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Review

On the Life History of the Honey Bee Superorganism

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Abstract

The Western honey bee, *Apis mellifera*, forms large colonies, which represent organisms in their own right, so-called superorganisms. Although the honey bee is one of the best studied species of insects, there are still contradictory explanations in use for characteristics as fundamental as colonial lifespan. In this review, considering colonies as potentially immortal is debunked due to a lack of conformity with biological convention. What has traditionally been referred to as honey bee colony represents a matrilineage of superorganisms. By proposing a refined colonial life cycle, the analogy between animals and superorganisms is taken further, thereby visualizing superorganismal traits in a new light. Zygotic, embryonic, fetal, juvenile and adult stages are identified during superorganismal ontogeny. An image of the honey bee superorganism emerges as viviparous with strictly sexual reproduction, which is engaged in various forms of maternal care. A multitude of pathways to sexual reproduction are analyzed. Since swarming precedes fertilization, it can be viewed as superorganismal autotomy rather than reproduction. While the prime swarm serves the function of allowing maternal superorganisms to survive reproduction, afterswarms are a means to produce more than one offspring per reproductive cycle. The implications of the findings for honey bee parasitology, monitoring and beekeeping are discussed.

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Introduction

Over a century ago, Wheeler (1910) identified the striking analogy between morphologically distinct castes of insect colonies and differentiated tissues of animals, and proposed treating such colonies as organisms in their own right, so-called superorganisms (Helanterä 2016). Backed by advances in our understanding of major evolutionary transitions, see e.g., Szathmáry (2015) and Boomsma and Gawne (2018), the superorganism has become the highest recognized level in a nested hierarchy of organismality, following unicellular and multicellular lifeforms. A prime example among the diversity of species, which are considered to form superorganisms, and likely the most extensively studied among them, is the Western honey bee, *Apis mellifera* (Boomsma and Gawne 2018).

A honey bee superorganism can be viewed as the somatic extension of the queen and consists of several thousand workers throughout its adult life (Wilson 1971, p. 443). Individual bees represent analogs of cells in multicellular organisms (Moritz and Southwick 1992). With just one physical worker caste, the various superorganismal tissues arise from the worker's temporal polyethism (Seeley 1982; Johnson and Linksvayer 2010). Honey bee superorganisms are perennial and rear new queens and drones in preparation for reproduction in spring or early summer in temperate climate zones (Seeley 1982). One or more swarms may be issued, the first of which is referred to as the prime swarm and includes the old queen. Subsequent swarms are called afterswarms and carry newly emerged, unmated queens. One of the new queens remains at the original nest, from which it takes mating flights and begins laying eggs to produce new worker bees. Swarms select and move into new nesting sites, where nest-building and -provisioning commences, and new worker bees are reared in

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preparation for the winter. New queens may also be reared to replace a fading, injured or lost queen (Fell and Morse 1984).

Despite the substantial knowledge about honey bees, which has been collected over centuries of scientific research, there are still different explanations in use for characteristics as fundamental as colonial lifespan (cf. Wilson 1971; Moritz and Southwick 1992). Wilson (1971, pp. 444-445) views new queens, which replace the old queens, as an integral part of one and the same colony. Since all constituent bees are then replaceable, the colony can be considered potentially immortal in the sense that it does not age. Moritz and Southwick (1992, pp. 62-67), on the other hand, argue that a honey bee colony possesses a genotype much like any other organism does, and that this genotype is defined by the queen and the drones she mated with. New queens carry different genotypes, such that the replacement of the old queens will result in different colonies. Owing to the senescence of queens, honey bee colonies, as described by Moritz and Southwick (1992), are therefore mortal in the sense that they age and have a limited lifespan.

The mortal and potentially immortal honey bee colonies as described by Moritz and Southwick (1992) and Wilson (1971), respectively, represent contradicting views of one and the same reality. This is not just a semantic debate, but has implications for how the biology of honey bees is quantified and understood. Apart from the potentially very different lifespans, consider, for instance, the respective survivorship curves. New potentially immortal colonies are created by casting swarms, which are faced with comparably low survivorship in their first year because they have to locate and move into suitable hollows, construct and provision the nests and produce winter bees before their first winter (Seeley 2017). Once a potentially immortal swarm has survived its first year, it stays in its nest. The mortality rate for the remaining years is therefore markedly lower (Seeley 2017). A high mortality rate early in life, followed by a lower mortality rate, is characteristic for a type III survivorship curve (Seeley 1978). A mortal colony, on the other hand, inherits its parent's nest and benefits from the lower mortality rate in its first year. Once the colony leaves its nest to make room for its offspring, however, it faces the lower survival rates associated with swarming. A low mortality rate early in life, followed by a higher mortality rate, is described by a type I survivorship curve. The opposing nature of the two views may have far-reaching consequences for honey bee life history, heritability and dispersal, describing two theoretically substantially differing organisms.

The potentially immortal view of honey bee colonies appears to be prevalent in the scientific literature, especially in the 21st Century, see e.g., Fell and Morse (1984), Allsopp and Hepburn (1997), Fries et al. (2006), Smith et al. (2016), Seeley (2017) and Kohl et al. (2022). In contrast, usage of the mortal view is rather rare and often intermixed with the potentially immortal view, see e.g., Wilson (1971) and Seeley (1978, 1985). Although Wilson (1971) described honey bee colonies as potentially immortal, the life cycle presented on page 98 implies the mortal view. With respect to the life history strategy of honey bee colonies, Seeley (1978) also used the mortal view by focusing on queens. For the colonial lifespan, however, Seeley (1978) reverted to viewing colonies as potentially immortal.

