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Ageing effects of social environments in 'non-social' insects

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It is increasingly clear that social environments have profound impacts on the life histories of 'non-social' animals. However, it is not yet well known how species with varying degrees of sociality respond to different social contexts and whether such effects are sex-specific. To survey the extent to which social environments specifically affect lifespan and ageing in non-social species, we performed a systematic literature review, focusing on invertebrates but excluding eusocial insects. We found 80 studies in which lifespan or ageing parameters were measured in relation to changes in same-sex or opposite-sex exposure, group size or cues thereof. Most of the studies focused on manipulations of adults, often reporting sex differences in lifespan following exposure to the opposite sex. Some studies highlighted the impacts of developmental environments or social partner age on lifespan. Several studies explored potential underlying mechanisms, emphasizing that studies on insects could provide excellent opportunities to interrogate the basis of social effects on ageing. We discuss what these studies can tell us about the social environment as a stressor, or trade-offs in resources prompted by different social contexts. We suggest fruitful avenues for further research of social effects across a wider and more diverse range of taxa.

This article is part of the discussion meeting issue 'Understanding age and society using natural populations'.

1. Introduction

That social interactions can have consequences for health and ageing is well-documented in humans and other animals with complex societies and social behaviours [1–9]. However, species typically considered 'non-social' may also have well-established and wide-ranging responses to variation in their social environment. This is because sociality is not a fixed set of social behaviours, but rather a spectrum covering simple to complex sets of social interactions [10–12]. At the simplest level, social interactions can refer to any interaction between conspecific individuals. At the other end of the sociality spectrum lie the eusocial insects, where kin selection has resulted in the evolution of complex social interactions occurring within a related social group. For example, there is division of labour among members of eusocial insect colonies, whereby closely related workers take on the bulk of resource gathering, offspring care and colony maintenance while the queen produces offspring [13,14]. Queens in some eusocial species are also remarkably long-lived, and it is suggested that it is their eusocial lifestyle that allows them to escape reproduction–lifespan trade-offs [15,16] (but see [17]). Thus, studies of eusocial insects have significantly shaped our knowledge of sociality, including its impacts upon ageing [13]. However, there are potential problems with an overreliance on social insects as models for ageing and lifespan. Queens living within protected, stable social environments face low extrinsic mortality risk, and hence slower rates of ageing [16]. The relatedness among individuals in eusocial groups may challenge their use as a general model to partition out the effects of social interactions *per se* separately from kin-selected effects. In this review, we address this by synthesizing across studies the effects of social interactions in lesser-studied non-social insect species to better understand the specific effects of social interactions on ageing and lifespan.

Studies in humans show a variety of impacts that social interactions may have on ageing patterns. Generally, negative social experiences, such as weak social connectedness [18], negatively correlate with health [19] and mortality risk [20]. However, this is not the case for all dimensions of health (e.g. [21]). For instance, the quality of social interactions (i.e. strength of the relationship) and an individual's perception of their connectedness within a social network seem to be key indicators of cognitive function in older adults rather than just the frequency of social interactions [22]. Moreover, increasing evidence suggests that social interactions that impact upon ageing trajectories, lifespan [23] and ultimately fitness are not restricted to species that show strong social or familial bonds [24] (electronic supplementary material, table S2). Therefore, it is plausible that the social environment can have widespread effects on senescence and lifespan, and that these effects could be trait-, context- and even sex-specific [25]. To fully understand the generality of these patterns requires investigation across species that vary in their social complexity.

One such example is the laboratory stalwart *Drosophila melanogaster* fruit fly. *D. melanogaster* has been used extensively as a model in the field of ageing [26,27] and increasingly to understand social behaviour and the effects of the social environment. *Drosophila* species have been described as communal [10,28] because overlapping generations share the same space, but elsewhere they are described as solitary and lacking complex social behaviour [13]. However, a growing body of work suggests that *Drosophila* fruit flies are highly responsive to their social environments [28–31]. This includes impacts of the social environment upon fly health, such as immune responses [32] and cancer progression [33]. Chronic social isolation reduces sleep [34] (critical to cognitive function) and induces hunger, causing flies to overeat [35]. The above examples demonstrate that even in a species with no noted kin structure the social environment can have strong effects on life-history traits. This raises two important questions that we address here of (i) whether the degree of social interactions either within or across sexes has general effects on ageing and lifespan, and (ii) whether these effects are found more generally across other insect/invertebrate taxa.

