# CHAPTER 5

# ECOLOGICAL DETERMINANTS OF SOCIAL EVOLUTION

Joan E. Strassmann and David C. Queller

The key evolutionary problem concerning the origin of eusociality, and of helping systems in general, is how genes could be selected when their effect is to decrease the reproduction of their bearers. Several theories attempt to account for cooperative behavior by denying that it is truly altruistic. Even though there may be some cost to the helping behavior, these theories posit some personal fitness gain that more than compensates for the cost. This compensatory gain may be an immediate, mutualistic one. For example, while joint defense against predators or parasites may carry some risks, it could cause a net increase in the personal fitness of all participants (Lin and Michener 1972). Alternatively, the gain may be delayed. Temporary helping may be favored if the helper eventually acquires a valuable territory (Emlen 1984, Woolfenden and Fitzpatrick 1984, Brown 1987) or reciprocal help comes at a later time (Trivers 1974, Emlen 1981). These theories may account for some cases of helping, but they do not explain truly altruistic behavior for which there is no compensating personal gain. In most eusocial insects there are no more than a few reproductives at a time, so the majority of individuals cannot gain any immediate personal advantage. Delayed benefits sometimes apply in eusocial insects: queen death may provide opportunities for others to reproduce. But this cannot be a general explanation for two reasons. First, the number of vacancies is low and the number of workers is large, so the average worker stands to gain very little. Second, in some species, the replacement egg-layers are individuals that did not help much, having focused instead on avoiding risks or establishing social dominance (e.g. Gadagkar and Joshi 1984).

---

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

Kin selection, indirect reproduction through helping relatives who tend to share the same genes, must provide the selective advantage for the many cases in which workers have little expectation of personal reproduction. Elements of the theory of kin selection were anticipated in various discussions of altruistic behavior (Darwin 1859, Fisher 1930, Haldane 1955, Williams and Williams 1957) as well as in the animal breeding literature (Lush 1947, Willham 1963). But it was Hamilton (1963 1964a 1964b 1970 1972) who combined a simple quantitative formulation of the idea with a recognition of its widespread importance in the natural world. Using Hamilton's assumptions one can write the condition necessary for selection to favor altruistic behavior as:

$$r^* \Delta w^* > r \Delta w \, . \qquad (1)$$

Here $\Delta w$ is the number of offspring lost by the altruist and $r$ is its relatedness to them (usually 1/2), while $\Delta w^*$ is the number of offspring gained by the beneficiary, and $r^*$ is the relatedness of the altruist to them.

Two classes of explanations of the evolution of eusociality emerge from Hamilton's rule. One focuses on differences in the $r$ terms and the other on differences in the $\Delta w$'s or costs and benefits. Both may operate together, but for purposes of clarity we discuss them separately. The next section discusses the role of relatedness in the evolution of eusociality and focuses on the haplodiploid hypothesis. The following sections subdivide hypotheses based on the costs and benefits side of Hamilton's rule into those invoking limited reproductive opportunities outside groups and those postulating ecological advantages to groups which result in higher inclusive fitness for group members. In each case, wasps of the genus *Polistes* are treated in detail because *Polistes* is one of the few genera (perhaps the only one) in which many of the hypotheses for group living and altruism have been investigated.

*Polistes* is especially appropriate for investigating the origin of eusociality because it is primitively social and lacks morphological castes. Its open-faced colonies are easy to find and study (FIGURE 1). This makes many of the key ecological parameters such as colony predation and parasitism much easier to document than is the case for the often cryptic colonies of ground and twig nesting bees and wasps (Michener 1964, Wilson

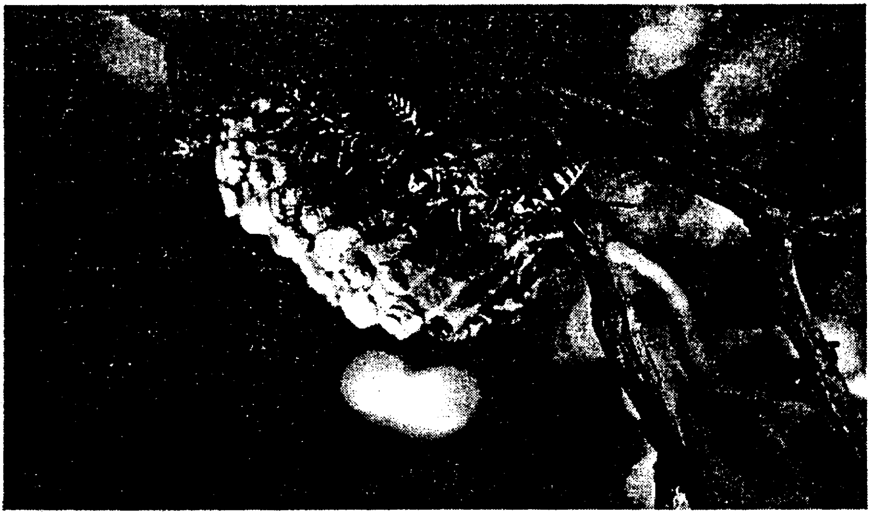

FIGURE 1. Colony of *Polistes exclamans.*

1971). [For a summary of the typical colony cycle of *Polistes* see Strassmann and Hughes (1986)].

