Received: 30 March 2019 | Accepted: 5 June 2019

DOI: 10.1111/1365-2435.13399

AN INTEGRATIVE VIEW OF SENESCENCE IN NATURE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Senescence in wild insects: Key questions and challenges

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Handling Editor: Jean-François Lemaître

Abstract

1. Insects are key laboratory models for research on the fitness effects, genetics and plasticity of senescence. It was long believed that insects almost never survive long enough to senesce in the wild, but it is now clear that senescence occurs and can exact substantial fitness costs in natural insect populations. Yet, given the practical challenges of obtaining longitudinal field data on small, motile animals, we still know remarkably little about the evolution, expression and fitness consequences of senescence in wild insects.
2. We argue that the study of senescence in wild insects is important because many insights and hypotheses based on laboratory experiments must be tested in natural populations.
3. Examples of research areas where conclusions from laboratory studies could be misleading include the roles of candidate senescence genes, the effects of nutrition and dietary restriction on life span and senescence patterns, and the roles of viability selection and sexual selection in shaping senescence through trade-offs and antagonistic pleiotropy.
4. Several emerging model species (such as antler flies, crickets, damselflies, dragonflies and butterflies) offer opportunities for field research on senescence using a range of observational and experimental techniques, as well as new genomic approaches.
5. Insects provide valuable and increasingly tractable models for research on senescence in natural populations. We believe that such work will shed light on many important questions in ecology and evolutionary biology.

KEYWORDS

ageing, dietary restriction, field study, life history, natural populations, plasticity

1 | WHY STUDY SENESCENCE IN WILD INSECTS?

A great deal of knowledge about the genetics, physiology and evolutionary ecology of senescence comes from laboratory studies on insects and other short-lived animals. Yet, many ecological and evolutionary inferences based on these findings are open to question because of the highly unnatural conditions in which laboratory animals are maintained, including constant abiotic factors (such as humidity, light, and temperature), high or controlled density, reduced or non-existent competition for resources and mates, sedentary lifestyle, unnatural diet (e.g. ad libitum availability of food and water), absence of predators and low exposure to parasites and pathogens. Hypotheses about the role of senescence in life-history evolution and trade-offs, the roles of key environmental factors such as diet and the genetic basis of variation in senescence and life span rely on the implicit assumption that the findings of laboratory studies are representative of effects that occur in natural populations. However, there are compelling reasons to question this assumption.

Senescence, which represents the decline in fitness components with age, and life span are highly plastic life-history traits that can be strongly influenced by the biotic and abiotic features of the ambient environment (Flatt, Amdam, Kirkwood, & Omholt, 2013), so much so that even subtle differences in rearing conditions in the laboratory can have substantial effects (Partridge & Gems, 2007). The unnatural environment of the laboratory could therefore lead to results that are non-representative of natural populations (for critical discussions of differences between laboratory and field study results, see Lambrechts, Perret, Maistre, & Blondel, 1999 (blue tits); Reznick & Ghalambor, 2005 (guppies); Kawasaki, Brassil, Brooks, & Bonduriansky, 2008 (insects); Reichard, 2016). Very few studies to date have attempted to compare life span and senescence in genetically similar populations under fully natural versus laboratory conditions, but the available evidence suggests that senescence can progress very differently in these contrasting environments. In some cases, senescence appears to progress more rapidly in the wild. For example, Tidière et al. (2016) compared life span and actuarial senescence rates in several mammal species in zoos versus natural populations and found that many species (especially those with a faster pace of life) exhibited shorter mean life spans and earlier age at the onset of senescence in the wild than in captivity. The only study that has attempted such a comparison in an insect species obtained similar results for one sex: Kawasaki et al. (2008) compared life span and actuarial senescence in genetically similar wild and captive cohorts of neriid flies (*Telostylinus angusticollis*) and found that males exhibited much shorter life spans and more rapid senescence in the wild than in captivity. By contrast, some studies detect senescence in captivity but fail to detect senescence in natural populations. For example, *T. angusticollis* females aged rapidly in captivity, but actuarial senescence could not be detected in females in the wild (Kawasaki et al., 2008). Similarly, Vrtílek et al. (2018) could not detect reproductive senescence in wild populations of an annual killifish (*Nothobranchius furzeri*), despite rapid reproductive senescence in captivity in this species. These findings are consistent with experimental evidence of the plasticity of life span and senescence rate in response to manipulation of environmental factors such as the juvenile or adult diet (Hooper, Spagopoulou, Wylde, Maklakov, & Bonduriansky, 2017; Hunt et al., 2004; Zajitschek, Jin, Colchero, & Maklakov, 2014; Zajitschek, Zajitschek, Friberg, & Maklakov, 2013), or the social environment (Adler & Bonduriansky, 2011; Zajitschek et al., 2013). The potential for environmental parameters to influence the evolution of senescence is also supported by theory (Ronget, Garratt, Lemaître, & Gaillard, 2017; Shokhirev & Johnson, 2014; Williams & Day, 2003). The plasticity of life span and senescence raises the possibility that genotypes or experimental treatments could interact strongly with environmental variables that differ between the laboratory and the wild, and that some findings of laboratory studies could therefore represent artefacts of the laboratory environment (Briga & Verhulst, 2015; Harshman & Hoffmann, 2000; Partridge & Gems, 2007).

