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Life history evolution in social insects: a female perspective

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Social insects are known for their unusual life histories with fecund, long-lived queens and sterile, short-lived workers. We review ultimate factors underlying variation in life history strategies in female social insects, whose social life reshapes common trade-offs, such as the one between fecundity and longevity. Interspecific life history variation is associated with colony size, mediated by changes in division of labour and extrinsic mortality. In addition to the ratio of juvenile to adult mortality, social factors such as queen number influence life history trajectories. We discuss two hypotheses explaining why queen fecundity and lifespan is higher in single-queen societies and suggest further research directions on the evolution of life history variation in social insects.

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Introduction

At a time at which deeper insights into the proximate basis of life history trade-offs are gained, including those in social insects [1,2], we take a fresh look at the evolutionary basis of life history traits in this group. Due to their social lifestyle, ants, termites, social bees and wasps exhibit not only extraordinary life histories [3–5], but also strong variation in these traits both within and between species [6••]. As this is in the social Hymenoptera especially true for queens and workers, we will focus here on female social insects.

Eusociality represents the latest of the major evolutionary transitions towards higher complexity [7,8]. In eusocial groups selection not only acts on individuals, though individual selection is an important selective force in many social insects [9], but on entire colonies as well, which represent the reproductive units here [10]. Therefore, life history traits of social insects include not only individual traits such as queen lifespan, but also colony-level traits, such as colony size or queen number [11••]. Like multicellular organisms, insect societies grow — in worker number instead of body size — and mature when colonies start to produce sexuals. However, in contrast to solitary individuals, they do not necessarily senesce [12••]. Polygynous colonies that re-adopt daughter queens, are potentially immortal [13], though their genetic composition changes over time in contrast to that of multicellular organisms. Interestingly in lower termites, the replacement of reproductives by neotenic can also lead to immortal colonies without with the link to polygyny [9]. Yet, in most single-queen, that is, monogynous societies, the colony's lifespan hinges on that of the queen and therefore selection on longevity led to extremely long queen lifespans [3,4]. Ant and termite queens can live for several decades, and their fertility may remain constant or even increase throughout their life [14,15]. A positive association between longevity and fecundity is apparent in queens and defies the predictions of life history theory [16], as both traits are usually traded-off against each other. The opposite is true for workers that show reduced lifespan and no or low fertility [15,17]. Evolutionary theories explain lifespan evolution by the declining force of selection with age with extrinsic mortality as the main driver. Colony life leads to low external mortality for queens, as the security of the nest shields her from predators and parasites and the care of the workers protects her from other environmental hazards such as starvation or desiccation [4]. In the following, we highlight the impact of colony size, reproductive strategies and social structure on the evolution of life history traits in social insects and emphasize the need to take these factors into account when studying life history evolution in eusocial societies.

