How to make a sterile helper

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The sterile worker castes found in the colonies of social insects are often cited as archetypal examples of altruism in nature. The challenge is to explain why losing the ability to mate has evolved as a superior strategy for transmitting genes into future generations. We propose that two conditions are necessary for the evolution of sterility: completely overlapping generations and monogamy. A review of the literature indicates that when these two conditions are met we consistently observe the evolution of sterile helpers. We explain the theory and evidence behind these ideas, and discuss the importance of ecology in predicting whether sterility will evolve using examples from social birds, mammals, and insects. In doing so, we offer an explanation for the extraordinary lifespans of some cooperative species which hint at ways in which we can unlock the secrets of long life.

Introduction

Altruistic behaviour is epitomized by the sterile worker castes found in the colonies of social insects. Instead of attempting to reproduce, workers invest in a variety of cooperative behaviours ranging from brood care and colony defence to forming bivouacs and tending fungus gardens [1]. In extreme cases, workers have become morphologically specialized to perform these tasks. For example, the heads of worker turtle ants, *Cephalotes varians*, are disc shaped, allowing them to act as living doors to their nests [2], while the swollen crops of large honeypot ant workers, *Myrmecocystus mexicanus*, permit them to act as storage vessels of sugar, water,

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and lipids [3]. These behaviours have an obvious benefit to the colony as a whole, but pose important questions about the process of natural selection [4, 5]: how can a gene for altruism spread when those carrying it are sterile?

Inclusive fitness theory, first proposed by W. D. Hamilton in the 1960s [6, 7], provides a solution to this problem. Altruistic individuals are able to transmit their genes to future generations indirectly by improving the reproductive success of relatives that carry the same gene. Family groups provide ideal conditions for the evolution of altruism, simply because family members are more likely to share genes, relative to the population as a whole. Relatedness in family groups can, however, still vary because of differences in the number of breeders contributing to the family gene pool. This led to the prediction that lifetime monogamy is necessary for the evolution of sterility because it ensures that helpers can pass on as many genes by raising full siblings as they can by having their own young [8–10]. However, not all monogamous cooperative species

have sterile helpers. Most notably, monogamy drives the evolution of cooperative breeding in vertebrates [11, 12], an entire lineage in which all helpers are able to reproduce [13, 14]. Why have sterile helpers evolved in some monogamous species but not in others?

Here, we argue that longevity plays a key role in determining which monogamous species evolve sterile helpers. To do so, we break down the evolution of sterility into two steps. The first step is the formation of a cooperatively breeding group in which helpers are not sterile, but retain the ability to breed later in life. Being long-lived makes this more likely to happen. The second step is the transformation of a cooperatively breeding group, where all individuals are fertile, to one with sterile helpers. For this to happen, helpers need to be able to invest in raising full siblings for the duration of their lives. This is possible if breeders live longer than their offspring that help. We then discuss what stops cooperative groups with fertile helpers from transforming into species with sterile helpers – this depends on the interplay between ecology and longevity. These arguments make sense of the remarkable lifespans of some cooperative species. For example, they help to explain why harvester ant queens, *Pogonomyrmex owyheei*, can live for up to 30 years [15] and why naked mole-rats, *Heterocephalus glaber*, have become a model organism for studying the mechanisms of aging, including cancer resistance [16–18].

Step 1: Form a cooperatively breeding group

The first step in the evolution of a sterile helper is the formation of a

cooperatively breeding group [23, 24]. Here, we define a cooperatively breeding group as a family in which offspring delay dispersal and help their parents in raising their siblings. The evolution of cooperative breeding is predicted to be more likely to happen from monogamous than from polyandrous non-cooperative ancestors [8–10]. This is because monogamy ensures a favourable exchange rate when helpers are weighing up whether they can pass on more genes by helping or by breeding (Box 1). Evidence from birds and mammals supports this prediction: cooperatively breeding species are more likely to evolve from monogamous than from polyandrous ancestors [11, 12].

Cooperative breeding birds are long-lived

In addition to being less polyandrous than non-cooperative species, cooperatively breeding birds are also long-lived. The cooperatively breeding red-winged fairy-wren, *Malurus elegans*, which weighs little more than a ballpoint pen, can live for up to 16 years [25], whereas the similarly sized non-

cooperative Zebra finch, *Taeniopygia guttata*, only lives for up to 5 years [26] (Fig. 1A and B). Similarly, pairs of cooperatively breeding Seychelles warblers, *Acrocephalus sechellensis*, may remain together for up to 9 years [27, 28], while non-cooperative bearded tits, *Panurus biarmicus*, live for 2 to 3 years on average [29] (Fig. 1C and D). This trend has been confirmed across bird species: cooperative breeders are longer-lived on average than non-cooperative species, after accounting for confounding factors such as latitude and body mass, which also influence longevity [30–32].