The purpose of this review is to determine which of the two views is simpler and in better agreement with biological convention governing descriptions of single-celled and multicellular organisms. The implications of the insights gained are discussed with respect to honey bee life history, parental care and superorganismal traits. In the following section, the two views are pitted against each other to resolve the issue. The colonial life cycle is discussed and further specified, followed by a review of colonial reproduction, the role of swarming and the extent of parental care. The paper concludes with a discussion of the consequences of the findings for honey bee parasitology, monitoring and beekeeping.

Parent or Offspring?

The opposing nature of mortal and potentially immortal honey bee colonies can be boiled down to one simple question: Which colony is the parent, and which is the offspring? To answer this question, the outcome of one reproductive cycle of an individual colony is analyzed, which results in the creation of the first filial generation. Consider the occupancy of three cavities at two points in

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time: year 1 before reproduction and one year later before the next reproductive cycle, see Table 1. It is assumed that no swarms occur from other colonies. To gain clarity, the year in between is treated as a black box at this stage. We return to this in the following section.

Table 1. Hypothetical case of cavity occupancy by a parental colony and its offspring before reproduction and one year later, with designation of parent and offspring for theoretically mortal and potentially immortal colonies.

	Cavity 1	**Cavity 2**	**Cavity 3**
Year 1 before reproduction	Mother queen and her workers	Not occupied	Not occupied
Year 2 before reproduction	Daughter queen and her workers	Mother queen and her new workers	Daughter queen and her workers
Year 2 before reproduction for potentially immortal colonies	Parent	Offspring	Offspring
Year 2 before reproduction for mortal colonies	Offspring	Parent	Offspring

In year 1, one colony is present in cavity 1, whereas the other two cavities are vacant. Since this colony is about to reproduce, its queen can be referred to as the mother queen. The parental colony survives reproduction and produces two filial colonies. In year 2, before the next reproductive cycle, cavity 1 is occupied by a daughter of the mother queen and workers, which developed from the daughter's eggs. Cavity 2 hosts the mother queen and her new workers, and cavity 3 hosts another daughter of the mother queen with her workers.

When honey bee colonies are viewed as potentially immortal, the colony in cavity 1 in year 2 represents the parent. Owing to the replacement of the mother queen with one of her daughter queens, the parental colony has undergone genetic transformation. The new genotype of the parental colony stems in part from the previous genotype, which was passed on from the mother queen to the daughter queen. The remaining part is contributed by other colonies via the mating of the daughter queen with drones. Here, we find many similarities with sexual reproduction at the level of the colony, which contradicts the view of the occupant of cavity 1 before and after a reproductive cycle as one and the same colony.

The potentially immortal colony in cavity 2 is viewed as offspring. Since it has the same genotype as the parental colony back in year 1 and even includes the actual physical mother queen, it should represent a clone. This suggests that reproduction is asexual. The colony in cavity 3 is also viewed as offspring. With the new genotype resulting from the daughter queen and the drones she mated with, reproduction appears to be sexual. While asexual and sexual modes of reproduction coexist in many species, in the present case, the view that the colony in cavity 2 is a clonal offspring of the original colony seems misleading.

For the theoretical case of mortal colonies, on the other hand, in year 2, the occupants of cavities 1 and 3 are viewed as offspring. Both filial colonies feature new genotypes, which are partly inherited from the parental colony, whereas the remaining parts originate from mating with drones of other colonies. Here, the similarities with sexual reproduction are in line with viewing the colonies with new genotypes as offspring. The colony in cavity 2 is viewed as the parent. The presence of the mother queen may simply imply that the parental colony has moved from cavity 1 to cavity 2.

When the two opposing views are compared, a substantial discrepancy in their simplicity becomes apparent. While one organism is potentially immortal, changes its genotype and reproduces sexually and asexually, but without yielding two genetically identical offspring, the other organism is mortal and reproduces sexually. There is also a discrepancy in how well the different views conform with conventional biology. While the world is teeming with mortal, sexually reproducing lifeforms, potential immortality is certainly not the norm. Changing the genotype of one and the same organism, involving genetic recombination from sexual reproduction, may even be viewed as a violation of fundamental biology. The difference between mortal and potentially immortal colonies in Table 1 is the referral of parent or offspring to the colonies in cavities 1 and 2. This suggests that the unique attributes of potentially immortal colonies merely stem from a confusion between parent and offspring.

The view of honey bee colonies as potentially immortal is unnecessarily complicated and does not conform with conventional biology. Honey bee colonies should therefore be viewed as mortal, which is simpler and in line with convention, and, as we will show below, helps us clarify several important aspects of honey bee biology.

Life Cycle

The purpose of this section is to shed light on the time between years 1 and 2 from Table 1. What was treated as a black box above, essentially, is the life cycle of the honey bee superorganism. For the sake of the argument, an alternative terminology is used below, which highlights the similarities between animals and superorganisms and may contextualize superorganismal traits in a new light.

