CHAPTER 6

MEASURING INCLUSIVE FITNESS IN SOCIAL WASPS

David C. Queller and Joan E. Strassmann

Since Hamilton's (1964a 1964b) seminal work, students of the evolution of social behavior have become accustomed to thinking in terms of the inclusive fitness effects of behaviors. For example, the inclusive fitness effect of an altruistic behavior is $c + rb$ where c is the fitness cost to the altruist, b is the fitness gain of the beneficiary and r is their relatedness. The sign of the inclusive fitness effect determines the expected direction of selection. If the inclusive fitness effect of a behavior is positive, then selection should lead to an increase in the frequency of genes causing the behavior.

Inclusive fitness theory provides a simple way to think about the evolution of social interactions. While it is not as rigorous as the recursion models of population genetics, it is much easier to use. Any insights from inclusive fitness theory can be checked, and sometimes modified, through the use of more rigorous models, but inclusive fitness thinking helps modelers know what to model.

The inclusive fitness method of accounting has also played an important role in empirical studies. The alternative of simply measuring personal fitness can sometimes be used (Grafen 1982), but only when all individuals have the opportunity to express the behavior under study. Here its value goes beyond mere simplicity. There is a good reason why inclusive fitness has been the tool of choice for field studies of the evolution of kin relations. The empirical advantage of inclusive fitness arises when expression of the behavior is conditional on some special circumstance, so that not all individuals bearing the genes for the behavior will actually express it. Such cases are common. For

---

Department of Biology, Rice University, P. O. Box 1892, Houston TX 77251, USA

In: The Genetics of Social Evolution
Michael D Breed and Robert E Page Jr eds.
Westview Press Boulder

example, among *Polistes* wasp foundresses, the most successful females are those who become queens of multiple-foundress associations, but obviously this alternative is not open to all foundresses. Those who are unable to attain this status must either nest alone or forego most of their personal reproduction by becoming a subordinate in a multiple-foundress association. Comparing the numbers of offspring of solitary nesters and subordinates is not sufficient for understanding how selection operates on this choice. To do so ignores the genes for the behavior that are transmitted by the offspring of the dominant queens. Just because the queens themselves do not express the choice of nesting alone or being a subordinate does not imply that they do not transmit the genes that affect this choice. The inclusive fitness solution is to assign those offspring of the queen that are in excess of what she would have had on her own and then devalue them by the relatedness of the subordinate to the queen. In effect, we use the observed behavior of some individuals, the subordinates, to predict the genes of other individuals who do not express the behavior, the queens. Some such procedure is necessary to make a complete accounting of the transmitted genes. Similar, and in some respects more sophisticated, methods are used by animal breeders (Lush 1947, Willham 1963, Falconer 1981). These could be used in some studies of social selection (Cheverud 1984), but in practice the simpler inclusive fitness method is generally preferred.

As inclusive fitness is the preferred method for dealing with this problem, it is curious that there have been so few attempts to measure inclusive fitness in social insects. More remarkable still is the fact that, after a small flush of studies conducted in the 1970's (Metcalf and Whitt 1977b, Gibo 1978, Noonan 1981, Strassmann 1981a) and later analyses of those studies (Grafen 1984, Queller and Strassmann 1988), there seem to have been no further serious attempts to measure inclusive fitness in social insects. While it is too soon to conclude that entomologists have given up on inclusive fitness, there is a distinct contrast with ornithologists, who continue to refine their inclusive fitness studies of helping in birds (e.g. Brown 1987, Woolfenden and Fitzpatrick 1984).

We can suggest two possible reasons for this difference. One might be a perception that we already understand the evolution of insect societies. This view may be held because of the widespread acceptance of Hamilton's (1964b) haplodiploid hypothesis which attributes the high incidence of eusociality in the haplodiploid Hymenoptera to the fact that super sisters are related by 3/4 instead of the usual 1/2. To the extent that this explanation is sufficient, there seems to be little left to explain. But recent reviews of the evolution of eusociality tend to downplay the special relatedness considerations that arise from haplodiploidy, pointing to costs and benefits as more important (Andersson 1984, Alexander and Noonan in press). It is clear that the question is not yet resolved and that field measurements of relatedness, costs, and benefits are important for its resolution.

The other reason for the rarity of studies of social insect inclusive fitness may be the difficulty of measuring important parameters. First, observation is difficult in most social insects because many important activities take place within an enclosed nest. It is no accident that *Polistes*, with its open nests, has been the favorite subject of inclusive fitness studies. Second, assigning paternity to individuals is very difficult because mated pairs do not remain together (except in termites). Finally, in many species, more than one female may oviposit in a single nest, making maternity difficult to assess as well. Some of these difficulties also apply to certain avian systems, but they arise more often and more consistently in social insects.

The solution to these difficulties is to devise methods that make inclusive fitness studies easier and more rigorous. The rest of the chapter is devoted to this task. We cannot address all the issues involved in measuring inclusive fitness so we focus on two recent efforts in our laboratory. One involves the measurement of relatedness and the other concerns a precondition necessary for accurate measurement of costs and benefits. We will use *Polistes* wasps as examples; however, the issues involved are of general interest.

