

POPULATION BIOLOGY OF SOCIAL INSECT CONSERVATION

PEKKA PAMILO^{1,2} AND ROSS H. CROZIER¹

¹ School of Genetics and Human Variation, La Trobe University, Bundoora 3083, Australia, and Victorian Centre for Conservation Genetics

² Program of Conservation Biology, Department of Genetics, Uppsala University, Box 7003, 750 07 Uppsala, Sweden

Abstract

Pamilo, P. and Crozier, R.H., 1997. Population biology of social insect conservation. *Memoirs of the Museum of Victoria* 56: 411-419.

Social insects, especially ants and termites, are keystone species in most non-arctic terrestrial ecosystems, but their special features have received little attention in conservation discussions. Both plants and other animals are affected by social insects as keystone species. Despite the abundance of species it may be that rather few in any one location are critical to understanding the ecosystem, because of the mosaic nature of the distributions of the dominant species. Social insects present a wide array of life patterns within the broad sway of sociality, varying in having colonies which are annual or perennial, multi- or single-nested, and multi- or single-queened. Populations of social insects may often be much more vulnerable than they appear on the basis of numbers of individuals; the reproductive division of labor means that the effective population size may be small for a species of apparently reasonable abundance. Factors increasing effective population size occur in many species, especially rare ones, but it is uncertain these represent adaptations to rareness. In eusocial Hymenoptera, many species, probably most, show inbreeding depression of a special kind due to the production of sterile males caused by homozygosity at the sex locus. In many termites, on the other hand, colonies pass naturally through cycles of inbreeding and outbreeding. Socially parasitic ants which habitually inbreed appear to have evolved a different means of sex-determination and do not show inbreeding depression. Differences in the mode of colony formation between species also lead to difference in the longevity of colonies, dispersal abilities, and the robustness of populations to disturbance. The greatest threats to social insects, apart from humans, are other social insects, and this applies also to invading ant pest species, which tend to have particularly strong impacts on native species. Social insects thus form a vital part of ecosystems, but also impel the need to accept long-term studies because of the slow pace at which their populations change.

Introduction

Invertebrates generally differ from vertebrates in the conservation problems they are prone to because of the scale on which they live. Even a small area can contain a large population, so that considerations such as the area of habitat required and problems of a small population size (leading, at least potentially, to inbreeding depression) can be less important and more easily solved. For such populations, habitat loss can remove whole populations without an intervening stage of fragility.

Social insects, however, differ in several important aspects from other invertebrates. We can recognize three major features that characterize social insects and are important in their population biology and in the population biological aspects of their conservation. First, the ratio of population size to biomass is small. Only a small number of individuals reproduce and the effective population size maintained in a given

area can be small and comparable to that of many vertebrates. Yet, the non-reproductive workers constitute a large biomass which affects both the food requirements of the population and the impact of the population on its environment. Second, the life of social insects normally centres around a nest, which makes them sedentary and can restrict dispersal. In that respect their population biology can resemble that of plants rather than of other insects. Third, most social insects (ants, bees and wasps) belong to the order Hymenoptera and have a male-haploid sex-determination system. This genetic mechanism affects some genetic population characteristics, particularly the effective population size and the genetic load resulting from the sex-determination mechanism.

Our aim here is to describe how these features, which are characteristic of social insects, affect their populations and in which ways they can influence their conservation.

The role of social insects in ecosystems

One criterion that can be used when setting priorities for conservation is to what extent other species depend on the species in question (Soulé, 1987). Without focusing on any single species, we can state that social insects in general form an important group both in ecosystems in general and in having important mutual relationships with other organisms, plants as well as animals.

The social life pattern has made social insects evolutionarily very successful, not so much in species diversity but in biomass. Social Hymenoptera make only about 10% of all described hymenopteran species, but the estimates from South-American tropical rainforests show that social insects make more than a quarter of all animal biomass, and c. 80% of all insect biomass (reviewed by Wilson, 1990). It is reasonable to assume that they have a key role in the energy budgets of many other ecosystems, although the ant biomass in temperate grassland areas is only 1–15% of all invertebrates (Pisarski, 1978). The diversities of social insect species are highest in the tropics, except of bumblebees that exist mainly in temperate areas. Of the major groups of social insects, termites and stingless bees occur mainly in tropics and subtropics. The major centres of social wasps are partly in south-east Asia (vespine wasps) and in neotropics (polybine wasps).