Why do we see this association between cooperative breeding and longevity? There are two possible reasons. Firstly, longevity may be a consequence of cooperative breeding. Living in a group has been suggested to protect group members from external causes of mortality, through increased predator vigilance for example, which in turn selects for longer life [33, 34]. Alternatively, longevity may be a cause of cooperative breeding. Theoretical models of the evolution of cooperative breeding find that long-lived species are more likely to make the transition to cooperative breeding than short-lived

species because long life enhances reproductive success once a nest is inherited [35, 36].

Whether long life is a cause or a consequence of cooperative breeding has been tested in birds [32]. If long life makes cooperative breeding more likely to evolve, then we would expect the ancestors of cooperative breeders to be longer-lived than the ancestors of non-cooperative species that do not evolve cooperation. If long-life is a consequence of the benefits of group living then longevity should increase after cooperative breeding has evolved. Ancestral state reconstructions have demonstrated that the ancestors of cooperative breeders had higher rates of annual survival (a proxy for longevity) than the ancestors of non-cooperative breeders, and there were no changes in annual survival after a species became cooperative [32]. These results confirm the prediction that long life makes the evolution of cooperative breeding more likely. This supports the idea that the opportunity to reproduce via nest inheritance plays an important role in the evolution of cooperative breeding, as predicted by theoretical models of the evolution of cooperative breeding [37–42]. It also appears that exceptionally long-lived cooperatively breeding birds, such as the red-winged fairy-wren, *M. elegans*, have higher rates of polyandry than non-cooperative species with similar lifespans. This suggests that when relatedness between helpers and offspring is low – hence reducing the opportunity for indirect fitness benefits – living for a long time is important for obtaining a breeding position to secure direct fitness benefits.

Patterns of longevity in cooperative mammals

There is mixed evidence as to whether cooperatively breeding mammals are long-lived. Among small ground-dwelling mammals (those weighing less than 60 kg), maximum lifespans are higher in cooperatively breeding species than in non-cooperative species [43]. In contrast, across all mammals, there appears to be no difference in the annual survival rates of cooperatively breeding and non-cooperatively breeding species [44]. In fact, the pattern is in the opposite direction to that predicted:

Box 1

The relatedness exchange rate

When should one individual (the actor) give up its own reproduction and help to raise someone else's (the recipient) young? Inclusive fitness theory predicts that altruistic helping of this kind will evolve when Hamilton's rule, $r_nB > r_oC$, is satisfied [19–21]. That is, when the number of offspring the actor helps the recipient to produce (B) – to whom the actor is related by r_n – is greater than the number of offspring the actor could produce if it did not help (C) – to whom it is related by r_o. The ratio of these relatedness coefficients effectively gives the actor an exchange rate that it can use to value the recipient's offspring against its own [22]. Clearly, cooperation is most easily favoured when the relatedness exchange rate (r_n/r_o) equals one, meaning that as long as there is some small efficiency benefit to cooperating ($B > C$), the actor can pass on more genes by helping than by breeding independently. In sexually reproducing species, the relatedness exchange rate equals one when offspring delay dispersal and help their parents in raising full siblings. On average, helpers are as related to their full siblings as they are to their own offspring. Hence, the prediction that the evolution of sterile helpers will happen in family groups in which the breeding female has mated monogamously [8, 9]. For sterility to evolve, however, the relatedness exchange rate needs to equal one for the duration of the actor's lifetime. This is only possible if helpers can invest in raising full siblings for the duration of their lifespans.
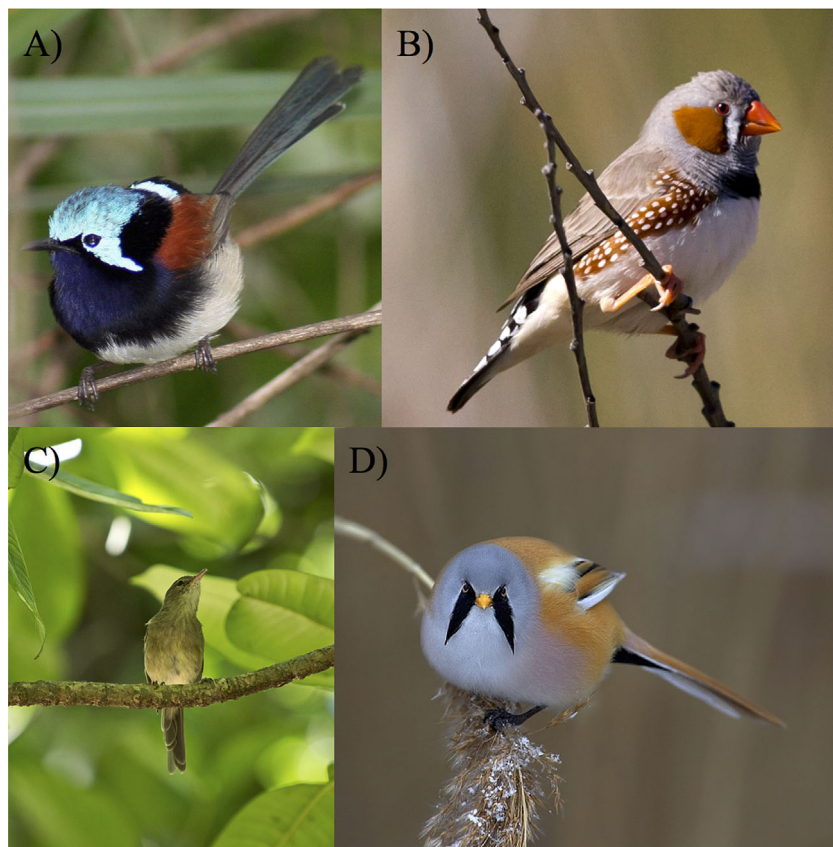

