mark (?) indicates that no host queens were described in the collection samples, but since the number of samples available is very small, queen intolerance is only suggested. A dash (—) indicates that no specimens of that caste were available for measurement. In the case of several *Pheidole* species there are two measurements for workers: one for major workers and one for minors. All specimens are from the Museum of Comparative Zoology at Harvard.

Parasite species			Host species		
Species name	Queen H.W.	Host-queen tolerant?	Species name	Queen H.W.	Worker H.W.
Subfamily Myrmeciinae					
<i>Myrmecia inquilina</i>	2.97	Yes	<i>Myrmecia nigriceps</i>	—	3.40
<i>Myrmecia inquilina</i>	2.97	Yes	<i>Myrmecia vindex</i>	4.40	3.40
Subfamily Pseudomyrmecinae					
<i>Pseudomyrmex leptosus</i>	0.69	No	<i>Pseudomyrmex ejectus</i>	0.68	0.69
Subfamily Myrmicinae					
<i>Anergates atratulus</i>	0.59	No	<i>Tetramorium caespitum</i>	1.37	0.90
<i>Doronomyrmex pacis</i>	0.65	Yes	<i>Leptothorax acervorum</i>	—	0.72
<i>Leptothorax</i> (=Myrafant)			<i>Leptothorax</i> (=Myrafant)		
<i>minutissimus</i>	0.48	Yes	<i>curvispinosus</i>	0.66	0.53
<i>Monomorium talbotae</i>	0.42	No?	<i>Monomorium minimum</i>	0.66	0.44
<i>Monomorium pergandei</i>	0.44	Yes	<i>Monomorium minimum</i>	0.66	0.44
<i>Myrmica hirsuta</i>	1.00	Yes	<i>Myrmica sabuleti</i>	1.30	1.08
<i>Myrmica microgyna</i>	0.91	Yes	<i>Myrmica rubra</i>	1.12	1.01
<i>Pheidole lanuginosa</i>	0.74	No?	<i>Pheidole indica</i>	1.44	1.35
					0.64
<i>Pheidole parasitica</i>	0.59	No?	<i>Pheidole indica</i>	1.44	1.35
					0.64
<i>Pheidole</i> (=Anergatides)			<i>Pheidole</i>		
<i>neokohli</i>	0.41	No?	<i>megacephala</i>		1.66
<i>Pheidole acutidens</i>	0.42	?	<i>melancholica</i>	—	0.53
			<i>Pheidole nitidula</i>	—	1.38
					0.63
<i>Pogonomyrmex anergismus</i>	1.77	No	<i>Pogonomyrmex rugosus</i>	—	2.32
<i>Pogonomyrmex colei</i>	1.76	Yes	<i>Pogonomyrmex rugosus</i>	—	2.32
<i>Tetramorium parasiticum</i>	0.56	?	<i>Tetramorium avium</i>	0.74	0.63
<i>Teleutomyrmex schneideri</i>	0.45	Yes	<i>Tetramorium caespitum</i>	1.37	0.90
Subfamily Formicinae					
<i>Formica talbotae</i>	1.03	No	<i>Formica obscuripes</i>	2.20	1.81

known from one Moroccan location, while dulotic *Chalepoxenus* species are found throughout the northern Mediterranean (Buschinger et al., 1988). Leptothoracines are parasitized by several genera of slave-makers and inquilines. The slave-makers (*Harpagoxenus* spp., *Leptothorax duloticus*, *Myrmoxenus gordiagini* and *Protomognathus americanus*) are almost uniformly more abundant than the inquilines (*Doronomyrmex* spp. and *L. minutissimus*). The common myrmicines, *Tetramorium caespitum* and *T. jacoti*, also fall victim to slave-makers and inquilines. Species of the dulotic

genus *Strongylognathus* are generally much more common than the inquilines (*Anergates atratulus*, *Teleutomyrmex schneideri*, *Tetramorium microgyna*, and *T. parasiticum*) some of which are probably among the rarest ant species (Buschinger, 1987; Hölldobler and Wilson, 1990). *Formica dirksi* and *F. talbotae* are the only known inquilines in that genus and both are quite rare (Wilson, 1976).

The fact that inquilines are rare and that their distributions often suggest they are relicts (Wilson, 1963; Hölldobler and Wilson, 1990) is consistent with the prediction of

TABLE 3. Bee and wasp inquilines. Comparison of average head width (H.W.) of inquiline queens with that of queens and workers of their host species (all in mm). A dash (—) indicates that workers and queens of that species cannot be distinguished morphologically; in such cases a single measurement is given that represents an average of females without distinction of caste. All specimens are from the Museum of Comparative Zoology at Harvard.