Conventional terms for honey bees, such as *colony*, *queen* and *drone*, preceded Darwin and Mendel as well as the superorganism concept by centuries, see e.g., Butler (1609). It is rather unlikely that this terminology would be in line with modern biological thinking. A mated queen, for example, represents the analog of a fertilized egg cell of an animal (Moritz and Southwick 1992, pp. 217-218). By means of symmetry, one may ask whether *mated queen* would be a suitable term for a zygote. Such a terminology for cells may lead to confusion, rather than an intuitive understanding of an animal's nature. Conventional terminology therefore likely obscures comparisons between superorganisms and multicellular organisms. An alternative terminology that works well to highlight the biology of honey bee superorganisms readily emerges by adopting the familiar terms for the various cell types, see Table 2.

Table 2. Conventional and alternative terminology for honey bees.

Conventional terminology	**Alternative terminology**
Drone	Sperm bee (gamete)
Virgin queen	Egg bee (gamete)
Mated queen	Fertilized egg bee (zygote)
Laying queen	Stem bee
Worker	Somatic bee
Colony/society	Superorganism

Drones are the equivalent of sperm cells in multicellular organisms (Moritz and Southwick 1992, pp. 216-218) and can therefore be referred to as *sperm bees*. The terminology for queens depends on the current stage of their life cycle. A virgin queen is analogous to an egg cell and can be called *egg bee*, which makes a mated queen a *fertilized egg bee* or *zygote*. Since a laying queen is the source for all other types of constituent bees throughout the life of a colony, she represents not only the germline, but the analog of a totipotent stem cell, and can therefore be referred to as *stem bee*. Finally, workers are *somatic bees* and the colony or society with its queen a *superorganism*.

Figure 1 shows the life cycle presented by Seeley (1985, p. 37), which was modified to fit the case of one parental superorganism with two offspring from Table 1, as well as the new terminology. The life cycle begins with the rearing of egg bees (Seeley 1985), after which it splits into three lines. The first, innermost circle follows superorganism 1 with the stem bee, which swarms into a new cavity as the prime swarm, where it resumes somatic growth. In the second circle, the first egg bee departs with the afterswarm as superorganism 2. After moving into another cavity, the egg bee is fertilized and superorganism 2 commences somatic growth. The third, outermost circle follows a second egg bee, which inherits the original nest to become a third superorganism. After fertilization, superorganism 3 commences somatic growth as well.

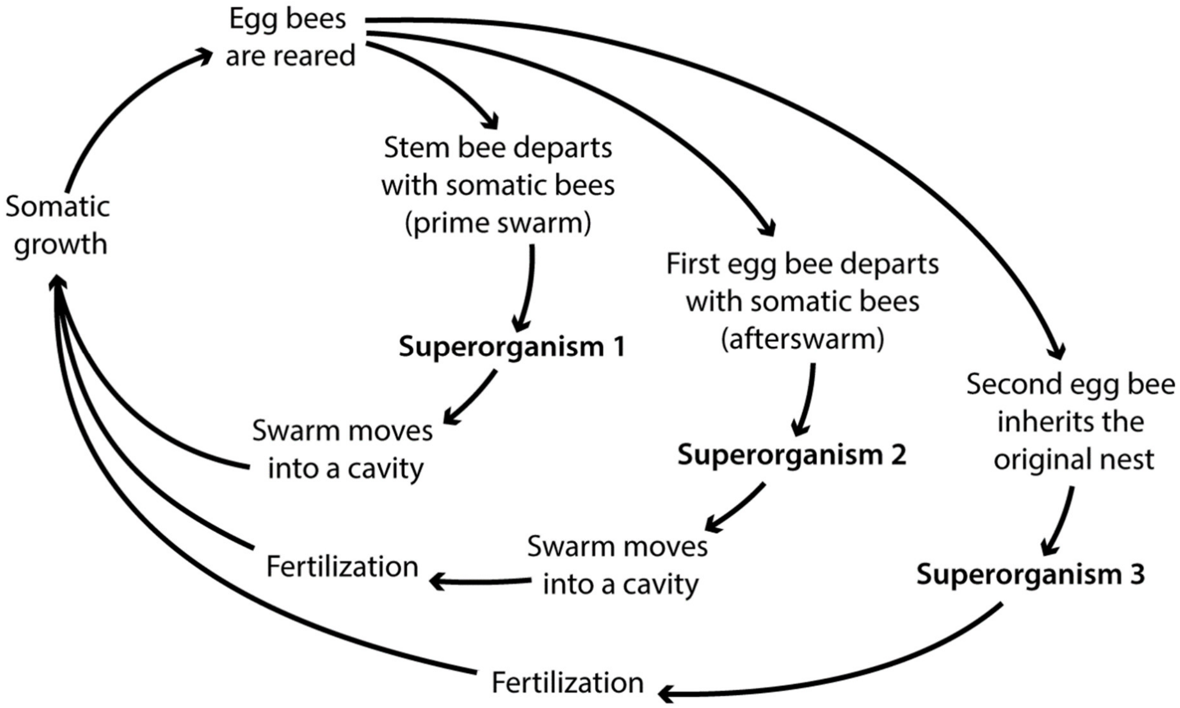

Figure 1. Honey bee life cycle modified from Seeley (1985, p. 37), which begins with the rearing of egg bees, followed by a division into three fractions. The prime swarm represents superorganism 1, which moves into a new cavity, where it resumes somatic growth. The afterswarm is superorganism 2, which moves into another cavity and commences somatic growth after fertilization. The bees remaining at the original nest represent superorganism 3, which commences somatic growth after fertilization (Figure created with Adobe Illustrator CS3).