(a) Aims of this review

To test the hypothesis that the social environment significantly affects lifespan and ageing in non-social invertebrates, we performed a systematic review of the literature. Our objective was to assess the taxonomic breadth of investigations, the types of social manipulations being performed and how researchers quantify the effects of social environment on lifespan and rates of ageing. From this, we aimed to use the results to detect any emergent themes such as key drivers and trade-offs, and identify any potential shared mechanisms involved. Specifically, we addressed the following questions:

(1) Do early life and/or adult social environments impact adult lifespan, potentially through trade-offs with other life-history traits?
(2) Do interactions within or across the sexes have widespread and consistent effects on ageing and lifespan? This was based on the rationale that we might expect the sexes to respond differently to opposite sex exposure, owing to sex-specific costs of reproduction. However, it is unclear how same-sex or mixed-sex interactions might impact lifespan in both sexes and across species with varying mating systems and social tendencies.
(3) What kinds of mechanisms are generally identified or tested in studies of the social environment, ageing and lifespan?

Although we included studies using manipulations of sex ratio, which inevitably causes differences in reproductive rates, hence lifespan, our aim was not to focus on costs of reproduction *per se*, discussed extensively elsewhere (e.g. [36]). Instead, we focused on how varying exposure to the same or the opposite sex (the sociosexual environment) can have sex-specific effects on lifespan and ageing. The interactions between sociality and ageing could be bidirectional. For example, individuals could change their social behaviour with age, as seen in humans (and non-human primates e.g. [37–41], could become more selective of social partners with age. However, we mainly focused here on the idea that the frequency or type of social interaction could alter lifespan and senescence.

2. Methodology

(a) Literature search

To test the hypothesis that the social environment affects lifespan and ageing we conducted a systematic search of the literature across invertebrate taxa. We followed the systematic review guidelines suggested by Foo *et al*. [42]. We identified empirical studies that measured lifespan or ageing following a manipulation of social context. We conducted a keyword search using the *ISI Web of Science* online database on 6 July 2023 using the following search string: (("social environment*" OR "social interaction*" OR "indirect genetic effects" OR "social behaviour" OR "social behavior" OR "social competition" OR "social contact*" OR "same-sex competitors" OR "male–male" OR "female–female" OR "social effects" OR "social perception" OR "rival*" OR "sex ratio" OR "sexual perception" OR "solitary and group") AND ("stress resistance" OR lifespan OR "life span" OR "life-span" OR mortality OR age OR ageing OR aging OR longevity OR senescence) AND (invertebrate OR insect OR drosophila OR fly OR beetle OR cricket OR moth OR butterfly)). After filtering the search results to include research articles only, 1758 unique records remained for title/abstract screening.

(b) Eligibility criteria

The review was restricted to studies of invertebrate taxa that include a measure of adult lifespan or ageing in response to the social environment. We included studies that manipulated the juvenile social environment if they then quantified lifespan or ageing in the subsequent adult life stage. We excluded studies during screening that (i) were reviews or theoretical papers, (ii) did not include a manipulation of the social environment, (iii) did not measure ageing or lifespan, (iv) investigated non-invertebrate taxa, or (v) focused on orders in which eusocial insects are found. We further excluded articles during full-text screening if they did not have suitable data on lifespan or longevity. Screening was carried out equally by all authors. After screening, we retained 80 eligible studies ([25,32,43–119]; electronic supplementary material, tables S12). The full search and inclusion/exclusion protocol is summarized in a PRISMA diagram (electronic supplementary material, figure S1). It should be noted that we only provide one reason for exclusion for each study, although studies could meet multiple exclusion criteria.