Parasite species		Host species		
Species name	Queen H.W.	Species name	Queen H.W.	Worker H.W.
Bees				
<i>Psithyrus rupestris</i>	3.28	<i>Bombus lapidarius</i>	3.02	2.26
<i>P. vestalis</i>	2.75	<i>B. terrestris</i>	2.92	2.30
<i>P. barbutellus</i>	2.92	<i>B. hortorum</i>	2.45	2.24
Wasps				
<i>Vespula austriaca</i>	4.20	<i>Vespula rufa</i>	4.21	3.52
<i>Dolichovespula adulterina</i>	4.15	<i>Dolichovespula saxonica</i>	4.05	3.45
<i>D. adulterina</i>	4.15	<i>D. norvegica</i>	4.02	3.49
<i>D. omissa</i>	4.18	<i>D. silvestris</i>	4.22	3.57
<i>D. arctica</i>	4.10	<i>D. arenaria</i>	4.15	3.42
<i>Polistes semenowii</i>	3.55	<i>Polistes dominulus</i>	3.60	—
<i>P. semenowii</i>	3.55	<i>P. nimpha</i>	3.49	—
<i>P. sulcifer</i>	3.78	<i>P. dominulus</i>	3.60	—

high extinction rates. That a substantial number of inquilines exist suggests that the evolution of inquilinism may be a relatively common event. In summary, the evolution of an inquiline life cycle in ants appears to correlate strongly with small population size and species rarity.

Prediction 6: Inquilinism and the Worker Caste.—If the loss of the worker caste occurs rapidly relative to the time workerless species can persist, then workerless inquilines should be more common than inquilines with workers. Hölldobler and Wilson's (1990) Table 12-1 summarizes all known cases of social parasitism in the Formicidae and includes 51 unambiguous workerless inquilines, but only six cases of what the authors consider inquilines with workers.

Prediction 7: Queen Size in Workerless Inquilines.—Queens of workerless inquilines should be of the same size or smaller than the host workers, such that the amount of food normally given a host worker larva is enough to push a female inquiline larva over her caste threshold.

We used head width, which is generally regarded as being a good indicator of biomass in the Hymenoptera (Oster and Wilson, 1978), to compare relative sizes. Although inquilines are very rare and we were limited to as few as one or two specimens

per species, the data do strongly suggest that workerless inquiline ant queens are consistently smaller than their host workers (in 18 out of 19 cases the parasites have equal or smaller head widths; $P = 0.001$, Wilcoxon signed-rank test). In the only reversal, *Pheidole lanuginosa*, the queens are larger than only the smallest host worker caste and considerably smaller than the host queens or their major workers (Table 2).

On the other hand, there is no queen miniaturization in annual bee and wasp social-parasitic species (Table 3). In 6 of the 11 cases the inquilines are, in fact, larger than their host queens. As argued above, in annual species inquilines take over colonies when the host workers are normally predisposed towards raising only sexual brood. This obviates the need for lower caste thresholds, and the results strongly suggest that without a queen/offspring conflict over larval development the selective advantages of large size for survival or host queen-killing are paramount. Many ant inquilines also appear to be host queen-intolerant, but miniaturization is unaffected (Table 2), although large size would also probably improve queen-killing efficiency. In ants, therefore, social conflicts within the nest seem to have the predominant evolutionary influence on queen size.

TABLE 4. Ant inquiline with workers. Comparison of average head width (H.W.) of inquiline queens and workers with that of queens and workers of their host species (all in mm). A dash (—) indicates that no specimens of that caste were available for measurement. All specimens are from the Museum of Comparative Zoology at Harvard.

Parasite species			Host species		
Species name	Queen H.W.	Worker H.W.	Species name	Queen H.W.	Worker H.W.
<i>Monomorium metoecus</i>	0.54	—	<i>Monomorium minimum</i>	0.66	0.46
<i>Manica parasitica</i>	—	1.03	<i>Manica bradleyi</i>	1.90	1.25
<i>Oxyepoecus inquilina</i>	1.25	0.80	<i>Pheidole radoszkowskii</i>	2.15	—
<i>Pheidole inquilina</i>	0.69	—	<i>Pheidole pilifera</i>	1.28	1.38
					0.60

Prediction 8: Queen Size in Inquilines with Workers.—Queens of inquilines with workers should be smaller than the host queen, but larger than the host workers; the degree to which the inquiline has lost its worker castes should be correlated with the degree to which it has become miniaturized.