Figure 1. Cooperatively breeding birds are relatively long-lived. The cooperatively breeding red-winged fairy-wren, *Malurus elegans* (**A**), is longer-lived than the similarly sized but non-cooperative zebra finch, *Taeniopygia guttata* (**B**). Similarly, the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis* (**C**), is longer-lived than the same sized but non-cooperative bearded tit, *Panurus biarmicus* (**C**). Images from Wikipedia Commons (**A–D**): Cas Liber, Jim Bendon, Christian Hauzar, and Martin Mecnarowski.

this species, newly founded social groups typically consist of sisters but from 15 to 35% of females are unrelated [51–53]. Nest-inheritance compensates for the low relatedness exchange rate and makes cooperation worthwhile: females that inherit the dominant position produce more offspring than do solitary females [54]. Furthermore, cooperative breeding ensures that young are raised to independence even if their parent dies, a mechanism known as assured fitness returns [55, 56]. Remarkably, subordinate females that are next in line to inherit the dominant position invest less in care than subordinate females that are unlikely to inherit a breeding position, further reflecting how cooperative behaviour is shaped by future direct fitness [57]. This example emphasizes that it is the opportunity to reproduce via nest inheritance that provides an incentive for cooperative breeding, and this occurs in both long- and short-lived species.

Step 2: Transform your cooperative group

Once a cooperative breeding group has formed, the second step in the evolution of a sterile helper is selection for reduced reproductive function in helpers [23, 24]. For this to happen, a helper needs to be able to re-invest its potential reproductive effort into raising full siblings for its entire lifespan rather than for just a fraction of it [8, 9]. When this is the case, the relatedness exchange rate equals one and drops out of Hamilton's rule (Box 1), and all that is required for sterility to evolve is a small efficiency benefit to helping ($B > C$). From this argument, it follows that two conditions are necessary for the evolution of a sterile helper. First, strict lifetime monogamy of the breeding female is required to ensure that helpers are investing in the production of full siblings [8, 9]. This appears to be the case: monogamy is the ancestral condition for all examined origins of eusociality in bees, wasps, and ants [67]. Second, a complete overlap of generations is required to ensure that a helper is able to invest in raising full siblings for the duration of its lifetime.

non-cooperative breeders have higher rates of annual survival than cooperative breeders, although this difference is not statistically significant. It is currently unclear why large size should make a difference to the relationship between cooperative breeding and longevity.

