deuterium ratio in a sample 24 years old. For samples many half-lives old, the fractional error in the age is small even if rates of production or deposition of the isotopes.

Although cyclotrons are expensive to build, their operating costs are relatively low. If several samples are dated per hour the cost per date may not be substantially higher than it is today for decay dating. There are already more than 50 cyclotrons in operation which have the potential to do radioisotope dating, and their application to important problems of dating and trace element analysis should prove very fruitful.

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Local Mate Competition and Parental Investment in Social Insects

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Kinship theory (*1*) and sex ratio theory (*2*) were used by Trivers and Hare (*3*) to predict the relative investments in reproductive males and females by various eusocial insects and their nonsocial relatives. They suggested that in eusocial species with haplodiploid sex determination, queens gain by a 1:1 (male: female) investment in reproductive offspring, while their sterile worker offspring gain by a 1:3 investment among reproductive siblings, and that (*3*, p. 250) ". . . a measurement of the ratio of investment is a measure of the relative power of the two parties . . ." From their measurements of investment patterns in various species, Trivers and Hare concluded that in single-queen (monogynous) ants, the investment pattern is "near 1:3," while in nonsocial bees and wasps, which lack sterile castes, the investment pattern "approximates 1:1." Their interpretation is that the interests of the workers are more nearly realized than are those of the queen. In support of this interpretation they also cite investment ratios from multiple-queen (polygynous) ants, slave-making ants, termites, and bumblebees. Their conclusions have been multiply cited (*4*).

We argue here that, on the contrary, (i) Trivers and Hare's predictions of 1:1 and 1:3 investment patterns are inappropriate for the insect groups they analyzed, (ii) they did not demonstrate such patterns, (iii) their data are not explained by their hypothesis, and (iv) their data for the most part conform to an alternative hypothesis, that is, Hamilton's (*5*) hypothesis of "local mate competition" (mating rivalry among close relatives), which they mention (*3*, footnotes 9, 53, and 96 and p. 251) but do not apply.

Trivers and Hare's predictions depend upon (i) monogamy or effective monogamy among laying females, (ii) inability of workers to lay eggs, and (iii) outbreeding without effects from local mate competition (LMC) (*6*). However, multiple matings by females, worker oviposition, and local mate competition may actually be typical of haplodiploid insects rather than rare or absent among them, as Trivers and Hare may have assumed in drawing their conclusions (*3*, p. 261).

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Multiple Matings by Queens

Multiple matings by queens of eusocial Hymenoptera have frequently been reported (*7–10*); Wilson, for example, cites multiple matings for eight species of eusocial Hymenoptera but only two instances in which it is believed that single mating by queens is the rule. (Obviously, multiple mating is easier to document than single mating.)

Multiple insemination has two effects. First, it reduces the predicted female bias in preferred investment ratios among sterile workers. In species with haplodiploid sex determination, full sisters share an average of 3/4 of their genes identical by (immediate) descent (IBD). If a female mates with *n* different males and uses their sperm randomly, her daughters average (1/4 + 1/2*n*) alike (*1*). On the basis of Trivers and Hare's approach, the worker offspring of a female who mates twice and uses the sperm of the males randomly maximize their reproduction by an investment pattern of 1:2. This is because they share, on the average, only twice as many genes IBD with their sisters as with their brothers, rather than three times as many, as under monogamy. If the sperm of the different mates of one female tend to clump separately, as is likely (*11*), the workers' interests are more female-biased than if the sperm do not clump; but with multiple matings by their queen the workers' interests would reach Trivers and Hare's 1:3 prediction only if workers were never required to tend half siblings, a condition we consider unlikely (*12*).

Multiple matings do not alter the relationship of a female's worker offspring to their brothers, which remains at 1/4. The mother is, in all cases, 1/2 like each offspring (in genes IBD), male or female.

Multiple mating by queens also produces mixed broods of full siblings and half siblings. This creates a potential for the expression of differences in reproductive interests within the brood. Only by using the sperm from one male (that is, being effectively monogamous) might a queen avoid reproductive differences of interest among her worker offspring. Even an abrupt transition from use of one male's sperm to use of another male's sperm would not cause quite the same effect as monogamy, since some workers would be required to tend less closely related siblings during the period of transition between the sperm of different males.

It would be interesting to know how changes in sperm use correlate with swarming in insects like honeybees, in which the old queen departs to a new nest site, leaving some of her worker offspring behind with a new queen, their sister. This new queen could be either a full sibling or a half sibling of the workers rearing her, depending on sperm use. Since half sisters average only 1/4 alike, workers with a half sister as their queen tend juveniles averaging only 1/8 like them. Also, workers tending the offspring of a full sister or a half sister share their sister queen's interest in the ratio of investment in the sexes, since workers are equally related to their nieces and nephews.