3. Results and discussion

(a) Taxonomic diversity

Our main aim was to formally identify the number of studies that have tested how the social environment influences lifespan or ageing in invertebrate species typically considered as 'non-social'. Overall, we identified 80 such studies, covering 49 invertebrate species, that manipulated the social environment and measured its effect on lifespan or ageing (figure 1). *Drosophila* species (*D. melanogaster*, *D. prolongat*a, *D. serrata*, *D. simulans*, *D. grimshawi*, *D. subobscura* and *D. pseudoobscura*) dominated, with around 40% of studies utilising these model species (n = 31 studies). Other Dipteran species (e.g. *Ceratita capitata* fruit flies, *Telostylinus angusticollis* flies) and model Coleopteran species (e.g. *Tribolium castaneum* [116] and *Gnatocerus cornutus* beetles [69,70]) were well represented (n = 11 and n = 10 studies, respectively) in the final set. Although our keyword search included other invertebrates, only 3 of the final 80 studies focused on non-insect invertebrates (the nematode worms: *Caenorhabditis elegans* [85], *C. remanei* [67] and the pelagic copepod: *Oithoca davisae* [92]).

(b) Early life social environments and their impact on lifespan

Resource competition during development can determine how individuals allocate resources towards reproduction and lifespan. Exposure to favourable environmental conditions in early life, such as low competition for resources, is expected to have positive effects on fitness-related traits (i.e. the 'silver-spoon' effect [120]), while the opposite is true for unfavourable or stressful early life conditions [6]. As such, there can be strong developmental effects on adult phenotypic variation and social behaviour that can influence fitness and senescence (but see [121]).

Our systematic review did find some evidence supporting the role of developmental social environment on adult lifespan or ageing (figure 2, electronic supplementary material, table S1). Out of the 80 studies, we identified 6 that manipulated density as a social stress (e.g. [62,68,81,102,114]). These studies generally reported a negative effect of high density on adult lifespan, and this effect was sometimes sex-specific (electronic supplementary material, table S1). For example, Gutiérrez and colleagues [114] tested potential trade-offs under two different stressors: nutritional environment and social environment, in *Acheta domesticus* crickets. They provided crickets with a low or a high diet (unbalanced versus balanced protein:carbohydrate diet) and then manipulated social environment (solitary versus group) throughout adult life stages. An unbalanced diet significantly increased development time for both sexes, increased female fecundity and reduced female lifespan [114]. However, the social environment significantly influenced cricket survival to adulthood in both sexes, whereby group-living crickets had poorer survival outcomes than did solitary crickets [114].

Phenotypic effects of larval density can also translate to behavioural changes in adults that can then affect fitness and longevity. In insects, resources accrued during development directly influence body size, which can then directly determine female fecundity and male competitive ability. For instance, adult *D. melanogaster* raised at low larval densities had higher courtship rates and longer lifespans, but produced offspring with poorer survival outcomes, than flies raised at high larval densities [122]. How insects acquire and invest nutritional resources may change depending on the environment in which they develop and the social environment they experience as adults. Developing individuals can use cues about their future social environment to modulate trait expression. Kasumovic and colleagues [73] manipulated the juvenile social environment (i.e. density) and the perceived future competitive environment by providing juvenile field crickets (*Teleogryllus commodus*) with variable call environments that signalled varying levels of competition (low, high or unpredictable). Call environment influenced age-specific calling effort and the rate of senescence of calling effort in males, and female responses to male calls [73]. Moreover, density, but not call environment, affected male lifespan, with males from lower-density treatments living