Our scenario suggests that an inquiline with workers is in an evolutionary transition towards losing the worker caste. There are few cases of inquilines with workers and several are disputed (Hölldobler and Wilson, 1990; A. Buschinger, pers. comm.), but these queens are more similar in size to their host queens than are workerless inquilines (Hölldobler and Wilson, 1990; Table 12-2). Collections are few in number, however, and we could examine none that include both workers and queens of the purported inquilines with workers (summary in Table 4).

Prediction 9: Workers in Workerless Inquilines.—The developmental scenario of workerless inquilinism predicts that workers are absent because the larvae are normally fed enough to push them over their lower caste threshold, and not because of an inability to produce workers. This suggests that workers should occasionally be found in the field and that restricting food to inquiline larvae might keep them below their caste threshold and elicit the production of workers in normally workerless species.

Elmes (1976) did obtain workers of the normally workerless *Myrmica microgyna*, an inquiline of *M. rubra*, while raising them in the laboratory. Likewise, A. Buschinger (pers. comm.) has found a small number of workers of *Doropnomyrmex pacis* and of *D. kutteri* (considered workerless inquilines) in

several field and laboratory colonies. Thus, workerless inquilines may have an atavistic ability to produce workers expressed only under periods of environmental stress. Examining this prediction experimentally would shed light not only on the importance of caste thresholds on inquiline development, but also on the general subject of development and caste determination.

CONCLUSIONS

The evidence presented here is consistent with the hypothesis that nonconspecific brood care in parasitic social insects provides an opportunity for developing parasite larvae to direct their own development into becoming queens. Thus the evolutionary stability of a parasite worker caste seems to be favored by worker-production of males, by social systems that maintain high intracolony relatedness, and by seasonal environments where hosts are unavailable during portions of the year. In contrast, the evolution of workerless inquilinism is possible under a wider variety of conditions. In ants, this state appears to occur through the reduction of the caste threshold for sexualization such that all parasite larvae become sexuals at a size smaller than the host workers, independent of whether the parasite queen kills the host queens. Conversely, inquiline wasps and bees (which have annual life cycles) show no reduction in caste threshold, which is consistent with a prediction of reduced queen/offspring conflict. The consequence of an inquiline life history for ants, however, is a restricted species distribution and small population sizes.

Although the patterns of social parasitism are generally consistent with our predictions, phylogenetic constraints may restrict

evolution in several groups. For example, it has been argued that only species in which brood learn their species identity late in development (as pupae or callow adults—e.g., *Formica*) are susceptible to social parasitism (Le Moli and Mori, 1987). Furthermore, social parasitism appears not to be distributed evenly in the Formicidae: when all *Bothriomyrmex* species are excluded, there are only five known species of ant social parasites that are not in the Myrmicinae or Formicinae (Table 1; Buschinger, 1990). This may be due in part to the other subfamilies having a higher proportion of species in aseasonal tropical environments, but this cannot be the sole reason for the apparent lack of parasitism in groups as large and diverse as the Ponerinae, for example. Even within the groups where parasitism is common, there are puzzling exceptions. *Camponotus* is a widespread formicine genus with species found in many of the same habitats and with similar social systems as the genus *Formica*. However, parasitism is common only in the latter genus. Clearly, then, our models may supply part of the answer for the evolution of social parasitism, but some taxonomic patterns still remain to be explained.

In summary, we present a series of hypotheses predicting certain characteristics of parasitic species, but not of the evolution of the parasite life habit itself (for reviews of hypothetical evolutionary pathways, see Alloway, 1980; Stuart and Alloway, 1982; Buschinger, 1986, 1990; Hölldobler and Wilson, 1990; Bourke and Franks, 1991). We make no statement as to why parasitism should be favored or evolve from an independent life history. Nor do we offer any insight on specific evolutionary transitions, such as whether slave-making evolves from predatory raids, territorial competition between mature colonies, or a polydomous population structure. Our goal is simply to propose that certain traits and habitats should correlate with given life histories, while others (such as a tropical slave-maker with an obligately-sterile worker caste) should be highly unlikely.

ACKNOWLEDGMENTS

We are grateful to the following persons for providing preprints, unpublished information, discussing our ideas, and/or criti-

cally reviewing the manuscript: A. Bourke, A. Buschinger, N. Carlin, J. Carpenter, S. Cover, P. Frumhoff, J. Heinze, J. Herbers, B. Hölldobler, L. Keller, W. Wcislo, D. Wheeler, E. O. Wilson, and two anonymous reviewers. J.E.T. was supported in part by a N.S.F. predoctoral fellowship.