ESTIMATING RELATEDNESS

The most common method of estimating relatedness uses pedigree path analysis (Cannings and Thomson 1981). A major advantage of this method is that it allows assignment of relatedness values between any pair of individuals whose pedigrees are known, but pedigrees are often very difficult to obtain for social insects. When pedigree data are inadequate, one can rely on assumptions, for example by assuming that all females mate only once with an unrelated male. It is better not to rely on untested assumptions. This uncertainty has led to increased reliance on protein electrophoresis data. The first studies used allozyme markers as an aid to pedigree construction (Metcalf and Whitt 1977a, Lester and Selander 1981, Pamilo 1982a, Page and Metcalf 1982). This can work quite well when there is only one kind of missing information. For example, if maternity can confidently be assigned through behavioral observations, then allozyme markers can then be used to estimate how many fathers each brood must have had, and relatedness of the brood can then be estimated. However, if there are too many unknowns, as is often the case, this method becomes difficult.

The solution to this problem is to jettison pedigree construction in favor of another approach. The alternative to the pedigree approach again makes use of allozyme data. The r in Hamilton's rule can be expressed as a genetic correlation or regression. Rather than going through an intermediate stage of pedigree construction, statistical estimates of these parameters are generated directly from allozyme data. The methodology for obtaining these estimates (Pamilo and Crozier 1982, Crozier *et al.* 1984, Pamilo 1984) has been employed in recent social insect studies in which pedigrees were hard to obtain (Craig and Crozier 1979, Pamilo and Varvio-Aho 1979, Ward and Taylor 1981, Pamilo 1982b, Pearson 1982, Ward 1983, Crozier *et al.* 1984, 1987, Ross and Fletcher 1985, Ross 1986, Schwartz 1986, 1987, Crozier and Pamilo 1986, Reilly 1987, Van der Have *et al.* 1988, see also Ross this volume, Kukuk this volume).

However, these statistical methods have at least two shortcomings. First, computer simulations show that the estimates of r are sometimes too low, particularly when there are data from relatively few social groups (Pamilo and Crozier 1982, Wilkinson and McCracken 1986). Second, these estimates yield only population averages, such as the average relatedness of foundresses to other foundresses on their nest. These population values are very useful, but it would also be helpful to have individual relatedness values. For example, we might wish to estimate the relatedness of foundresses on one nest only, or we may wish to compare their relatedness with that of foundresses on another nest. The methodology for attacking questions of this type has not been worked out.

Solving these problems (Queller and Goodnight, in press) should make allozyme studies considerably more valuable. A detailed treatment cannot be given here, but a summary will convey the main features of our approach. The quantity to be estimated is

$$r = \frac{\sum_{A}(p_y - \bar{p})}{\sum_{A}(p_x - \bar{p})} \qquad (1)$$

where the p's are Grafen's (1985) "p-values" which are usually interpreted as gene frequencies: $\bar{p}$ is the population frequency; p_x is its frequency in the actor, x; and p_y is its frequency in the actor's partners, y. The summations are taken over all altruistic acts, A, that are induced by the gene in question. This measure is closely related to the more familiar genetic regression, but it is slightly more general, that is, it makes Hamilton's rule work under a broader range of assumptions (Grafen 1985). The crucial difference is that our measure (1) takes deviations from the mean of the whole population while a regression measure takes deviations from the separate means of the actors and their partners ($r = \Sigma(p_y - \bar{p}_y)(p_x - \bar{p}_x) / \Sigma(p_x - \bar{p}_x)^2$).

The new measure (1), though less familiar than the regression coefficient, actually has a simpler interpretation in terms of selection for social behavior. If the p's represent frequencies of the gene for altruism, $p_y - \bar{p}$ represents the difference of a beneficiary from the population frequency and $p_x - \bar{p}$ represents the difference of an altruist from the same average. As selection affects a gene frequency to the extent that selected individuals differ from the population mean (there would be no genetic change if the selected group matched the population mean), the numerator and denominator of (1) must represent the relative importance of beneficiaries and altruists as vehicles for selection on the altruism gene. That is why this measure acts as a proper coefficient to scale the relative values of costs and benefits. Considered from the standpoint of a single copy of the altruism gene in an altruist, its identity with genes in the beneficiary is p_y, while its identity by chance alone is $\bar{p}$. Therefore $p_y - \bar{p}$ represents a measure of total identity minus identity by chance, in other words, identity by descent. Similarly $p_x - \bar{p}$ represents the allele's identity by descent with its own genotype (including itself, so $p_x \geq 1/2$ for diploids).