Interspecific competition among ants has led to dominance hierarchies between species, and the dominant species can largely influence the composition of the whole ant community. This has led to so called ant mosaics (Leston, 1978; Majer, 1993), found particularly in tropical forests. Replacement of the dominant species can lead to a large change in the assemblage not of only ant species but also of other arthropods (perhaps even vertebrates) as well. In fact, Gilbert (1980) suggested as one of the research priorities for neotropical conservation biology 'autecology of link species, keystone mutualists and dominant ant species'. Majer (1993) notes that ant mosaics become rarer as one moves away from the tropics.

Social insects affect their environment also by building nests and by manipulating the foraging areas. These activities create niches for many other organisms, and indeed, the nests of social insects harbour many different guests — and parasites. Some of the best studied examples come from the *Maculinea* butterflies, the big blues, whose caterpillars live in colonies of the *Myrmica* ants and whose life cycles depend com-

pletely on the host ants. There have been several national extinctions of *Maculinea* species in western Europe (five species live in Europe). The conservation of the butterfly populations requires simultaneous attention on the host ant populations, and active management on these lines has been carried out to reintroduce the large blue (*M. arion*) in Britain (Elmes and Thomas, 1992; Thomas, 1995). Similar situations are expected in Australia, where the lycaenid butterflies include species depending on the care provided by ants (New, 1993).

As regards the plants, the main roles of social insects are in protecting them against herbivores (which has led to the evolution of special domatia, extrafloral nectaries and food bodies by some plants (Beattie, 1985)), in spreading seeds, and as pollinators. For example, Handel et al. (1981) counted that 13 of 45 herbaceous plant species in a mesic forest had seeds dispersed by ants, and they comprised ca 40% of the above-ground herbaceous biomass. Ants contribute significantly to the population dynamics of such myrmecochores and shape the structure of the whole plant community. They are also important for the viability of some rare and endangered plant populations. Although bees are major pollinators of angiosperms, social bees have generally a less important role. They can, however be locally important. Some bees visit only a few closely related species of plants, and the protection of such oligolectic bees relies on the preservation of these plants. At the same time specialist pollinators can be important for the success of the plant populations. Such a close relationship exists between *Aconitum septentrionale* and its pollinator, the bumblebee *Bombus consobrinus*, both of them being rare and endangered in northernmost Europe (Pekkarinen, 1979).

The relatively low species diversity of social insects, at least when compared to many other insects, makes it feasible to use the phylogenetic approach for defining priority areas to protect the worldwide species diversity. Bumblebees of the *Bombus sibiricus*-group comprise one of the first taxonomic groups where this approach has been applied, although the authors note that conservation of bumblebees is not yet generally considered to have a high priority (Williams et al., 1993). There are, however, reports indicating that bees are generally declining (O'Toole, 1993).

Social insect life patterns

Social insect life patterns vary enormously, and their societies can be classified on several bases.

We present here some basic features (Crozier and Pamilo, 1996), all of these adding important aspects also to conservation, mainly because they affect either the effective population size or dispersal.

Annual vs perennial colonies. Bumble bees, many primitively social bees, and many social wasps have annual colonies. They have a solitary phase, with a female (or a group of females) starting a colony and taking care of the first brood, after which the offspring will stay as helping individuals raising additional broods. The colony has first an ergonomic stage when it grows, and the sexual offspring are produced towards the end of the season when the colony moves to a reproductive stage (Oster and Wilson, 1978). Honeybees, stingless bees, swarm-founding wasps, and all ants and termites have perennial colonies. A colony can have a short solitary period if a single female establishes the colony, but after that the colony can survive several years and produce sexuals repeatedly.