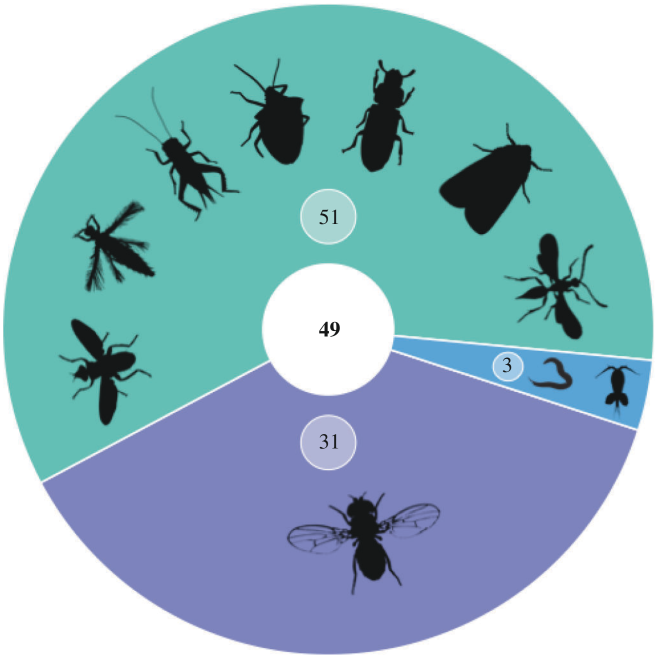
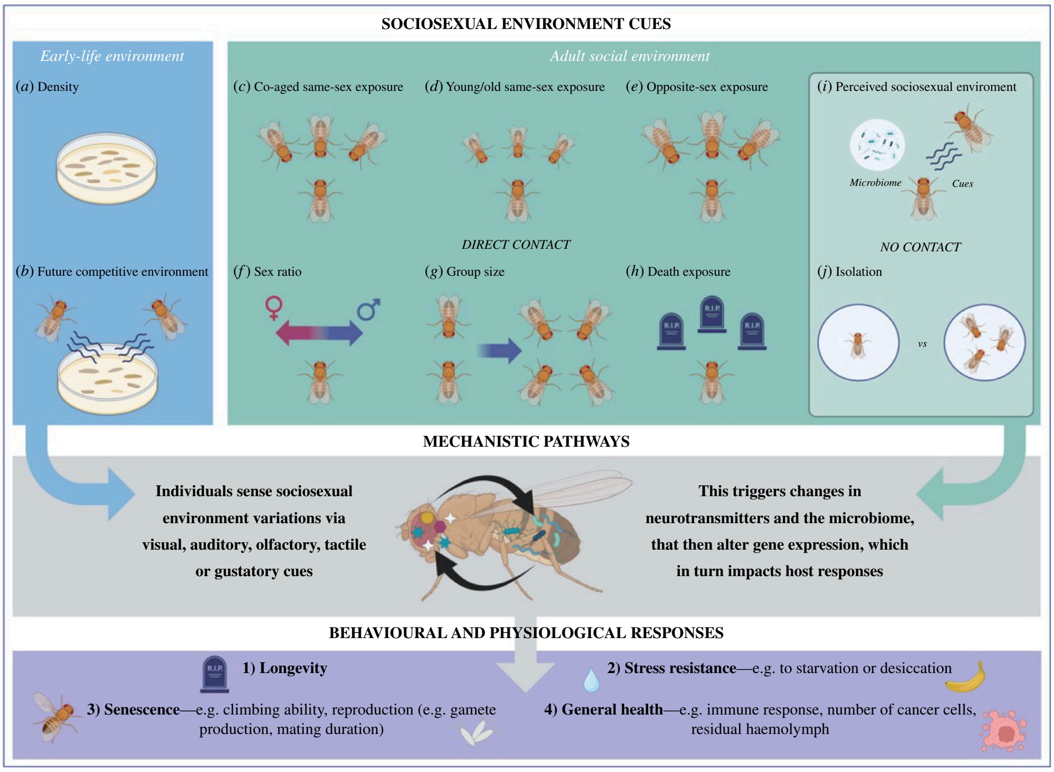


Figure 1. Taxonomic diversity observed across the 80 unique studies that tested how social environments influence lifespan or ageing in insects/invertebrates. The centre circle reflects the total number of unique species represented in the 80 studies. The smaller circles show the number of studies that use a *Drosophila* species (purple), another insect species (green) or an invertebrate species (blue). Silhouettes represent some of the invertebrate orders present in the different studies.



Individuals sense sociosexual environment variations via visual, auditory, olfactory, tactile or gustatory cues

This triggers changes in neurotransmitters and the microbiome, that then alter gene expression, which in turn impacts host responses

Figure 2. The types of social environment manipulations researchers use to examine social effects on ageing and lifespan using *Drosophila* as an example. Some studies manipulate the early life or developmental social environment, either through density (*a*) or using cues from adults (*b*), and then measure their effects on adult life-history traits. Studies that manipulate the adult social environment tend to manipulate exposure to the same sex (co-aged (*c*), or older/younger (*d*)), the opposite sex (*e*) or both (*f,g*), or even exposure to deceased conspecifics (*h*) to test for sex-specific effects of the social environment on lifespan and ageing. Mechanistic studies tend to manipulate how males and females respond to cues about their social environment (*i*). Finally, many studies tend to use social isolation (*j*) as a 'control' social environment to compare the effects of different social manipulations. Individuals detect these cues using multiple senses and respond to them using neuronal, microbial and genetic pathways (grey box). They then plastically adjust their behaviour and physiology to maximize their potential fitness (purple box), with trade-offs occurring between (1) longevity, (2) stress resistance, (3) senescence and (4) general health. Figure created using BioRender.com.

significantly longer than males from higher-density treatments [73]. Thus, cues received during development can influence the plasticity of trait expression and preferences in adults.