Nest inheritance is associated with cooperative breeding in social insects

All of the evidence discussed so far concerning the role of longevity and the evolution of cooperative breeding has come from vertebrates. Is the evolution of cooperative breeding in family groups in other clades also associated with longevity? Evidence suggests that it is. The ancestral termite is likely to have been a long-lived cooperatively

breeding cockroach [45]. This conclusion is based on comparisons between extant termites and the cockroach genus *Cryptocercus*, which form a monophyletic group. *Cryptocercus* are wood-feeding cockroaches that provide bi-parental care in family groups [46]. They live in chambers and burrows chewed into the logs they feed on. This provides a relatively safe nesting environment, which means they are relatively long-lived: their life-cycle takes 8 years to complete from hatch to hatch. As in birds, nest inheritance resulting in the opportunity to reproduce is thought to have been an important incentive for philopatry and the evolution of cooperation in prototermites [45, 47–49].

The opportunity for nest inheritance is not restricted to long-lived species. For example, the paper wasp, *Polistes dominulus*, has an annual life-cycle and relatively high mortality rates [50]. In
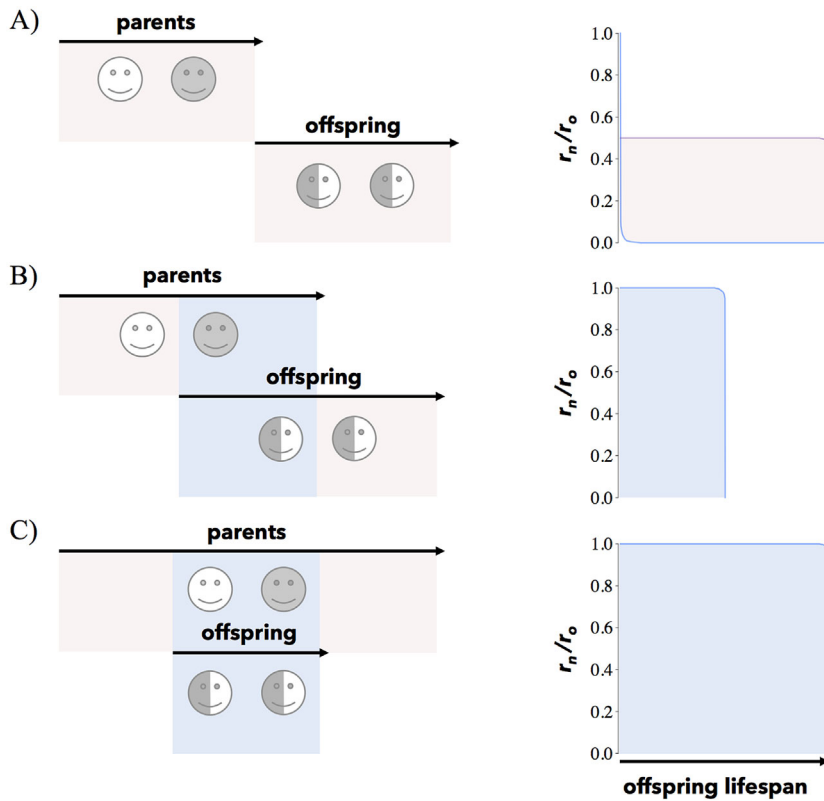
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Figure 2. Generational overlap affects the lifetime relatedness exchange rate. **A:** When there is no overlap between parents and offspring, social groups will consist of siblings. In this case, the relatedness exchange rate (r_n/r_o) is equal to a half (pink-shaded region). **B:** When there is some generational overlap, offspring can do as well by helping to raise full siblings as they can by breeding independently while their parents are alive (blue-shaded region). **C:** When there is complete generational overlap and parents are longer-lived than their offspring, offspring can invest in raising full siblings for the duration of their lifespans, favouring lifetime commitment to a non-reproductive role. This can be achieved in different ways: through divergent selection on the lifespans of breeders and helpers or through the co-option of a bivoltine life-cycle.

The extent of generational overlap influences the lifetime relatedness exchange rate. Consider the three following examples. In the first, parents die before their young reach reproductive maturity resulting in non-overlapping generations (Fig. 2A). At best, members of the same cooperative group will be full siblings and the relatedness exchange rate will equal one half. This appears to characterize some cooperatively breeding species. For example in co-foundress associations of the paper wasp, *P. dominulus*, and in breeding groups of long-tailed tits, *Aegithalos caudatus*, group members are often siblings [51–53, 68, 69]. As expected from Hamilton's rule, in these species the benefits of cooperating are high and the costs are low which compensates for helping to raise the offspring of

siblings [54, 70]. In the second example, there is a degree of generational overlap between parents and offspring (Fig. 2B). Here, offspring can raise full siblings for some of their lifespans, but not all. While their parents are alive, offspring often delay reproduction to help, but once their parents die, independent reproduction becomes a better fitness-maximizing strategy than helping. This stops lifetime commitment to a sterile role. As seen earlier, a degree of overlap between reproductive generations appears to typify the life histories of most cooperatively breeding vertebrates and some social insects. In the third example, parents live longer than their offspring, resulting in completely overlapping generations (Fig. 2C). Consequently, helpers can invest in raising full siblings for the duration of their

lives. The indirect fitness gains from helping are therefore always as profitable as the direct fitness gains from breeding independently, hence eliminating conflict over reproduction and permitting the evolution of sterile helpers.