Independent vs dependent colony foundation. There are two major modes of nest foundation: independent and dependent. Independently founding females establish new nests without any help from workers, either singly or in small groups. Dependent nest founding relies on workers helping the queen. Dependent nest foundation commonly takes place by budding or fission, in which a new nest is established by workers and queens departing from the parental nest. New nests can also in some ants be established by help of alien species, in form of temporary social parasitism. The queen intrudes into a host colony, and the host workers raise the first brood, after which the colony gradually turns into that of the intruding species.

Monogynous vs. polygynous colonies. Many social insects have a single reproductive female, a queen, in their nests and the colonies are called monogynous. This is the case in the honeybees, most other eusocial bees, many eusocial wasps, the majority of termites and many ants. This is, however, not a rule and about half of the European ant species have polygynous colonies, ie. they have several to many reproductive females per nest (Buschinger, 1974). Some wood ants of the *Formica rufa* group have up to hundreds of queens in their mounds (Rosengren and Pamilo, 1983). Even if a colony has many queens, they may not share reproduction evenly and their contributions have a non-zero variance, ie. there exists a reproductive skew (Keller and Reeve, 1994; Pamilo and Crozier, 1996)

Monodomous vs. polydomous colonies. A single nest usually forms a colony and defends its

nest and/or foraging area against competing colonies. Such single-nest colonies are termed monodomous. It is, however, common particularly in some ants that neighbouring nests are connected to each other and exchange individuals, brood and food. Such multinest colonies are termed polydomous. It is evident that such polydomous colonies can effectively occupy and dominate a habitat patch. In an extreme form, when the network of interconnected nests covers a large area, it has been called a supercolony, and if there is no hostility within the whole population, the population is termed unicolonial. Unicolonial species appear to become pests more often than other species, but this apparent trend may simply indicate that many unicolonial species remain to be detected.

Effective population size

Vulnerability of populations can be caused by deterministic or stochastic factors. Stochastic factors depend on the population size and its fluctuations, and on the environmental stochasticity. As mentioned above, the ratio of effective population size to biomass is generally low, or very low, in social insects. The territory of a single ant nest can cover several hectares, yet there may be just one reproductive female in the nest. The density of social insect populations can therefore be low, even though the worker ants are abundant.

The concept of effective population size (N_e) refers to the genetic effects of a finite population size. There are various concepts of N_e , and the one commonly used is the inbreeding effective size. In diploid populations, this N_e is affected by biased sex ratios as follows

$$N_e = 4N_f N_m / (N_f + N_m)$$

where N_f and N_m refer to the numbers of reproductive females and males, respectively. In male-haploid insects, e.g., in ants, bees and wasps,

$$N_e = 9N_f N_m / (2N_f + 4N_m)$$

which for the same numbers of females and males (N_f and N_m) yields smaller effective sizes than in a diploid population, unless the sex ratio is very female-biased. The sex ratios refer to those among breeding individuals, and the effective population size therefore depends on the numbers of matings of males and females. Both sexes are known to mate multiply in many species, but the number of matings by females is commonly low. Many species typically have once-mating females, and the effective number of matings rarely exceeds 2. Exceptions are the honeybees with up to 30 matings in *Apis cerana*,

social wasps of the genus *Vespula*, and leaf-cutting ants (Crozier and Pamilo, 1996).

Whereas multiple mating by females increases the effective population size, multiple mating by males decreases it, because the effect is that several females in the population would carry sperm of the same male. Multiple mating by males is known in several ants, but its general occurrence and genetic effectiveness are poorly known. Males of many species are known to mate only once, as they either die or lose their genitalia when mating (e.g., honeybee).

A further factor reducing effective population size is worker reproduction in social Hymenoptera. Workers in many species are sterile, but in others they can lay haploid eggs developing into males, sometimes workers are assumed to be the major source of males. Even though worker reproduction increases the number of reproductive individuals, it decreases (slightly) the effective population size, because it does not increase the gene pool but simply adds a further step for stochastic fluctuations and increases the variance of male allele frequencies (Crozier, 1979).