It is easy to see how neutral allozyme markers can be used to estimate r. Suppose we have available x altruists scored for k variable marker loci with a allele copies at each (here we mean allele copies, not allelo*morphs*, hence a always equals two for diploids). A reasonable estimator of (1) is

$$r = \frac{\sum\limits_{\overset{x}{\cancel{y}}} \sum\limits_{\cancel{y}\,k} \sum\limits_{a} (p_y - \bar{p}^*)}{\sum\limits_{\underset{\underset{\text{indiv}}{\uparrow}}{x}} \sum\limits_{\underset{\underset{\text{loci}}{\uparrow}}{k}} \sum\limits_{\underset{\underset{\text{alleles}}{\uparrow}}{a}} (p_x - \bar{p}^*)} \qquad (2)$$

In effect, we sum all identities by descent of altruist marker genes with beneficiary genes and divide by the sum of all identities by descent of altruist marker genes with genes in their own genotypes. (Note that to avoid clutter we have not indexed the p-values for alleles, but they do change according to which allele is currently being summed over). Often we are interested not so much in actual altruists as potential ones. If we let x be an index for potential altruists and y for potential beneficiaries, the formula (2) still applies.

The only complication concerns the estimate of the population frequency for any allele. Instead of $\overline{p}$, we have written it as $\overline{p}^*$ to indicate a necessary bias correction when a small number of altruists or potential altruists are sampled. Here $\overline{p}^*$ is the population mean frequency of the allele currently being summed over, but calculated after omission of the current altruist, x, and its beneficiaries, y. To understand the rationale for this, consider the effect of not excluding these individuals. In a large population these individuals' genes make a negligible contribution to the actual population gene frequency, but they would make a sizable contribution to an estimate calculated from a small sample. This presents no problem for an estimate of the population frequency itself, but it leads to biased estimates of $p_x - \overline{p}$ and $p_y - \overline{p}$. For example, since each x individual contributes an artificially large proportion to $\overline{p}$, the difference, $p_x - \overline{p}$, will be artificially reduced. The solution is to omit x (and its genetically similar relatives, y) from the estimate of $\overline{p}$, so that the difference, $p_x - \overline{p}^*$, is now taken using an estimate of the population frequency which, like the true population frequency, is essentially unaffected by individuals currently being considered. Failure to make such a correction causes the previously noted (Pamilo and Crozier 1982, Wilkinson and McCracken 1986) downward bias of the regression estimator. Simulations show that using $\overline{p}^*$ does in fact correct this bias (Queller and Goodnight, in press).

The second useful feature of this method is that it provides a clear and simple way to estimate individual *r* values rather than just population averages. By individual *r* values we mean either the average relatedness between one altruist and its beneficiaries or the relatedness within one particular social group. For individual estimates, the regression measure has a zero denominator and is, therefore, undefined. One can visualize this by recognizing that there is no unique regression line that can be fit to a single point. In contrast, individual *r* values obtained directly from formula (1) are defined. Summations are performed for the single altruist in question (or for all the members of the single group of interest) instead of the entire sample. It is important to remember, however, that the $\overline{p}^*$ values must still be calculated using *other* individuals. What is important is how much the altruist and its beneficiary differ from the population mean, so it is still necessary to gather genetic information from more than just the individuals of interest.

Because the estimates of individual *r*'s are highly dependent on the genotypes of just a few individuals, they are expected to be much more variable than estimates of average population relatedness. This means that they will be fairly unreliable unless there is a great deal of genetic information available. Although each individual value may be quite variable, they can be used together to test interesting hypotheses. Suppose, for example, we want to know if foundresses who associate before March 25 are more closely related than those that first associate after this date. We can calculate average *r*'s for each group, but we need to know something about the dispersion of values to test for statistical significance. One simple way to determine the dispersion is to estimate *r* separately for each foundress association and use a non-parametric Mann-Whitney U test to compare those formed before and after March 25. Simulations have shown that this kind of procedure can be quite successful at detecting differences in relatedness, even when the individual estimates are quite unreliable (Queller and Goodnight, in press).

We have not yet applied these methods to many examples of real data, but the following example gives another indication of the kinds of hypotheses that can be investigated. At the end of a reproductive season, *Polistes* colonies rear reproductive males and females. The females will overwinter and begin new nests the following spring, often in association with natal nestmates. It is, therefore, of interest to know the relatedness of reproductive females on their natal nests, and whether relatedness differs on different kinds of nests. For example, one might hypothesize that relatedness might be lower on natal nests that produce many reproductives because the queen might have had more trouble monopolizing reproduction on larger and more productive nests. FIGURE 1 shows data from a study we have conducted with Colin R. Hughes on *Polistes instabilis* from McAllen, Texas that can be used to test this hypothesis. Two polymorphic loci were scored for all females taken from 41 fall nests. The plot of colony relatedness values versus number of females shows that the hypothesis is not supported. There is a trend in the opposite direction: relatedness tends to increase with higher productivity (though the Spearman's rank correlation coefficient of .247 is not significant).

COSTS AND BENEFITS

Fitness is always a difficult parameter to define and to measure. Measurement of costs and benefits, which are components of fitness, should share the same difficulties. However, it is not these difficulties that we want to address here. Approximate measures, such as counting offspring at a certain stage, are as acceptable in social behavior as they are in other fields. But there are two problems that are peculiar to inclusive fitness studies, and we focus on these.