(c) How do the sexes each respond to same versus opposite sex exposure?

Studies that manipulated the adult social environment (n = 61 of the 80 studies) manipulated exposure to the same or opposite sex to test for sex-specific effects of the social environment on lifespan and ageing. More specifically, these studies either manipulated exposure to (i) same-sex rivals (e.g. male–male competitive scenarios; n = 21 studies), (ii) the opposite sex (i.e. mating rate or mating costs; n = 18 studies) or (iii) varied exposure to both sexes (i.e. sex ratios; n = 37 studies). Social exposure generally occurred through physical interactions between individuals, but some studies did manipulate exposure to cues of the same or opposite sex. Interestingly, many studies used social isolation as a 'control' social environment. There was no strong sex bias in the focal sex across these 80 studies; 23 studies focused only on male responses to the social environment and 18 focused on females, while the remaining 39 measured the responses of both sexes.

When considering same-sex interactions, male lifespans appear to be more sensitive to same-sex exposure than females. A possible reason for this is that males are generally more aggressive to each other than are females [123,124]. For example, Kudo [112] compared the lifespan of male and female *Drosophila prolongata* flies from four different strains, including a 'hyperaggressive' strain, when kept alone or in same-sex groups. Grouping reduced the lifespan of males from the 'hyperaggressive' strain to a much greater extent than in other strains. Moreover, the difference in lifespan between these two different social environments for males was greater than that for females, even for the 'hyperaggressive' females [112]. In insects, damage accrued during male–male combat is likely to be cumulative as the exoskeleton cannot be easily repaired or replaced. In this way, aggressive male–male interactions can induce somatic deterioration and shorten lifespan. Adler and colleagues [102] experimentally tested the link between male condition, the level of male–male competition and somatic deterioration using neriid flies, *T. angusticollis*. They found that high-condition males (i.e. males optimized for male–male contest ability) that were kept in all male groups suffered higher rates of somatic damage and had shorter lifespans than low-condition males or males kept in mixed-sex groups [102].

Intrinsic male condition can influence success in male–male competition, and hence fitness outcomes. However, males can plastically adjust their resource allocation towards traits associated with reproduction (i.e. fighting ability and mating duration) and traits positively associated with lifespan (i.e. somatic maintenance) in response to their social environment. Indeed, many studies have demonstrated an increased investment into pre- or post-copulatory sexual traits, and an equivalent decrease in male lifespan, in response to same-sex rivals (e.g. [47,66,103]). Lifetime exposure to rival males increased male calling effort in *T. commodus* crickets [98], while *D. melanogaster* males that had been exposed to rivals took longer to mate, but mated for longer, than isolated males [52,94]. These plastic responses to rivals not only occur when there are direct interactions among males, such as male–male contests, but also following exposure to one or more sensory cues of rival presence (e.g. [71,97]). Such plasticity is thought to occur when the sociosexual environment reliably signals either the current or future competitive environment [125]. This suggests that, even in the absence of direct interactions between males, cues of the sociosexual environment can modulate trade-offs between reproduction and lifespan.

While males are more sensitive to the presence of same-sex rivals, females exposed to males can experience dramatic lifespan loss. This may be owing to sex-specific costs of reproduction, whereby the energetic demands of reproduction for females are generally greater than, or different from, those of males [126]. We found that many studies examined these costs of reproduction on male and female lifespan by varying the operational sex ratio (OSR) from heavily female-biased to heavily male-biased (e.g. [57,75,83,89,107]). Females consistently had the longest lifespans when kept alone or with only other females [100,109,117], while increased male exposure decreased female lifespan (e.g. [127,128]). While studies of sex ratios are valuable for quantifying the costs of reproduction for male and female lifespan, we found that far fewer studies then tested how variation in exposure to the opposite sex influenced rates of ageing in both sexes (but see [92,104]). This is an important distinction as the general loss of lifespan associated with increased investment into reproduction might mask more subtle sex differences in mortality risks and the onset of senescence associated with varied exposure to the same and opposite sex. For example, Adler & Bonduriansky [119] found that variation in the OSR had strong, sex-specific effects on lifespan and ageing patterns in *T. angusticollis* flies. For males, early life mortality rate increased, and lifespan decreased, as the OSR became increasingly male-biased. Females, however, consistently lived less long than males regardless of the number of males in their social group [119]. Therefore, studies that examine how males and females each respond to varying social contexts are important for understanding sex differences in ageing and lifespan.

