

*Life Cycles in Social Insects: Behaviour, Ecology and Evolution.*

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## **Steps toward a general theory of the colony cycle in social insects**

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**Abstract** – *The fundamental character of the colony cycle in social insects has long been recognized, and the basic pattern for most major groups has been known for roughly a century. Nonetheless, we are only at the beginning of an attempt at a theoretical understanding of how colony cycles are shaped by natural selection. It is proposed to initiate this process by taking advantage of a) a structural resemblance between colony cycles and the life cycles of individual organisms, and b) the substantial body of theory concerning life cycles (life-history theory).*

*A review of the basic parameters of life cycles shows that most of these are readily applicable by analogy to colony cycles. The main exception appears to be sex ratio, which has no evident meaning at the colony level. Some basic ideas in life-history theory are reviewed, with a view to illustrating some kinds of hypotheses about colony cycles that are suggested by analogy.*

*Finally, an appeal is made for the establishment of a permanent central database for social-insect colonies, partly in the service of advancing a general theory of the colony cycle. It is suggested that this can be a feasible, cost-effective undertaking for the International Union for the Study of Social Insects (IUSSI).*

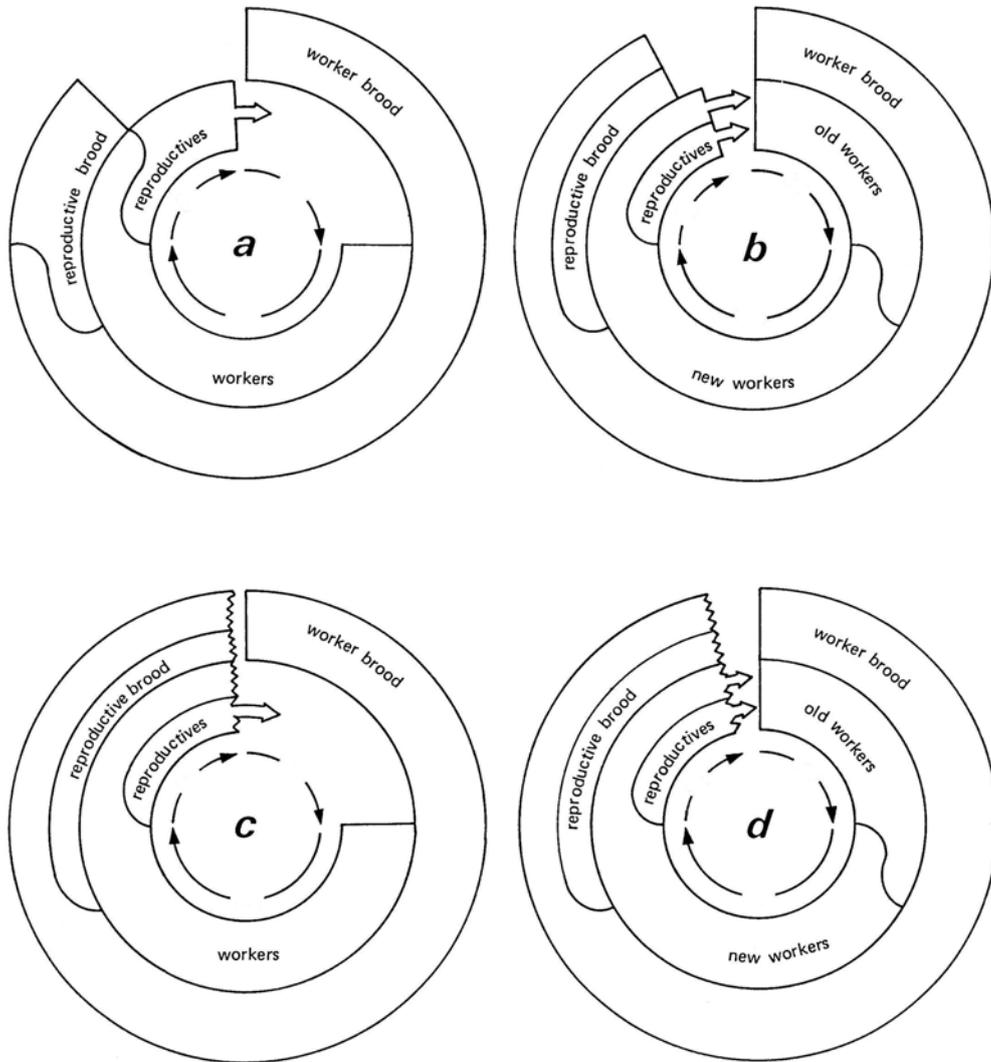
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### **Introduction**

"A comprehensive life history theory for social insects should aim to explain, first, why the basic ant [colony] cycle is [indeterminate] and [independent founding] .... Next, it should explain the nature, timing and scale of each part of the basic [colony] cycle, and especially how resources are partitioned between investment in growth (worker production) and investment in reproduction (sexual production). Lastly, it should uncover the reason why variants in the basic pattern evolve." Bourke and Franks (1995: 300)

The social insect colony typically comprises a queen or royal pair, a large number of workers (and sometimes soldiers), immature brood at various stages, and sometimes new reproductive individuals, all enveloped in a stationary nest.

These different types of individuals are more or less constant in form, while the colony as a whole is not. For any species, a colony of a given size has a characteristic mix of phena, and it resists any disturbance of this mix. However, overall colony size is not constant.



**Figure 1.** Schematic representation of four types of colony cycles.

- a. Determinate independent-founding, exemplified by paper wasps (*Polistes*).
- b. Determinate swarm-founding, exemplified by nocturnal hornets (*Provespa*).
- c. Indeterminate independent-founding, exemplified by most termites.
- d. Indeterminate swarm-founding, exemplified by honey bees.