The first, innermost, circle in Figure 1 follows one and the same superorganism 1 with its stem bee, which moves to a new nesting site for each year or reproductive cycle. As such, it corresponds with the mortal view of honey bee superorganisms. However, this first circle does not feature the generational shift and renewal associated with biological life cycles. Instead, it can be interpreted to describe what the parental superorganism 1 is doing, while its offspring develop elsewhere. The second and third circles, on the other hand, do represent conventional life cycles in the sense that they progress one generation for each round. The presence of two distinct life cycles suggests that there are multiple pathways that lead to honey bee superorganismal reproduction.

An issue with the life cycle from Figure 1 is brought to light by the new terminology, namely that filial superorganisms appear to be created before fertilization takes place. Additionally, the sperm bees are left out, which are required for fertilization. Moreover, as discussed in the following section, there are further pathways to reproduction, which are not featured in Figure 1. By continuing the line of thought from Moritz and Southwick (1992), a single life cycle is drawn in Figure 2, which resolves the aforementioned issues and unites the various circles from Figure 1.

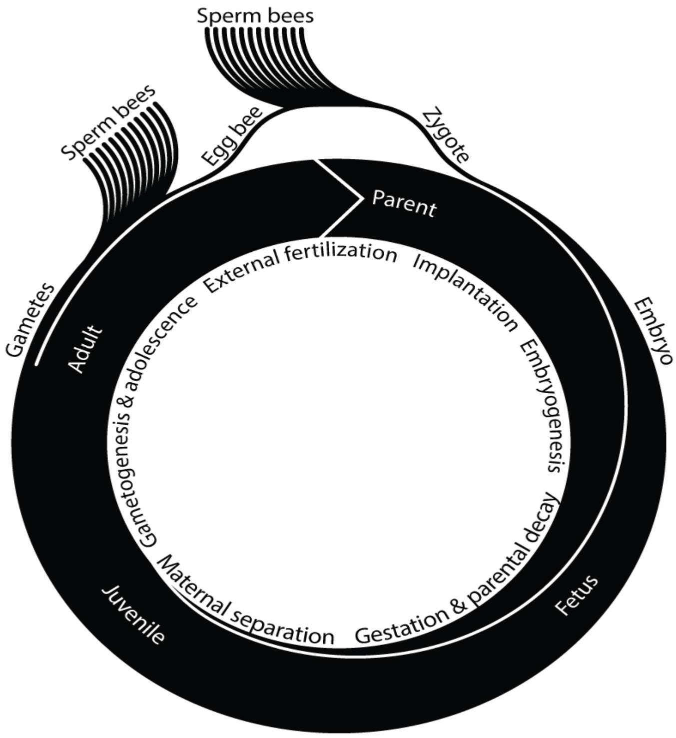

Figure 2. Proposed honey bee life cycle, which begins with external fertilization between gametes to produce a zygote. After implantation of the zygote in the maternal superorganism, embryogenesis commences. During gestation, the maternal superorganism decays with the passing of its somatic bees until maternal separation is completed. The filial superorganism develops from embryo to fetus and juvenile, and closes the circle with gametogenesis and adolescence. The proportions between the parental and filial sections of the circle are intended to illustrate, in principle, the growth of the offspring and decay of the gestating parent. They do not correspond with the actual proportions between the respective numbers of bees found in nature. Neither does the thickness of the circle account for fluctuations in the numbers of bees for varying brood activities or swarming events (Figure created with Adobe Illustrator CS3).

The proposed life cycle shown in Figure 2 begins with the external fertilization of an egg bee by sperm bees to create a filial superorganism. The fertilized egg bee represents the zygote of the filial superorganism, which returns to its maternal superorganism, where it is implanted in the brood area of the nest. Since all somatic bees at this stage are from the maternal superorganism, the offspring develops inside its mother, which can be referred to as gestation. Embryogenesis commences with the first egg laid, from whereon the fertilized egg bee represents the stem bee. The laying of eggs and their development into somatic bees is analogous with cellular division for multicellular organisms to produce the various tissues of the filial superorganism. As time progresses, the maternal somatic bees are gradually replaced by those of the filial superorganism, such that the offspring becomes separated from its mother. The cycle is then closed with gametogenesis at the level of the superorganism. Spermatogenesis results in sperm bees and oogenesis results in egg bees. In a form of somatic gametogenesis, sperm bees can also develop parthenogenetically from haploid eggs of somatic bees, and egg bees may arise via thelytoky (Allsopp and Hepburn 1997). Both sperm and egg bees leave their respective parental superorganisms for external fertilization to begin a new cycle.

The development of the filial superorganism can be divided into several stages, as shown in Table 3. Following the initial zygotic stage, an embryonal stage can be defined, beginning with the presence of eggs laid by the filial stem bee. These eggs and the larvae and pupae developing from them can be interpreted as rudiments for the various superorganismal tissues. With the emergence of somatic bees, a fetal stage can be identified. Here, young somatic bees represent the tissues of the superorganism. However, since young somatic bees perform only the first few required functions, such as cleaning and brood tasks (Seeley 1982), these tissues do not yet constitute a fully functional organism. Consequently, the juvenile stage occurs, when the somatic bees can perform all the required functions inside and outside the nest and thereby constitute all fully functional superorganismal tissues and organs. Adulthood can then be defined with the onset of sexual maturity, i.e., when sperm bees and later egg bees are present. Finally, fertilization transforms the superorganism into a parent. It should be noted that brood breaks, e.g., from swarming, dearth and also overwintering, can lead to an absence of eggs, larvae and pupae during juvenile, adult and parental stages.