## RELATEDNESS AND THE EVOLUTION OF EUSOCIALITY

Besides devising the general inclusive fitness formula, Hamilton (1964a,b) developed a specific relatedness-centered hypothesis for the origin of eusociality. He noted that the haplodiploid genetic system possessed by this group leads to some peculiar relatedness properties. Specifically, a female who helps to rear super sisters would obtain a particularly favorable $r^*$ value of 3/4, instead of the usual 1/2 for diploids (formula 1). Selection could then sometimes favor rearing super sisters instead of offspring even if $\Delta w^* < \Delta w$. This hypothesis, called the haplodiploid hypothesis, would account for the fact that most of the origins of eusociality occurred in the haplodiploid Hymenoptera and for the fact that workers in this group are exclusively female.

Though elegant, the haplodiploid hypothesis has encountered a series of problems. First, females are related to their brothers by only 1/4 (Crozier 1970), so that a haplodiploid female helping to rear an even mixture of super sisters and brothers would obtain an average $r$ to brood of only 1/2, exactly the same value as in diploid systems. The haplodiploid advantage could be saved if female workers could avoid aiding brothers, either because of a female-biased sex ratio or by laying the male-destined eggs themselves (Hamilton 1972, Trivers and Hare 1976). Worker laying of male-destined eggs occurs, but is far from universal (Hamilton 1972, Trivers and Hare 1976, Bourke, 1988). Female-biased sex ratios also occur (Trivers and Hare 1976, Nonacs 1986), but their significance in selecting for eusociality is not entirely clear for two reasons. First, once workers succeed in biasing the sex ratio to their optimum (3 females : 1 male under the simplest conditions), the haplodiploid advantage disappears because the rarer males become more valuable than females (Trivers and Hare 1976, Grafen 1986). The maintenance of eusociality must therefore be explained in some other way. Second, there is also a problem for the origin of eusociality because it requires two simultaneous changes: helping and the female-biased sex ratio (Charnov 1978). Still the haplodiploid hypothesis can be rescued under certain conditions. Seger (1983) and Grafen (1986) have described circumstances in which a female-biased sex ratio will be favored among the progeny of only some mothers, setting up the opportunity for their daughters to stay and rear mainly sisters, without females being devalued relative to males.

While these adjustments to the haplodiploid hypothesis make it more logically sound, it is still questionable whether it actually describes the critical condition for the origin and maintenance of eusociality (Lin and Michener 1972, Alexander 1974, Evans 1977, West-Eberhard 1975 1978, Eickwort 1981, Brockmann 1984, Andersson 1984, Stubblefield and Charnov 1986, Alexander and Noonan *in press*). First, it cannot account for the diploid termites. Some special mechanisms could increase relatedness in this group (Luykx and Syren 1979, Bartz 1979, Lacy 1980 1984, Pamilo 1984), but it is not clear tha these mechanisms operated in the early termites (Leinaas 1983 Crozier and Luykx 1985). Nor can the relatedness hypothesi account for helping in diploid vertebrates, from the apparently eusocial naked mole rats (Jarvis 1981) to the many species with less developed social systems (Vehrencamp 1979, Emlen 1984, Brown 1987).

It is also far from clear that the haplodiploid hypothesis explains eusociality even in the Hymenoptera. The value of $r^* = 3/4$ depends on having one singly-mated egg layer per colony. Multiple mating is widespread in insects (Parker 1970, Thornhill and Alcock 1983) including some eusocial Hymenoptera (reviewed by Page 1986), though one can only speculate about the mating habits of the ancestral species in which eusociality first appeared. Multiple egg laying individuals are also widespread in eusocial colonies (Wilson 1971, Jeanne 1980). Moreover, it is probable that queen death led to multiple (sequential) egg layers in the earliest eusocial species (West-Eberhard 1978); prior to having evolved special longevity, a mother would usually die before her daughters, leaving the nest to another egg layer. Thus sociality probably first evolved with an average relatedness among female brood of less than 3/4. Whatever the theoretical arguments, measurements of relatedness make it clear that eusociality is maintained in some species with relatedness to female brood of less than 1/2 (Craig and Crozier 1979, Pamilo and Varvio-Aho 1979, Ward and Taylor 1981, Pamilo 1982a 1982b, Pearson 1982, Ward 1983, Crozier *et al.* 1984, Ross and Fletcher 1985, Ross 1986).

Two separate studies of *Polistes exclamans* found relatedness values between workers and brood of about 0.38, which is lower than worker relatedness to their own young (Lester and Selander 1981, Strassmann 1985b). These are the only such studies in *Polistes*. It is especially interesting that workers usually remain on their natal nest in this species in spite of low relatedness as workers of *P. exclamans* sometimes leave their natal nest to begin a new (satellite) nest of their own (Strassmann 1981a). The decisions of other workers to join such a satellite nest depend on their relatedness to the queen of the satellite; they join her if their relatedness is high (Strassmann 1981b). These results indicate that workers sometimes respond to alternatives, make choices based on relatedness, and yet usually choose to remain on their natal nest in spite of the presence of an alternative (nesting alone) which would yield higher relatedness to the brood. Coming back to Hamilton's rule, the available evidence on relatedness indicates that ecological factors must be important in the origin and maintenance of eusociality.