Worker Oviposition

In some eusocial insects, workers are known to lay eggs. Wilson notes in (*10*, p. 333) that "Worker oviposition is widespread in the ants, from the primitive Myrmeciinae to the advanced Myrmicinae, Dolichoderinae, and Formicinae. . . . By feeding queens of *Myrmica* P^{32} and thus labeling their eggs, Brian (1968) was able to show that the workers lay in the presence of the queens and that most males are derived from worker-laid eggs" (*13*). Sex ratio data are sensitive to variations in the number of unfertilized laying females. There are several ways in which unfertilized females may become egg-layers in haplodiploid species: as workers in slave-making species which take over colonies, as microgynes or secondary reproductives in their mother's nest, as mated queens who have used all of their sperm, as unfertilized queens, as laying workers in a nest with a normal queen, or as laying workers when the queen is lost. One way to correct for this factor would be to eliminate from consideration all nests that produced only males; another would be to assume that, if nests that produce all males are included, then, in terms of Trivers and Hare's hypothesis, unless proportions of unfertilized laying individuals have been consistent enough for fertilized queens to adjust sex ratios in their broods accordingly, the data are male-biased.

When some workers lay eggs, the workers do not collectively share the same genetic interests, so that complex questions are raised about how individual, short-lived workers could function to achieve their "preferred" investment pattern in the sex ratio of reproductives produced by the colony as a whole. This problem is particularly evident in ants, in which a worker may live a maximum of 1 to 3 years while the queen lives for several times as long (*10*, pp. 426–430) and the colony, moreover, often produces only males while it is small, and only females (or both sexes) later (*3*, footnote 44, p. 262). Many workers in such colonies only interact with one sex of reproductives and, indeed, many workers in social insects probably fail to interact with any reproductives at all (for example, workers in the *Formica rufa* group; *10*, p. 163). Any analogy with the somatic cells of a metazoan producing a sex ratio in their gametes breaks down when eusocial workers in a colony do not have identical genetic interests, as in cases when workers lay eggs or when queens mate with more than one male (*14*).

Interpreting Trivers and Hare's discussion of this problem is difficult since they assume (*3*, figure 1 caption) that their "p" represents the ". . . fraction of male-producing eggs laid by the queen (p), where the remainder are laid by a *single* laying worker" (emphasis added). What Trivers and Hare envision as the "preferred" sex ratios of the three "interested parties" (that is, the queen, the laying workers, and the nonlaying workers), if most or all workers have the potentiality of laying eggs, is unclear, in spite of their explanation (*3*, note 19, p. 261). For example, if at least some workers are able to produce sons, the problem becomes one of understanding how a laying worker would apportion her male-directed beneficence among brothers (produced by her mother and, on average, 1/4 like her in genes IBD), nephews, 1/8 to 1/4 like her, and her own sons, 1/2 like her.

Trivers and Hare appear to avoid specifying these preferences for each species by assuming that few, if any, laying workers exist. They state (*3*, p. 254), "In some ants, such as *Atta* and *Solenopsis* . . . all males appear to be produced by the queen, and in other monogynous ants (single queen per nest) laying workers appear to be a relatively uncommon source of males (compared to eusocial bees and wasps) . . . so that the ratio of investment in ants should often approach 1:3." In view of the information presented above, the uncommonness of oviposition by females lacking sperm and thus the appropriateness of this prediction is open to question.

Local Mate Competition

Local mate competition refers to mating rivalry among genetic relatives. Its effects may derive from such competition not only between siblings or between parent and offspring, but also among more distant relatives, for mates that may be either related or unrelated to those competing for them. In one extreme, if all of a parent's daughters are fertilized only by their brothers, parents will benefit by producing only enough males to fully inseminate all their daughters. For "insects having usual sibmating," Hamilton (*5*) cites sex ratios within broods which vary from 1:2 to 1:46; males in such species, moreover, are usually smaller than females.

As evidenced by likelihood of sibling or parent-offspring matings, LMC may be widespread among both social and nonsocial haplodiploid insects (*15–17*) as, apparently, are the predicted female-biased investment patterns (*18–20*). Trivers and Hare's data from monogynous ants, for example range from 1:1.57 to 1:8.88 with a geometric mean investment ratio of 1:3.45 (the arithmetic mean is 1:3.94). For "five of the six species with the best data" (*3*, p. 254) the range is 2.99 to 4.14, with a geometric mean of 3.36 (arithmetic mean, 3.39), essentially the entire range of variation thus falling outside the predictions of their hypothesis, even if the queens involved were monogamous and there were no unfertilized laying females. At least one ant species known to mate within the family (*21*) appears to produce investment patterns like those found by Trivers and Hare. We have been able to find satisfactory information regarding the likelihood of intrafamilial mating rivalry for only one ant species listed by them (*3*, table 2, p. 254), *Myrmica schencki*. In this species, sibling matings are appropriately suspected (*17, 18*) and the investment ratio is 6.45 (*3*, table 2). Since a hypothesis (other than inadequate data) exists to explain investment ratios greater than 1:3, findings in this range do not support Trivers and Hare's argument.

We examined Trivers and Hare's list of nonsocial Hymenoptera (*3*, table 4) for possible variations in effects from LMC. We considered that species in which individuals nest solitarily and siblings mature together are most likely to undergo such effects, thus to have female-biased investment patterns. By contrast group-nesting species (or solitary nesters which deposit their eggs singly) should be less affected by LMC and thus should have investment patterns nearer 1 : 1. Four species in the first category [13th, 14th, 16th, and 17th in the list in (*3*, table 4)] averaged an investment pattern of 1:1.81; in the second category (that is, all the rest with complete data) 12 species averaged 1:0.99. The direction of the difference is thus as predicted, and the two distributions differ significantly ($P < .03$, *t*-test).