The outer and inner circles indicate which types of brood and adults, respectively, are present. Labelled arrows inside the inner circle name the phases in the colony cycle, as follows: Fo – founding, Gr – growth, Rp – reproductive. A jagged line across the two circles indicates that the original colony continues past the end of the reproductive phase.

The relative numbers of different sexes, castes and life stages change and with them the character of the colony.

There are some marked regularities in these changes, so that it is meaningful to speak of a species-characteristic colony life cycle, or colony cycle. Fig. 1a shows a relatively simple colony cycle with three distinct phases, or stages, based on unequivocal events. While different authors have given these phases different names, there is little disagreement about their identity.

The cycle illustrated in Fig. 1c differs in one respect: A healthy colony undergoes several distinct reproductive phases, rather than disintegrating after just one. And that shown in Fig. 1d differs from this latter in that a new colony is founded not just by one or more queens (and kings in termites) but by a group of queens together with workers, so that workers are continuously present.

**Table 1.** Colony cycles classified according to two major variables (see Fig. 1). Known or supposed examples are given within each box.

	Independent founding	Swarm founding
Determinate	<i>Stenogastrinae</i> <i>Polistes</i> <i>Mischocyttarus</i> many <i>Ropalidia</i> Vespinae except <i>Provespa</i> social Halictinae <i>Bombus</i>	<i>Provespa</i> a few ants
Indeterminate	most ants most (all?) termites	many <i>Ropalidia</i> most Epiponini <i>Apis</i> Meliponini Dorylinae Ecitoninae

These three patterns describe the cycles of the great mass of eusocial insect species (Tab. 1). We can readily extract two basic points from a comparison of them:

1. In most species, we can meaningfully conceive of the establishment of a new nest as the start of the cycle (founding) and the production of new colony propagules as the event toward which the cycle is directed. Accordingly, it is convenient to define colony death – the end of the cycle – as the time when there are no longer any workers present.

2. Variation among taxa is expressed in two main parameters. First, Fig. 1a illustrates a determinate cycle, ending after one reproductive phase, while in Figs. 1c and 1d the cycle is indeterminate, with the possibility of many reproductive episodes. (The frequently used terms "annual" and "perennial" are a geographic special case of the same distinction.) Second, there is a distinction between independent-founding (Figs. 1a, 1c) and swarm-founding (Fig. 1d) species, depending on whether the founding group includes workers. (In non-parasitic

ants, "dependent founding" is a synonym of "swarm founding".) Except in a few species of ants, social insects do not appear to make frequent use of both founding modes.

A virtue of these two parameters is that each represents a distinct dichotomy.

Recognition of two main parameters suggests a fourth pattern, a determinate cycle with swarm founding. Does this type of colony cycle exist in nature? It is characteristic of at least two of the three species of nocturnal hornets, *Provespa* (Matsuura, 1991, 1999) and is known or expected from a few ants (K. Tsuji, pers. comm.). However, the association of swarm founding with a determinate colony cycle is evidently a rarity among social insects. It is not hard to suggest plausible reasons why this should be so. However, as far as I am aware, no one has even drawn attention to the fact that this particular pattern is so very rare.

The colony cycle is generally recognized as a fundamental property of social insects. Nesting biology is at the heart of insect sociobiology, and the colony cycle forms the framework of nesting biology, so that the proposition that colony cycles are a product of natural selection – with the corollary that this part of the phenotype should be as open to comparative treatment as are nest structure, foraging behavior, etc – is uncontroversial. It is, in fact, almost a first principle of insect sociobiology in our time.

The colony cycle of the western honey bee, *Apis mellifera*, has been well known for many centuries. It is now about a century since the main pattern of founding and colony cycle in ants and swarm-founding social wasps has been known at least in outline. Comparable knowledge is older for vespine wasps and bumble bees, somewhat more recent for termites and halictine bees, and about half a century old for army ants. As these examples show, the colony-cycle pattern is well established in all groups that have received major attention. As a result, early in almost any general treatise on a group of social insects – such as vespine wasps (Edwards, 1980; Matsuura and Yamane, 1990; Spradbery, 1973), *Ropalidia* wasps (Gadagkar 2001), bumble bees (Goulson 2003), honey bees (Gould and Gould, 1988; Seeley, 1995), ants (Hölldobler and Wilson, 1990); leaf-cutter ants (Weber, 1972), army ants (Gotwald, 1995) or termites (Grassé, 1982–86; Krishna and Weesner, 1969–70) – one finds a substantial description of the typical colony cycle and important variations on it. The first chapter of Heinrich's (1979) book on bumble bees is titled simply "The Colony Cycle", and Schneirla's (1971) book on army ants is structured around this theme.

At the same time, we still do not have even a rough draft of a general theory of the colony cycle in social insects. This is illustrated by the table of contents of any treatise or textbook on social insects as whole (e.g. Buschinger, 1985; Kipyatkov, 1991; Wilson, 1971). The colony cycle is not treated as a general subject but separately in chapters on different groups. Accordingly, when it was learned that at least some nocturnal hornets typically found new colonies by means of swarms, it was a surprise just because all other vespine wasps appear to be strictly independent-founding, not because of any theoretical reason to expect that the nocturnal hornets or any other vespine should found one way or the other. Stated another way, this question has yet to go beyond the inductivist phase of its development.

My purpose here is quite modest. It is to put the search for a general theory of colony cycles on the agenda of insect sociobiology and suggest some steps in this direction. By "general theory" is meant a framework of ideas that will draw attention to phenomena that require explanation and highlight other fruitful questions. The timing is good for such an undertaking. As seen in remarks by Jeanne (1996), Seeley and Mikheyev (2003), and especially Bourke and Franks (1995: Chapters 9–10), others have been thinking along similar lines, so that the approach taken here will hopefully have a familiar flavor for some readers.