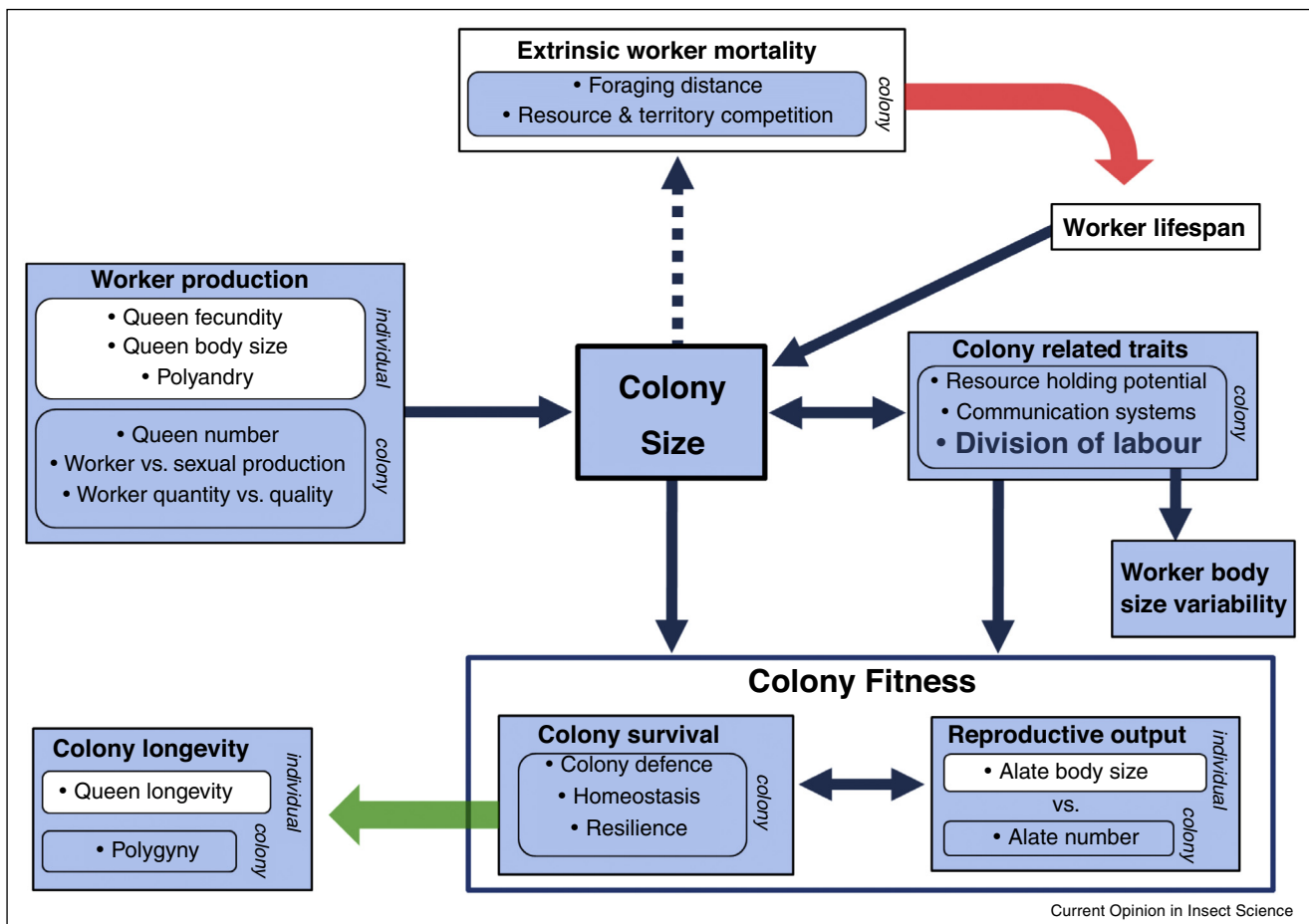
The effect of colony size on life history evolution in social insects

Just as body size in solitary organisms, colony size in eusocial societies has important consequences, but in social insects individual as well as colony-level life history

traits are affected [11^{**},18]. Species with larger colonies exhibit increased social complexity, communication skills and resource holding potential and intraspecific comparisons show that larger colonies benefit from improved colony survival and reproductive output [Figure 1]; [19–23]. Division of labour and task specialization mainly explain these fitness-relevant traits of colonies and leading to caste differentiation and the evolution of divergent ageing phenotypes [24,25^{**},26]. In species with larger colonies, life history traits of queens and workers, such as body size, fecundity, and longevity increasingly diverge [Figure 1]; [6^{**},24,25^{**}]. According to the evolutionary theory of ageing, differences in lifespan between queen and workers, may be explained by colony size-associated changes in extrinsic mortality [2,27–29]. In larger colonies, queens are better protected from extrinsic

sources of mortality and benefit from higher survival due to improved colony defence, homeostasis and resilience [Figure 1]; [6^{**},23,30–32]. Yet, how the relationship between worker lifespan and extrinsic mortality shifts with colony size both within and between species is less clear. Increasing colony size causes a rise in resource demand, which in turn leads to increased foraging distances with higher risks of desiccation, predator and parasite encounters. Species with larger colonies also have a higher potential to control resources and are more likely to engage in intra-specific or interspecific fights [Figure 1]; [32,33]. As a consequence an increase in extrinsic worker mortality could result in relaxed selection for worker longevity [Figure 1]; [29]. Alternatively, the overall fitness benefits of increased colony size could select for increased longevity in workers [Figure 1]; [34^{*}].

Figure 1



This figure illustrates the central role of colony size in life history evolution of social insects. The flowchart depicts the influence of size-related changes on the evolution of individual (in white) and group-level (in blue) life history traits. Dark blue arrows indicate causal relationships, which are condition-dependent when lines are dotted. Colony size affected selective pressures are shown by large arrows, the colour of which indicate the direction of selection (positive: green; negative: red). Colony size largely depends on worker production and worker lifespan, which in turn is influenced by the extrinsic mortality of workers. Intra-specific and interspecific comparisons revealed an increase in division of labour, improved resilience and colony defense, better resource holding potential and communication systems in larger social insect colonies. Although species with stronger division of labour are likely to evolve morphological divergence within the worker caste, increased colony survival selects for colony longevity and in turn for increased queen lifespan or queen replacement, for instance via secondary polygyny.