Because they are the offspring of single reproductives, most eusocial insect colonies are like nonsocial solitary-nesting species in which siblings mature together. In other words, according to our classification of nonsocial species, eusocial insects are likely to have female-biased investment patterns as a result of LMC (see also *18–20*). If the 12 nonsocial species least likely to be affected by LMC are removed from Trivers and Hare's nonsocial list, the remaining nonsocial species have an average investment pattern almost identical to that of all of their social species combined.

We infer that effects from LMC may be rather common and that these effects are most obvious among the Hymenoptera, whose haplodiploid system of sex determination makes them particularly capable of reducing deleterious consequences by sex ratio adjustments. Haplodiploidy also occurs in beetles and mites with "usual sibmating" (*5*). Together with Borgia (*22*) we hypothesize that haplodiploidy may actually spread and be maintained as a consequence of LMC.

Nonsocial, Trapnested Bees and Wasps

Trivers and Hare suggest that ratios of investment in nonsocial trapnested bees and wasps support their hypothesis that female-biased investment ratios in eusocial species result from worker domination. They state (*3*, p. 258), "Although there is considerable scatter, the species are closer to a 1:1 ratio of investment than to a 1:3." We do not believe that ratios of investment in nonsocial species trapnested by Krombein (*23*) can legitimately be used in this context for two reasons. First, patterns reported by Krombein plainly depended on the manner of trapnesting. He put out nests of various diameters, and sex ratios varied dramatically with nest bore: the larger the bore, the higher the percentage of females—with the smallest cavities sometimes having all males, the largest all females. Overall investment patterns obviously depended on the proportions of nests of each size that Krombein put out, and the significance of the size range he used would vary among species of differing body sizes. Thus, we disagree with Trivers and Hare's conclusion (*3*, p. 257) that no systematic bias is expected.

Second, Krombein usually bundled trapnests together, most often in groups of six. He thereby created a situation resembling colony breeding, in which outbreeding is likely. Should trapnested species be able to adjust sex ratios accordingly, 1:1 investments in the situation created by Krombein would not properly describe the investments of this group of Hymenoptera. D. P. Cowan (unpublished data) has discovered that, when females of *Euodynerus foraminatus* (Vespidae : Eumeninae) are trapnested in groups, they bias the sex ratios of their broods toward males more than when trapnested singly; data for this species were obtained by Krombein and used by Trivers and Hare (*3*, table 5). The possibility that trapnesting Hymenoptera may generally be able to vary the ratios of investment according to the likelihood of LMC indicates that trapnesting bee and wasp data currently available cannot be used to test the outcome of parent-offspring conflict.

Polygynous Ants

Trivers and Hare suggested that polygynous ant colonies are collections of the daughters or granddaughters of a single queen, living in association with their queen mother. Even though this may not always be the case (*24*), they predicted male-biased investment patterns (*3*, p. 256) among polygynous species because (*3*, p. 255) "If a reproductive daughter is permitted to settle within or near the maternal nest when unrelated females would not be so permitted, then one must assume that the daughter thereby inflicts a cost on her mother . . . This cost can be treated as a component of investment and raises the relative cost of a reproductive female." This argument is apparently derived from a consideration of *Acacia* ants (*25*), in which multiple colonies are founded on one tree by apparently unrelated queens, with each queen then behaving so as to replace, if possible, the other queens with her daughters. It may be more appropriate to view *Acacia* ant aggregations as groups of monogynous colonies rather than as a polygynous colony. In addition, it is probably inappropriate to view polygynous ants generally as parallels to the peculiar *Acacia* ant situation, in which the small colonies inhabit different hollow thorns. A queen of a subterranean species, for example, who allows her daughter to remain in her nest as an incipient queen, may be preparing a replacement for herself; further, a pair of sister queens in one nest is not appropriate to Trivers and Hare's interpretation, in spite of their footnote 61 (*3*, p. 262).

Trivers and Hare cite investment ratios from five species in the genus *Myrmica* as support for their polygynous ant hypothesis. In terms of decreasing female-bias in investment ratios, the five *Myrmica* species are ordered (*3*, figure 4C and p. 256): *M. schencki, M. sulcinodis, M. ruginodis, M. sabuleti*, and *M. rubra*. Trivers and Hare state (p. 256) that "The ratios of investment for these species are ordered exactly according to the parameters we have outlined (see Fig. 4C)."

We suggest that this ordering might be the result of several other factors, not taken into account by Trivers and Hare. For example, *M. schencki* probably mates within the family (*17, 18*), and it has the most female-biased investment ratio in the genus (1:6.45). Since unfertilized females can only produce males in haplodiploid species, oviposition by varying numbers of such females will tend to bias population-wide investment ratios toward males. Thus, it is important to know what proportions of nests in the polygynous sample produced only males, a factor that Trivers and Hare do not take into account despite their footnote 44 (*3*, p. 262). From data they used (*3*, tables 2 and 3), in *M. sulcinodis* 13 of 21 colonies produced only males while 1 produced only females (*26*), in *M. sabuleti* 25 of 35 colonies produced only males and none produced only females (*27*), and in *M. rubra* 9 of 11 colonies produced only males while none produced only females (*27*). Similar data for *M. ruginodis* are unpublished (*3*, footnote 66, p. 262).