Table 3. Characteristic stages in the ontogeny of honey bee superorganisms.

Zygote	**Fertilized egg bee**
Embryo	Stem bee with laid eggs and later larvae and pupae
Fetus	Stem bee with laid eggs, larvae, pupae and somatic bees performing a subset of the required functions
Juvenile	Stem bee with somatic bees performing all functions (optional: laid eggs, larvae, pupae)
Adult	Stem bee with somatic bees performing all functions, sperm bees and/or egg bees (optional: laid eggs, larvae, pupae)
Parent	Stem bee with somatic bees performing all functions and at least one fertilized egg bee (optional: laid eggs, larvae, pupae, sperm bees, egg bees)

As proposed in the life cycle in Figure 2, the reproduction of honey bee superorganisms encompasses external fertilization, implantation, embryogenesis and fetal development to produce a filial superorganism. This set of stages and steps can be said to underlie the second and third circles of the life cycle shown in Figure 1. The distinct circumstances under which honey bee superorganisms are able to reproduce are discussed in the following section.

Reproduction

During the reproductive phase, honey bee superorganisms produce both male and female gametes and are therefore simultaneous hermaphrodites (Moritz and Southwick 1992, p. 219). As with anisogamous multicellular organisms, there is asymmetry between the contributions of males and females to reproduction. Male superorganismal reproduction is restricted to the fertilization of egg bees, which requires the production, maintenance and release of sperm bees. Female superorganismal reproduction, on the other hand, is more involved, covering fertilization and gestation, which can be realized via various pathways.

The arguably simplest form of female superorganismal reproduction is supersedure, i.e., the replacement of the maternal stem bee with one of her egg bees within one and the same nest. At the level of the superorganism, supersedure implies the replacement of a maternal superorganism by a filial superorganism, which develops inside its mother. In this light, a temporary presence of both the maternal stem bee and the filial egg or stem bee inside a nest is therefore not a case of one colony with two queens (Kleckner and Ellis 2025), but rather, a maternal superorganism pregnant with one of its offspring. Once the maternal stem bee stops laying eggs, the maternal superorganism decays with the passing of its somatic bees until it ceases to exist. Supersedure therefore entails obligate maternal death and represents a form of terminal reproduction. Since one parent is replaced by one offspring, supersedure is reproduction without multiplication. Supersedure is one of the pathways to female reproduction, which are missing in the life cycle shown in Figure 1.

A second pathway to female reproduction occurs at the original nest in conjunction with the issuing of one or more swarms, as depicted by the outermost circle in Figure 1. The reproduction and development of the filial superorganism are then essentially identical as with supersedure. However, the offspring now develops within a fraction of its mother, and the mother may survive reproduction by moving to a different nesting site as the prime swarm. As in the case of supersedure, reproduction after the issuing of only the prime swarm produces only a single offspring per reproductive cycle. If the maternal superorganism manages to complete more than one reproductive cycle, however, multiplication is possible.

After the departure of the prime swarm, one or more afterswarms may be issued (Seeley 1985). In such cases, the fraction of the parental superorganism at the original nest further divides and departs with egg bees to proceed along a third pathway to female reproduction. Afterswarms construct nests for their respective filial superorganisms at different nesting sites. As in the original nest, these fractions of the maternal superorganism decay with the passing of the maternal somatic bees during gestation.

A fourth pathway to female reproduction involves the sudden loss of the stem bee, which may lead to spontaneous reproduction. When a stem bee is severely injured or perishes, the superorganism can no longer renew its soma and is faced with certain death. The superorganism reacts by rearing egg bees from the remaining eggs and larvae, which has been referred to as emergency rearing. The term *emergency* is somewhat misleading in this context, as there is nothing the superorganism can do to evade its impending death. What it can do in such a situation, however, is to invest its remaining resources into one last attempt to maximize its fitness and reproduce. The circumstances for reproduction after the loss of the stem bee are similar to those for supersedure. However, since reproduction is spontaneous rather than planned, there are minor differences. The types of cells in which egg bees are reared, for instance, differ from those during supersedure (Fell and Morse 1984). Furthermore, the rearing of egg bees first after the loss of the stem bee, results in a longer brood break than for the more seamless transitions during supersedure and after the issuing of swarms.

Another form of spontaneous reproduction may occur, if there are no eggs or suitable larvae available for rearing egg bees after the loss of the stem bee. In such a case, somatic bees may start laying haploid eggs, which develop into sperm bees (Seeley 1985). At the level of the superorganism, this can be viewed as somatic gametogenesis in order to maximize fitness in the face of certain death. Sperm bees developing from eggs of somatic bees may succeed to fertilize egg bees of other superorganisms. Genetically, this would be the same as if the laying somatic bees would instead have developed into stem bees, whose superorganisms succeed in fathering offspring. Like that, a dying superorganism can become a paternal grandmother, without having produced the paternal superorganism in between generations.