## The superorganism analogy

In the 1870s there arose in sociology the idea that a human society could usefully be analogized with an organism. It was soon seen that the analogy could be extended to embrace societies of other animals (Espinas, 1877), and about a century ago Wheeler (1911) explicitly treated the social-insect colony as a "superorganism" with broad functional similarities to a multi-cellular organism.

This concept of the colony is with us today, although in quite different form from its first incarnation. It is most meaningful with respect to a) organization of the immediate work of the colony, and b) colony cycles. The first is the substance of the thriving research programme of social physiology and self-organization (Camazine *et al.* 2001; Detrain *et al.*, 1999; Moritz and Southwick, 1992; Pasteels and Deneubourg, 1987; Seeley, 1995), with marked advances in our understanding of how colonies forage, build nests, and maintain a suitable microhabitat, all drawing inspiration from the analogy with organisms.

The second, in contrast, has received almost no attention. That is, the modern superorganism concept tends to treat colonies as systems for efficient foraging, nest construction and maintenance of suitable microclimatic conditions, but not as systems geared to replicating themselves. Might this be because there is no body of general ideas on (individual-level) life cycles to suggest analogous features in colony cycles? Not at all.

## Life-history theory

"[Life history theory] has successfully explained: why organisms are small or large, why they mature early or late, why they have few or many offspring, why they have a short or long life, and why they must grow old and die." (Stearns, 1996)

"Life history theory has been extraordinarily successful in providing a framework within which to understand evolutionary change." Roff (2002: 459)

Half a century ago, Cole (1954) set forth the mathematical framework for analyzing the consequences of differences in life-history traits. Today life-history theory is a robust sub-discipline of population biology with a number of recent book-length treatments (Charnov, 1993; Roff, 1992, 2002; Stearns, 1992). A simple indication of its maturity is seen in the standard set of demographic notation that has long been uniformly accepted.

As Heinze (pp 49–61 of this volume) notes, almost no connection has yet been made between insect sociobiology and life-history theory. The one substantial attempt in this direction of which I am aware is in Bourke and Franks's (1995: Chapters 9–10) book on ants, which demonstrates considerable variation in details within the scope of a common pattern applicable to most species. The reasons for this general mis-connection are not obscure: The colony cycle is not recognized as a topic within life-history theory, and the life-cycles of individual social insects have little relevance apart from the colony cycle.

Still, the large existing body of (individual-level) life-history theory can serve as a ready-made source of inspiration in initial steps toward general formulations regarding the colony cycle. In what follows, my first concern is to propose how we might utilize existing theory as analogical stepping stones. In so doing, I hope we can take our distance from one particular aspect of Bourke and Franks's treatment. Although they do not say so explicitly, it is implied that a general theory of the colony cycle will form an integral part of life-history theory. In my view, it is preferable at present to treat the analogy between developmental

cycles in individuals and colonies as a valuable source of conjectures, to be received with scepticism. It will serve this purpose if the term "life cycle" is no longer applied indifferently to individual organisms and to colonies. Only the first sense is used here.

Allied with this shortcoming is a tacit tendency to equate the colony cycle in some cases with the life cycle of the queen. They are often very closely tied to each other in monogynous colonies without queen replacement, but they are not the same.

I will review some features of life-history theory, with a view to reaching a preliminary judgement of their analogical relevance to the study of colony cycles. In so doing, one is automatically drawn into a sort of triage, setting to one side those features that obviously (perhaps trivially) apply, to the other side those that obviously do not apply, and investing the uncertain ones with especial interest

Two obvious outstanding general differences between a colony and a metazoan animal merit early emphasis.

First, the individual parts of the colony are physically uncoupled. One important result of this is that there is more than one fundamental way to reproduce the colony.

Bonner (1993: 24) noted with some puzzlement that most animals and plants pass through an extreme size bottleneck in their life cycles, by starting out as tiny embryos. Why do they go to all this bother? "Would it not be much easier", he asked, "simply to pinch in two and regenerate the missing half ...?" The answer seems to be that they do so because there is no good way to avoid it. Social insect colonies, in contrast, are not obliged to pass through this bottleneck, and in roughly 10% of species they bypass it through swarm founding. Why, then, is independent founding the rule in social insects? This is among the key questions that any general theory will have to address.

Second, the components are genetically heterogeneous, not a clone, so that there are necessary genetic conflicts of interest within the colony. No one before W.D. Hamilton seems to have given this point any weight, yet it is the largest pillar of today's insect sociobiology (no references needed). Should a general theory of the colony cycle take kin conflict into account? In time, it must. As an example, the colonies of many north-temperate social wasps turn rather abruptly to a phase of brood slaughter – the "couvain abortif" of Deleurance (1950, 1952) – toward the end of the season. A general theory should be able to predict whether such brood cannibalism is adaptive at the colony level or if it only makes sense from the point of view of those adults who kill and eat. For the present, however, I believe we can legitimately set kin conflict aside under the simplifying assumption that it does not shape the main differences between taxa in their colony cycles. Still, this "present" may be short-lived, as we are already seeing attempts to model the role of kinship in shaping colony cycles (e.g. Bourke and Chan, 1999; Crozier and Pamilo, 1996; Herbers *et al.* 2001; Peters *et al.*, 1999; Reuter and Keller 2001).

While Fig. 1 simplifies the diversity of known colony cycles, it is not a gross oversimplification. This narrow variation in colony cycles, compared with what is found in the life cycles of individual organisms, facilitates our purpose. To give an example, alternation of (colony) generations is unknown in social insects. No free-living species has alternating sessile and errant generations, and no social-parasitic species has both an intermediate and a definitive host.