To resolve this issue, more empirical data comparing colony size-related changes in extrinsic mortality and worker lifespan both within and between species are needed.

Life history theory predicts a trade-off between offspring quality and quantity [35], which appears to shift in insect societies with colony size [36]. Within a species, larger colonies produce fewer alates, but the body size of new males and queens increases (Figure 1; [11^{••},23]). Queen body size is associated with better independent founding success and faster colony growth within ant and bee species [37–39]. Hence, smaller colonies focus on producing more queens of lower quality and aim for quantity, whereas larger colonies invest more in offspring quality, which can lead to an increased founding success [23,37]. Similarly, worker quality and quantity could be traded-off [Figure 1]; [29,40,41], albeit it is less clear what characterizes worker quality. As workers do not normally reproduce, the quality of a worker can be regarded as its contribution to the reproductive output of a colony. As in most social insects, per-worker productivity decreases with colony size [42,43], is worker quality thus lower in larger colonies? A facet of worker quality could be size, but there is little evidence that worker size decreases with colony size [6^{••}]. A comparison of non-invasive and invasive species revealed that the supercolonial invasive ants have smaller workers [44]. Yet, they differ in so many traits from non-invasive species that it remains unclear whether colony size differences alone explain this pattern. Variation in worker body size clearly increases with colony size both during colony ontogeny and in interspecies comparisons and is associated with higher degree of specialization and task efficiency in larger colonies [Figure 1]; [21,25^{••}]. Species with polymorphic workers exhibit diverging worker morphologies as their colonies grow adding the highly specialized larger worker castes (majors) only later in colony development [45]. An exception is fungus-growing termites, in which the early production of soldiers decreases the growth of incipient colonies [46]. As reduced investment into each worker may help colonies to grow faster, many species with monomorphic workers increase worker size over early colony ontogeny [47].

Fecundity is another life history trait that can be affected by colony size. Although the likelihood of worker reproduction is reduced in highly eusocial species, queen reproductive output is associated with colony size especially among monogynous species [Figure 1]; [11^{••},31,48[•]]. Furthermore, increased fecundity is associated with physiogastry in army ant and termite queens with colonies of several million of individuals [45,49,50]. In monoandrous social Hymenoptera, a queens' total lifetime production of diploid offspring may be limited by the amount of sperm she receives from a male during her only mating flight. Evolution of large colony size may thus

favour polyandry or several mating events during a queens' social life [Figure 1]; [51–55]. Alternatively, fecundity constraints of body size and sperm availability and the strong fitness dependence on the queens' lifespan, are overcome by multiplying the number of reproductives in secondary polygynous species [Figure 1]; [3,56[•]].