The effective size of a social insect population depends clearly not only on the nest density, but on the number of reproductive individuals in the nests, on the reproductive skew among these individuals, and on the genetic mechanisms. The genetically effective population size depends on the effective levels of polygyny and polyandry, and when the contributions of different queens, or those of the males copulating with the same female, are unequal, the effective number of individuals is lower than the actual number. When an individual i contributes a fraction x_i to a colony's production, the effective number of reproductives in the colony is $1/\sum x_i^2$.

Wilson (1971) noted that polygyny tends to occur commonly in rare ant species, habitat specialists and social parasites. He argued that polygyny increases the survivorship of such colonies and populations and that this may have selected for polygyny in these species. Hölldobler and Wilson (1977) developed the idea that polygyny is particularly selected for in two kinds of ants: those with frequently-fragmenting colonies (tramp species) and habitat specialists where the habitat patches are fragmented. Although the pattern is far from clear, it does suggest that rare species associated to specific habitat types can have locally large effective populations because of polygyny. Crozier (1979) further suggested that unicoloniality is an adap-

tation to rarity, with selection on local aggregations occurring as for colony-level selection.

When estimating population sizes in rare species, it is important to not only count the nests but to estimate the number of reproductive females in them. Genetic studies of an endangered ant *Formica cinerea* in northern Europe gives an example. This is a ground-nesting species living in open sandy habitats. Such habitats are rare in northern Europe and constitute either of areas where the retreat of ice stopped for a longer period at the end of last glaciation, or of coastal sand fields. The species is considered vulnerable in Sweden, and it has very fragmented populations in both Sweden and Finland, with some populations occupying only tens of square metres of suitable habitat. Preliminary genetic studies indicate that in some populations the nests are polygynous, whereas in other populations the nests have a single queen (Lindström et al., 1996). Clearly, the effective size, and perhaps vulnerability, of the populations depend also partly on their social organization.

Patterns of population size fluctuations vary among different taxonomic groups. Bumblebees and most social wasps have annual colonies, and their populations fluctuate as a function of weather conditions. Honeybees, stingless bees, ants and termites have perennial colonies, and consequently their populations are more stable. Ant queens can live 10–20 years (Hölldobler and Wilson, 1990), and an estimate of the mean longevity of queens in the ant *Formica exsecta* in natural conditions was over 20 years (Pamilo, 1991). Evaluating the vulnerability of their colonies and estimating the effective population size require information on the age structure of the population.

Baroni Urbani et al. (1973) give some guide lines for estimating population densities of ants, but very few data exist on the demographic parameters needed for population viability analysis. The mortality of incipient colonies, when resulting from independent founding, is high in all groups of social insects. It can take a long time for successful colonies to reach maturity. In annual colonies, this ergonomic stage takes place during a summer, but perennial colonies can grow several years before they start producing sexuals.

Scherba (1963), and Pamilo (1991) estimated annual death rates of nests in two related species of *Formica* ants to be 5–9%, and Scherba estimated the birth rate to be 5–13%. It is a general observation in many ants that mature colonies

outnumber young colonies and populations look very stable (Wilson, 1971: 445). However, demographic data on the turnover rate of nests may not tell about the turnover rate of reproductive individuals if a nest has more than one queen. Wilson (1971) remarked that colonial organization serves as a homeostatic device in damping fluctuations in the numbers of individual insects. It would be important to know if there is any correlation between the density of nests and the number of reproductive individuals per nest in populations where the number of nests shows temporal variation. Elmes (1987) found in a long time series of an ant *Myrmica sulcinodis* in a heathland habitat regenerating after a fire, that the number of queens in the nests fluctuated synchronously in the population, and the fluctuations seemed to follow a cycle of 4–5 years, which probably coincides with the life-span of the queens.

Three categories of colonies can be extremely stable, and in theory immortal (Wilson, 1971: 444), namely polygynous colonies that recruit new queens, colonies that reproduce by budding or fission (resembling vegetative growth), and monogynous colonies that can raise replacement reproductives in the case the colony queen (or either member of the royal pair in termites) dies. It is an important task for population studies of endangered social insect species to try to estimate the relevant demographic parameters and the social organization of colonies. Such information is needed also for common species, as the data on population dynamics of social insects, particularly those with perennial colonies, are few. Yet, these can be keystone species with a significant influence on other taxa in the ecosystem (LaSalle and Gauld, 1993). Vulnerability of even major ecosystem components can in some cases be reduced to simple population size effects in a few keystone species.