There are today two basic approaches in life-history studies: optimization and genetic. Optimality analyses commonly assume enough genetic variation to let organisms evolve the best combination of features within external constraints. This approach fits social-insect

colonies well and is expected to predominate in colony-cycle studies for the foreseeable period. After all, interactions among life-history variables occur in every individual of every generation over evolutionary time, so that we should expect fine-tuning of those interactions that determine inclusive fitness.

It is noteworthy that theory about social-insect evolution has long been based on genetic models, yet information about genetic bases of social variation has been slow in coming, especially with respect to between-colony differences. The one known case in which dimorphism or polymorphism of a colony trait is controlled by one or a small number of genes – that of the monogyne and polygyne forms of the fire ant *Solenopsis invicta* (Ross and Shoemaker, 1997; Valles and Porter 2003) – is evidently very unusual. There is no indication that distinct polymorphism of colonies within a population is at all common in social insects.

The basic substance of life-history theory is the schedules of birth and death, so that the terms  $l_x$  and  $m_x$  – survival to age  $x$  and reproduction at age  $x$ , respectively – are used without unambiguity and often without definition. Calculation of lifetime fitness involves computing the manner in which birth and death rates change with such factors as age and size. The key parameters in this calculation are: a) size at birth, b) growth pattern, c) age at maturity, d) size at maturity, e) number and size of offspring, f) sex-ratio of offspring, g) age- and size-specific reproductive investments, and h) length of life.

It is plain that each of these parameters except (f) sex-ratio of offspring is analogically applicable to colony cycles. That is, it is meaningful to speak of (a) the number of individuals in a colony at founding, (b) the pattern of increase in number of individuals over time, etc. As an opening conjecture, one can suggest that each of the meaningful analogical parameters will be found to have much the same place in a general theory of the colony cycle as it does in life-history theory.

You can confirm the reasonableness of this view by reading a representative passage from one of the general treatments of life-history theory as if it were about colony cycles. What results in most cases is a series of statements that sound like they might be true and are, in any case, not nonsensical. Still, in hardly any case has the question yet been posed of whether such statements are, in fact, true.

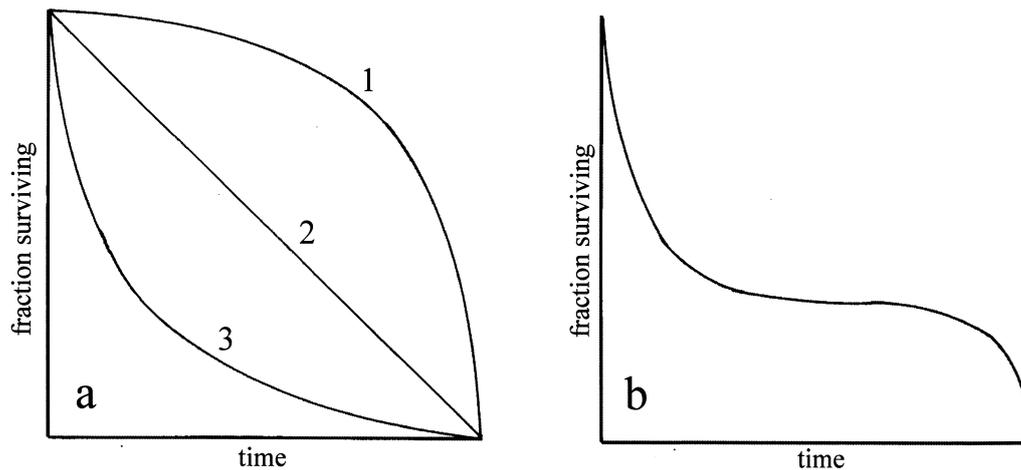
In a spirit of skeptical appreciation, I would like to consider some features of life-history theory, with a view to suggesting how they might serve our purpose.

## Life tables and survivorship curves

Survivorship curves are commonly divided into three types (Fig. 2a). Type 2, which assumes a constant probability of dying in all intervals, is the simplest. It is also the least expected in nature, including at the colony level, as there is good reason to expect that mortality rates will, in fact, be markedly inconstant. Mortality rates of individuals are age-specific, although age per se appears not to be a generally important factor. Rather, other factors that tend to vary with age – such as developmental stage, body size, reproductive status – are key. It seems almost certain that colonies will show a strong analogy in this respect, as has long been known for the western honey bee.

Of the three ideal survivorship curves, Type 3 is probably the most widely applicable to social-insect colonies, and it may be the strong general rule among independent-founding species. Colonies, like organisms, are likely to escape from some important predators as they grow. Anyone who has noticed the huge numbers of ant and termite reproductives that fall

prey to lizards, birds and ants and then has seen large nests of the same species continuously inhabited year after year will have little difficulty with this untested generalization. Consistent with this view, only 1.3% of colonies of the harvester ant *Pogonomyrmex occidentalis* survive to the end of their first year (Cole and Wiernasz 2002).



**Figure 2.** Idealized survivorship curves, with fraction surviving on a logarithmic scale. *a.* The most commonly recognized curves, taken from any textbook of population biology or life-history theory. *b.* Hypothetical colony survivorship curve resulting from i) high mortality in the independent-founding phase, ii) very low mortality during the growth and most of the reproductive phases, and iii) maximum lifespan set by the life of the (irreplaceable) queen.

In the biology of independent-founding social wasps, the founding stage is commonly regarded as a time of exceptionally high colony mortality, although few hard data are available. One clear indication that founding-phase colonies of independent-founding social wasps are at high risk is provided by Queller (1996: Tab. 13.1): In six species in which both haplometrosis and pleometrosis are frequent, pleometrotic colonies have a markedly higher probability of surviving to the growth phase. In one of the very few formulations of a colony-level life table, Miyano (1980: Fig. 1) found patterns strikingly consistent with a Type-3 curve in two of three populations of *Polistes chinensis*, with a clear improvement in survivorship around the end of the founding phase (see also Turillazzi, 1984: Fig. 2.1 on *P. nimpha*). This makes sense if the emergence of the first workers coincides with the colony growing more or less abruptly out of risk from some important enemies.