Myrmica rubra, the species with the least female-biased investment ratio in the polygynous ant series, deserves further consideration. For this species, Brian (*27*, p. 50) noted that the colonies he studied were ". . . subject to disturbance by the trampling of cattle . . . causing colonies to be . . . difficult to retain . . . for study for more than a few years." If *M. rubra* tends to produce only males when colonies are young (see above), this, and not the number of queens, may well explain the low investment ratio (4:1) recorded for this species by Trivers and Hare and therefore its ranking in their polygynous ant series. *M. rubra* is also one of the species for which there is evidence of population-wide mate competition (*10*, p. 38).

Slave-Making Ants

Trivers and Hare believe that their analysis of slave-making ants supports their hypothesis because they found investments showing "a highly significant deviation ($P < .001$) toward a 1:1 ratio" (*3*, p. 255) (apparently meaning significantly less than 1:3). Slave workers, they argue, have lost the ability to produce 1:3 investments in the nests of queens of slave-making species, who have evolved to extract from the slaves their preferred 1:1 investment. Slave-making workers, they suppose, must gain more by bringing to their nests slaves that will help their mothers produce a 1:1 investment than by remaining as workers themselves and producing their "preferred" 1:3 ratio; Trivers and Hare do not identify the nature of this gain. Their data on slave-makers are, like those on other species, averages from many colonies (in this case, 58 for *Harpagoxenus sublaevis* and 96 for *Leptothorax duloticus*) and standard deviations in sex ratios are not given. This is important because Wilson (*10*, p. 370) notes that in *H. sublaevis* "morphologically complete queens are relatively scarce," and that in a closely related species, *H. americana*, 16 of 32 colonies examined were populated exclusively by slave-making workers and their slaves. Worker queens are likely to be unfertilized, therefore able to produce only males, potentially creating male biases in samples of investment ratios which are unrelated to Trivers and Hare's explanation.

Regarding the likelihood of LMC among slave-makers, Wilson notes (*10*, p. 324) that "The exact extent of true brother-sister mating is unknown . . . in the only test of this kind of which I am aware, Wesson (1939) did find that the queens and males of the dulotic ant *Harpagoxenus americanus* prefer to mate with unrelated individuals." Wesson (*28*) also reported a sex ratio of 1.9:1 for 19 colonies of this species, including 11 colonies with laying workers. *H. sublaevis*, a closely related slave-maker, was reported (*3*, table 2) to have a sex ratio of 1.38:1 and the second least female-biased investment ratio (1.25) listed. Wilson also notes (*10*, p. 370) that "The rather fragmentary information available suggests that *L. duloticus* is basically similar to *Harpagoxenus* in its biology." The other slave-maker listed by Trivers and Hare, *L. duloticus*, invests the least in females of any formicid (0.87). At least these facts indicate that insufficient information was provided. At most, they suggest that the apparent bias toward 1:1 investments by the two slave-making species is due to different causes from those which Trivers and Hare postulate (that is, unfertilized queens or population-wide mate competition).

Trivers and Hare separate their data on slave-making ants from those on ants that are not slave-making (*3*, figure 4B), and those on polygynous ants from those on monogynous ants (*3*, figures 4C and 4A). The basis for their conclusions about formicid investment ratios (and those of all other social and nonsocial groups as well) are their tests of whether or not these separated sets of data resemble 1:1 or 1:3 investment slopes (but see below). In no case do they test whether or not these sets of data actually differ from one another. In contrast to this treatment, they consolidate, respectively, all data for termites (*3*, figure 5), all data for trapnested nonsocial Hymenoptera (*3*, figures 7 and 8), and all data for naturally nesting nonsocial Hymenoptera (*3*, figure 6). It is not clear to us, however, that the data in (*3*, figures 5–8) are any more unitary than are those in (*3*, figures 4A–C), if those in the latter case are appropriately combined (*3*, figures 4, A and B, and 4, A and C).

Termites

The termites may represent Trivers and Hare's most important comparison, since Isoptera do not have haplodiploid sex determination. This means that, according to Trivers and Hare's approach, termite investment ratios should be 1:1. Unfortunately, the data are scant, consisting of figures for nine species from two genera (*3*, figure 5). Trivers and Hare combine these data and obtain a geometric mean ratio of 1:1.62 (arithmetic mean, 1:1.91). They describe this (*3*, p. 256) as not significantly different from the slave-making ant data but different from the monogynous ant data.

We believe that a closer look at these data is warranted for two reasons. First, the two sets of data for different genera average, respectively, just more than 1:1 and 1:2.5, values not remarkably different from those reported for various social and nonsocial Hymenoptera. The two sets of data, moreover, differ from one another ($P < .05$; *t*-test). Second, if we use the same kind of test that Trivers and Hare used, the combined termite data are significantly biased toward 1:3 (that is, are different from 1:1). The implication is that the same factor or factors may influence investment ratios in both the Isoptera and the Hymenoptera.