Egg bees may also be produced by somatic gametogenesis when somatic bees lay diploid eggs by means of thelytoky (Hepburn 1994). One such egg may develop into the stem bee of the filial superorganism, which replaces the dying maternal superorganism (Allsopp and Hepburn 1997). An egg bee produced via thelytoky can be considered a clone of the laying somatic bee (Goudie and Oldroyd 2014). Again, this is genetically the same as if the laying somatic bee would instead have become a stem bee. The resulting filial superorganism, therefore, genetically represents the offspring of the dying maternal superorganism.

It is striking that a single species of superorganisms exhibits a total of four pathways to female reproduction. On top of that, honey bee superorganisms may utilize at least three such pathways during a single reproductive cycle. By making full use of the phenotypic plasticity, which comes with a body made of bees, the superorganism splits into several fractions, which can independently raise offspring at different nesting sites. Filial superorganisms may be produced at the original nest and via afterswarms at new nesting sites, while the prime swarm may supersede or spontaneously reproduce after losing the stem bee in yet another nest.

Swarming

Swarming has traditionally been described as reproduction, analogous to strictly asexual modes of reproduction such as fission, fragmentation or budding (Wilson 1971; Moritz and Southwick 1992). However, Moritz and Southwick (1992) argue against this analogy with respect to honey bee superorganisms, since it poorly captures the complex genetic mechanisms at play. According to Moritz and Southwick (1992), only the prime swarm represents asexual reproduction, and swarming in general involves a mix of asexual and sexual reproduction. In this section, we provide arguments for viewing honey bee superorganismal reproduction as strictly sexual. Furthermore, the concept of swarming as reproduction is challenged, and an alternative explanation for the function of swarming is offered.

Reproduction by fission, fragmentation or budding involves the division of an organism into two or more fractions, followed by a phase of regeneration or growth to produce one or more clones. Initially, swarming may be analogous to such modes of asexual reproduction, since the superorganism divides into two or more parts. However, only the prime swarm, which carries the stem bee, is able to regrow its soma. The other fractions shrink with the passing of their constituent bees until they cease to exist. As discussed above, the prime swarm is not a clone, but rather the parental superorganism on the move. Swarming, therefore, does not result in clones, which means that asexual reproduction can be ruled out.

Phenotypically, the issuing of a swarm shows many similarities with the birth of a new organism. At the time of swarming, however, there exists no new organism to give birth to. This is because swarming precedes fertilization. Swarming alone does not result in reproduction, which still requires fertilization, implantation, embryogenesis and so on. For both male and female reproduction, swarming is not needed.

The issuing of the prime swarm does not lead to an increase in the number of offspring produced per reproductive cycle. The same number of offspring can be achieved without swarming, which is one. This is because there are two pathways to female reproduction that do not involve swarming, i.e., supersedure as well as spontaneous reproduction, initiated by the loss of the stem bee. Although afterswarms do not represent offspring, they do set the stage for the production of more than one offspring per reproductive cycle.

All bees involved in swarming are constituents of an adult superorganism, which divides into two or more fractions. Instead of a new organism, a swarm is therefore a fraction of an adult superorganism. Since the prime swarm includes the stem bee, it represents the fraction that can continue to live as the adult superorganism at a different nesting site. If a superorganism does not issue a prime swarm before reproduction, it will have no chance to survive reproduction. The issuing of a prime swarm, therefore, represents a survival mechanism rather than a reproduction mechanism.

By issuing a prime swarm, the superorganism essentially divides in order to avoid death, which is not unheard of in the animal kingdom. Certain species of lizards, for example, divide to survive predation in a process called autotomy (Congdon et al. 1974). After the tail of a lizard is shed, it continues to live for a while and wriggles to deter a predator (Higham and Russell 2010). Similarly, the fraction of the honey bee superorganism left behind in the original nest continues to live for a limited period of time to fulfill the function of producing offspring. The frontal part of the lizard, on the other hand, may grow a new tail, much like the prime swarm may grow back to full strength at its new nesting site. Swarming can therefore be viewed as superorganismal autotomy. This line of thought may not be entirely new with respect to social insects, as the division of termite superorganisms has been referred to as sociotomy (Wilson 1971, p. 462).

Autotomy is not only employed exclusively to escape predation, but also as a means to increase reproductive success (Emberts 2019). Afterswarms may fit the latter, since they have the function to increase the number of offspring for a given reproductive cycle. It can be concluded that swarming in itself is not reproduction, but rather, a form of autotomy to facilitate maternal survival, multiplication and parental care.

Parental Care

The way the superorganismal life cycle is portrayed may matter greatly for our understanding of honey bee parental care. The life cycle in Figure 1 can be interpreted to convey only limited parental care. The parental superorganism swarms away as the prime swarm, to leave its offspring to fend for itself. The life cycle from Figure 2, on the other hand, draws an entirely different picture, reminiscent of viviparous animals. While paternal care into filial superorganisms appears to be absent, the various forms of maternal care are discussed below.

After fertilization, the nurse bees of the maternal superorganism collectively provide a nourishing environment similar to a uterus, in which the embryonic larvae develop. Here, milky food secretions by maternal nurse bees can be viewed as analogous to uterine milk. The first nurse bees of the filial superorganism may be interpreted to function as a placenta, which transmits nectar and pollen from the maternal somatic bees to the developing embryo and fetus. When interpreted that way, the ability to produce extraembryonic superorganismal tissue makes stem bees totipotent. When the maternal foragers have been replaced by those of the filial superorganism, the placental function ceases, and the offspring becomes metabolically independent. During gestation, the protection of the developing filial superorganism by the maternal guard bees constitutes an additional form of parental care.

