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Evolution: Plastic Sociality in a Sweat Bee

How and why do bees become social? A transplant experiment shows that sweat bees can adopt a solitary or social lifestyle in response to their environment.

Michel Chapuisat

Cooperation plays a central role in the major evolutionary transitions that produced the integrated hierarchy of biological organization, from genes within cells to organisms within societies [1]. Cooperation between individual organisms reaches extreme forms in the eusocial insects, where some individuals permanently forfeit reproduction to help rearing the offspring of other individuals. How did this highly integrated form of social organisation evolve? Does it require major genetic innovations? In this issue of *Current Biology*, Field *et al.* [2] report that a species of sweat bee flexibly shifts between solitary and social life when moved between cold and warm environments. This experiment indicates that phenotypic plasticity underlies an ongoing evolutionary transition between solitary parental care and eusociality in this group.

Most wild bee species are solitary — each female builds and provisions her own nest, in which she cares for her offspring. In contrast, some species, like the honeybee, form well-coordinated societies in which only one female, the queen, reproduces. Sweat bees (Hymenoptera, Halictidae) are particularly interesting for the study of social evolution because members of this family exhibit the full range of behaviour, from strictly solitary to

permanently eusocial [3]. The mapping of the social behaviour on the phylogeny of the group has revealed three independent origins of eusociality, but also as many as twelve reversions from eusocial to solitary lifestyle [4]. In fact, a few halictid species appear to be in the middle of these social transitions. These species are socially polymorphic, with solitary and social colonies, which makes them particularly appropriate to elucidate the mechanisms and selective pressures leading to social transitions.

Field *et al.* [2] studied one of these socially polymorphic sweat bee species, *Halictus rubicundus*. In the British Isles, bees from northern or high elevation populations are solitary (each female raises her own offspring with no help), whereas bees from southern and low elevation populations are social (many of the first generation offspring become non-reproductive helpers; Figure 1). When the authors transplanted foundresses between the ‘solitary’ and ‘social’ populations, most of their offspring adopted the social system of the sites they were transplanted into, rather than the system of their site of origin. In addition, the authors used genetic markers to show that one female monopolized reproduction in social nests. They also performed a control transplant between two ‘solitary’

populations to verify that the transplant itself did not alter the social organization.

The conclusion from these experiments is straightforward: these bees show phenotypic plasticity for solitary or social behaviour. Individuals with a given genotype can develop either into independent mothers or into social helpers in response to the environment in which they were reared. The decision is independent of the origin of the genotype of the bee, which may come from either a solitary or a social population. This impact of environmental conditions on sociality can be explained by the fact that annual bees need a long growing season to become social (Figure 1). Indeed, sociality requires an overlap of generations that can only be obtained by provisioning two consecutive generations in the same year [5]. In cold climates time constraints prevent bees from rearing a second generation, which forces them to be solitary. If the conditions are unpredictable or if bees frequently move between cold and warm habitats, a flexible response to environmental conditions appears to be a good strategy to make the best of both worlds.

In warm climates, becoming social appears to be adaptive, because it permits an individual to rear a new generation in an established nest and with the workforce of a group rather than trying to rear offspring alone from scratch, which is likely to be a risky enterprise [6]. An adaptive link between climate and sociality is supported by the geographic distribution of solitary and social behaviour within and across species of sweat bees [7,8]. The data collected by Field *et al.* [2] also suggest that the behaviour of *H. rubicundus* helpers