What matters for the evolution of sterility is that helpers can invest in raising full siblings for the duration of their lifespans. Most commonly, this will happen when breeders are relatively longer-lived than helpers: whether helpers live for a few days or for several years, they will have a life-long supply of full siblings to raise if their parents live longer than they do. It is possible, however, that helpers can invest in raising full siblings for their entire lifespans with minimal overlap between parent and offspring generations. For example, if the queen dies once her last eggs are laid, as long as older helpers can invest in raising this brood for their entire lives, selection can favour sterility. This requires that older helpers only live for the period of dependency of the last brood. If older helpers were alive when this last brood reaches independence, it would be better for them to retain the ability to reproduce and raise their own young.

The rate of extrinsic mortality influences lifespan evolution

An obvious question that arises is how do breeders become longer-lived than helpers? Evolutionary theories of the evolution of aging predict that a key factor shaping an organism's lifespan is the rate of extrinsic mortality that occurs, for example, due to predation or disease [33, 71, 72]. When extrinsic mortality is low, selection favours long-term investment in survival, whereas when extrinsic mortality is high, investment in early reproduction is favoured over investment in survival. Recent support for this prediction comes from a study on how the ability to fly has shaped the evolution of mammal and bird lifespans [73]. Flight is assumed to reduce the rate of extrinsic mortality by allowing species to escape predation and unfavourable conditions. Across 1,368 species of birds and mammals the study found that species capable of flight have longer lifespans than

similar-sized species that are not capable of flight. Theory and evidence therefore suggest that the rate of extrinsic mortality can shape lifespan evolution.

Division of labor leads to differences in the lifespans of breeders and helpers

A reproductive division of labor is vital to the evolution of lifespan differences between breeders and helpers. This is because it gives the unusual condition that individuals within the same social group may experience very different rates of extrinsic mortality. For example, if helpers protect breeders from predation, they would experience elevated rates of extrinsic mortality while the breeders would experience reduced rates. Evidence suggests that individuals in different roles within social groups do indeed experience different rates of extrinsic mortality, which leads to differences in longevity. In the weaver ant, *Oecophylla smaragdina*, and in the leaf-cutting ant, *Acromyrmex brunneus*, large helpers perform riskier tasks than smaller helpers, and in line with the prediction that the rate of extrinsic mortality shapes investment in

lifespan, small helpers live longer than large helpers [74, 75]. Similarly, breeder and helper naked mole-rats, *H. glaber*, both live for over 25 years in captivity, where they are protected from extrinsic mortality; however, in the wild, helpers live for 4 years on average, while breeders live for over 17 years [17, 76]. The proximate factors underlying these differences in the lifespans of individuals with the same genome provide a unique opportunity for developing our understanding of the aging process (Box 2).

Insect life-cycles and lifespans

Solitary insect species with bivoltine life-cycles have two broods per year as an adaptation to seasonality. The first brood is produced early in the year and develops fully, while the second brood is produced later in the year and enters diapause until the cycle begins anew the following year. Inherent in a bivoltine life-cycle is the ability to produce a short-lived helper caste early in the season which helps to rear a relatively long-lived breeding caste later in the year, which then overwinters. The co-option of a bivoltine life-cycle has been argued to explain why first brood

females in *Polistes* wasps help to rear second broods [77]. Because helpers from the first brood are typically raising full siblings for their entire lifespans (they die at the end of the breeding season), the condition that the relatedness exchange rate is equal to one for the duration of the helper's lifespan is satisfied. Similar processes are thought to explain lifespan differences in other lineages, including the bumble bee, *Bombus terrestris* [78, 79]. These life-cycles further emphasize the point that it is complete generational overlap, rather than life span per se, that is key for the evolution of sterility. While the two are usually correlated, in bivoltine species, a shorter lifespan does not reduce the probability of overlap.