If one wants to estimate population size in order to evaluate genetic aspects, one should estimate the number of effectively reproducing individuals. However, for estimating population viability, it may be sufficient to estimate the birth and death rates of colonies, if one assumes that these variables do not interact with changing queen numbers when the population declines. Most life history models of social insects have focused on the growth of colonies (Oster and Wilson, 1978; Bourke and Franks, 1995), and in consequence the dynamics of the whole population are still poorly understood.

Dispersal and fragmentation of populations

The sedentary life style of social insects affects both the turnover of individuals in local populations and dispersal and differentiation between populations. A clear indication of limited dispersal of females in social insects with polygynous colonies is that the coexisting queens are genetically related to each other (Crozier and Pamilo, 1996), and the females therefore seem to have a tendency to stay in their natal colony after mating.

Dependent nest founding, particularly when based on splitting of existing nests, includes limited dispersal (at least of females) and is expected to lead to genetic differentiation of local populations. A comparison of conspecific populations, or pairs of closely related species with different modes of colony foundation and social organisation, suggest that this indeed is the case. A pattern emerging from such comparisons suggests that populations with colony budding have greater genetic differences among subpopulations than populations with independent founding (Table 1). The observed pattern indicates that occasional immigrating females have been frequently eliminated by local ants.

Table 1. Genetic differentiation of populations with different colony types. Differentiation is measured as F_{ST} , and the colony types are M-M: monogynous and monodomous colonies, and P-P: polygynous and polydomous colonies. The study areas range from 1 to 20 km, except in *F. aquilonia*, where it is 400 km.

Species	F _{ST}		Reference
	M-M	P-P	
<i>Formica truncorum</i>	0.04	0.19	Sundström (1993)
<i>Formica aquilonia</i>	—	0.18	Pamilo (unpubl.)
<i>Myrmica ruginodis</i>	0.02	—	Seppä and Pamilo (1995)
<i>Myrmica rubra</i>	—	0.20	Seppä and Pamilo (1995)

It is interesting to note, as remarked by Wilson (1971), that the species which reproduce by budding have traded dispersal capacity for longevity of the existing nests. This pattern of colony foundation also means that a species can be slow in recolonizing and re-establishing areas where it has gone extinct. This, however, does not apply to all species in this category, as some of the quickly spreading pest ants have a highly polygynous and polydomous colonial structure.

It is still unclear to what extent social insect populations are subdivided due to restricted dispersal. Hill-topping behaviour of mating swarms has been described in some species, and genetic differentiation within a homogeneous habitat in a population of *Formica transkauca-sica* strongly suggests that dispersal of sexual individuals is restricted in spite of a lack of physical barriers, even though the size of habitat is only 200×1000 m, distances that could be moved by a flying ant (Pamilo, 1983).

The low ratio of population size to biomass, and the restricted dispersal at least in many (but not all) social insect species, suggest that any analyses of population viability should pay attention to the spatial scale even in apparently continuous populations (Lande, 1987).

Inbreeding depression

One of the on-going debates in conservation biology is whether inbreeding depression and genetic erosion contribute significantly to extinction of populations, or whether ecological factors cause extinction before inbreeding has time to significantly influence demography. Hymenopteran species, because of their male-haploidy, have been both predicted (Crozier, 1985) and shown (e.g., Pamilo et al., 1984) to have lower levels of allozyme variation than other insect orders, and variation is particularly low in social species. It is, however, difficult to think that such a lower level of heterozygosity would largely affect the viability of populations (see also Unruh and Messing, 1993). Another consequence of male-haploidy is that recessive, deleterious mutations are effectively selected against in haploid males, and this can reduce inbreeding depression (but see Crozier, 1985, and Werren, 1993, for some complications).