(d) Age of social partners

Many studies used experimental cohorts with non-focal individuals that are themselves co-ageing with the focal individuals (figure 2, electronic supplementary material, table S1). However, we identified four studies that did use social partners of different ages relative to the focal individual [106,109,110,117]. Social relationships are known to change with age, with older individuals becoming more socially selective by interacting with fewer social partners and being less connected in their social networks (e.g. in forked fungus beetles, *Bolitotherus cornutus* [129]). A further study in *B. cornutus* published in this issue shows that male fitness is reduced by interacting with older males, whereas populations with older age profiles reduce female fitness [130]. It has also been suggested that the age of social partners might influence health outcomes [131]. The studies in *D. melanogaster* that alter social partner age generally find a negative trend between social partners' age and longevity, i.e. young same-sex partners are beneficial but older partners deleterious to lifespan [106,109,110,117]. In addition to extending lifespan, young social partners also seem to increase physiological indicators of health. Both Ruan and Wu [106] and Cho and colleagues [117] showed that exposure to young social 'friends' improved the climbing ability and stress resistance in old flies. Likewise, Lin and colleagues [109] found that exposure to old 'friends' reduced resistance to environmental stressors, though not to oxidative stress, and decreased male courtship activity. Leech and colleagues [110] (see below) suggest that young social partners have less effect than co-ageing social partners on age-related changes to the microbiome. Additionally, the presence of older non-focal individuals—specifically adult males during larval development—reduced lifespan of both sexes. It is worth noting that these *Drosophila* studies do not isolate the social effects *per se* from consequences or relatedness amongst individuals on lifespan and ageing, so further studies are needed to establish whether such effects are a general phenomenon.

(e) Mechanisms linking social environments and ageing

There are multiple potential biological pathways linking social environments to ageing [1]. A major advantage of laboratory-based invertebrate studies is that they facilitate mechanistic experimental approaches to understanding how environmental information is mediated through physiological and molecular mechanisms into ageing patterns. Indeed, we found several studies that tackled this through altering the perception of social partners, identifying the involvement of specific genes, genetic pathways and the microbiome (figure 2, electronic supplementary material, table S1).

The effects of an individual's own perceived isolation may differ from those caused by being physically socially isolated. Therefore, the respective sensory inputs operating via potentially different sensory modalities may initiate different responses. In fruit flies, olfaction seems to be a key trait. For example, the cuticular hydrocarbon repertoire of young flies extends lifespan [117] while receipt of female pheromones without the ability to mate reduces male lifespan [97,132]. Moreover, using mutants that are impaired in their olfactory or gustatory senses (the genes *Orco* and *pickpocket*, respectively) reduces the lifespan-extending benefit of young social partners, at least in females [117]. Olfaction also plays a role in the lifespan reduction of females sensing dead conspecifics, but here vision is critical and sufficient to induce lifespan changes [133]. In other traits, sensing and responding to the social environment may use combinations of cues [134]. *D. melanogaster* males require any paired combination of sound, smell and touch in order to mount a response to predicted sperm competition [127], but what is unknown is whether the same sensory inputs also influence lifespan.