The first is an accounting problem that we treat very briefly as it has been discussed by Grafen (1982). While traditional personal fitness models allocate all offspring to their parents' fitness, inclusive fitness models allocate offspring to the fitness of the individual that is responsible for them. When a helper increases its sister's reproduction, inclusive fitness models augment the fitness of the helper. However, care must be taken not to allocate the same fitness units to more than one

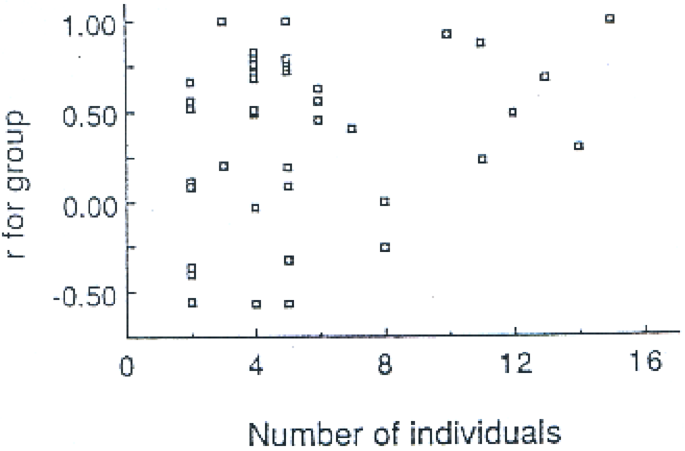

FIGURE 1. Relatedness of *Polistes Instabilis* females as a function of group size. Each value represents relatedness within one colony collected in the fall just prior to overwintering.

individual. In the example above, the offspring cannot also be added to the sister's fitness. Grafen (1982) noted that inclusive fitness has often been defined in ways that incorporate such double counting, but that this has less often been a problem in actual measurements of inclusive fitness. Measurements are usually done using Hamilton's rule, and the structure of this rule forces us to think in a way that avoids double counting.

However, there remains a second general problem with trying to estimate costs and benefits. Costs and benefits are defined as fitness effects of a behavior (Hamilton 1964). That is, they are *differences* due to the behavior; they are each defined as a fitness actually achieved minus the fitness that would have pertained if the behavior had not occurred. The special problem with measuring inclusive fitness lies with this second part. How do we estimate the number of offspring that would have been produced in the absence of the behavior?

As an example, consider the choice facing an overwintered *Polistes* female who would not, for whatever reason, be able to attain dominant queen status in a multiple-foundress association. She can accept the status of a subordinate and help to rear the queen's offspring or she can establish a nest on her own. This is the choice investigated in most inclusive fitness studies of *Polistes* (Metcalf and Whitt 1977b, Gibo 1978, Noonan 1981, Strassmann

1981a, Grafen 1984, Queller and Strassmann 1988). What are the costs and benefits of joining as a subordinate? The cost is a subordinate's personal fitness minus the fitness she gave up by not nesting alone. Similarly, the benefit is the fitness that the subordinate adds to her relative. Estimating this requires knowing what the relative's fitness would have been without the subordinate's help. Neither the cost nor the benefit is directly measurable. In the inclusive fitness studies cited above, the way out of this dilemma was to use the fitness of solitary foundresses to represent both how well a subordinate would have done if she had nested alone and how well a queen would have done without the help of any helpers. As the authors of these studies recognized, this requires an assumption that other things are equal. This is a familiar assumption in studies of adaptation, and it often works well, but there is a special reason to distrust it in this case. Note that there are two assumptions required: that subordinates and solitary foundress would be equally capable at nesting alone, and that queens and solitary females would be equally capable. Each assumption seems plausible enough by itself, but together they imply that queens and subordinates are equally capable at nesting alone. Yet queens and subordinates are unequal in some respects; otherwise the queen would not be able to dominate her subordinates. Queens and subordinates, depending on the species and population, differ in factors such as size, ovarian development, hormone levels, and fat content (Pardi 1946 1948, West-Eberhard 1969, Turillazzi and Pardi 1977, Röseler *et al.* 1980 1984, Dropkin and Gamboa 1981, Turillazzi *et al.* 1982, Sullivan and Strassmann 1984). While some of these differences could be partly a result of dominance interactions, it is clear that queens and subordinates are not identical. Moreover, it has been argued that dominance should be expected to reflect reproductive ability (West-Eberhard 1978). To the extent that this is true, the standard assumptions of inclusive fitness analyses are false, and the inclusive fitness estimates are in error.

It is possible that, in spite of the behavioral, morphological, and physiological differences between queens and subordinates, they would still be equally capable of nesting alone. But given the importance of the assumption, and the distinct possibility that it is false, it needs to be tested. We have attempted to do so during the course of a study of *Polistes bellicosus* at Brazos Bend State Park near Houston, Texas. Full details of this study will be presented elsewhere (Queller and Strassmann, in preparation). Here we focus on the single issue of the reproductive equivalence of queens and subordinates.