Maternal care is not limited to the rearing of egg bees, matrotrophy during gestation and protection. Even before fertilization, maternal superorganisms invest heavily in their offspring by building and provisioning nests (Moritz and Southwick 1992). Here, a distinction is meaningful between nests that were established in the previous year and newly founded nests, see Seeley (2017). The most elaborate and provisioned nests can be expected to be passed on to offspring for cases of supersedure and spontaneous reproduction in an established nest. Since swarms deprive a nest of portions of both provisions and bees (Seeley 1985), maternal investment in offspring developing in an established nest after swarming is lower. The lowest maternal investment is found for filial superorganisms that develop in afterswarms. However, even here, the respective fraction of the maternal superorganism selects a nesting site for its future offspring and begins to construct and provision the nest before fertilization. During gestation, it will continue to do so until no maternal somatic bees remain.

Filial superorganisms are always provided with a nest by their mother or a fraction of their mother. An established nest is provided after the departure of the prime swarm in the original nest, and newly founded nests are passed on by afterswarms. Both established and newly founded nests are possible for supersedure and spontaneous reproduction. Since superorganisms have many fathers and a single mother, all of which may construct a multitude of nests during each reproductive cycle, terms such as *parental*, *maternal* or *natal nest* may be rather unspecific. Herein, the term *original nest* is used to refer to the nest of an adult superorganism from which it may swarm to a new nesting site (Moritz and Southwick 1992, p. 63).

The construction and provisioning of a nest by a swarm is associated with risks and considerable labor, resulting in lower chances of surviving the coming winter than in an already established nest (Seeley 2017). Interestingly, honey bee parental care goes as far as providing the offspring with the security associated with an established nest, while the maternal superorganism puts its life at risk by swarming away with a fraction of its soma. Filial superorganisms that develop inside afterswarms also face lower survival rates associated with swarming. The various pathways to reproduction have the effect that honey bee superorganisms do not possess just one characteristic survivorship curve. On the basis of the survival rates from Seeley (2017) with annual swarming, superorganisms born in established nests exhibit a higher survival rate in their first year and a lower rate associated with swarming in following years, which yields in a type I survivorship curve. Being raised by an afterswarm, on the other hand, results in a constant survival rate and, therefore, a type II survivorship curve, since a new nest is founded every year.

In addition to nest-building and -provisioning and subsequent matrotrophy, honey bee superorganisms may also engage in postnatal maternal care. However, this is dependent on when a honey bee superorganism is considered to be born. As discussed in the previous section, it is not meaningful to consider swarming as the birth of a new superorganism. Birth normally refers to the exit of the internal environment of a mother. However, this does not occur for honey bee superorganisms, since filial superorganisms remain in the nest in which they have developed, whereas the mother slowly fades away until maternal separation is completed. Instead, birth can be defined as the rather inconspicuous onset of the juvenile stage, see Table 3, i.e., when the various tissues of a filial superorganism are fully developed, but may not yet have grown to full size. It is thus the transition to foraging of the first filial somatic bees that marks the onset of the juvenile stage and, thereby, the birth of the filial superorganism.

Postnatal parental care occurs when maternal bees are still present in the nest after birth. In conjunction with reproduction after the issuing of one or more swarms, considerable time may pass until a filial superorganism reaches the juvenile stage. Owing to the short lifespan of somatic bees during the foraging season, the maternal bees still present after the birth of the filial superorganism are therefore expected to be foragers, and possibly guard bees. Postnatal parental care may therefore be rather limited and include feeding and possibly protection.

During a certain period, both maternal and filial foragers are present inside the nest. The waggle dance of maternal foragers may then constitute additional instances of postnatal parental care. When a filial forager follows the waggle dance of a maternal forager, the maternal superorganism essentially guides its offspring to a food source. Teaching may also be involved, since the intricacies of the waggle dance are at least partly learned by young foragers observing more experienced foragers (Dong et al. 2023).

Supersedure likely represents a special case with respect to the extent of postnatal maternal care. The maternal stem bee may remain in the nest for a period of time, while the filial superorganism already commences its development, see e.g., Kleckner and Ellis (2025). Moreover, during supersedure later in the season, long-lived maternal winter bees may already be present, which could care for a filial superorganism for several months throughout the winter. Postnatal parental care may therefore be more comprehensive in conjunction with supersedure than for reproduction following swarming.

The various characteristics of the four pathways to female reproduction are summarized in Table 4. The parental care administered for all four includes nest building and provisioning as well as nurturing, protecting, feeding, guiding and teaching, all of which are exclusively carried out by the maternal superorganism. Parental care for individual filial superorganisms is therefore characterized by a distinct asymmetry between the sexes.

Table 4. Characteristics of the four pathways to female honey bee superorganismal reproduction.