There is one reason to predict that social hymenopteran species can suffer seriously from inbreeding depression. The sex in the honeybee is determined by a single locus in such a way,

that individuals heterozygous for the locus develop into females (workers or new queens), while other genotypes develop into males. Normal males are haploid (hemizygous), but diploid individuals that are homozygous for a sex allele develop also into males. Diploid males are shown to be sterile or inviable. It has been proposed that the same, or similar, sex-determining mechanism exists in most social hymenopterans (Cook and Crozier, 1995). There is clearly strong frequency-dependent selection maintaining allelic diversity at the sex locus. Decreasing variation increases the proportion of diploid males and causes a genetic load. When a female mates once and the male and the female carry an identical sex allele (matched mating), half of the diploid offspring are males.

In the introduced fire ant, *Solenopsis invicta*, in northern America colonies started by a single female producing diploid males do not survive to maturity (Ross and Fletcher, 1986). Some *Formica* ants produce rather high frequencies of diploid males, and monogynous colonies with matched mating can survive the founding stage and reach maturity (Pamilo et al., 1994). The *Formica* females have dependent nest founding, as they take over established nests of another species (subgenus *Serviformica*). The proportion of nests producing diploid males is particularly high in isolated island populations that have very few colonies.

Diploid males occur in *Formica* nests only at a time of normal sexual production. During other times, only workers are produced and diploid males are apparently eliminated at an early developmental stage, as also happens in the honeybee. This effectively reduces the load caused by diploid males, once the colony has survived the founding stage. As the species have evolved mechanisms to eliminate some of the load caused by diploid males, it is too early to conclude how significantly diploid male production contributes to the vulnerability of small and isolated populations (Table 2).

In many termites colonies enter a cycle of inbreeding, when the primary reproductives die and are replaced. The replacement reproductives originate from the same colony and inbreed in it, and a cycle of inbreeding can continue several generations. Such a naturally high level of inbreeding is effective in eliminating any harmful recessive alleles in the same way as male-haploidy in the Hymenoptera, and it can be predicted that termites are unlikely to suffer severely from inbreeding depression when the population size decreases.

Table 2. Possible genetic effects in sparse and fragmented ant populations as a function of colony type (M-M and P-P as in Table 1).

	M-M	P-P
N_c	small	large
Genetic differentiation	gradual	distinct
Sex alleles	few	affected by bottlenecks when colonizing
Genetic load	Diploid male production can cause a load	Dependent nest foundation diminishes the load

Social parasites

Socially parasitic species are known in bees, wasps and ants, but not in termites. Females of socially parasitic species take over nests of other, commonly closely related species, and let the host species raise the larvae. The parasite populations are naturally smaller than those of the host species, and the parasites are often very species specific.

Social parasitism has according to the so called Emery's Rule evolved between two closely related species, or the parasite has evolved directly from the host. Parasitism in ants is particularly common in leptothoracine ants, and many parasitic species are found in isolated populations in mountain areas (Buschinger, 1989). Many of the social parasites are extremely rare and have a restricted geographical distribution.

Because of low population densities, socially parasitic ants are known to inbreed frequently and the sex-locus system of other ants has been evolutionarily replaced (Buschinger, 1989). It is evident that they have often small and isolated populations, and parasitic ants belong to those of the rarest and most endangered species. Hölldobler and Wilson (1990: 212-213) note that parasitic species have a tendency to be polygynous (as many other rare ants do), which increases their effective population sizes.

Introduced species

Some social insects that have been introduced to new areas, accidentally or on purpose, have led to a need to protect the native fauna.

The introduced ants *Solenopsis invicta* (the imported fire ant), *Linepithema humile* (the Argentine ant), *Pheidole megacephala*, and

Wasmannia auropunctata are spreading in different islands and continents. They are all characterized by highly polygynous and polydomous (or unicolonial) colonial structures, and they replace native ants of similar ecological requirements. Whereas the Argentine ant occupies largely urban and other disturbed habitats (at least in Australia), the other three species have also penetrated native ecosystems.