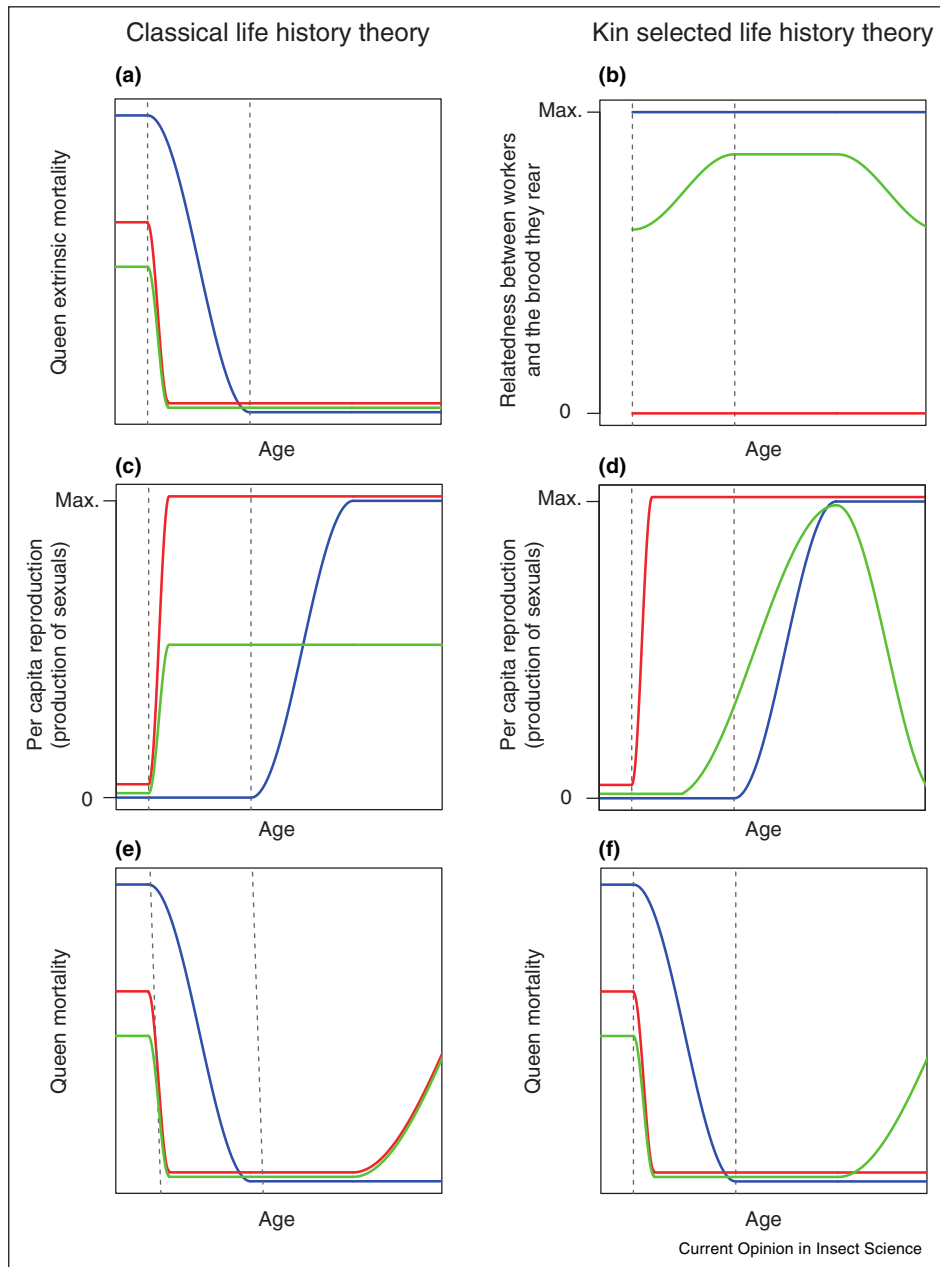
Social structure and reproductive strategies

Social insects exhibit a diversity of reproductive strategies, often associated with the social organization of their colonies. Whereas ants and termites invariably form long-lived societies, many social bees and wasps are shorter lived and often exhibit an annual semelparous lifestyle [44,57]. Life history theory predicts that a species should reproduce only once in life, if adult mortality exceeds juvenile mortality [58]. The semelparity of bees and wasps in temperate climates [44,57], could thus be an evolutionary consequence of high overwintering mortality of established nests. If however, juvenile mortality is higher than adult mortality, several reproductive events are selected for. Albeit a semelparous lifestyle is hard to abandon [*Cole's paradox*; [59^{••}]], there are several transitions to perennial iteroparous life, for example in the ancestors of the ants, termites, honey and stingless bees [3,28]. Reproductives of these taxa benefit from a lower adult mortality due to well-developed nest defences against predators and parasites [32], but suffer from a high juvenile mortality due to a dangerous mating flight and colony foundation phase [31,60].

Obligate eusociality is believed to have evolved under lifetime monogamy [61,62,63[•],64], yet many eusocial lineages have secondarily developed multi-queen breeding (i.e. polygyny; [30,31,65,66]). Monogyny and polygyny are associated with distinct life-history syndromes [65], as queens of polygynous species are typically shorter-lived, less fecund and smaller compared to queens from monogynous ones. According to classical life history theory, these differences in queen lifespan can be explained by the higher juvenile to adult mortality in monogynous queens (Figure 2a), which disperse over longer distances and found new colonies independently [30,31,67,68]. Contrastingly, queens from polygynous colonies suffer lower juvenile to adult mortality because they often mate in or near their natal nests and start to reproduce either in the mother colony or establish new nests with the help of workers. This relaxes selection for longevity thus favouring early reproduction (i.e. production of sexuals; Figure 2c). That queen number is less important than the founding mode becomes apparent when looking at the monogynous honeybees, where young queens return to the mother nest and show fast reproduction and relatively short lifespans.