We began observing *Polistes bellicosus* colonies from the time of their founding in late March, 1985 (Strassmann *et al.* 1987). Nests were usually begun by a single female but were often subsequently joined by others. On April 6 we performed our experimental manipulation. At this stage most nests had early instar larvae and three quarters of the colonies had more than one female, all of which had been marked with enamel. Multiple-female colonies were randomly assigned to three treatment groups. We removed all but the largest female from 1/3, all but the smallest female from 1/3 and left the rest untreated. A fourth group, which we did not alter, consisted of the colonies that only had one female to start with. Our main interest here is in the three treatments in which a single female is left to maintain the nest.

If the largest female in a colony is usually the queen and the smallest female is usually a subordinate, then our two experimentally manipulated groups would consist primarily of queens forced to nest alone and subordinates forced to nest alone. Size is a well-known correlate of dominance in *Polistes* foundresses (Turillazzi and Pardi 1977, Noonan 1981, Sullivan and Strassmann 1984) and *Polistes bellicosus* is no exception. Due to the large numbers of colonies in our experiment, we did not assess behavioral dominance directly. But queenship could be inferred from dissections of wasps from collected colonies. In ten out of fourteen complete colonies collected, the largest female was judged to be the queen on the basis of clearly having the best-developed ovaries. On only one was the smallest female the queen. This trend was confirmed by dissections of females from the colonies that were partially collected during the experimental manipulation. When we collected all but the largest female from some colonies, we obtained a sample of smallest females for dissection, and when we collected all but the smallest females we obtained a sample of largest females. Dissections showed the largest females to have significantly better developed ovaries than the smallest females for every measure taken ($p<0.05$, Mann Whitney U tests for: number of layable eggs, number of oocytes per ovariole, number of oocytes with yolk in the best-developed ovariole, lengths of the largest and the second largest oocytes in that ovariole). We conclude that largest females are usually queens and smallest females almost never are. Therefore, even

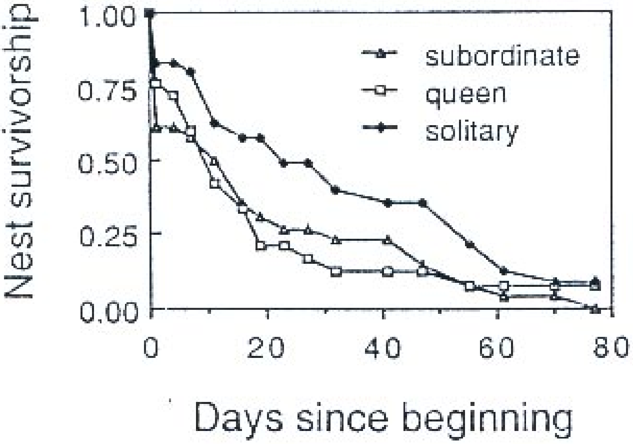

FIGURE 2. Survivorship of colonies tended by three categories of single females after experimental manipulation on April 6. Subordinates and queens are individuals who had those roles on multifemale associations prior to the removal of their nestmates on April 6. Solitary females are those who were already nesting alone prior to April 6.

though there are likely to be a few exceptions, we will call the largest females queens and the smallest females subordinates.

Did queens fare better than subordinates when forced to nest alone? The answer was no. We censused nests repeatedly until June 21, by which time nearly all had failed. Failures were due either to death of all adults, desertion by all adults, or predation on the nest comb (after failure due to the latter two causes, females may begin or join another nest, but our measures of success pertain only to the original nests). Queens nesting alone did not maintain their colonies for a longer time than subordinates nesting alone (FIGURE 2). Nor were there any significant differences, at any census date after the experimental manipulation, in any measures of brood rearing success (number of cells, eggs, larvae, or pupae). In all respects, queen colonies and subordinate colonies fared equally well.

Actually, it would be more accurate to say that the two groups fared equally poorly, and this shift in emphasis may have some significance in the interpretation of our results. The fact that queens and subordinates fared poorly when nesting alone is shown by comparison with the colony survivorship of natural colonies of solitary foundresses. The females who chose to nest on their own maintained their colonies for significantly longer than those that we forced to nest alone (FIGURE 2). The explanation would seem to lie in the fact that, prior to our manipulation, the experimental colonies had a brief history as multiple-foundress colonies. Because of this, the experimental nests were larger than the control solitary nests (FIGURE 3). By removing foundresses from a nest, we may have overburdened the remaining foundress with a larger brood than she would have chosen to raise if she had been a solitary foundress from the beginning. Her response could be to increase foraging, thereby increasing risk of mortality, or she might opt to desert the nest and go elsewhere. We cannot distinguish between these alternatives, but either could account for the decreased survivorship of experimental colonies.