## COSTS AND BENEFITS OF EUSOCIALITY

Perhaps because of the limitations of the haplodiploid hypothesis, current opinion seems to favor explanations that stress costs and benefits (Lin and Michener 1972, Alexander 1974, Evans 1977, West-Eberhard 1975 1978, Eickwort 1981, Brockmann 1984, Andersson 1984, Stubblefield and Charnov 1986, Alexander and Noonan *in press* ). If there is no special relatedness advantage, then the best case (in an outbreeder) is helping full sibs: $r^* = r = 1/2$. This means that even in the best of circumstances eusociality cannot be favored unless the benefit of helping is greater than the cost, $\Delta w^* > \Delta w$ (see formula 1).

Therefore, at the very least, we need to explain how an individual can rear more of a relative's offspring that it can rear of its own. Compared to the theoretical work on relatedness, this area has been relatively neglected. A few theoretical studies have addressed the question of how the organization of work within colonies can evolve to make the colony more efficient (Oster and Wilson 1978, Wilson 1985, Jeanne 1986), but in the early stages of eusociality, efficient work patterns would not yet have evolved. Moreover, it is not clear that these mechanisms always give the required efficiency. From collections of colonies of social insects, Michener (1964) found that *per capita* productivity declines with colony size in most species. This suggests that the most productive colony size is one, and that each worker adds less to the colony than it could have reared on its own; the $\Delta w^* > \Delta w$ requirement is not met. There are, however, two general ways of reconciling the observation with the requirement that $\Delta w^* > \Delta w$. The first hypothesizes differences in reproductive potential among individuals, and is commonly referred to as 'best of a bad job' (e.g. Brockmann 1984). The second postulates fitness gains to individuals in groups that would not be detected in studies like Michener's (1964). This is where true ecological advantages to grouping fall. These two categories of costs-and-benefits explanations for eusociality will be discussed in the next two sections.

## BEST OF A BAD JOB AND THE EVOLUTION OF EUSOCIALITY

Extrinsic or intrinsic constraints may limit an individual's reproductive ability when it nests alone. Extrinsic constraints include shortages of nesting sites or territories, shortages of mates, and shortages of time for nesting (e.g. Brown 1987, Herbers 1986, Strassmann *et al.* 1987). Intrinsic constraints make some females less capable of laying eggs than they are of tending another female's brood (Craig 1983). Both types of constraints can result in selection on females to join groups rather than nest alone. They are both consistent with Michener's finding of decreasing *per capita* fitness with group size because some individuals may be incapable of nesting alone, so that even if they add relatively little to the colony success, they are still opting for the best alternative in a bad situation. These are discussed below with special reference to *Polistes.*

## Nest Site Constraints

One of the most important requirements for any organism that displays parental care is to have a safe site in which to raise the young. This is particularly important when the young are immobile and defenseless, as is the case in altricial birds (e.g. Brown 1987), many carnivores (e.g. Moehlman 1986), and most insects that exhibit parental care (e.g. Eickwort 1981). If a particular feature of the environment renders it more protected than other areas, then the number of such locations may limit the numbers of individuals that can raise young. If all safe sites have been filled, an individual may achieve higher inclusive fitness by helping a relative rear additional progeny in a safe location than it could raise by starting its own nest in an unsafe location.

Demonstrations that this principle is important in group nesting require identification of the limiting habitat, demonstration that all sites are filled, and observation that non-breeders can help breeders in the safe sites. Experiments can verify that group size diminishes when additional nest sites are added. To our knowledge the only study of this was conducted by Herbers (1986) on *Leptothorax longispinosus.* Polygyny (queens sharing a nest) decreased when nest sites were added to the acorns and hollow twigs usually used for nests. Other examples of limited nest sites are caves, holes in the ground and hollow trees. The re-use of natal nest sites even when facing the disadvantages of parasites that have accumulated in such sites also suggests that nest sites are limited. This is common in a variety of social insects (e.g. Batra 1966, Starr 1975, Evans and Hook 1982, Strassmann 1983, Kukuk and Eickwort 1987, Michener 1985, Itô *et al.* 1985, Hook 1985 1987). In fact, re-use of the natal nest or the natal nest site is a common way for groups to begin in primitively social bees and wasps. Re-use of the natal nest may not fall under best-of-a-bad-job conditions if it is the simplest way of finding relatives (which then allow individuals to obtain ecological advantages), or if there is a substantial saving in time and expense necessary to construct a new nest.