Alternatively, differences in queen lifespan between monogynous and polygynous social Hymenoptera that

Figure 2



Conceptual model of social insect life history traits according to classical (left) and kin-selected life history theory (right). Queen age is represented by three phases, the dispersal phase, the ergonomic phase and the reproductive phase (from left to right), separated by the grey dashed lines. Blue lines represent queens from monogynous species, green lines queens from polygynous species and red lines inquiline social parasites.

adopt mated queens may be driven by kin selection [59^{••},69–71]. Central to this kin selected life history theory, is that worker loyalty erodes over the lifetime of a queen in polygynous colonies, driven by the replacement of workers from older queens by workers from newly adopted ones [72,73]. A decrease in worker loyalty may result from a switch from worker to sexual production over the reproductive life of a queen. Worker daughters from resident queens are expected to raise eggs of newly adopted queens

into workers (Figure 2b). These workers will contribute to the future reproductive success of their mother, corroding the loyalty of the workforce to the older queens with negative consequences on their reproductive success (Figure 2d). Hence, kin selected life history theory predicts a reduction in queen reproductive success over time and thus relaxed selection for longevity once species have evolved obligate polygyny (Figure 2f). This hypothesis thus depends on workers behaving altruistically depending

on the degree of relatedness, hence nepotistic. Yet, evidence for true kin recognition and nepotistic behaviour in social insect colonies remains scant [63*].

Although both classical and kin selected life history theory predict lower queen longevity in polygynous versus monogynous species, the key mechanisms hampering the evolution of queen lifespan in polygynous species markedly differ (Figure 2). One promising avenue to distinguish between these two alternatives is to focus on species where the predictions of classical and kin selected life history theory diverge. In particular, kin selected influences on life history evolution are entirely negated in socially parasitic species (e.g. inquilines), which exploit the workforce of another species to raise their often exclusive sexual brood [31,74,75]. Thus, (most) inquiline social parasites do not produce workers and can instead maximally invest in sexual offspring (Figure 2c,d). In inquilines that disperse and usurp host colonies, the extrinsic mortality risk during early life phases may resemble that of independently founding, non-parasitic queens. However, early mortality risk of inquilines that circumvent risky dispersal and colony usurpation by intranidal mating may be comparable to the polygynous strategy. In the latter, theory thus predicts that the age-dependent extrinsic mortality resembles that of polygynous species, in the absence, but not in the presence of kin-selected life history evolution (Figure 2e,f).

Conclusions

The social lifestyle reshapes common life history trade-offs, such as the one between longevity and fecundity, but it is less clear what exactly allows queens to be both highly fecund and long-lived. Although the field currently focusses on revealing how genetic pathways were reset in social insects [1], it is worth investigating the impact of ultimate factors such as resource availability or extrinsic mortality as well. We have revisited some of the evolutionary drivers of the remarkable life histories of female social insects and highlight four future research areas:

1. Colony size is a colony-level trait tightly connected to intraspecific and interspecific variation in life histories. However, the relative importance of possible underlying factors, such as division of labour, resource holding potential and foraging strategies including communication skills are still unclear. We suggest to study how and why queen and worker mortality, lifespan and body size change with colony size both within and between species. In this context, we consider division of labour of particular importance.
2. As predicted by life history theory in general, the relationship between juvenile and adult mortality should also affect social insect reproductive strategies. However, reliable field data on extrinsic mortalities for social insect queens during mating flight, colony foundation and adult life are scarce. Trapping sexuals, mapping and tracking colonies combined with genetic

methods [76,77] allows to obtain these data that will lead to a better understanding of life history evolution.

3. The dependency of colony survival on queen survival is loosened in polygynous social Hymenoptera and in the lower termites, which can replace queens by their daughters. Although this is linked in Hymenoptera to polygyny, this is not necessarily the case in the lower termites, which allows to test whether social structure itself or the possibility to replace the mother queen is associated with relaxed selection and shorter lifespans in social insects.
4. Polygyny-associated shifts in queen life history traits may be imposed by their social rather than their physical environment. The conflict of interest between queens and workers in polygynous species paves the way for intraspecific exploitation, and ultimately inquiline social parasitism [59**,64,75,78,79]. Although the role of life history strategies in the evolution of inquilinism has received considerable attention, social parasites are generally excluded from comparative life history studies. Our conceptual model however emphasises that inquiline life history data could be particularly instrumental to test the predictions of kin selected life history theory.

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