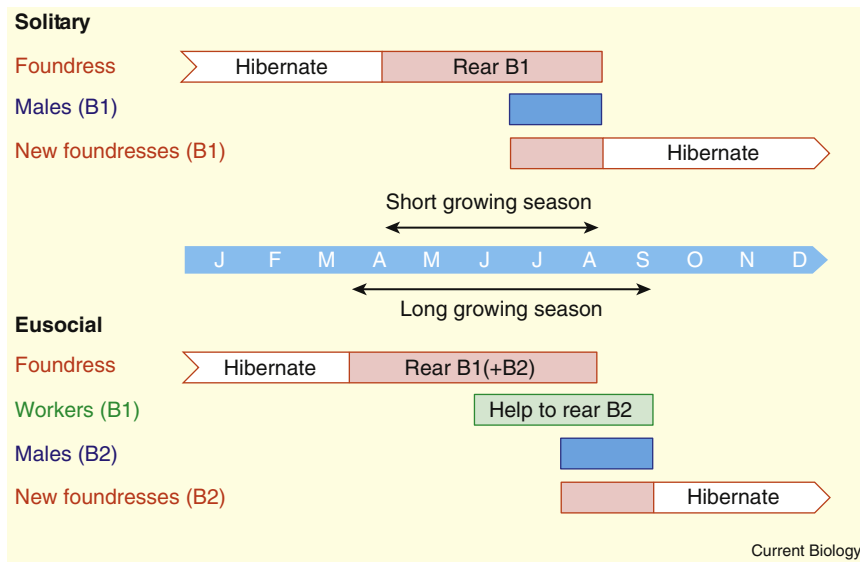


Figure 1. Life cycle of the socially polymorphic sweat bee *Halictus rubicundus*.

Top panel: in populations where the growing season is short, the bees are solitary. The foundress rears one brood (B1) of males and females. The B1 females leave the nest to overwinter and start their own nest in the next spring. Bottom panel: in populations where the growing season is long, the bees are eusocial. Most of the B1 females become non-reproducing workers that help to rear a second brood (B2).

increases their inclusive fitness. First, there were more helpers in nests that had produced their first females early in the season: helpers at these nests had indeed more time left to increase group productivity. Second, nests in which the foundress was still alive had more helpers than nests in which a daughter had replaced the foundress. This pattern is predicted by kin selection, as helpers have more indirect genetic benefits to gain if they rear brothers and sisters than nieces and nephews, which are less related to them. This is correlational evidence. A definitive proof that the polymorphism observed in the study populations of *H. rubicundus* is adaptive would require experimental data on the cost of helping (how many offspring does a helper forfeit?), its benefits (how many additional individuals will be reared because of the worker's help?) and the genetic relatedness between the helper and the extra brood.

The social behaviour of *H. rubicundus* comprises multiple strategies: reproducing in the presence of the mother or only after the mother has died, possibly drifting to other nests, or helping [2,9]. Other members of the social group may also enforce altruism by constraining the options of the developing females [10]. In particular, the foundresses that

provision the offspring have the possibility to limit the amount of food provided to their first generation of daughters in order to force them to stay at home and help to rear the second generation. This reflects the full complexity of insect sociality, which not only combines direct and indirect gene transmission, but also involves constraints, power and information of multiple group members with partially divergent genetic interests [11,12]. With their small annual colonies, sweat bees are eminently tractable for detailed quantitative studies on the costs, benefits and mechanisms involved in social life [3].

An interesting twist of the story is that *H. rubicundus* probably is descended from eusocial ancestors [4,8]. Hence, the plasticity observed in Europe might have been regained or retained to cope with an unpredictable climate. Gene flow is also maintained among populations of the British Isles [7]. In contrast, social and solitary populations form genetically differentiated clusters in North America [13]. It would be of interest to experimentally test if bees from the North American populations are also phenotypically plastic, or if they have become genetically specialized for either solitary or social life.

The experimental demonstration of phenotypic plasticity for social behaviour in sweat bees [2] has important implications for the evolution of eusociality, because it suggests that switching between solitary and social lifestyles can be fairly easy and reversible. The social polymorphism may indeed be generated by simple decisions altering the life-cycle and reproduction — stay or leave, lay eggs or help [14]. Such alterations may not require major genetic innovations once the appropriate developmental switches have evolved. Hence, the evolution of eusociality may be based on pre-existing gene-by-environment interactions influencing developmental switches, rather than on novel 'genes for altruism'. The switches may in turn be influenced by various external stimuli and social factors, such as day length, temperature, food quality and quantity, presence of a mother or availability of mates [15,16].