Accordingly, I propose as a candidate principle of the colony cycle that colony mortality in independent founders is by far highest during the founding phase, the very period in which the colony does not enjoy the advantages of sociality. It is called a "principle" advisedly, as the existence of such a high-risk stage early on must shape the cycle as a whole. Such a principle seems to be in harmony with present thinking about social insects (e.g. Bourke and Franks, 1995: 304), although it remains without broad empirical support.

A comparable general hypothesis for swarm-founding species is not so readily at hand. It seems likely that the colony is at somewhat greater risk right after division than right

before, but it is far from obvious whether this difference should usually be large. Furthermore, if there is a substantial risk involved, is it mainly from decreased colony size or the loss of the nest? This question would seem quite open to experiment with a species in which one can induce either an in-place reduction in size or an intact absconding swarm. However, even in so intensively studied a species as the western honey bee, I am aware of no strong evidence pointing to a Type-3, Type-2 or Type-1 survivorship pattern. If the death of wild colonies is usually due to senescence of the queen, the latter curve would seem to apply. What does seem obvious is that there is no reason to propose that swarm founders in general are at any extraordinary risk during the founding or any other phase of the colony cycle.

It should be noted that these three are not the only possible idealized patterns, and it seems likely that others exist in nature. For example, an ant species might plausibly combine high early mortality with very low mortality after the founding phase and a maximum lifespan set by queen longevity, giving rise to a sigmoid curve with high survivorship in the middle part (Fig. 2b).

### **Relationships among parameters: Trade-offs**

"The basic hypothesis underlying most analyses of the evolution of life history traits is that variation is constrained in large measure by trade-offs between traits." (Roff, 1992:1)

Life-cycle syndromes are "suites of characters that covary and function together" (Dingle, 1986), so that a change in one stage or parameter may well have consequences in another. For example, generation time shows a distinct positive correlation with adult body size across a very broad range of taxa (Harvey and Pagel, 1991: Fig. 1.1). Larger organisms may tend to live longer simply because they must, as a combination of large body size and short life cycle will usually not work.

There are two things of note in this relationship. First, it is allometric. Within a given taxon, and to lesser extent among taxa, many physiological and ecological variables – including those relevant to life-history theory – relate to each other at least approximately by a power function  $y=c+bx^a$ , in which the allometric constant  $a$  is not equal to 1. If  $y$  is generation time and  $x$  is body length, for example, then  $a\approx 0.82$  across a broad taxonomic range of organisms (based on Harvey and Pagel, 1991: Fig. 1.1).

There is now a large literature on how other life-history traits vary with body size (Roff 2002: Tab. 4.10). It is reasonable to expect various colony-level variables to vary with colony size in similarly lawful ways, yet the exploration of these relations has only just begun. As an example, parasite load in some social insects is known to increase allometrically ( $a > 1$ ) with colony size (Schmid-Hempel, 1998, pp. 37–48 of this volume).

Second, any such relationship between two parameters can be posed so that the correlation is negative. In the example just cited, the fraction of parasite-free colony members correlates negatively with colony size.

In itself, this second is a trivial feature, but it serves to highlight a central concept from life-history theory that can be imported intact and without hesitation into any general theory of the colony cycle. A trade-off is a causal relationship that constrains simultaneous evolution of two or more traits. This is a very accessible concept, with many examples available in such areas of everyday life as home economy and sport. A successful decathlete,

for example, is celebrated for minimizing the consequences of a series of trade-offs. What it means for our purposes is that the colony cannot do everything, that choices must be made. A trade-off is not a compromise, although it may demand a compromise.

Charnov (1993: Tab. 5.1 and 5.4) compared the expected and observed correlations between pairs of four life-history variables for mammals. With the exception of one pair, in which the expected correlation was uncertain, the direction of the observed correlation matched the expected.

**Table 2.** *Life history traits involved in trade-offs. A trade-off is demonstrated or inferred between each pair of these nine traits, a total of 45 pairs. From Stearns (1992).*

- |                         |
|-------------------------|
| 1. Current reproduction |
| 2. Parental survival    |
| 3. Future reproduction  |
| 4. Parental growth      |
| 5. Parental condition   |
| 6. Number of offspring  |
| 7. Size of offspring    |
| 8. Offspring condition  |
| 9. Offspring survival   |

The most studied trade-offs in organisms are: a) current reproduction vs parental survival, b) current reproduction vs future reproduction, c) reproduction vs growth, d) reproduction vs offspring condition, and e) number and quality of offspring (Stearns, 1992; Tab. 2). A noteworthy feature of such trade-offs is that, despite the very strong logic behind them, it can be surprisingly difficult to demonstrate them in practice. To give two illustrations from Roff (1992: Tab. 6.3 and 6.8), a) a review of studies of correlation between reproduction and survival in 17 animal species showed the expected negative correlation in only four species, against a positive correlation in four, and no significant correlation in the other nine, and b) in only seven of 13 studies of the manipulation of brood size in birds was a significant effect on the next brood shown.