Breeders are longer-lived than helpers in some cooperative species

An important consequence of a reproductive division of labor and bivoltinism is that breeders can evolve to be longer-lived than helpers. This gives us our second necessary condition for the evolution of sterility – a complete overlap of generations. Are breeders longer-lived than helpers? This appears to be the case in some cooperative species. For example, there are considerable differences in the lifespans of breeders and helpers in many species of ants, wasps, and bees, and the magnitude of the difference in lifespans appears to be positively associated with colony size [80]. Furthermore, the queens of ant and termite colonies are extremely long-lived, with average lifespans of 10 and 11.5 years, respectively [15, 81]. This is particularly striking given that the average lifespan of non-cooperative insect species is 0.1 years [81].

Although differences in the lifespans of breeders and helpers exist in some cooperative species, the extent to which these differences are associated with sterility has not been quantitatively explored. As Fig. 3 demonstrates, in some species with large differences in longevity between breeders and helpers, helpers are completely sterile, lacking functional ovaries. In other species, however, helpers are capable

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Box 2

One genome, different lifespans

What are the proximate mechanisms underlying differences in longevity between individuals with the same genome? In the Western honey bee, *Apis mellifera*, being fed royal jelly determines which females become queens. Queens have an average lifespan of between 1 and 2 years, while helpers have an average lifespan of 6–8 weeks [58–61]. Mating itself also seems to contribute to longer life. In Ansell's mole rat, *Fukomys anselli*, sexual activity appears to enhance the lifespans of breeders, which live about twice as long as non-breeders, despite being equivalent in intrinsic quality [62, 63]. Similarly, in the ant, *Cardiocondyla obscurior*, queens mated to either a fertile or a sterilized male lived significantly longer than virgin queens [64]. In this species, the expression of a putative aging gene, *NLaz*, is related to queen longevity, and the changes in gene expression with age are in the opposite direction to those seen in the common fruit fly, *Drosophila melanogaster* [65]. *Juvenile Hormone* may also play a key role in regulating differences in longevity between breeders and helpers. *Lasius niger* ant queens that were experimentally treated with *Juvenile Hormone* laid fewer eggs, had increased activity rates, reduced maternal care, and higher mortality when exposed to a fungal pathogen compared to a control group with un-manipulated levels of *Juvenile Hormone* [66].
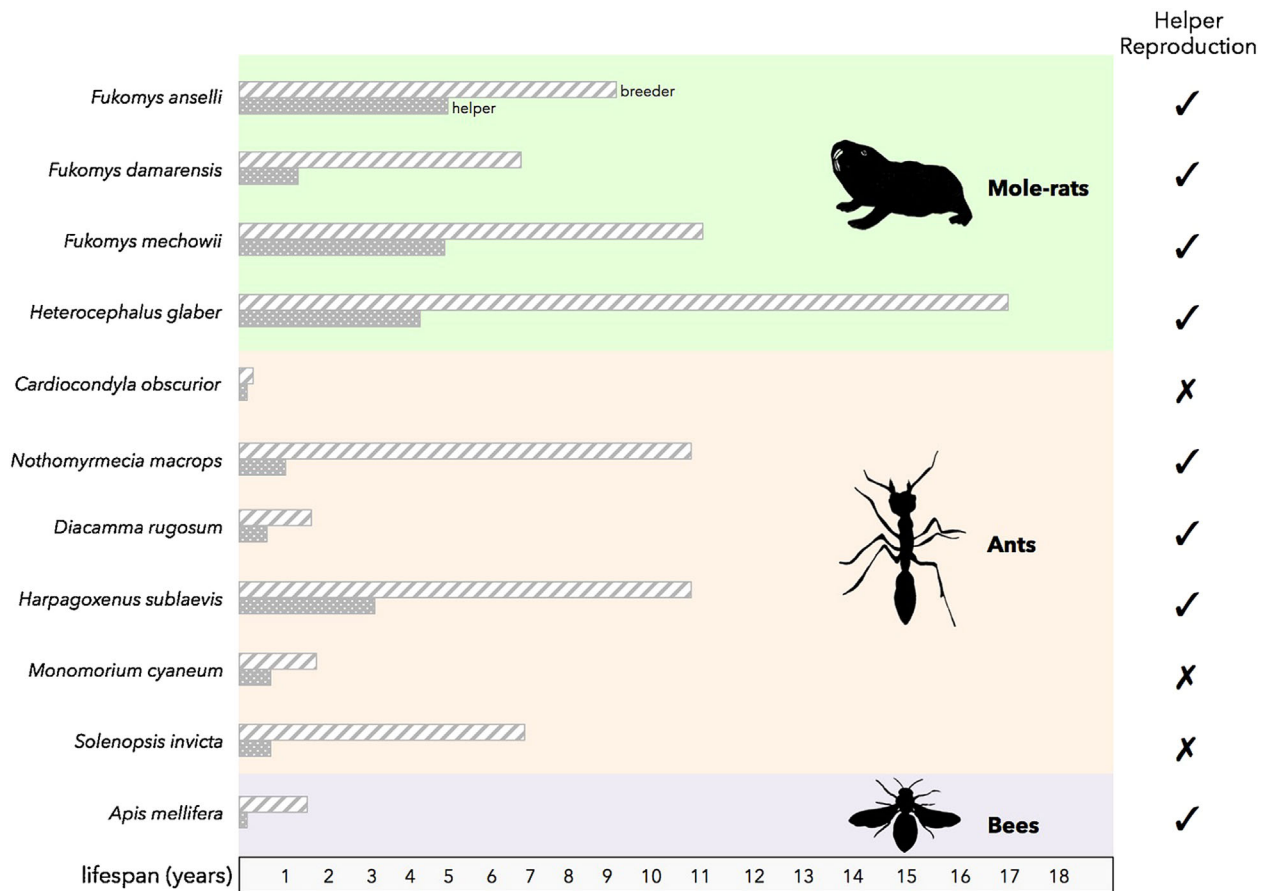