Conceivably, the differences between termite genera and the wide scatter in all investment ratio data may be due to variations in LMC. Since termite eusociality has been attributed to inbreeding (*20, 29*), it may not be unreasonable to assume that some species undergo LMC. If they do, and if female-biased investment ratios reflect this fact, we still do not know how any diploid species accomplishes such adjustment. Several possibilities are apparent, such as sex-differential destruction of gametes or juveniles, or sex-differential adjustments of investment in individual offspring. Termites, however, possess a means of adjusting investment in the sexes that may be unique and may have been important in their evolving eusociality. Unlike Hymenoptera, the nonreproductive castes of termites include both sexes, and, as with hymenopteran females, whether or not a given juvenile of either sex will be reproductive or nonreproductive is determined only when the juvenile is already partly grown—in termites it may already be an effective worker. This means that a termite colony has a continuing reservoir of nonreproductive juveniles of both sexes from which numbers and proportions of reproductives that are appropriate to any given circumstance be drawn. Apparently, no other species share this remarkable attribute.

Problems with Interpreting Data

Selection of specimens. All investment ratio data presented by Trivers and Hare may be consistently biased away from 1:1 because of the method of gathering them. They state (*3*, footnote 46, p. 262) that "More than half of the specimens weighed were sent to us by other scientists in response to our request for five specimens of each sex that were typical by size." If, as may be likely, cooperating scientists tended to pick males and females which did not resemble each other (that is, were "typically" male or female), and if females weigh more than males do, a consistent bias might well be introduced.

Grouping of data. Wide variation in the original sex ratio data on which Trivers and Hare's article is based make the consistent use of grouped data unacceptable. As an example of the original data from which the authors draw their conclusions, consider their use of investment patterns of *Prenolepis imparis* (*3*, lower dot, figure 4; also, table 2). Their inverse investment ratio is based on sex ratios of 11 colonies of this species. In the article from which these data are drawn (*30*), information is reported for 20 colonies, only 12 of which possessed reproductives (a total of 2009). Trivers and Hare used 11 of the 12. Of the 12 colonies, one had males only (162), one had females only (15), one had a strongly female-biased ratio (9 males:26 females), and nine had male-biased ratios, varying from 1.9:1 to 21:1. The sex ratio of six colonies dug up at Tiffin, Ohio, was 5.8:1, and that of the six from St. Charles, Missouri, was 8.7:1. These data were apparently averaged to produce a sex ratio of 8.36:1 (*3*, table 2).

Intraspecific variation. Sample sizes of 1 to 66 were used in a single table (*3*, table 2) for weight-ratio measurements; what determined each sample size is not indicated. For most weight data, standard deviations are not given and are needed. The need for such is illustrated by data from the genus *Atta*. For *Atta sexdens* females, the standard deviation is almost 40 percent of the mean weight of the ten females sampled; nonetheless, the weight ratio of *A. laevigata* is based on a sample of six, five of which are males. For *Solenopsis invicta*, the sex ratio is based on a sample of 200,491, while the weight ratio sample size was 14 (again, no standard deviation is given for the weight of either sex). In addition, sample sizes are sometimes omitted from tables (for example, *3*, table 3) as are weight ratios and inverse investment ratios (for example, table 4).

Inappropriateness of regression analyses. Trivers and Hare presented and analyzed their data with regressions. Unless a systematic deviation in variance is corrected for, however, their linear regression analyses are inappropriate. Because they computed sex ratios by dividing the number of males by the number of females, their figure 4 and the others are asymmetric: when males outnumber females, the points are widely spread out; but when females outnumber males, the points are clustered between 1 and 0. This has two consequences. First, as the proportion of males increases, the total possible variance around any predicted line (1:1 or 1:3) also increases, thus violating an assumption of linear regression analysis; where "p" is the proportion of males, "q" is the proportion of females, and "n" is the sample size, the variance of the quantity "males/females" is nonhomogeneously distributed as (p/nq^3) (*31*). Second, this means that even investment ratios as far different from the hypothesized 1:3 ratio as 1:7.9 and 1:8.88 are caused, in their graphs, to appear to support the 1:3 hypothesis.

Trivers and Hare draw their conclusions exclusively from testing such questions as whether or not a set of investment ratios "approximates 1:1" (*3*, p. 258) or is "biased toward females" (*3*, p. 258) (or males, *3*, p. 259); whether or not the results were "significantly different from a 1:3 slope" (*3*, p. 254); whether they "tend to scatter around the 1:3 line of investment instead of the 1:1" (*3*, p. 254); or whether or not termite investment ratios (*3*, p. 256) or those of solitary bees and wasps (*3*, p. 257) were "significantly closer to 1:1 than are the ratios for monogynous ants . . . ." The answers to such questions could be conclusive if the postulated investments of 1:1 and 1:3 were appropriate, if the hypotheses advanced were the only ones that could account for the data, and if regression analyses were appropriate. Since none of these preconditions is met, a reanalysis of their data seems warranted. Using principal components analysis (*32*) on total investment in females as a function of total investment in males, we estimated 95 percent confidence intervals for investment ratios. This treatment revealed that only monogynous ants' investments and those of all nonsocial, nontrapnested bees and wasps combined (but see above) differ. If the 95 percent confidence intervals are used, investment ratios of monogynous ants, termites, bumblebees, and nonsocial trapnested bees and wasps all overlap.

That almost every set of data presented by Trivers and Hare has an overall female bias implies some cause other than that, under haplodiploidy, worker interests are being realized. The wide scatter in their data is also prejudicial to their hypothesis in view of the apparent precision of their procedure of weighing adults in species in which juveniles are tended or provisioned to adulthood (that is, weighing them at termination of parental care) (*2*). Both the variability in their data and female biases beyond their predictions, on the other hand, support a hypothesis of varying amounts of LMC.