Our conclusions, then, are less straightforward than we might have hoped, but still revealing. A simple comparison of queens and subordinates suggests that they are reproductively equivalent when nesting alone, so that the equivalence assumption implicit in the use of Hamilton's rule seems justified. But the experimental reduction in foundress numbers may have stressed the remaining females, and this conclusion could be challenged on two grounds. First, it might be argued that our experimental treatment was unnatural and that, therefore, the results could not be taken as indicative of the actual abilities of queens and subordinates under normal circumstances. But in fact the stress engendered by the experiment is not unnatural. Mortality of *Polistes* foundresses is high and reduction of multiple-foundress colonies to a single female is a common event. Indeed, we found that the death or disappearance of all foundresses was the most common cause of colony failure prior to the emergence of workers.

It could also be argued that we did not test all of the abilities required to nest alone. Specifically, if our queens and subordinates were overburdened with brood after the experimental manipulation, one would not expect them to lay additional eggs, so our experiment would not test their ability to perform this task. The data in FIGURE 3 confirm that former queens and subordinates did not add new cells to their nests after the experimental removal of other females. However, FIGURE 3 also suggests that this is the normal pattern for solitary females during this period since the unmanipulated single-foundress nests did not grow either. Apparently solitary females begin a cohort of brood and then concentrate on rearing that brood before laying

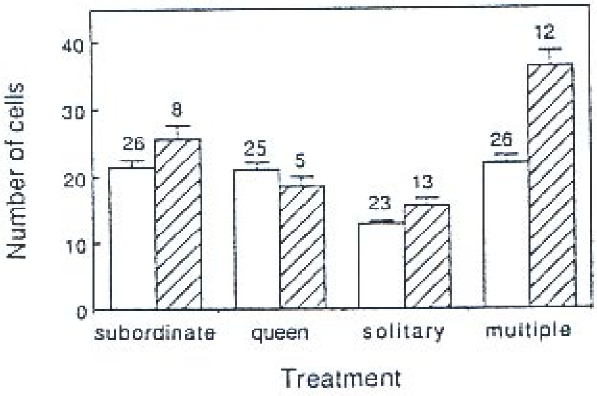

FIGURE 3. Average numbers of cells in nests on the day of the experiment, April 6 (open bars), and 22 days later (hatched bars). Categories of nests are as in FIGURE 2, with the addition of "multiples", which are colonies with more than one foundress before April 6 that did not have any females removed.

additional eggs. In contrast, multiple-foundress nests continue to grow throughout this period.

We can conclude, then, that our experiment lends some support to the assumption that queens and subordinates are reproductively equivalent in their brood-rearing abilities. While we did not test relative egg-laying abilities, this is not very relevant at the time of year when our study was conducted anyway.

DISCUSSION AND CONCLUSIONS

We have not discussed all the issues relevant to conducting accurate and meaningful inclusive fitness studies in wasps like *Polistes*. But we have removed two serious obstacles. On the one hand, we have developed a statistical estimator of relatedness that is both unbiased and flexible enough to estimate individual relatedness values. On the other, we tested a critical assumption required for rigorous measurement of costs and benefits and we have failed to find anything wrong with it. Of course, these two advances do not eliminate the hard work that will be necessary to measure relatedness, costs, and benefits. But they do suggest that such efforts will yield valid information. Perhaps the time is ripe for a renewal of interest in inclusive fitness studies of social insects.

Even measurements of relatedness alone, without costs and benefits, can be valuable in answering important questions. What benefit/cost ratio is required for sociality to pay, or in other words, how efficient do groups have to be? How do individuals use their information about relatedness in making behavioral choices? To what extent do intraspecific differences in *r* predict differences between species in the extent of altruism? With Colin Hughes, we are currently trying to answer such questions for several Texas *Polistes* species. Beyond a few temperate *Polistes* and vespines (Ross 1986), almost nothing is known of relatedness in social wasps. Some of the tropical polybiine wasps offer some especially intriguing opportunities for relatedness studies. Many of these species are characterized by multiple queens, suggesting that relatedness may be quite low. In addition, most of these species reproduce by swarming and it would be very interesting to know what role relatedness plays in behavioral decisions during the colony fissioning stage.

Similarly, much remains to be learned about costs and benefits. The testing of alternatives focusing on costs and benefits is still in the early stages (see Strassmann and Queller, chapter 5). Particularly needed are demonstrations of how an altruist can give more, in terms of fitness, to its relative than it could give to itself. *Polistes* is the best-studied group, and some important benefits of helping have been proposed (West-Eberhard 1969, Metcalf and Whitt 1977b, Gibo 1978, Gamboa 1978 1980, Noonan 1981, Strassmann 1981b, Strassmann *et al.* 1988), but it is probably fair to say that no general picture has yet emerged. Once again, there has been far too little work on the polybiines, with the exception of *Mischocyttarus,* which is behaviorally rather like *Polistes* (Jeanne 1972, Litte 1977 1979). Studies of the costs and benefits of sociality in other polybiines could be particularly illuminating with respect to the evolution of castes because this group contains species with different grades of morphological caste differentiation, including none at all.

Acknowledgements

We thank Carlos Solís for field assistance and for doing the figures, Keith Goodnight for writing the computer program for estimating relatedness, and Colin Hughes for help with field work and for generating the electrophoresis data of FIGURE 1. Part of the work reported here was conducted at Brazos Bend State Park under Texas Parks and Wildlife permit number 16-85, and we thank D. Riskind, L.