Hypotheses

Figure 3. The difference in the lifespans of breeders (hatched bars) and helpers (dotted bars) varies across social species. Despite considerable differences in the lifespans of breeders and helpers in some species, helpers are still able to reproduce. Sources: *Fukomys anselli* [62], *Fukomys damarensis* [106], *Fukomys mechowii* [63], *Heterocephalus glaber* [17], *Cardiocondyla obscurior* [64], *Nothomyrmecia macrops* [107], *Diacamma rugosum* [83], *Harpagoxenus sublaevis* [108], *Monomorium cyaneum*, *Solenopsis invicta* [109], *Apis mellifera* [110].

of reproducing despite expecting to live less than half as long as breeders. For example, there appears to be an asymmetry in the lifespans of breeders and helpers in naked mole-rats, *H. glaber* [17]. In this species, less than 1% of females within a colony ever get to breed, and physical aggression by the breeding female appears to suppress sexual maturation. Individuals less than 8 months old are capable of reproducing, however, should the opportunity arise [16]. Similarly, queens in the slave-making ant, *Harpagoxenus sublaevis*, inhibit ovarian development in their helpers, who can otherwise produce sons [82]. In the Japanese ant, *Diacamma rugosum*, which lacks a morphologically differentiated queen caste, the dominant female mutilates

the thoracic appendages of other females to stop them from mating, although some do manage to reproduce (Fig. 3) [83, 84]. These patterns suggest that an asymmetry in the lifespans of helpers and breeders does not guarantee the evolution of complete sterility. Our argument, however, is that without completely overlapping generations lifetime commitment to a non-reproductive role cannot be favoured by selection. Although not all species with an asymmetry in the lifespans of helpers and breeders will have evolved sterility, species with sterile helpers will have completely overlapping generations, at least ancestrally.

Other factors may have also played a role in the evolution of worker sterility. For example, there may be physical

constraints on the ability of very small workers to maintain their ovaries, and as the size of the colony increases, the chance of any one worker reproducing becomes negligible, hence diminishing the strength of selection for investment in reproduction [23, 85]. Selection may also favour the retention of ovaries among workers. For example, female workers produce sons following queen loss in some haplodiploid species (such as ants, bees, and wasps) where workers also regularly produce trophic eggs. Indeed, although workers are usually committed to a life-long non-reproductive role in haplodiploids, the loss of ovaries among workers appears to be rare [86–90]. Determining how these factors influence the evolution of sterility and how they interact with longevity remains to be addressed.

Protect the queen

Although low levels of female polyandry favour the evolution of cooperative breeding in vertebrates, a complete

overlap of generations, which is required for the evolution of sterile helpers, is absent from most species [91, 92]. This is surprising given that there is a clear reproductive division of labor in many cooperatively breeding species [13, 14, 92] which, as argued above, sets the scene for helpers and breeders to experience different rates of extrinsic mortality, eventually resulting in complete generational overlap. The question this raises is why breeders and helpers in most cooperative vertebrates do not experience different rates of extrinsic mortality despite a reproductive division of labour?