There is no good evidence that nest site constraints are important factors selecting for grouping in *Polistes.* Many species nest in vegetation, on cliffs, and on eaves where nest sites seem to be nearly infinite (e.g. West-Eberhard 1969, Strassmann 1979, Strassmann and Hughes 1986). It may be argued that space is limited on a cliff or eave (Noonan 1979, Cervo and Turillazzi 1985, Queller and Strassmann 1988). However, such arguments are susceptible to the criticism that the nests could have been packed more closely together. *P. carolinus* may exemplify grouping because of nest site constraints as it nests in dark places like artificial nest boxes and hollow trees. This species uses the same nest boxes year after year and prepares them for re-use by tearing down the nest at the end of the season (Hughes and Strassmann, unpublished). Nests are begun by 2.2 foundresses on average (the range is 1 to 7), a larger average number of foundresses than other species in the area (Hughes and Strassmann in press). However, average foundress numbers per nest did not change from 1982 to 1987 even though numbers of new nest boxes varied annually. Thus, the addition of nest boxes does not cause the decrease in foundress association size that would be expected if females group because of the lack of suitable nest sites.

Habitat constraints, which are in many respects similar to nest site constraints, are favorite explanations for helpers at the nest in many bird species (e.g. Koenig and Mumme 1987, Woolfenden and Fitzpatrick 1984). While habitat is certainly restricted in a number of bird species with helpers, it is not clear that this is the driving force behind helping (Brown 1987, Austad and Rabenold 1985). For example, Koenig and Mumme (1987) noted that adding or removing granaries did not have a marked effect on group size in acorn woodpeckers.

## Subfertility

A related best-of-a-bad-job hypothesis supposes that some individuals are in poor condition (or "subfertile"; West-Eberhard 1978) such that they are unlikely to succeed at reproducing alone. These individuals could make the best of their situation by helping, provided that they are not also handicapped in their abilities to help (Craig 1983). In some cases, the poor condition may be imposed by parental manipulation (Alexander 1974) in order to force some progeny to be helpers. This kind of hypothesis must certainly apply to many higher eusocial insects with differentiated castes. Workers are less capable of being productive egg layers, indeed sometimes completely incapable. However, attempts to find support for this hypothesis in social insects without distinct castes have failed (Haggard and Gamboa 1980, Sullivan and Strassmann 1984, Kukuk and Eickwort 1987, Queller and Strassmann, this volume). This failure is serious if the hypothesis is to explain the origin of eusociality as eusociality presumably evolved prior to the development of castes. But the failure should perhaps come as no surprise since the hypothesis requires the uncoupling of talents for foraging from those for egg laying (Craig 1983).

The subfertility hypothesis has been accepted as pivotal in the evolution of eusociality in part because it is so logical and attractive an explanation. Here we summarize the results of our attempts to find support for the hypothesis in *P. annularis* (Strassmann 1979, Sullivan and Strassmann 1984, Queller and Strassmann 1988). We also addressed the subfertility hypothesis in *P. bellicosus* (Queller and Strassmann, this volume).

According to the subfertility hypothesis, poor quality females that are not capable of nesting alone should join relatives on nests where they will function as subordinates. In *P. annularis* we measured female quality in two ways: size (Sullivan and Strassmann 1984, Strassmann 1983) and whether or not they had been deprived of honey during the winter (Strassmann 1979). Both measures had significant effects on female fitness. However, neither small females nor females that had been deprived of honey were found in larger groups. Thus grouping was not a response of females to their overall lowered condition. The only study that seems to support the subfertility hypothesis demonstrated that under laboratory conditions some females of *P. fuscatus* failed to initiate nests (Gibo 1974). However even females of singly-founded species frequently fail to build nests in the laboratory because of the artificial conditions, so this experiment cannot be regarded as support for the subfertility hypothesis.

When females are infected with stylopid parasites, reproduction is reduced more drastically than is the ability to work, as the first effect of the parasite is to sterilize the female (Strambi 1965, Strambi and Strambi 1973). Selection might favor such females working on a sister's nest because the female could work but not lay eggs. But she would probably be better off staying away from all relatives as she might pass on the parasites to the brood she reared, thus having a net negative effect on the relative's progeny. Also stylopid parasites are not common enough to account for most workers.

Therefore, we conclude that there is no evidence that either nest site constraints or subfertility have been important in the evolution of eusociality. However there have been so few empirical tests of either hypothesis that it is entirely possible that this position could change with the publication of new studies that focus on these questions, particularly on previously unstudied taxa.

## Ecological Advantages of Eusociality

If the best of a bad job explanation fails, then group members should have higher inclusive fitness than solitary individuals. Solitary individuals may occur in species that ordinarily nest in groups if they cannot find any relatives with whom to nest (Noonan 1981). A comprehensive study of all individuals in a given area from colony inception to the production of reproductives should reveal the advantages of group nesting. Detailed studies of the correlates of reproductive success should also reveal the specific selective factors that give groups their special advantages over solitary individuals. This is particularly likely if the study is conducted in native habitats where the selective factors for grouping are likely to be operating.