**Table 3.** *Suggested colony-level states of some social-wasp genera with respect to r-selected traits. The traits are: 1) rapid development, 2) a high rate of increase, 3) early reproduction, 4) small size, and 5) semelparity (Pianka 1970). The scoring is based on my own experience as an observer of social wasps and in places is more impressionistic than quantitative. IF – independent-founding species, SF – swarm-founding species.*

Genus	1	2	3	4	5
<i>Polistes</i>	+	+	+	+	+
<i>Mischocyttarus</i>	+	+	+	+	+
<i>Ropalidia</i> IF	+	+	+	+	+
<i>Ropalidia</i> SF	-	-	?	-	?
<i>Polybia</i>	+	-	+	-	-
<i>Vespa</i>	+	+	+	-	+
<i>Vespula</i>	+	++	+	-	+
<i>Dolichovespula</i>	+	+	+	±	+
<i>Parischnogaster</i>	?	-	?	++	+

Despite these practical difficulties, the study of possible trade-offs at the colony level is a necessary part of understanding the colony cycle. I suggest that the most demonstrable trade-offs are likely to be: a) production of many small vs few large workers, b) in termites, production of workers vs soldiers, c) reproduction vs further growth, and d) size of colony propagules, with emphasis on independent-founding vs swarm-founding. Especially in ants, it should be feasible to manipulate features of the colony to test these propositions. The focus below is on aspects of the last two kinds of trade-offs.

At the same time, there is a limitation inherent in the study of simple trade-offs within pairs of parameters. This is recognized in the concept of r- and K-selection, as outlined in almost any population-ecology textbook. The focus of these opposing terms shifted after they were first proposed to describe selection in density-regulated and -unregulated environments (MacArthur and Wilson, 1967), so that they came to be associated with suites of characters (Tab. 3). The terms have fallen into some discredit, yet a presumption remains that two alternative sets of traits approximating these represent a widespread reality (Stearns, 1992).

If not too much is made of it, it is a reasonable working hypothesis that analogous sets of characters are to be found at the colony level in social insects, something that must have occurred to many in our discipline. The pattern of conjectures shown in Table 3 is consistent with the view that a general theory of the colony cycle will develop around the functional understanding of syndromes of characters much more sophisticated than the simple beginning illustrated in Fig. 1.

### **Reproduction: Now or later?**

"We are still far from understanding why some organisms are semelparous and others are iteroparous. In particular, does semelparity result from extreme reproductive effort, or is death inevitable and extreme reproductive effort a response to it?" (Roff, 1992: 394)

"One way to understand the adaptive design of the life history of a social insect colony is to view the colony as having an investment policy whereby it allocates limited resources among the various physiological functions fostering its growth, survival, and reproduction." (Seeley and Mikheyev 2003)

The presumed trade-off between present and future reproduction is at the heart of the distinction between semelparity and iteroparity (or monocarpy and polycarpy, respectively, in plants). Iteroparity – the tendency to reproduce in several episodes over an extended period – appears to be more common, overall, in multicellular organisms. Examples of semelparous species – in which all reproduction comes in a single burst toward the end of the parents' life – are many insects, Pacific salmon, bamboos, some oak trees, and annual plants. As with much else in life-history theory, it is very easy to enumerate the relative advantages of each habit and very difficult to say why a given habit is found in these taxa but not in these others. A closely analogous situation is seen in the distinction between determinate and indeterminate colony cycles.

The question of the circumstances in which it is worthwhile to devote less or more of one's resources to reproduction goes back at least to Fisher (1930). Reproduction by an organism is logically assumed to come at a cost to its future reproduction and/or expected longevity. If it did not, the organism should start reproducing as early as possible, which most do not. Reproductive effort (RE) is the proportion of available energy devoted to

reproduction, rather than into self-maintenance or growth, during a given period (Hirshfield and Tinkle, 1975). This is often taken to refer only to surplus energy, beyond that needed to keep the organism alive, so that it becomes primarily a question of growth versus reproduction. The age schedule of reproduction is a reflection of how this trade-off is resolved.

As a rule, organisms and colonies become larger with age, and fecundity tends to increase with size. We expect, then, a definite positive correlation between age and fecundity, even if the causal link is weak. The relationship between size and fecundity has been extensively studied at the organismal level (Roff, 1992:126–28). As expected, there is a distinct tendency for larger individuals to reproduce more. The allometric constant varies widely among taxa, with a suggestion that larger individuals tend, on the whole, to be more fecund per body mass. There is no necessary problem in the allometric nature of the relationship or in the great variation between taxa, as long as size and fecundity remain positively correlated.

Colonies face the same question as do organisms with respect to the timing of reproduction: Is it better to reproduce a smaller number of propagules early or to delay in expectation of producing more when one is bigger? In its direct form, with relation to single organisms, this question has been with us for at least 50 years. With respect to colonies in relatively non-seasonal environments, it is almost untried, although I imagine that most of us have puzzled over it, as did O. W. Richards. Based on his experience with many species of social wasps in Guyana, he asked why colonies of some species persist for a year or more and grow to very large size, while others stay small and break up after a few months (Richards and Richards, 1951; Richards, 1953). It is easy enough to frame a conjecture in terms of bet-hedging, as is often done where attacks by army ants are common and irresistible, but why do species in the same locality hedge their bets so variously? Richards's sketch of a working hypothesis was that small-colony species tend to have a higher RE and invest less in such things as resistance against natural enemies, but my own experience leaves me far from satisfied that any such clear trend exists. Still, I am not aware that we have even a plausible alternative hypothesis in this important question.

Models of social insects in strongly seasonal environments predict that the colony should delay the reproductive phase as long as external conditions allow it to remain productive (Bourke and Franks, 1995; Oster and Wilson, 1978). One of the very few broad theoretical generalizations about colony cycles is that it is optimal for the reproductive phase to start abruptly, with no new worker eggs laid after the first reproductive eggs (Macevicz and Oster, 1976; Oster and Wilson, 1978; modified by Cassill 2002 to accommodate indeterminate colony cycles). This "bang-bang" hypothesis is accessible and attractive, yet it remains almost untested. This is really quite puzzling, as in most social insects it is exceptionally easy to detect the change-over from worker to reproductive production in the colony. In the one explicit test of which I am aware, Greene (1984) found only an indifferent fit between the observed and expected patterns in vespine wasps and gave reasons to predict a departure from bang-bang. Archer (1981) similarly found an overlap in the initiation of worker and reproductive brood in two other vespines.