Fowler, and C. VanBaarle for their cooperation. This work was partially supported by NSF grant BSR-8695026.

LITERATURE CITED

Alexander, R. D. and K. M. Noonan. In press. The evolution of eusociality. In *The natural history and social behavior of naked mole rats*, P. W. Sherman, J. Jarvis and R. D. Alexander, eds.

Andersson, M. 1984. The evolution of eusociality. *Ann. Rev. Ecol. Syst.* 15:165-189.

Brown, J. L. 1987. *Helping and communal breeding in birds: ecology and evolution.* Princeton University Press:Princeton, NJ.

Cannings, C. and E. A. Thomson. 1981. *Genealogical and genetic structure.* Cambridge University Press:Cambridge, U. K.

Cheverud, J. 1984. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. *Evolution* 38:766-777.

Craig, R. and R. H. Crozier. 1979. Relatedness in the polygynous ant *Myrmecia pilosula. Evolution* 33:335-341.

Crozier, R. H. and P. Pamilo. 1986. Relatedness within and between colonies of a queenless ant species of the genus *Rhytidoponera* (Hymenoptera: Formicidae). *Entomol. Gener.* 11:113-117.

Crozier, R. H., P. Pamilo and Y. C. Crozier. 1984. Relatedness and microgeographic genetic variation in *Rhytidoponera mayri*, an Australian arid zone ant. *Behav. Ecol. Sociobiol.* 15:143-150.

Crozier, R. H., B. H. Smith and Y. C. Crozier. 1987. Relatedness and population structure in the primitively eusocial bee *Lasioglossum zephyrum* (Hymenoptera: Halictidae) in Kansas. *Evolution* 41:902-910.

Dropkin, J. A. and G. J. Gamboa. 1981. Physical comparisons of foundresses of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Can. Entomol.* 113:457-461.

Falconer, D. S. 1981. *Introduction to quantitative genetics.* 2nd ed. Longman:London.

Gamboa, G. J. 1978. Intraspecific defense: advantage of social cooperation among paper wasp foundresses. *Science* 199:1463-1465.

Gamboa, G. J. 1980. Comparative timing of brood development between multiple and single-foundress colonies of the paper wasp, *Polistes metricus. Ecol. Entomol.* 5:221-225.

Gibo, D. L. 1978. The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): a field study of the effects of predation on productivity. *Can. Entomol.* 110:519-540.

Grafen, A. 1982. How not to measure inclusive fitness. *Nature* 298:425-426.

Grafen, A. 1984. Natural selection, kin selection and group selection. In *Behavioural ecology: an evolutionary approach,* J. R. Krebs and N. B. Davies, eds. Sinauer:Sunderland, Mass. pp. 62-84.

Lush, J. L. 1947. Family merit and individual merit as bases for selection. *Am. Nat.* 81:241-261.

Hamilton, W. D. 1964a. The genetical evolution of social behavior. I. *J. Theoret. Biol.* 7:1-16.

Hamilton, W. D. 1964b. The genetical evolution of social behavior. II. *J. Theoret. Biol.* 7:17-52.

Jeanne, R. L. 1972. Social biology of the neotropical wasp *Mischocyttarus drewseni. Bull. Mus. Comp. Zool. Harvard* 144:63-150.

Lester, L. J. and R. K. Selander. 1981. Genetic relatedness and the social organization of *Polistes* colonies. *Am. Nat.* 117:147-176.

Litte, M. 1977. Behavioral ecology of the social wasp, *Mischocyttarus mexicanus. Behav. Ecol. Sociobiol.* 2:229-246.

Litte, M. 1979. *Mischocyttarus flavitarsus* in Arizona: social and nesting biology of a polistine wasp. *Z. Tierpsychol.* 50:282-312.

Metcalf, R. A. and G. S. Whitt. 1977a. Intra-nest relatedness in the social wasp *Polistes metricus*: a genetic analysis. *Behav. Ecol. Sociobiol.* 2:339-351.

Metcalf, R. A. and G. S. Whitt. 1977b. Relative inclusive fitness in the social wasp *Polistes metricus. Behav. Ecol. Sociobiol.* 2:353-360.

Noonan, K. M. 1981. Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. In *Natural selection and social behavior: recent research and new theory,* R. D. Alexander and D. W. Tinkle, eds. Chiron Press:New York pp. 18-44.

Page, R. E. and R. A. Metcalf. 1982. Multiple mating, sperm utilization, and social evolution. *Am. Nat.* 119:263-281.

Pamilo, P. 1982a. Multiple mating in *Formica* ants. *Hereditas* 97:37-45.

Pamilo, P. 1982b. Genetic population structure in polygynous *Formica* ants. *Heredity* 48:95-106.

Pamilo, P. 1984. Genetic correlation and regression in social groups: multiple alleles, multiple loci, and subdivided populations. *Genetics* 107:307-320.

Pamilo, P. and R. H. Crozier. 1982. Measuring genetic relatedness in natural populations: methodology. *Theoret. Popul. Biol.* 21:171-193.