Unfortunately, relatively few such studies have been carried out on primitively eusocial insects (e.g. Batra 1966, Jeanne 1972, Sakagami 1977, Litte 1977, 1979, Noonan 1979, 1981, Pickering 1980, Strassmann 1981c, Queller and Strassmann 1988, Strassmann in preparation, Strassmann and Hughes in preparation). These studies indicate that the probability that a colony will fail is critical in assessing the costs and benefits of grouping. Smaller groups of females are, in general, more likely to fail in their nesting attempts than are larger groups of females. Failure may be due to loss of all tending adults, or to loss of the nest to predation and the subsequent failure to build a new nest successfully. This advantage of larger groups would not be detected in a study in which nests were collected at one time because the failed nests would not be represented in the collection. Following colonies over longer periods of time is necessary to assess the importance of predation on adults and brood, as was noted by Michener (1964). Predation on brood in nests and predation on adults may confer an advantage to larger groups.

Brood may be killed individually by parasitoids or all at once by a nest predator which removes the entire nest and consumes the contents. Larger associations may be better protected from predators and parasitoids due to increased vigilance, or more effective stinging attacks (Alexander 1974). Defense against parasitoids is often cited as an advantage of early grouping in colonies (e. g. Evans 1977). Such an advantage should translate into greater *per capita* fitness for females in groups and could be detected simply by collecting colonies. Since such collections do not usually indicate that there is a *per capita* advantage (Michener 1964), this is unlikely to be the key factor favoring grouping. In contrast, increased abilities for defense of the entire nest from destruction by a predator would not be detected by a collection, and may be a major advantage to group nesting (Alexander 1974). However, we are unaware of any study that has documented lower predation rates for colonies defended by greater numbers of primitively eusocial insects. In *Polistes* there is no evidence that larger groups deter parasitoids more effectively (Strassmann 1981c). Nor is there any evidence in this genus that larger groups of individuals are more effective at predator deterrence (Gibo 1978, Strassmann 1981c, Strassmann *et al.* 1988).

Even if the group is not successful at defense, it may be better at building a new nest after the original nest is destroyed. This is the case in *Polistes bellicosus* in which larger groups of individuals were better able to build a new nest and successfully rear brood in it (Strassmann *et al.* 1988). We removed 49 nests and their brood without harming the adults and then monitored the subsequent behavior and reproductive success of the adults (Strassmann *et al.* 1988). After 44 days those females which were originally in groups of 4 or more had much higher *per capita* fitness rates than did females in smaller groups, because the rebuilt nest was less likely to fail. In fact, among successful nests there was no relationship between numbers of adults produced after 44 days and group size. Including the failed nests in the analysis resulted in a *per capita* advantage to larger groups. As nests are destroyed very frequently in this population of *P. bellicosus*, it is critical to include nest failure in any analysis of the advantage of group size. The key advantage that we observed would not be detected in a simple collection of nests and their associated brood. In summary, groups are better able to recover from predation events than are solitary individuals. No such advantage has been detected for defense against either predators or parasitoids. Therefore it is critical that studies of the costs and benefits of group nesting follow colonies long enough to measure the effects of nest predation.

## Demographic Advantages

One disadvantage of trying to rear young alone is that death of the parent leads to the death of all its dependent young. This may be particularly severe for insects in which high adult mortality rates are combined with extended periods of complete dependency of young. For example, in the wasps *Polistes exclamans* (Strassmann and Orgren 1983, Strassmann 1985a) and *Mischocyttarus drewseni* (Jeanne 1972) the average adult worker longevity as an adult is considerably less than the time required to rear an offspring to independence. Most individuals, if they nested alone, would therefore fail completely. Cooperative care of the young can help circumvent this problem in two related ways.

First, when a worker or a co-foundress dies, its investment in still-dependent young is protected by the presence of other adults who can rear the young to the age of independence. Thus the investment in brood of a group-nesting individual is insured against that individual's death by the presence of others that would continue to rear the young. In *Polistes* having at least one foundress survive to the worker emergence stage is an important advantage of foundress associations (Metcalf and Whitt 1977, Queller and Strassmann 1988). Even though colonies tend to be larger later in the colony cycle, the same advantage probably also applies to workers remaining on the natal nest. Even in mid-summer the main cause of colony failure in *Polistes exclamans* is the death or disappearance of all adults (Strassmann 1981c). Larger colonies are less likely to fail for this reason than smaller ones.

There is a related, but distinct, advantage of cooperative brood care in the face of high adult mortality and extended parental care. Besides having another adult to carry on one's investment after one's death, it is also possible to carry on investment that others have started (Queller submitted). This is not necessarily the same as the first advantage. For example, a worker staying on its natal nest can obtain an advantage by carrying on the queen's initial brood investment even if the queen is still alive. The advantage to the worker is a reproductive head start. If it had nested alone, it would have to wait at least the length of the entire developmental period and run the risk of dying and failing to realize any of its investment. As a worker, however, it can begin to realize some of its reproductive investment very quickly because it can invest in young that are already partly grown. If it is unlucky enough to suffer an early death, it will still have realized some of its reproductive investment. Analysis of demographic data on four species of polistine wasps shows this to be a strong advantage favoring worker behavior (Queller submitted). Termite workers have a special head start advantage as juveniles can function as workers but cannot yet reproduce on their own (Alexander and Noonan in press).