Sensing the social environment and initiating behavioural responses to that environment are likely to involve the nervous system. Therefore, neuronal mechanisms could influence ageing patterns. Flintham and colleagues [25] investigated this idea using male *D. melanogaster* flies with feminized nervous systems and female flies with masculinized nervous systems. This had the effect of inducing male-specific courtship behaviour and aggression in masculinized females and male–male courtship and reduced aggression in feminized males. In control flies, consistent with other studies [44,104,113], males suffered reduced lifespan in same-sex groups, whereas females did not. However, females with masculinized nervous systems showed patterns similar to control males. This was likely owing to such individuals receiving male behaviours (e.g. aggression) rather than the cost the cost of producing those behaviours themselves. Flintham *et al*. [25] pointed out that these findings could help to explain why sex differences in ageing trajectories exist. However, other studies have found little evidence that males held with other males suffer aggressive interactions or being excluded from food [32,94]. Activity between social partners seems crucial. Ruan and Wu [106] suggest that the benefits of young helpers are only realized if they have fully functional motor skills and can fully interact with the older partners. Housing with flies carrying mutations in the circadian rhythm gene *period* (defective in daily activity patterns) increases lifespan in females and, notably, males in single sex groups [135]. Therefore, behaviours that are not so intuitively stressful as aggression, such as the amount of activity or the quality of sleep, could be affected when in groups.

A further potential mechanism translating social environments into ageing is the microbiome, and there is increasing attention on the dysbiosis of the microbiome in old age [136]. The ecosystem of microbes that inhabit a host is likely to be altered by the host's social environment. Social contact aids horizontal transmission of microbes, and social partners are more likely to share similar environments and resources such as food, a major determinant of the microbial community. Indeed, cohabitation, social group membership or social networks can determine microbiome variation in mammals [137]. Stress can feed into the 'gut–brain axis', potentially driving microbiome dysbiosis. For example, social stress in mice alters the gut microbial community [138] and isolation behaviours can be induced in socialized mice using faecal transfers from isolated individuals [139]. Such impacts could mediate social effects on ageing, as microbiomes can have substantial effects on host health and ageing patterns [128,140–142]. Leech *et al*. [110] found that same-sex grouping increased bacterial diversity in both sexes. Importantly, the community structure of grouped males became distinctive at older ages. This only occurred if the grouped males were co-aged rather than replenished with young males. This study also identified an effect of the developmental social environment on adult lifespan: being raised with adult males during development reduced subsequent lifespan of both sexes and altered the microbiome at the pupal stage.

While the relationship between socially determined microbiome community structure and lifespan needs further direct testing, Leech *et al*. [110] suggested how these changes to the microbiome could be functionally important. They used known interactions between bacterial genes/metabolites and fly genes to predict the *Drosophila*-specific genetic pathways that would be differentially enriched by changes in microbial community. Focusing on five pathways critical to ageing and immunity, generally sex differences in enrichment were more apparent in groups rather than when alone. Additionally, age had a bigger effect on pathway enrichment when males were grouped with co-ageing rather than young social partners. There is a suggestion that social conditions lead to a conserved transcriptional response: for example, social adversity in humans has a signature of immune- and inflammation-associated gene expression [143]. Certainly, social environments alter gene expression in insects (e.g. [98,144], but the pattern is not always consistent, e.g. [111]). The role of such gene expression changes could be tested with the use of mutants and transgenics (e.g. [106]).

(f) Linking laboratory and field studies in nature

Almost all of the studies were performed in the laboratory, which could yield contrasting patterns to those found in the field [26]. At present, studies of ageing in the wild are otherwise dominated by those conducted on social mammals (e.g. [2,7–9,38,40]). The longevity of large mammals can be challenging for studies of ageing because many years of continuous observation are required to accrue data. An alternative to long-term studies of wild vertebrate populations is to track the lifespans of invertebrates in the field. A notable example comes from Rodríguez-Muñoz and colleagues [145]. *Gryllus campestris* crickets are one of the few insect systems in which individual adults can be tracked and assessed in the field and this has so far yielded more than 10 years of long-term data [146]. In relation to ageing, Rodríguez-Muñoz and colleagues [145] measured actuarial senescence (change in probability of dying with age) and physical senescence (calling) across years (where there is one discrete generation per year). Across their study period, the sex ratio varied from strongly female-biased to an even sex ratio. Both sexes showed faster actuarial senescence when there were more males in the population. Baseline mortality was higher for females in more female-biased years, consistent with the idea that they are protected from predators when associating with males at their burrows [147]. Males showed a decline in calling with age if there was a more equal sex ratio, in contrast to no senescence in calling when the population was strongly female-biased. This may indicate a cost of competing with rival males. In the closely related cricket *Teleogryllus bimaculatus*, being housed with a rival male reduced lifespan, which the authors attribute to direct interactions between males [98]. Additionally, as mentioned above, in *T. bimaculatus,* hearing other males alters gene expression including in stress/immune response pathways [148] which may have consequences for the lifespan. As sex ratio was not experimentally manipulated in the field, it is difficult to know whether it was causal to the patterns observed; there could have been an environmental variable that altered both sex ratio and ageing. Nevertheless, it is highly suggestive of patterns observed in the laboratory reflecting key components in nature.