It has long been recognized that phenotypic plasticity plays a pivotal role in insect sociality [17]. Indeed, kin-selection theory predicts that the genes promoting altruistic behaviour must be carried by both workers and queens, and therefore must be conditionally expressed only in workers and not queens [18]. This remains a central tenet of insect sociobiology, even if purely environmental caste determination is less common than previously thought and genetically-based caste determination prevails under some conditions, particularly in complex hybrid systems [18]. Phenotypic plasticity is also important in other evolutionary transitions [19]. The cells in an organism differentiate into specialized forms as a result of controlled modifications in gene expression. In a multicellular green alga, *Volvox carteri*, the gene inducing the permanent suppression of reproduction in somatic cells evolved from a gene involved in the temporary suppression of reproduction in response to stressful environmental conditions in a related solitary unicellular alga, *Chlamydomonas reinhardtii* [20]. This study on the evolution of individuality shows striking conceptual similarities with Field *et al.*'s [2] demonstration that phenotypic plasticity is important in the early stages of the transition between parental care and eusociality. More generally, such studies show that a full

understanding of the evolution of cooperation and sociality requires knowledge of how genes and environment interact in shaping the life-history trajectory and social development of individuals.

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Gene Regulation: Global Transcription Rates Scale with Size

Is bigger better? Scientists have long puzzled over the potential relationship between cell size and the rate of mRNA production. A recent report builds a strong case that global transcription rates scale with size.

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While the size of organisms varies over an almost incomprehensible range, the average size of cells is remarkably invariant between species [1,2]. These observations suggest that cells have an active mechanism to ensure cell size homeostasis. Excessive growth would produce cells of ever increasing size. Conversely, unrestrained proliferation in the absence of adequate growth could result in a mitotic catastrophe. Put simply, cells must have a means of coordinating their rate of cell growth with their rate of division.

Collectively, the term ‘cell growth’ refers to the metabolic processes involved in macromolecular anabolism, and the bulk of this consists of DNA, RNA, and protein synthesis. DNA replication occurs only during a discrete phase of the cell cycle. In contrast, protein and RNA synthesis

are continuous processes. While cell proliferation is inarguably exponential, it is considerably less certain if cell growth is exponential. Exponential growth dictates a dependence upon size; large cells grow proportionally faster than small ones. Thus, exponential growth puts a premium on cell size.

The potential importance of size has been a hot topic that has teased the minds of philosophers and scientists for hundreds of years. Modern marketers continually batter ‘pop culture’ with the concept that bigger is better. Sometimes the evidence in favor of this idea is inescapable. Strength is nearly always proportional to size, and evidence suggests that longevity and metabolic rates scale with size [1,3]. Large organisms are long-lived, perhaps because they are more metabolically efficient. The average domesticated elephant lives 30–100 times longer than the average laboratory mouse [1]. However,

considerably less is known about the relationship between size and basic cellular processes like RNA production. For example, as cells enlarge, their DNA to protein ratio declines (Figure 1). Thus, with respect to their mass, the relative gene dosage of each cell decreases. Does this result in a concomitant decrease (or increase?) in global transcription rates? In this issue of *Current Biology*, Zhurinsky *et al.* [4] re-examine the relationship between the rate of mRNA synthesis and cell size.

With respect to global mRNA production, two very general processes occur with cell cycle progression. First, in order to produce nearly identically sized daughters, cells continually increase in size as they advance towards cytokinesis. Second, cells replicate their DNA during S-phase. What remains to be resolved is how each of these events affects global RNA transcription. Initial experiments conducted in synchronized yeast cultures suggested that mRNA transcription rates abruptly doubled after DNA replication [5,6]. Similar results were obtained in HeLa or CH-Don-C cells [7–9]. Since the sharp rate change for mRNA production was not mirrored by the rate at which cells increased in size, these data were more consistent with a gene