Pamilo, P. and S.-L. Varvio-Aho. 1979. Genetic structure of nests of the ant *Formica sanguinea*. *Behav. Ecol. Sociobiol.* 6:91-98.

Pardi, L. 1946. Richerchi sui polistini. V. La poliginia iniziale in *Polistes gallicus* L. *Boll. Ist. Ent. Univ. Bologna* 15:25-84.

Pardi, L. 1948. Dominance order in *Polistes* wasps. *Physiol. Zool.* 21:1-13.

Pearson, B. 1982. Relatedness of normal queens (macrogynes) in nests of the polygynous ant *Myrmica rubra* Latreille. *Evolution* 36:107-112.

Queller, D. C. and K. F. Goodnight. in press. Estimation of genetic relatedness using allozyme data. *Evolution*.

Queller, D. C. and J. E. Strassmann. 1988. Reproductive success and group nesting in the paper wasp, *Polistes annularis*. In *Reproductive success: studies of individual variation in contrasting systems*. T. H. Clutton-Brock, ed. University of Chicago Press:Chicago. pp. 76-96.

Reilly, L. M. 1987. Measurements of inbreeding and average relatedness in a termite population. *Am. Nat.* 130:339-349.

Röseler P.-F., I. Röseler and A. Strambi. 1980. The activity of corpora allata in dominant and subordinated females of the wasp *Polistes gallicus. Insectes Sociaux* 27:97-107.

Röseler P.-F., I. Röseler, A. Strambi and R. Augier. 1984. Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, *Polistes gallicus. Behav. Ecol. Sociobiol.* 15:133-142.

Ross, K. G. 1986. Kin selection and the problem of sperm utilization in the social insects. *Nature* 323:798-800.

Ross, K. G. and D. J. C. Fletcher. 1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 17:349-356.

Schwartz, M. P. 1986. Persistent multi-female nests in an Australian allodapine bee, *Exoneura bicolor* (Hymenoptera: Anthophoridae). *Insectes Sociaux* 33:258-277.

Schwartz, M. P. 1987. Intra-colony relatedness and sociality in the allodapine bee *Exoneura bicolor. Behav. Ecol. Sociobiol.* 21:387-392.

Strassmann, J. E. 1981a. Wasp reproduction and kin selection: reproductive competition and dominance hierarchies among *Polistes annularis* foundresses. *Fla. Entomol.* 64:74-88.

Strassmann, J. E. 1981b. Parasitoids, predators and groups size in the paper wasp, *Polistes exclamans. Ecology* 62:1225-1233.

Strassmann, J. E., D. C. Queller and C. R. Hughes. 1987. Constraints on independent nesting by *Polistes* foundresses in Texas. In *Chemistry and biology of social insects*, J. Eder and H. Rembold, eds. . Verlag J. Peperny:München. pp. 379-380.

Strassmann, J. E., D. C. Queller and C. R. Hughes. 1988. Predation and the evolution of sociality in the paper wasp, *Polistes bellicosus.* Ecology 62:1225-1233.

Sullivan, J. D. and J. E. Strassmann. 1984. Physical variability among nest foundresses in the polygynous social wasp, *Polistes annularis. Behav. Ecol. Sociobiol.* 15:249-256.

Turillazzi, S. and L. Pardi. 1977. Body size and hierarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera Vespidae). *Monitore Zool. Ital. (N.S.)* 11:101-112.

Turillazzi, S., M. T. Marino Piccioli, L. Hervatin and L. Pardi. 1982. Reproductive capacity of single foundresses and associated foundress females of *Polistes gallicus* (Hymenoptera Vespidae). *Monitore Zool. Ital. (N.S.)* 16:75-88.

Van der Have, T. M., J. J. Boomsma and S. B. J. Menken. 1988. Sex investment ratios and relatedness in the monogynous ant *Lasius niger* (L.). *Evolution* 42:160-170.

Ward, P. S. 1983. Genetic relatedness and colony organization in a species complex of ponerine ants. *Behav. Ecol. Sociobiol.* 12:285-299.

Ward, P. S. and R. W. Taylor. 1981. Allozyme variation, colony structure and genetic relatedness in the primitive ant *Nothomyrmecia macrops* Clark (Hymenoptera: Formicidae). *J. Aust. Entomol. Soc.* 20:177-183.

West-Eberhard, M. J. 1969. The social biology of polistine wasps. *Misc. Publ. Museum Zool. Univ. Mich.* 140:1-101.

West-Eberhard, M. J. 1978. Polygyny and the evolution of social behavior of wasps. *J. Kansas Entomol. Soc.* 51:832-856.

Wilkinson, G. S. and G. F. McCracken. 1986. On estimating genetic relatedness using genetic markers. *Evolution* 39:1169-1174.

Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19:18-27.

Woolfenden, G. E. and J. W. Fitzpatrick. 1984. *The Florida scrub jay: demography of a cooperatively breeding bird.* Princeton University Press:Princeton, NJ.