My own more casual observations with independent-founding social wasps are consistent with those of Greene and Archer, as is implied in Fig. 1a. That is, although few workers are produced after the start of reproductive production, there is significant overlap. I suggest that the now rather sterile question of whether social insects adhere to a bang-bang pattern or not should give way to a more fruitful comparative one: What is the diversity among

species in departure from strict bang-bang, and how can it be explained? To begin with, it should be easy to devise a one-dimensional goodness-of-fit index and apply it to coexisting species of independent-founding polistine wasps, or to conspecific populations in different habitats. Predicting or explaining differences in departure from strict bang-bang – or even saying why there should be differences at all – will be more of a challenge.

At the colony level the size-frequency allometry is at the heart of a long-standing conundrum. In surveying data on reproductive output in social hymenoptera, Michener (1964) found that as a colony grows its total reproductive output increases, but output per adult female decreases. Accordingly,  $a < 1$ , where  $y$  is number of colony offspring and  $x$  is colony size. Unlike at the individual level, this "reproductivity effect" (Wilson, 1971: 338) poses a problem. While a large multicellular plant or animal does not have the option to divide into two or more smaller individuals, social-insect colonies usually can do just this. If  $a < 1$ , any large colony would do better to break up immediately into smaller units, so that no species should characteristically develop large colonies. Similarly, swarm founding should not exist, as the parent colony would do better to invest in independent-founding queens.

Discussions of the reproductivity effect tend to focus on the fact that Michener's analysis did not take into account colonies that have zero reproductive output because they fail early, and to suggest that larger colonies enjoy greater survivorship. The tacit assumption, then, is that colony survivorship approximates a Type-3 curve. However, I am unaware of any attempt to reach a more definite solution to this problem.

Social insects would appear to have exceptional flexibility in the allocation of resources to reproductive vs non-reproductive brood, according to the immediate situation. The developmental period is short, relative to that in metazoan animals of the same cumulative body mass. And in swarm-founding species the decision regarding the fraction of workers to allocate to the swarm can wait until close to the time of departure. It is as if an animal could wait until the moment of giving birth to decide what fraction of her substance to invest in the offspring.

The trade-off between reproduction now or later may also in many cases be a question of reproduction vs survival. Although it can be difficult to demonstrate, it seems very likely that for colonies of most species reproduction poses distinct risks to survival. What is far from clear is whether these risks are generally high, and it will probably be difficult to seek answers in a well-controlled fashion.

## **The number and size of offspring**

Do larger colony propagules fare better? This question would seem to be especially acute for swarm-founders. Swarms are necessarily very few in number, and any swarm substantially depletes the size of the parent colony. It appears almost self-evident that a larger swarm will have greater reproductive value (expected lifetime reproductive output) than a smaller one. This is corroborated in the few species studied to date (Winston, 1987:189; Jeanne and Nordheim, 1996), and there is every reason to expect that such a positive correlation is general and strong.

Given such a correlation, what is the shape of the curve? It would be hard to explain any simple curve, as this would select either for independent founding or for the whole colony as a swarm, and a straight line would seem decidedly unnatural. It is predicted that colony reproductive value as a function of swarm size will show a sigmoid function, with modal

swarm size where the slope is steepest. This can be tested experimentally by the induction of absconding swarms of varying size in a swarm-founding wasp. The difficult part, it seems to me, will be to devise a convenient index of colony productivity that is proportional to expected reproductive success.

In independent-founders, as well, the colony has a choice of investing in many smaller or few larger reproductives, and it is generally supposed that in queens, at least, larger size confers an advantage. As a rule, males are about the size of workers, but in most ants and some other social hymenoptera queens are substantially larger. The common question with respect to this discrepancy has to do with why workers are so small, but let us turn this around and ask why queens are so large.

The evidence, while mostly fragmentary and indirect, seems unequivocally in favour of the view that larger queens do better than smaller ones, as in organisms as a whole, as the founding stage is likely to put severe demands on a their body reserves (Wheeler and Buck, 1996). In one of the few direct studies of this question, Wiernasz and Cole (2003) found a strong positive correlation between size and survivorship in *Pogonomyrmex occidentalis* queens. In addition, as a rule in ants, queens are significantly larger in haplometrotic than pleometrotic species (Wiernasz and Cole 2003). The working hypothesis suggested by these results is that colonies of independent-founding species produce large queens at a cost in numbers because large queens have a decided advantage in the founding stage. The observation that the (short-lived) males are smaller is consistent with this hypothesis. Against this hypothesis, it would appear, is the observation that in termites, queens and kings are usually the same size and not strikingly bigger at final moult than workers.

At the individual level among related species, those with larger females tend to produce larger offspring and at the same time to produce more of them, so that investment per offspring is a compromise between a constant absolute amount and a constant proportion (Clutton-Brock, 1991; Fox and Czesak 2000). Does a similar pattern obtain at the colony level? With correction made for phylogenetic effects, this seems like quite a tractable question in both independent-founding and swarm-founding taxa.