Pathway to reproduction:	**supersedure**	**after departure of prime swarm in original nest**	**via afterswarm**	**spontaneous after loss of stem bee**
Provided nest:	established or newly founded	established	newly founded	established or newly founded
Provided stores:	all	fraction	all	all
Maternal care by:	entire or fraction of superorganism	fraction of superorganism	fraction of superorganism	entire or fraction of superorganism
Postnatal maternal care:	potentially high	low	low	very low or potentially high when reproduction occurs late in the season
Survivorship curve:	type I in established nest or II in newly founded nest	type I	type II	type I in established nest or II in newly founded nest
Fate of maternal superorganism:	reproduction entails obligate death	may survive reproduction	may survive reproduction	reproduction initiated by impending death

Possible number of offspring per reproductive cycle:	1 (replacement of maternal superorganism)	1 (may lead to multiplication)	2 or more (may lead to multiplication)	1 (replacement of maternal superorganism)

Discussion

A colony of honey bees may appear to be phenotypically perennial because of the renewal of all its constituent bees, thereby fostering the idea of potential immortality. However, a change of the queen entails a transition into a new colonial genotype (Moritz and Southwick 1982). Since a new genotype implies a new organism, potential immortality can be debunked on the grounds of inconsistency with biological conventions. What has traditionally been referred to as *honey bee colony* represents, in reality, a lineage of superorganisms, which uninterruptedly occupies a certain nesting site. Since the nest is passed on from mother to offspring, this is a matrilineage. Viewing honey bee superorganisms as mortal instead of potentially immortal paves the way for new insights into honey bee biology, ranging from life history, parental care and the role of swarming to research on pathogens and parasites, as well as monitoring and beekeeping. In general, correctly applying ecological and evolutionary theories and concepts to superorganisms requires the correct identification of evolutionary individuals.

In conjunction with research on the effects of the ectoparasitic mite *Varroa destructor* on honey bees, the lifespan of potentially immortal colonies has been documented, see e.g., Fries et al. (2006). However, this is not the lifespan at all, but rather, represents the duration of uninterrupted nest occupancy by consecutive generations of superorganisms. The fact that a nest may become vacant 3 to 5 years after an initial infestation with *Varroa destructor* (Korpela et al. 1993) may mean that the great-great-great-granddaughter of the original superorganism succumbs to the infestation. During that period of time, the initially infested superorganism may have moved elsewhere and multiplied successfully to contribute to a population that may thrive, despite exposure to varroa. A continuous nest occupancy of merely a few years does not imply that a population of honey bee superorganisms cannot cope with a varroa infestation. The duration of continuous nest occupancy, therefore, represents a rather abstract characteristic of questionable significance. Studies based on nest site occupancy may need to be revisited in light of the insights gained from the current review.

Another subject of research, which employs the traditional view of potentially immortal colonies, is honey bee demography in the wild, see e.g., Kohl et al. (2022). Birth, age and death rates are highly dependent on whether superorganisms are treated as mortal or potentially immortal. The lifespan presented by e.g., Seeley (2017) represents the duration of nest site occupancy by a matrilineage of superorganisms. The monitoring of nest site occupancy several times a year, such as that described by Moro et al. (2024), is likely inconclusive with respect to the occurrence of supersedure, usurpation (Danka et al. 1992), absconding (Seeley 1985) as well as swarming and the number of swarms issued. Even if honey bee superorganisms are treated as mortal, such monitoring protocols would deliver merely a subset of the data required to describe their demography. Genetic sampling of individual nests, on the other hand, may suffice to register supersedure, but cannot differentiate between swarming and supersedure and does not yield information about the number of swarms issued or their fate. It appears that the elusive nature of the honey bee poses a number of challenges for researchers seeking to document their demography.

A common practice in beekeeping is requeening (Gray et al. 2020), i.e., the manual replacement of the queen with one that is usually not her daughter. Manual requeening involves the killing of the old queen and, thereby, implies the killing of the associated superorganism. The subsequent implantation of a new queen forces the dying superorganism to gestate the offspring of other superorganisms. Surprisingly, regular requeening is considered good hive management (Gray et al. 2020). The replacement of at least 50% of queens is recommended for beekeepers to minimize losses during winter (Gray et al. 2020). This recommendation means killing and replacing at least every other superorganism in summer, with the goal of decreasing the number of deaths during the winter. The acceptance of such a practice likely stems from viewing honey bee colonies as potentially immortal. Apparently, not only are new queens from supersedure and swarming considered to be part of one and the same colony, but also unrelated queens that are manually implanted by a beekeeper. As should be clear from the present review, however, such a view is not compatible with conventional biology.

The analogy between honey bee superorganisms and animals has been weakened by unconventional characteristics attributed to superorganisms, such as unique combined sexual and asexual reproduction (Moritz and Southwick 1992, p. 227) and potential immortality (Wilson 1971, pp. 444-445). The present review provides arguments for viewing superorganisms as mortal, with strictly sexual reproduction. Consequently, terms such as *fragmentation*, *budding* and *fission* may be misleading with respect to honey bee superorganisms, since they imply asexual reproduction. Swarming in itself is not reproduction, but rather a form of autotomy, which occurs prior to reproduction to facilitate maternal survival and increased reproductive output. The developmental stages and viviparity discussed herein substantiate the validity of the analogy between honey bee superorganisms and animals.

The issue with the immortal view of honey bee superorganisms can be boiled down to a confusion between parent and offspring, yielding misleading data for a multitude of essential characteristics, ranging from life span, dispersal and heritability to parental care and beyond. The importance of using the mortal view can, therefore, not be emphasized enough. By taking the analogy between animals and honey bee superorganisms further, this review contextualizes superorganismal traits in a new light, hopefully opening new lines of thought and inquiry even for other taxa. In the spirit of Boomsma and Gawne (2018), the insight presented herein calls for rigor in both the definition and use of superorganismal terminology. Superorganismality affirms itself as a fruitful paradigm to gain insight and understanding of life at the top of the organismal hierarchy.

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