LITERATURE CITED

- ALLOWAY, T. M. 1980. The origins of slavery in lepto-thoracine ants (Hymenoptera: Formicidae). *Am. Nat.* 115:247–261.
- BOOMSMA, J. J. 1989. Sex-investment ratios in ants: has female bias been systematically over-estimated? *Am. Nat.* 133:517–532.
- BOURKE, A. F. G. 1988a. Dominance orders, worker reproduction, and queen-worker conflict in the slave-making ant *Harpagoxenus sublaevis*. *Behav. Ecol. Sociobiol.* 23:323–333.
- . 1988b. Worker reproduction in the higher eusocial Hymenoptera. *Q. Rev. Biol.* 63:291–311.
- . 1989. Comparative analysis of sex investment ratio in slave-making ants. *Evolution* 43:913–918.
- BOURKE, A. F. G., AND N. R. FRANKS. 1991. Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biol. J. Linn. Soc.* 43:157–178.
- BOURKE, A. F. G., T. M. VAN DER HAVE, AND N. R. FRANKS. 1988. Sex ratio determination and worker reproduction in the slave-making ant *Harpagoxenus sublaevis*. *Behav. Ecol. Sociobiol.* 23:233–245.
- BUSCHINGER, A. 1986. Evolution of social parasitism in ants. *Trends Ecol. Evol.* 1:155–160.
- . 1987. *Teleutomyrmex schneideri* Kutter 1950 and other parasitic ants found in the Pyrenees. *Spixiana* 10:81–83.
- . 1989. Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). *J. Evol. Biol.* 2:265–283.
- . 1990. Sympatric speciation and radiative evolution of socially parasitic ants—Heretic hypotheses and their factual background. *Z. Zool. Syst. Evolutionsforsch.* 28:241–260.
- BUSCHINGER, A., AND T. M. ALLOWAY. 1979. Sexual behaviour in the slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and sexual pheromone experiments with *H. canadensis*, *H. americanus* (Emery), and *H. sublaevis* (Nylander) (Hymenoptera; Formicidae). *Z. Tierpsychol.* 49:113–119.
- BUSCHINGER, A., AND U. WINTER. 1978. Echte arbeiterrinnen, fertile arbeiterrinnen und sterile wirt-sweibchen in völkern der dulotischen ameise *Harpagoxenus sublaevis* (Nyl.) (Hym., Form.). *Insectes Soc.* 25:63–78.
- BUSCHINGER, A., W. EHRHARDT, K. FISCHER, AND J. OFER. 1988. The slave-making ant genus *Chalepoxenus* (Hymenoptera, Formicidae). I. Review of literature, range and slave species. *Zool. Jahrb. Syst.* 115:383–401.
- CHARNOV, E. L. 1978. Sex-ratio selection in eusocial Hymenoptera. *Am. Nat.* 112:317–326.
- CHOE, J. C. 1988. Worker reproduction and social evolution in ants (Hymenoptera: Formicidae), pp.