Honeybee is introduced and maintained by humans, and bumblebees are also cultured and introduced for pollination purposes. These introduced bees, particularly the honeybee, can compete with the native bee fauna and can, at least potentially, have undesirable effects on the local bee diversity (see New (1994) for a discussion on this problem).

One important conservation aspect is to preserve the native faunas, because they play important roles in the native ecosystems.

Conclusions

We have shown that social insects, a major part of many ecosystems, have many differences from other invertebrates in characteristics important for conservation. Low dispersal rates and small effective population sizes (in relation to the biomass) make many species liable to be easily endangered (and associated species threatened). This potential vulnerability is increased for hymenopterans by their male-haploidy and the single-locus sex determination system (Table 2). The long life-span of colonies means that population change is slow, necessitating acceptance of the need for studies to be long-term. There is a significant need for manipulation experiments to ascertain the extent of ecosystem-wide effects of changes in the composition of the social insect community.

Acknowledgements

We thank the Environmental Protection Board and the Natural Science Research Council of Sweden for research support to PP, and the Australian Research Council for supporting RHC's research; PP's visit to La Trobe University was made possible by a CRA/La Trobe University Distinguished Visitor award.

References

- Baroni-Urbani, C., Josens, G. and Peakin, G.J., 1978. Empirical data and demographic parameters. Pp. 5–44 in: Brian, M.V. (ed.), *Production ecology of ants and termites*. Cambridge Univ. Press: Cambridge.
- Beattie, A.J., 1985. *The evolutionary ecology of ant-plant mutualisms*. Cambridge Univ. Press: Cambridge.
- Bourke, A.F.G. and Franks, N.R., 1995. *Social evolution of ants*. Princeton Univ. Press: Princeton, New Jersey.
- Buschinger, A., 1974. Monogynie und Polygynie in Insektensozietäten. Pp. 862–897 in: Schmidt, G.H. (ed.), *Sozialpolymorphismus bei Insekten*. Wiss. Verlagses.: Stuttgart.
- Buschinger, A., 1989. Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera: Formicidae). *Journal of Evolutionary Biology* 2: 265–283.
- Cook, J.M. and Crozier, R.H., 1995. Sex determination and population biology in the Hymenoptera. *Trends in Ecology and Evolution* 10: 281–286.
- Crozier, R.H. 1979. Genetics of sociality. Pp. 223–286 in: Hermann, H.R. (ed.), *Social insects. Vol. I*. Academic Press: New York.
- Crozier, R.H., 1985. Adaptive consequences of male-haploidy. Pp. 201–222 in: Helle, W. and Sabelis, M.W. (eds), *Spider mites, their biology, natural enemies and control, Vol. 1a*. Elsevier: Amsterdam.
- Crozier, R.H. and Pamilo, P., 1996. *Evolution of social insect colonies, sex allocation and kin selection*. Oxford University Press: Oxford.
- Elmes, G.W., 1987. Temporal variation in colony populations of the ant *Myrmica sulcinodis*. I. Changes in the queen number, worker number and spring production. *Journal of Animal Ecology* 56: 559–571.
- Elmes, G.W. and Thomas, J.A., 1992. Complexity of species conservation in managed habitats: interactions between *Maculinea* butterflies and their ant hosts. *Biodiversity and Conservation* 1: 155–169.
- Gilbert, L.E., 1980. Food web organization and the conservation of neotropical diversity. Pp. 11–33 in: Soulé, M.E. and Wilcox, B.A. (eds), *Conservation biology, an evolutionary-ecological perspective*. Sinauer Ass.
- Handel, S.N., Fisch, S.B. and Schatz, G.E., 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108: 430–437.
- Hölldobler, B. and Wilson, E.O., 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64: 8–15.
- Hölldobler, B. and Wilson, E.O., 1990. *The ants*. Springer Verlag: Berlin.
- Keller, L. and Reeve, H.K., 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution* 9: 98–102.
- Lande, R., 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130: 624–635.
- LaSalle, J. and Gauld, I.D., 1993. Hymenoptera: their diversity, and their impact on the diversity of other organisms. Pp. 1–26 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Leston, D., 1978. A neotropical ant mosaic. *Annals of the Entomological Society of America* 71: 649–653.
- Lindström, K., Berglind, S-A, Pamilo, P. 1996. Variation of colony types in the ant *Formica cinerea*. *Insectes Sociaux* 43: 329–332.
- Majer, J.D., 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia — its structure and influence on arthropod diversity. Pp. 115–141 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- New, T.R. (ed.) 1993. *Conservation biology of Lycaenidae (Butterflies)*. IUCN: Gland, Switzerland.
- New, T. R., 1994. *Exotic insects in Australia*. Glenagles Publ.: Glen Osmond, Australia.
- Oster, G.F. and Wilson, E.O., 1978. *Caste and ecology of social insects*. Princeton Univ. Press: Princeton, New Jersey.
- O'Toole, C., 1993. Diversity of native bees and agroecosystems. Pp. 169–196 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Pamilo, P., 1983. Genetic differentiation within subdivided populations of *Formica* ants. *Evolution* 37: 1010–1022.
- Pamilo, P., 1991. Life span of queens in the ant *Formica exsecta*. *Insectes Sociaux*. 38: 111–119.
- Pamilo, P. and Crozier, R.H., 1996. Reproductive skew simplified. *Oikos* 75: 533–535.
- Pamilo, P., Sundström, L., Rosengren, R. and Fortelius, W., 1994. Diploid males and colony-level selection in *Formica* ants. *Ethology, Ecology Evolution* 6: 221–235.
- Pamilo, P., Varvio-Aho, S-L. and Pekkarinen, A., 1984. Genetic variation in bumblebees (*Bombus psithyrus*) and putative sibling species of *Bombus lucorum*. *Hereditas* 101: 245–251.
- Pekkarinen, A., 1979. Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica* 158: 1–60.