Quantifying Effects of Local Mate Competition

Local mate competition, as Hamilton (*5*) used the term, refers to competition among genetic relatives for mates. Its effects are to devalue the competing individuals as contributions to the inclusive fitness of other relatives, including parents. These effects may be sexually symmetrical or asymmetrical. At least three means exist by which they may be alleviated. In most organisms, dispersal of potentially competing relatives may reduce or eliminate effects of LMC. Sexually asymmetrical effects may be alleviated by parents adjusting investments in the two sexes of their offspring. Among humans, marriage rules may be employed by collectives of interested, powerful relatives in fashions which reduce devaluations of kin as a result of LMC.

Quantification of the effects of LMC obviously is complex and must proceed along several different lines. Here we suggest only a few (see also *5*). In most species, sexual competition is more severe among males than among females, with the possible outcome that brothers will devalue the parental effort invested in them when they compete for the same mate (or mates). In one kind of extreme, if a female produced in her brood two sons that competed solely with each other for every mate secured by either of them, the two sons would be of no more value to her than a single son. If they competed solely with each other for half the mates secured by both of them, they would be worth 3/4 as much as two sons who never competed.

When brothers simultaneously compete for a female also being competed for by nonsibling males, whether or not they are devalued for their participation depends upon their effect on the likelihood that one of their mother's sons will secure the copulation; if their simultaneous presence doubles the chances, they are not devalued. If they cooperate in some fashion so as to more than double the chances of one of their mother's sons being successful, their individual values to their mother will be enhanced.

It is commonly assumed that Fisher's explanation of sex ratio selection (*2*) always holds in outbreeding populations, only failing when inbreeding occurs. But consanguineous matings can occur without effects from LMC, and vice versa. One reason for the confusion of inbreeding with LMC may be that when matings are frequent between siblings, brothers are likely to compete with each other for copulations with their sisters. If all matings are between siblings and if males do not invest parentally, a mother will partition her investment optimally between the sexes when she produces the minimum number of males necessary to inseminate her daughters fully and when the investment in these males is barely sufficient to enable them to accomplish this insemination. Because dispersal tends to reduce the likelihood that brothers will compete for mates, species in which premating dispersal occurs are not usually thought to be affected by LMC. This is not necessarily true. For example, brother-brother competition may not be unlikely in species among which males gather at crowded leks within which most females in the vicinity are inseminated, as in honeybees (*33*).

We emphasize that even competition for mates between rather distant relatives, such as cousins, may be deleterious to near and distant relatives of both. The question, for any species, seems to be whether or not cost-effective means are available for reducing these deleterious consequences.

Conclusions

The idea of testing the power of individuals (for example, a parent) against the collective power of groups of individuals (for example, a brood of similarly related offspring), as Trivers and Hare have attempted to do, is of broad significance in understanding the levels in the hierarchy of life at which natural selection has most consistently been effective. Current theory in evolutionary genetics seems, temporarily at least, to have taken the direction of supposing that selection is effective essentially only at the genic level, despite arguments to the contrary (*34*), the evident integrity of the genome, even in sexual organisms, and the widespread opinion that "the primary focus of evolution by natural selection is the individual" (*35*, p. 7).

We believe that because Trivers and Hare did not consider any hypotheses other than their own to explain the ratios of investment in the two sexes by social and nonsocial insects, and because of the manner in which they gathered and interpreted data, the significance of their arguments is diminished. Their data may possibly reflect the existence of both local mate competition and parent-offspring conflict. However, while ample evidence implicates the former hypothesis, in light of the reservations we outline, there is yet little or none to support the latter. The conclusion, therefore, that in modern eusocial Hymenoptera the workers' interests are being realized contrary to their queen's interest, is at least premature (*36*).

Summary

Efforts to develop formulas for contrasting genetic interests of workers and queens in social Hymenoptera are complicated by many factors, including multiple matings by queens, oviposition by unmated females, and mating rivalry among genetic relatives (Hamilton's "local mate competition"). Because of haplodiploid sex determination in Hymenoptera, when such influences are absent, queens benefit from 1:1 sex ratios of investment (male : female) in reproductive offspring, workers from 1:3 ratios among reproductive siblings. Reports of variable ratios, including many well above 1:3, and female biases in nonsocial Hymenoptera and diplodiploid termites, implicate local mate competition and raises questions about previous interpretations that workers have their way.