### **Conclusion: What is to be done?**

"Animal sociology remains, in comparison [to human sociology], at its very beginning. To be sure, outstanding specialists have accumulated an enormous mass of facts and have published a great many substantial works in recent decades, from which we have gained deep insights into the biology and organization of animal societies. However, it is only in very recent times that we have seen any attempt to analyse this material from a sociological perspective." (Eidmann, 1928)

"There are virtually no general predictions in life history theory, because some organism can always be found with a tricky and unexpected trade-off that violates the assumptions, because the predictions themselves depend on the state of the life history, and because we do not yet have reliable source laws to predict the critical trade-offs." Stearns (1992: 208)

This, then, is the present status of our understanding of colony cycles in social insects:

1. The basic pattern is well known in a wide variety of taxa.
2. The analogy with individual-level life cycles remains very little exploited.
3. Where the analogy is recognized, the untested assumption that results can be carried over from individual-level life-history theory prevails.

4. The task of explaining differences in colony cycles among taxa has hardly begun.

Michener's (1964) reproductivity effect has been subject to very few tests. On the one hand, this is baffling, as the reproductivity effect has never been treated as comfortable conventional wisdom. At most, it seems to be uncomfortable conventional wisdom and so should serve as an attractive target of new inquiries. On the other hand, it is no mystery why no one has set out to replicate and expand Michener's analysis from existing data. The data are scattered, fragmentary and often ambiguous for the purposes of any broad comparative test. Similarly, anyone testing for colony-level trade-offs across a variety of taxa would likely find the task rather frustrating. Like much of population biology, life-history theory is very fact-intensive, and it is not yet close to a state where the mass of facts ceases to bewilder.

The relevant parameters are by no means obscure or peripheral, yet, as Tschinkel (1991) has noted, the collection and publication of any basic data that do not serve an immediate hypothesis have become quite unfashionable in insect sociobiology. As a result, even such a valuable and easily measured parameter as average colony size at maturation is calculated in very few independent-founding social wasps, for example, and virtually never unless it serves to address an immediate question.

To cite another example, Hölldobler and Wilson's (1990: Tab. 3–2) compilation of colony sizes in ants probably represents the bulk of published data. To anyone outside of our discipline, it would probably appear shocking that this fundamental data-set comprises just 135 species – of which 57 are based on just one colony and another 19 on two – with about 40% derived from a single paper (Wilson, 1959), and is not consistently based on mature colonies.

The key problem is not exactly a paucity of data. Rather, what is missing is a centralized database of colony-level parameters. That is, it is mainly an information-retrieval problem. When researchers undertake a broad comparative study, the customary approach to amassing the data is the same as it was a generation ago: survey the literature and then put out an appeal for unpublished or obscurely published data. Electronic search and communication methods contribute speed to this procedure, but it is fundamentally archaic. A freely accessible repository for both published and unpublished data could do much to promote and democratize the analysis of insect societies.

There is a good model for such a database. The Human Relations Area File (HRAF, <http://yale.edu.hraf/>), based at Yale University, has existed since 1949 to accessibly store data on human societies. The HRAF stores data on about 365 ethnic and religious groups according to a detailed classification. Nothing even remotely comparable exists for the study of insect societies. It is a brake on progress in our discipline that well-rounded, publishable data-sets and especially more fragmentary, obscure, and unpublished data do not automatically go into a central database and are therefore not accessible with Internet ease.

It is certainly not because of any intrinsic difficulty that the HRAF model has not been emulated in insect sociobiology. The number of "species" is of course larger, but the number of data categories would certainly be much smaller (see Tschinkel, 1991: Tab. 1, and the appendix to this paper) than the hundreds recognized by the HRAF. All in all, this is not a daunting enterprise. The main value of such a database would likely be in the understanding of colony cycles, but the uses of a good data-set commonly go well beyond those originally conceived.

The central practical problem is that a general database on social insects is not the obvious responsibility of anyone in particular. Who, then, should manage it? One option is

to seek an institutional base, like that enjoyed by the HRAF and a new electronic database of ant taxonomy (<http://www.antbase.org>). An alternative is to adopt it as a major, permanent initiative of the International Union for the Study of Social Insects (IUSI), the organizing body for our discipline.

This second option may seem quite radical in an age when scientific societies have long since almost entirely stopped organizing research and restricted themselves to facilitating discussion and publication. Nonetheless, there is much in favour of it. Management of the database need not be especially expensive – requiring perhaps one full-time staffer – and until such a resource has the weight of tradition there are risks in entrusting it to the hospitality of an institution. It seems fair to predict that a well-run database would quickly gain enough popularity among insect sociobiologists to ensure outside funding and its continuation by the IUSI.

This proposal is hereby laid before the IUSI as a formal motion for implementation.

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## Appendix

*Draft list of sociometric parameters for a database on social insects. The list is limited to that part of the database needed for a description of the colony cycle, leaving aside such areas as nest structure, feeding habits, and within-colony kinship. For an alternative classification of much the same subject area see Tschinkel (1991: Table 1).*

Modal numbers of colony-founding group members

a) Queens, b) males/kings, c) minor workers, d) major workers, e) brood according to each stage (in swarm-founding species, distinguish between mother and daughter colonies).

Modal numbers of colony members at the start of the growth phase

a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal numbers of colony members at the start of the reproductive phase

a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony-founding group members

a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony members at the start of the growth phase

a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony members at the start of the reproductive phase

a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Forms that undergo seasonal diapause

Duration of seasonal diapause

Mean egg-to-emergence time

a) Queens, b) males/kings, c) minor workers, d) major workers/soldiers.

Schedule of production (sequence of emergence) of new individuals according to sex and caste

Ratio of minor/major workers (or workers/soldiers) according to colony age

Ratio of minor/major workers (or workers/soldiers) according to colony size

Mean duration of the founding phase

Mean duration of the growth phase

Mean colony generation time

Colony survivorship through the founding phase  
(in swarm-founding species, distinguish between mother and daughter colonies)

Colony survivorship through the growth phase

Colony survivorship according to age

Colony survivorship according to number of workers

Number of colony propagules according to age

Number of colony propagules according to number of workers