- Pisarski, B., 1978. Comparison of various biomes. pp. 326–371 in: Brian, M.V. (ed.) *Production ecology of ants and termites*. Cambridge Univ. Press: Cambridge, U.K.
- Rosengren, R. and Pamilo, P., 1983. The evolution of polygyny and polydomy in mound-building *Formica* ants. *Acta Entomologica Fennica* 42:65–77.
- Ross, K.G. and Fletcher, D.J.C., 1986. Diploid male production — a significant colony mortality factor in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 19: 283–291.
- Scherba, G., 1963. Population characteristics among colonies of the ant *Formica opaciventris* Emery (Hymenoptera: Formicidae). *Journal of the New York Entomological Society* 71: 219–232.
- Seppä, P. and Pamilo, P., 1995. Gene flow and population viscosity in *Myrmica* ants. *Heredity* 74: 200–209.
- Soulé, M.E., 1987. Introduction. Pp. 1–10 in: Soulé, M.E. (ed.), *Viable populations for conservation*. Cambridge Univ. Press: Cambridge.
- Sundström, L., 1993. Genetic population structure and sociogenetic organization in *Formica truncorum*. *Behavioral Ecology and Sociobiology* 33: 345–354.
- Thomas, J.A., 1995. The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. Pp. 180–197 in: Pullin, A.S. (ed.), *Ecology and conservation of butterflies*. Chapman & Hall: London.
- Unruh, T.R. and Messing, R.H., 1993. Intraspecific biodiversity in Hymenoptera: implications for conservation and biological control. Pp. 27–52 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Werren, J. H., 1993. The evolution of inbreeding in haplodiploid organisms. Pp. 42–59 in: Thornhill, N.W. (ed.), *The natural history of inbreeding and outbreeding*. University of Chicago Press: Chicago.
- Williams, P.H., Vane-Wright, R.I. and Humphries, C.J., 1993. Measuring biodiversity for choosing conservation areas. Pp. 309–328 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Wilson, E.O., 1971. *The insect societies*. Harvard Univ. Press: Mass., USA.
- Wilson, E.O., 1990. *Success and dominance in ecosystems: the case of the social insects*. Ecology Inst.: Oldendorf/Luhe, Germany.