Our systematic review has identified a taxonomic bias towards Dipteran species for studies of ageing (figure 1; electronic supplementary material, table S2), which are useful models for laboratory-based, experimental studies. However, there are many other insect species where individuals within a population can potentially be studied over the course of their lifetime [149,150]. Species with high site fidelity can be easily monitored in the field (e.g. *Coenagrion puella* damselflies [151]), while the interactions of group-living invertebrates, like some social spiders, could be studied over time in their communal space (e.g. [152,153]). Moreover, sessile invertebrates, like some marine bryozoans, experience ‘static’ social environments for part of their life (e.g. [154]). Longitudinal studies of such species could provide useful insights into the effects of competition and density on ageing.

4. Conclusions and future perspectives

Our systematic review found evidence for social impacts on ageing in ‘non-social’ insects (electronic supplementary material, table S1), which could be tested in the future via meta-analysis. Nevertheless, our review revealed that social environments do have key impacts on lifespan and ageing across a range of invertebrate taxa. First, we expected that negative early life experiences would decrease lifespan. Indeed, several studies that exposed juveniles to high competition did report reduction of lifespan (except for [67,90,96]). Second, we expected to find strong, negative impacts of male presence on female lifespan, but not on male lifespan. There were more studies that focused on the effects of opposite-sex exposure on lifespan than for any other social context, and these studies did tend to report lifespan reduction for females in the presence of males. Interestingly, where social isolation would be assumed to be stressful in studies of humans and other socially complex animals, often this state was described as a control in studies that we identified. It might be fruitful in either group to simply describe differences in social experience, and to assess whether either state is stressful from the outcome of the assays used. Third, studies investigating the effect of same-sex exposure on male lifespan often reported negative impacts of same-sex competition (except when rivals were younger; see [106,109,110,117]), but there was also frequently a negative impact of female competition on female lifespan. These surprising effects warrant further investigation into the costs of same-sex competition in females and whether these are generally associated with social interactions (i.e. dominance interactions) or resource competition.

Social environment impacts were often measured as differences in lifespan but some of the studies that we found measured senescence in physiological traits and behaviours, potentially indicating differences in ‘health span’ [155] (see electronic supplementary material, table S2). Including a range of traits in future studies of senescence would be a major advance because recent studies show that lifespan differences that are dependent on social environment are driven by differences in actuarial senescence (e.g. [156]). A further gap in our knowledge is why sex differences in response to the same environmental manipulations exist [107,156]. The underlying reasons could be addressed by using the mechanistic approaches available for model insects. Indeed, progress has been made in studying social effects mechanistically from sensory inputs to physiological outputs, taking advantage of the relatively easy experimental manipulation and genetic resources available in some species. Future studies could use isolines/strains that differ in their genetic propensity to be social (e.g. [157]) or test for indirect genetic effects (e.g. [107]). Many of the investigations of the effects of social environments have been made in *Drosophila*, and greater taxonomic breadth would be useful. For example, although biomarkers of ageing such as telomeres and DNA methylation are absent in *Drosophila*, these tools are available for other insects [158,159]. Most of the studies reviewed use designs that do not allow individuals to choose their social environment, and it remains unclear whether animals living in fluid groups form stable social networks (as in *Drosophila* [30]). Whilst this may be difficult to examine in natural populations of most insects, semi-natural mesocosm-type experiments could be useful.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The end point of our systematic review is provided online as a supplementary table, which includes publication information and categorizes aspects of the study designs [160].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.M.H.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; E.R.C.: data curation, visualization, writing—review and editing; M.F.: data curation, writing—review and editing; C.H.S.: data curation, funding acquisition, writing—review and editing; T.C.: conceptualization, data curation, funding acquisition, writing—review and editing; A.B.: conceptualization, data curation, funding acquisition, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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