Ecology is likely to play an important role. In the social insects, two ecological syndromes are associated with the evolution of sterility: fortress defence and life insurance [20]. Fortress defenders feed and live in a protected site and include some termites, social aphids, social shrimps, social thrips, and ambrosia beetles. Life insurers feed outside the nest and include ants, bees, and wasps. In both fortress defenders and life insurers, the nest is a valuable, defensible resource [23]. Crucially, this nest protects the queen from predation while helpers may be exposed to predation when foraging or defending the nest for example. In contrast, among most cooperatively breeding vertebrates, the nesting site does not predictably guarantee that breeders and helpers experience different rates of extrinsic mortality as it does in fortress defenders and life insurers. For example, in one of the most socially advanced birds, the obligately cooperative white-winged chough, *Cyanocorax melanorhamphos*, breeders and helpers perform all of the same tasks ranging from building the nest to guarding the young [93, 94]. This difference in ecology means that in most cooperatively breeding vertebrates all individuals within the social group are exposed to similar rates of extrinsic mortality independently of whether they are a helper or a breeder. The only exception to this generality are the mole-rats. Mole-rats live and feed in a network of subterranean burrows as do fortress defenders [95]. As seen, differences in the lifespans of breeders and helpers suggest that they are exposed to different levels of extrinsic mortality in the wild [17, 76].

How to quantify differences in the ecology of cooperatively breeding species with and without sterile helpers is an empirical challenge. Although the distinction between fortress defenders and life insurers is useful, and it has been argued that vertebrates show a combination of these two syndromes [96], what seems essential is the extent to which the queen is protected from predation relative to workers.

Post-reproductive sterility can evolve in multi-generational families

Another interesting difference between the social insects and some social vertebrates is the existence of multi-generational families in the latter. In our own species for example, parents, their offspring and their grand-offspring may all live within the same family group [97–99]. In social insects, however this appears to be rare. Group members within ant and termite colonies are typically parents and their offspring [1, 67]. This makes group kin-structure more predictable in social insects than it is in social vertebrates living in multi-generational families, which undergo age-related changes in relatedness. For example, grandmothers are less related to their daughter's offspring than their own, while daughters are equally related to their mother's offspring and their own.

From a theoretical perspective these sorts of asymmetries in relatedness that arise with age can lead to conflict over reproduction within social groups, and ultimately drive the evolution of post-reproductive lifespans [100, 101]. Support for this prediction comes from a study on the evolution of menopause in the killer whale, *Orcinus orca* [102]. In killer whales, male and female offspring are both philopatric, and mating occurs between groups, meaning that females become more closely related to group members as they age, thus favouring investment in helping the group late in life. There is also evidence from our own species to suggest that age related changes in relatedness may favour the evolution of post-reproductive lifespans. In societies with female-biased dispersal, immigrant females are only related to their own offspring in their adopted groups, while older females

are related to other group members, including the immigrant females' offspring. This favours younger females in reproductive competition with older females who are still able to gain indirect fitness benefits by helping late in life [103, 104].

Predictions and conclusions

We have shown that making a sterile helper requires the evolution of cooperative breeding followed by selection for reduced reproductive function in helpers. This requires two conditions to be satisfied: the group's breeding female should be monogamous, and there should be a complete overlap of generations. These conditions ensure that helpers can do as well by helping as they could do by breeding for the duration of their lives, thereby eliminating conflict over reproduction. The second condition is satisfied when breeders and helpers are exposed to low and high rates of extrinsic mortality respectively or through the co-option of a bivoltine life-cycle. Further empirical observations on individual species, and comparative analyses across species, should be used to confirm that there is complete generational overlap in species with sterile helpers. Ancestral state reconstructions of worker and breeder lifespans can then be used to explore their co-evolution. We expect that differences in breeder and worker lifespans should be greatest in the ancestors of species with sterile helpers. One difficulty in testing this hypotheses is that once sterile helpers have evolved, the colony becomes the unit of selection, meaning that complete overlap of generations may be lost [105].

Overall, cooperative behaviour accounts for the exceptional 30-year lifespans of harvester ant queens, *P. owyheei*, and for cancer resistance in naked mole-rats. Because the same genome can produce vastly different lifespans, social species provide an ideal system for studying the epigenetics of senescence and other proximate mechanisms underlying the aging process. This could help us unlock the secrets to designing extraordinary lifespans.

Hypotheses

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