In summary, the combination of high mortality with an extended period of parental care makes it unlikely that any given adult will successfully rear offspring on its own. Cooperation is advantageous under these conditions because an individual can successfully reproduce even if it survives for a relatively short period. This kind of advantage would not be evident in Michener's (1964) studies of colony productivity because one-time collections give no information about individuals that have died. Further research on the demography of social insects is necessary to determine the generality and magnitude of this factor in selecting for group living.

## CONCLUSIONS

If Evans' (1977) plea for more empirical studies of the insects important in the evolution of eusociality had been heeded, now would be the time for a definitive review. Instead we review a small list of field studies with predominantly negative results. Cooperating individuals are usually related to each other, but in most species worker to brood relatedness is not higher than worker to progeny relatedness. To date, neither subfertility or nest site constraints have been demonstrated to have played a major role in the early evolution of eusociality. By a process of elimination we conclude that there must be real ecological advantages to group nesting. This conclusion seems to be supported by the enormous ecological success of social insects (reviewed in Wilson 1987, Jeanne and Davidson 1984). Collections of colonies reveal a declining *per capita* output with group size but group living persists. Therefore, all indicators point to colony failure as a critical variable in the evolution of eusociality. Groups are protected against failure by their enhanced abilities to recover after loss of both nest and brood. Groups can also protect against the loss of all adults and subsequent starvation of the brood. Future studies would do well to focus on colony failure in looking for advantages to eusociality. However the number of empirical studies of native populations is so small that additional studies of relatedness levels, subfertility, or nest site constraints in appropriate populations may change this focus.

## Acknowledgements

We thank Colin Hughes for collaborating on many of the cited field studies which were conducted at Brazos Bend State Park under Texas Parks and Wildlife permit numbers 15-82, 11-83, 8-84, 16-85, 20-86 and 18-87. We thank D. Riskind of the Texas Parks and Wildlife Department and L. Fowler and C. VanBaarle of Brazos Bend State Park for their cooperation. This research was partially supported by NSF BSR86-05026.

## LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 4:325-383.

Alexander, R. D. and K. M. Noonan. In press. The evolution of sociality. 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.

Austad, S. N. and K. N. Rabenold 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren. *Behav. Ecol. Sociobiol.* 17:19-27.

Bartz, S. 1979. Evolution of eusociality in termites. *Proc. Natl. Acad. Sci. USA* 76:5764-5768.

Batra, S. W. T. 1966. The life cycle and behavior of the primitively social bee, *Lasioglossum zephyrum* (Halictidae). *Univ. Kansas Science Bulletin* 46:359-423.

Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. Q. Rev. Biol. 63:291-311.

Brockmann, H. J. 1984. The evolution of social behavior in insects. In *Behavioural Ecology, An Evolutionary Approach*, J. R. Krebs and N. B. Davies, eds. Second Edition. Sinauer Assoc. Inc.:Sunderland, Mass. pp. 340-361.

Brown, J. L. 1987. *Helping in Communal Breeding Birds: Ecology and Evolution.* Princeton University Press:Princeton, N.J.

Cervo, R. and S. Turillazzi. 1985. Associative foundation and nesting sites in *Polistes nimpha. Naturwissenschaften* 72:48-49.

Charnov, E. L. 1978. Evolution of eusocial behavior: offspring choice or parental parasitism. *J. Theor. Biol.* 75:451-465.

Craig, R. 1983. Subfertility and the evolution of eusociality by kin selection. *J. Theor. Biol.* 100:379-397.

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

Crozier, R. H. 1970. Coefficients of relationship and the identity of genes by descent in the Hymenoptera. *Am. Nat.* 104:216-217.

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. and P. Luykx. 1985. The evolution of termite eusociality is unlikely to have been based on male-haploid analogy. *Am. Nat.* 126:867-869.

Darwin, C. 1859. *The Origin of Species by Means of Natural Selection or The Preservation of Favored Races in The Struggle for Life.* Modern Library:New York.

Eickwort, G. C. 1981. Presocial insects. In *Social Insects*, H.R. Herman,ed. Academic Press, New York pp.199-280.

Emlen, S. T. 1981. Altruism, kinship, and reciprocity in the white-fronted bee-eater. In *Natural Selection and Social Behavior*, R. D. Alexander and D. W. Tinkle, eds. Chiron Press:New York pp. 217-230.

Emlen, S. T. 1984. Cooperative breeding in birds and mammals. In *Behavioural Ecology, An Evolutionary Approach*, J. R. Krebs and N. B. Davies, eds. Sinauer Assoc. Inc.:Sunderland, Mass. pp. 305-339.

Evans, H. E. 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. *BioScience* 27:613-617.

Evans, H. E. and A. W. Hook. 1982. Communal nesting in the digger wasp, *Cerceris australis* (Hymenoptera: Sphecidae) *Aust. J. Zool.* 30:557-568.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection.* Clarendon Press:Oxford. (Reprinted and revised, 1958. Dover:New York).