References and Notes

1. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
2. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).
3. R. L. Trivers and H. Hare, *Science* **191**, 249 (1976).
4. E. O. Wilson, *Sociobiology* (Harvard Univ. Press, Cambridge, Mass. 1975); in *Insects, Science, and Society*, D. Pimentel, Ed. (Academic Press, New York, 1975), pp. 25–31; J. Krebs and R. M. May, *Nature (London)* **260**, 9 (1976); R. Dawkins, *The Selfish Gene* (Oxford Univ. Press, Oxford, 1976); and others.
5. W. D. Hamilton, *Science* **156**, 477 (1967).
6. Hamilton has noted that "Fisher's principle" of the sex ratio (*5*, p. 477) ". . . is restricted to the actually unusual case of population-wide competition for mates." Trivers and Hare imply, by contrast, that population-wide competition is usual by stating (*3*, p. 251): "Values more female biased than 1 : 3 are only expected where extreme patterns of dispersal occur . . ." Trivers and Hare also state (in our opinion, erroneously) (*3*, p. 251) "The important point regarding ratios of investment is that such ratios are never expected to be more female biased than 1 : 2 on the effects of inbreeding alone. All values between 1 : 2 and 1 : 3 must reflect worker performances [*sic* : preferences?] for sisters over brothers."
7. For examples, see H. St. J. K. Donisthorpe, *British Ants: Their Life-History and Classification* (Routledge, London, ed. 2, 1927), p. 115.
8. W. C. Roberts, *Glean. Bee Cult.* **72**, 255 (1944).
9. F. Ruttner, *Bee World* **37**, 3 (1956); S. Tabor III, *J. Econ. Entomol.* **47**, 995 (1954); G. A. Parker, *Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970); F. Ruttner, J. Woyke, N. Koeniger, *J. Apic. Res.* **12**, 21 (1973); J. Woyke, *ibid.* **14**, 153 (1975).
10. E. O. Wilson, *The Insect Societies* (Belknap, Cambridge, Mass., 1971), p. 330 and references therein.
11. S. Taber III [*J. Econ. Entomol.* **48**, 522, (1955)] found that proportions of offspring from multiply mated queen honeybees sampled weekly did not form a homogeneous binomial series. Although his data suggest that *Apis mellifera* sperm clump to some extent, it is also true that the progeny of at least two mating types appeared in every group of workers he sampled; Roberts (*8*) obtained similar results in a parallel experiment. Further, Taber's figure 1 (p. 525) suggests that the process of "switching" from predominant use of one type of sperm to predominant use of another lasts 3 to 5 weeks. Unless workers always discriminate between their half siblings and their full siblings, Taber's report suggests that they are consistently required to tend both.
12. The only possibility of the occurrence of this situation appears to be in a hypothetical species in which a polyandrous queen herself tends her first offspring by a second male during the transition between use of the sperm of different males.
13. See also M. V. Brian, *Insectes Soc.* 16, 249 (1969). Wilson's 1968 reference to Brian is "Regulation of Sexual Production in an Ant Society," *Colloques Internationaux du Centre National de la Recherche Scientifique, Paris*, No. 173, pp. 61–76 (1967).
14. See also M. J. West-Eberhard, *Q. Rev. Biol.* **50**, 1 (1976).
15. Sibling matings are appropriately suspected in the various ant species with wingless males and with wingless or partially winged microgyne females, as well as in species in which mating occurs in the nest. For examples, see Donisthorpe (*7*, pp. 78, 86, 102, 107, 123, 129); H. St. J. K. Donisthorpe, *The Guests of British Ants: Their Habits and Life-Histories* (Routledge, London, 1927), p. 82. Although P. B. Kannowski [*Insectes Soc.* **6**, 115 (1959)] concludes that "intranidal mating is an exceptional process, not a normal one," he reports numerous apparent instances among bog ants in Michigan; see also L. Passera, *ibid.* **15**, 327 (1968); P. B. Kannowski, *Symp. Genet. Biol. Ital.* **12**, 74 (1963); E. O. Wilson (*10*).
16. J. H. Sudd, *An Introduction to the Behavior of Ants* (St. Martin's, New York, 1967).
17. M. Talbot, *Am. Midl. Nat.* **34**, 504 (1945).
18. See Trivers and Hare's data (*3*). In species known to mate in the nest, moreover, sex ratios are female-biased. Such sex ratio skews probably indicate female-biased investment ratios since, according to Trivers and Hare, female ants are from 1.73 to 25.4 times heavier than conspecific males. Thus, for *Monomorium pharaonis*, Sudd in (*16*, p. 140) states that "Many other crevice-nesters, including *Monomorium pharaonis*, also mate in the nest." See also M. A. Bellevoye, *Insect Life* **2**, 230 (1890). In describing the mating flight activities of *Myrmica schencki*, Talbot in

(*17*) states that "winged ants stayed close to the nests and never flew in numbers. . . ," and she concludes that ". . . contrary to the procedure for *Lasius* and *Prenolepis*" (in which she had reported conspicuous mating flights) "*Myrmica* produced more females than males."