- 163–187. In J. C. Trager (ed.), *Advances in Myrmecology*. E. J. Brill, Leiden, Belgium.
- DOUWES, P., K. JESSEN, AND A. BUSCHINGER. 1988. *Epimyrma adlerzi* sp. n. (Hymenoptera, Formicidae) from Greece: Morphology and life history. *Entomol. Scand.* 19:239–249.
- ELMES, G. W. 1976. Some observations on the microgyne form of *Myrmica rubra* L. (Hymenoptera, Formicidae). *Insectes Soc.* 23:3–22.
- FRANKS, N. R., AND A. F. G. BOURKE. 1988. Slaves of circumstance. *New Scient.* 119:45–49.
- FRANKS, N. R., B. IRELAND, AND A. F. G. BOURKE. 1990. Conflicts, social economics and life history strategies in ants. *Behav. Ecol. Sociobiol.* 27:175–181.
- HÖLLDOBLER, B., AND E. O. WILSON. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, MA USA.
- HUNG, A. C. F. 1973. Reproductive biology in dulotic ants: Preliminary report (Hymenoptera: Formicidae). *Entomol. News* 84:253–259.
- KELLER, L., L. PASSERA, AND D. CANTONI. 1992. Repeated mating by queens results in a single insemination in the Argentine ant *Iridomyrmex humilis*. In J. Billen (ed.), *Biology and Evolution of Social Insects*. Leuven University Press, Leuven, Belgium. *In press*.
- KUTTER, H. 1969. Die sozialparasitischen Ameisen der Schweiz. (Vierteljahrsschr. Naturforsch. Ges. Zurich 113:1–62.
- LE MOLI, F., AND A. MORI. 1987. The problem of enslaved ant species: Origin and behavior, pp. 333–363. In J. M. Pasteels and J.-L. Deneubourg (eds.), *From Individual to Collective Behavior in Social Insects*. Birkhäuser, Basel, Switzerland.
- NONACS, P. 1986. Ant reproductive strategies and sex allocation theory. *Q. Rev. Biol.* 61:1–21.
- . 1992. Male parentage and sexual deception in the social Hymenoptera, pp. 384–401. In D. L. Wrensch and M. A. Ebbert (eds.), *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman and Hall, N.Y., USA.
- OSTER, G. F., AND E. O. WILSON. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, NJ USA.
- OTTO, D. 1960. Zur Erscheinung der Arbeiterinnenfertilität und Parthenogenese bei der kahlrückigen roten Waldameise (*Formica polyctena* Först.) (Hym.). *Dtsch. Entomol. Z. (N.F.)* 7:1–9.
- PAGE, R. E. 1986. Sperm utilization in social insects. *Annu. Rev. Entomol.* 31:297–320.
- PAMILO, P. 1981. Genetic organization of *Formica sanguinea* populations. *Behav. Ecol. Sociobiol.* 9:45–50.
- . 1982a. Multiple mating in *Formica* ants. *Hereditas* 97:37–45.
- . 1982b. Genetic population structure in polygynous *Formica* ants. *Heredity* 48:95–106.
- PAMILO, P., AND R. ROSENGREN. 1983. Sex ratio strategies in *Formica* ants. *Oikos* 40:24–35.
- . 1984. Evolution of nesting strategies of ants: Genetic evidence from different population types of *Formica* ants. *Biol. J. Linn. Soc.* 21:331–348.
- PAMILO, P., AND S. VARVIO-AHO. 1979. Genetic structure of nests in the ant *Formica sanguinea*. *Behav. Ecol. Sociobiol.* 6:91–98.
- RATNIEKS, F. L. W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat.* 132:217–236.
- ROSENGREN, R., L. SUNDSTROM, AND W. FORTELIUS. 1993. Monogyny and polygyny of *Formica* ants—a result of alternative dispersal tactics? In L. Keller (ed.), *Queen Number and Sociality in Insects*. Oxford University Press, London, UK. *In press*.
- SAVOLAINEN, R., AND K. VEPSÄLÄINEN. 1988. A competition hierarchy among boreal ants: Impact on resource partitioning and community structure. *Oikos* 51:135–155.
- SMEETON, L. 1981. The source of males in *Myrmica rubra* L. (Hym. Formicidae). *Insectes Soc.* 28:263–278.
- STUART, R. J., AND T. M. ALLOWAY. 1982. Territoriality and the origin of slave raiding in leptothoracine ants. *Science* 215:1262–1263.
- SUDD, J. H., AND N. R. FRANKS. 1987. *The Behavioural Ecology of Ants*. Chapman and Hall, N.Y., USA.
- TOBIN, J. E. 1990. Nourishment, caste thresholds, and workerless social parasites in the Formicidae, pp. 649–650. In G. K. Veeresh, B. Mallik, and C. A. Viraktamath (eds.), *Social Insects and the Environment*. Oxford and IBH Publishing Co., New Delhi, India.
- TOPOFF, H. 1990. Slave-making ants. *Am. Sci.* 78:520–528.
- TRIVERS, R. L., AND H. HARE. 1976. Haplodiploidy and the evolution of the social insects. *Science* 191:249–263.
- WCISLO, W. T. 1987. The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea). *Biol. Rev.* 62:515–543.
- WESSON, L. G. 1939. Contributions to the natural history of *Harpagoxenus americanus* Emery (Hymenoptera: Formicidae). *Trans. Am. Entomol. Soc.* 65:97–122.
- . 1940. Observations on *Leptothorax duloticus*. *Bull. Brooklyn Entomol. Soc.* 35:73–83.
- WHEELER, D. E. 1986. Developmental and physiological determinants of caste in social Hymenoptera: Evolutionary mechanisms. *Am. Nat.* 128:13–34.
- WILSON, E. O. 1963. Social modifications related to rareness in ant species. *Evolution* 17:249–253.
- . 1971. *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, MA USA.
- . 1976. The first workerless parasite in the ant genus *Formica* (Hymenoptera: Formicidae). *Psyche* 83:277–281.
- WINTER, U., AND A. BUSCHINGER. 1983. The reproductive biology of a slavemaker ant, *Epimyrma ravouxi*, and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). *Entomol. Gener.* 9:1–15.
- . 1986. Genetically mediated queen polymorphism and caste determination in the slave-making ant, *Harpagoxenus sublaevis* (Hymenoptera: Formicidae). *Entomol. Gener.* 11:125–137.

Corresponding Editor: J. Seger