Gadagkar, R. and N. V. Joshi. 1984. Social organization in the Indian wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae). *Z. Tierpsychol.* 64:15-32.

Gibo, D. L. 1974. A laboratory study on the selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae). *Can. Entomol.* 106:101-106.

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. 1986. Split sex ratios and the evolutionary origins of eusociality. *J. Theor. Biol.* 122:95-121.

Haggard, C. M. and G. J. Gamboa. 1980. Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Can. Ent.* 112:101-106.

Haldane, J. B. S. 1955. Population genetics. *New Biol.* 18:34-51.

Hamilton, W. D. 1963. The evolution of altruistic behavior. *Am. Nat.* 97:354-356.

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

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

Hamilton, W. D. 1970. Selfish and spiteful behavior in an evolutionary model. *Nature* 228:1218-1220.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in the social insects. *Ann. Rev. Ecol. Syst.* 3:193-232.

Herbers, J. M. 1986. Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. Behav. Ecol. Sociobiol. 19:115-122.

Hook, A. W. 1985. *The comparative ethology of communal nesting in the Philanthinae (Hymenoptera:Sphecidae).* Ph. D. Dissertation, Colorado State Univ.:Fort Collins, Colorado 142 pp.

Hook, A. W. 1987. Nesting behavior of Texas *Cerceris* digger wasps with emphasis on nest reutilization and nest sharing (Hymenoptera:Sphecidae). *Sociobiology* 13:93-118.

Hughes, C. R. and J. E. Strassmann. Foundress mortality after worker emergence in social wasps (*Polistes*) *Ethology* in press.

Itô, Y.,O. Iwahashi, S. Yamane and Sk. Yamane 1985. Overwintering and nest reutilization in *Ropalidia fasciata* (Hymenoptera: Vespidae). *Kontyû* 53:486-490.

Jarvis, J. V. M. 1981. Eusociality in a mammal: Cooperative breeding in naked mole-rat colonies. *Science* 212:571-573.

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

Jeanne, R. L. 1980. Evolution of social behavior in the Vespidae. *Ann. Rev. Entomol.* 25:371-396.

Jeanne, R. L. 1986. The evolution of the organization of work in social insects. *Monitore zool. ital. (N.S.)* 20:119-133.

Jeanne, R. L. and D. W. Davidson. 1984. Population regulation in social insects. In *Ecological Entomology,* C. B. Huffaker and R. L. Rabb, eds. John Wiley and Sons:New York pp. 559-587.

Koenig, W. D. and R. L. Mumme. 1987. *Cooperatively breeding acorn woodpecker.* Princeton Univ. Press:Princeton, NJ. 435pp.

Kukuk, P. F. and G. C. Eickwort. 1987. Alternative social structures in halictine bees. In *Chemistry and Biology of Social Insects,* J. Eder and H. Rembold, eds. Verlag J. Peperny:Munich. pp. 555-556.

Lacy, R. C. 1980. The evolution of eusociality in termites: a haplodiploid analogy? *Am. Nat.* 116:449-451.

Lacy, R.C. 1984. The evolution of termite eusociality: reply to Leinaas. *Am. Nat.* 123:876-878

Leinaas, H. P. 1983. A haplodiploidy analogy in the evolution of termite eusociality? A reply to Lacy. *Am. Nat.* 121:302-304.

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

Lin, N., and C. D. Michener. 1972. Evolution of sociality in insects. *Quart. Rev. Biol.* 47:131-159.

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

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

Lush, J. L. 1947. Family merit and individual merit as bases for selection. *Am. Nat.* 81: 241-261, 362-379.

Luykx, P., and R.-M. Syren. 1979. The cytogenetics of *Incistitermes schwarzi* and other Florida termites. *Sociobiology* 4:191-209.

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

Michener, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. *Insectes Sociaux* 11:317-341.

Michener, C. D. 1985. From solitary to eusocial: need there be a series of intervening species? In: *Experimental Behavioral Ecology,* B. Hölldobler and M. Lindauer, eds. Stuttgart pp. 293-305.

Moehlman, P. D. 1986. Ecology of cooperation in canids. In *Ecological aspects of social evolution*, D. I. Rubenstein and Richard W. Wrangham, eds. Princeton Univ. Press.:Princeton, NJ pp 64-86.

Nonacs, P. 1986. Ant reproductive strategies and sex allocation theory. *Quart. Rev. Biol.* 61:1-21.

Noonan, K. M. 1979. *Individual strategies of inclusive fitness maximizing in the social wasp, Polistes fuscatus (Hymenoptera:Vespidae).* Ph.D. Dissertation University of Michigan:Ann Arbor, Michigan.

Noonan, K. M. 1981. Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. In *Natural selection and social behavior*, R. D. Alexander and D. W. Tinkle, eds. Chiron Press:New York pp. 18-24.

Oster, G. F., and E. O. Wilson. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press:Princeton, NJ

Page, R. E., Jr. 1986. Sperm utilization in social insects. *Ann. Rev. Entomol.* 31:297-320.