19. A female-biased sex ratio has been reported for *M. pharaonis* (range between nests is 1 : 1.1 to 1 : 5.3) by A. D. Peacock, *Entomol. Mon. Mag.* **87**, 185 (1951).
20. W. D. Hamilton, *Annu. Rev. Ecol. Syst.* **3**, 204 (footnote) (1972).
21. We attempted to compute the investment ratio for *Monomorium pharaonis*, a species in which brothers likely compete with each other for mates (*10*, pp. 40–41; see also *18, 19*). We used a mean sex ratio of 1 : 2.19 (*19*). We did not have specimens to weigh, nor could we find published weights for reproductives of this species. Therefore, we used the body length ratio given by D. W. Hall and I. C. Smith [*Entomol. Mon. Mag.* **87**, 217 (1951)] as an indicator of the difference in size between males and females; this ratio is 1 : 1.39. Taken together, these data yielding a probable inverse investment ratio near 4.43 (5.84, using body lengths cubed), figures well within the range of many species listed by Trivers and Hare in Table 2 (*3*). Because *Monomorium pharaonis* founds nests by swarming (*10*), the actual investment in females is somewhat higher (if one regards workers accompanying a new queen as part of the investment in her).
22. G. Borgia, in preparation. M. J. West Eberhard has pointed out to us that LMC may have promoted evolution of eusociality in haplodiploid species because female biases within broods would increase the average relationship between an incipient worker and her siblings. Similarly, LMC may reduce numbers of laying workers by devaluing males.
23. K. V. Krombein, *Trap-nesting Wasps and Bees: Life Histories, Nests and Associates* (Smithsonian Institution Press, Washington, D.C., 1967).
24. Wilson (*10*, p. 324) states that "We also understand very little of the adaptive significance of polygyny, and, more importantly, the degree of kinship of queens that live together in polygynous colonies. A definitive judgment cannot be made until more data are available on these subjects."
25. See *3*, footnote 60, p. 262; D. H. Janzen, *J. Anim. Ecol.* **42**, 727 (1973); *10*, pp. 51–55.
26. G. W. Elmes, *Oecologia (Berlin)* **15**, 337 (1974).
27. M. V. Brian, *Ekol. Pol.* **20**, 43 (1972).
28. L. G. Wesson, Jr., *Trans. Am. Entomol. Soc. (Philadelphia)* **65**, 97 (1939).
29. N. Lin and C. D. Michener, *Q. Rev. Biol.* **47**, 131 (1972).
30. M. Talbot, *Ecology* **24**, 31 (1943).
31. E. D. Rothman, personal communication.
32. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 526–532. In our analysis, the ordinate (I_f) = number of females × mean female weight, abscissa (I_m) = number of males × mean male weight; investment ratios are I_f/I_m. Since a logarithmic transformation of both I_f and I_m is necessary to produce normality, I_f/I_m is the antilogarithm of the intercept for the first principal component line, with the origin at ($\bar{I}_m$, $\bar{I}_m$). Confidence intervals are found from the intersections of the ordinate with the 95 percent confidence elipse for the bivariate mean.
33. C. Zmarlicki and R. A. Morse, *J. Apic. Res.* **2**, 64 (1963); G. E. Strang, *J. Econ. Entomol.* **63**, 641 (1970).
34. I. Franklin and R. C. Lewontin, *Genetics* **65**, 707 (1970); E. Mayr, *Biol. Zentralbl.* **94**, 377 (1975).
35. R. C. Lewontin, *Annu. Rev. Ecol. Syst.* **1**, 1 (1970).
36. We thank David P. Cowan for permission to use unpublished information and Robert K. Colwell for generous assistance with statistical interpretations. We also thank Gerald Borgia, Kent L. Fiala, R. Glenn Ford, Katharine M. Noonan, George F. Oster, and Edward D. Rothman for assistance. The Miller Foundation at the University of California, Berkeley, supported P.W.S.

The Elusive Rise in the American Birthrate

Although fertility is now very low, a substantial increase in the near future appears unlikely.

Campbell Gibson

In an article published in *Science* in 1975 (*1*), Sklar and Berkov concluded "that the American birth rate may have bottomed out and that the country is likely to see a rise in reproduction." Their analysis was based on fertility trends in California (through 1974) and in four other states (through 1973) where legal abortion is also readily available, and on selected national data on marriage (through 1974), fertility (through 1973), and family-size expectations (through 1974).

Fertility in the United States continued to decline through 1976 (Table 1), although at a lower rate after 1973 than in the three preceding years (*2, 3*). In view of the continued decline, the purpose of this article is to review Sklar and Berkov's interpretations and to examine data pertinent to more recent fertility trends (*4*). More specifically, this article addresses three issues: (i) the implications of survey data about the family-size expectations of young wives for fertility trends during the next few years; (ii) the usefulness of fertility trends in California as an indicator of national fertility trends; (iii) the possible role of economic factors in determining recent trends in fertility.

Family-Size Expectations and Fertility

With regard to the prospects for an increase in fertility over the next several years, Sklar and Berkov cited recent survey data showing that a high proportion of young married women were childless, that most Americans have an aversion to childlessness and to the one-child family, and that only a small proportion of married women under 30 expected to bear fewer than two children in their lifetimes (*1*, p. 695). Their conclusion follows (*1*, p. 696): "If these young women are to realize their desires and expectations with respect to family size, they cannot postpone childbearing much longer. Within the next few years many will have to begin 'making up' the births they delayed in previous years."

More recent data on child spacing and first-order birthrates support the conclusion that there has been some postponement of childbearing in recent years (*5, 6*). For purposes of this analysis, it is assumed that the postponed childbearing of young married women will be made up and that, in the aggregate, the family-size expectations of these women will be realized, although it should be noted that such expectations are subject to error and to change (*7*).

Sklar and Berkov pointed out that only 16 percent of married women under 30 in 1974 expected to have fewer than two children (*1*, p. 695). However, those same data suggested also that all women 18 to 29 years old in 1974 (the birth cohorts of 1945 to 1956) will complete childbearing with an average of only 2.1 births (*8*, pp. 23, 122). The explanation of this apparent inconsistency is twofold: first, married women under 30 expected an average of only 2.25 births, in part because only 10 percent expected four or more births (*9*); second, generalization of the expectations to all women requires a downward adjustment to allow for the fact that women who have not yet married or who will never marry will have lower average fertility than currently married women (*8*, p. 23; *9*, p. 33).

If lifetime fertility rates are projected for these cohorts consistent with their

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