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 relatedness and evolution of insect sociality. *Behav. Ecol. Sociobiol.* 15:241-248.

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

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev. Cambridge Philos. Soc.* 45:525-567.

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

Pickering, J. 1980. *Sex ratio, social behavior and ecology in Polistes (Hymenoptera: Vespidae), Pachysomoides (Hymenoptera: Ichneumonidae) and Plasmodium (Protozoa, Haemosporida).* Ph. D. Dissertation, Harvard Univ.:Cambridge, Mass.

Queller, D. C. The evolution of eusociality: a head-start hypothesis. Submitted.

Queller, D. C., and J. E. Strassmann. 1988. Reproductive success and group nesting in the paper wasp, *Polistes annularis*. In *Reproductive Success: Studies in Individual Variation in Contrasting BreedingSystems*, T. H. Clutton-Brock, ed. University of Chicago Press:Chicago. pp. 76-96.

Ross, K. G. 1986. Kin selection and the problem of sperm utilization in 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.

Seger, J. 1983. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* 301:59-62.

Sakagami S. F. 1977. Seasonal change of nest survival and related aspects in an aggregation of *Lasioglossum duplex* (Dalla Torre), a eusocial halictine bee (Hymenoptera: Halictidae). *Res. Popul. Ecol.* 19:69-86.

Starr, C.K. 1975. Nest reutilization by *Polistes metricus* (Hymenoptera:Vespidae) and possible limitation of multiple foundress associations by parasitoids. *J. Kansas Entomol. Soc.* 49:142-144.

Strambi, A. 1965. Influence du parasite *Xenos vesparum* Rossi (Strepsiptère) sur la neurosécrétion des individus du sexe femelle de *Polistes gallicus* L. (Hyménoptère, Vespidae). *C.R. Acad. Sci. Paris* 260:3767-3769.

Strambi, A. and C. Strambi. 1973. Influence du développement du parasite *Xenos vesparum* Rossi (Insecte, Strepsitère) sur le système neuroendocrinien des femelles de *Polistes* (Hyménoptère, Vespidae) au début de leur vie imaginale. *Arch. d'anotomie microscopique et de morphologie expérimentale* 62:39-54.

Strassmann, J. E. 1979. Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. *Science* 204:207-209.

Strassmann, J. E. 1981a. Evolutionary implications of early male and satellite nest production in *Polistes exclamans* colony cycles. *Behav. Ecol. Sociobiol.* 8:55-64.

Strassmann, J. E. 1981b. Kin selection and satellite nests in *Polistes exclamans*. In *Natural selection and social behavior*, R. D. Alexander and D. W. Tinkle, eds. Chiron Press:New York pp. 45-58.

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

Strassmann, J. E. 1983. Nest fidelity and group size among foundresses of *Polistes annularis* (Hymenoptera: Vespidae). *J. Kans. Entomol. Soc.* 56:621-634.

Strassmann, J. E. 1985a. Worker mortality and the evolution of castes in the social wasp, *Polistes exclamans. Insectes Sociaux* 32:275-285.

Strassmann, J. E. 1985b. Relatedness of workers to brood in the social wasp, *Polistes exclamans* (Hymenoptera: Vespidae). *Z. Tierpsychol.* 69:141-148.

Strassmann, J. E. and C. R. Hughes. 1986. Latitudinal variation in protandry and protogny in polistine wasps. *Monitore zool. ital. (N.S.)* 20:87-100.

Strassmann, J. E. and Orgren, M. C. 1983. Nest architecture and brood development times in the paper wasp, *Polistes exclamans* (Hymenoptera: Vespidae). *Psyche* 90:237-248

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:Munich. 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* 69:1497-1505.

Stubblefield, J. W., and E. L. Charnov. 1986. Some conceptual issues in the origin of eusociality. *Heredity* 57:181-187.

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.

Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems.* Harvard Univ. Press:Cambridge, Mass.

Trivers, R. L. 1974. The evolution of reciprocal altruism. *Quart. Rev. Biol.* 46:35-39, 45-47.

Trivers, R. L. and H. Hare. 1976. Haplodiploidy and the evolution of social insects. *Science* 191:249-263.

Vehrencamp, S. L. 1979. The roles of individual, kin and group selection in the evolution of sociality. In *Handbook of Behavioral Neurobiology, vol. 3. Social Behavior and Communication,* P. Marler and J. Vandenbergh, eds. Plenum:New York pp. 351-394.

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. of the Museum of Zool, U. of Michigan* 140: 1-101.

West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.* 50:1-33.

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

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

Williams, G. C. and D. C. Williams. 1957. Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution* 11:32-39.

Wilson, E. O. 1971. *The insect societies.* Belknap Press of Harvard Univ. Press:Cambridge, Mass.

Wilson, E. O. 1985. The sociogenesis of insects colonies *Science* 228:1489-1495.

Wilson, E. O. 1987. Causes of ecological success: the case of the ants. *J. Anim. Ecol.* 56:1-9.

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