Current data on senescence and life span in natural populations are also strongly biased taxonomically. A large majority of existing studies have been carried out on large, long-lived vertebrates such as red deer (*Cervus elaphus*, Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006) and Soay sheep (*Ovis aries*, Hayward et al., 2015), and this taxonomic sampling bias is also reflected in comparative studies (Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013; Promislow, 1991). By contrast, very little is known about senescence and life span in natural populations of insects, or other small-bodied animals (Nussey et al., 2013; Zajitschek & Bonduriansky, 2014). In other words, laboratory research on senescence is largely carried out on species in which senescence has not been studied in the wild and, conversely, field studies are mainly carried out on species that are rarely used in laboratory experiments. This taxonomic bias in the literature is problematic because, despite the generality of basic life-history principles, it is clear that there are considerable differences in physiology, reproductive scheduling and selection on late-life performance between large-bodied, long-lived animals such as ungulates and small-bodied, short-lived animals such as flies. Given such differences, generalization of findings across taxa and between laboratory and natural environments can be problematic.

This problem is most acute in relation to inferences that relate to selection on senescence or trade-offs between senescence and other life-history traits, because fitness and its components can be highly environment-dependent (Fernández & López-Fanjul, 1997; Fry, 2008; Roles, Rutter, Dworkin, Fenster, & Conner, 2016). The rate and pattern of senescence, as well as the effects of genes and environmental factors, could vary considerably between natural and laboratory environments, and inferences that concern the evolution or ecology of senescence therefore require corroboration in natural populations. Such work could also help to identify key environmental factors that could be manipulated in laboratory studies to gain a better understanding of how well laboratory results generalize to natural populations (Briga & Verhulst, 2015).

The dichotomy between laboratory and field-based studies stretches across research fields and reflects a tug-of-war between approaches that emphasize the dynamic complexity in nature and approaches that seek reductionist standardization in the laboratory (we are referring to methodological reductionism, see Fang & Casadevall, 2011). Both strategies have their merits, but to determine which outcomes of laboratory studies can be generalized to natural populations, it is necessary to investigate the relationship between ageing phenotypes in the laboratory versus under natural conditions. Below, we outline some specific cases where, we believe, research on natural populations is needed to establish whether conclusions from laboratory studies apply to natural populations and environments where long-term adaptation occurs.

2 | HOW LABORATORY STUDIES COULD PRODUCE MISLEADING RESULTS: SOME EXAMPLES

2.1 | Effects of diet composition and dietary restriction

Many studies have shown that diet composition and intake rate can have dramatic effects on senescence and life span in a wide range of

TABLE 1 Evidence of functional, reproductive or actuarial senescence in natural insect populations

Order	Species	Trait	Technique	Senescence detected?	Reference
Diptera	*Protopiophila litigata*	Mortality Reproductive effort (Mating rate) Nutrient effects	CMR, Nutrient supplementation	Yes (males) Yes (males)	Bonduriansky and Brassil (2002), Bonduriansky and Brassil (2005), and Mautz et al. (2019)
	Telostylinus angusticollis	Mortality	MRR	Yes (males) No (females)	Kawasaki et al. (2008)
	Anopheles gambiae	Mortality	MRR (Re-analysis)	Yes (females)	Ryan et al. (2015)
Orthoptera	*Teleogryllus commodus*	Mortality	CMR	Yes (males) Yes (females)	Zajitschek et al. (2009)
	Gryllus campestris	Mortality	CMR, Videotracking	Yes (males: in 9 years)/ No (males: in 1 year)	Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al. (2019) and Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al. (2019)
		Reproductive effort (Male calling effort)		Yes (in 5 years) /No (in 4 years)	
		Dominance in fights Search activity Latency to mate		Yes (males) No (males) No (males)	Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al. (2019)
Odonata	*Coenagrion puella*	Mortality	CMR	Yes (males) Yes (females)	Sherratt et al. (2010)
		Reproductive effort (Mating rate)		No (males) No (females)	Hassall et al. (2015)
	35 species	Mortality	CMR (Re-analysis)	Yes (32 species) No (three species)	Sherratt et al. (2011)
Hymenoptera	*Apis mellifera*	Mortality	MRR	Yes (foragers)	Dukas (2008b)
		Foraging success		Yes (foragers)	Dukas (2008a)
	Atta cephalotes	Leaf cutting efficiency		Yes (foragers)	Schofield, Emmett, Niedbala, and Nesson (2011)
Lepidoptera	Six species	Mortality	CMR (Re-analysis)	Yes	Carroll and Sherratt (2017)

Abbreviations: CMR, capture–mark–recapture; MMR, mark–release–recapture; Re-analysis, fitting demographic models that allow for age-dependent mortality to previously published MRR or CMR data.

animals and other organisms (Heilbronn & Ravussin, 2003; Masoro, 2005). For example, in insects, protein restriction can lead to dramatic extension of life span (Adler, Cassidy, Fricke, & Bonduriansky, 2013; Lee et al., 2008; Maklakov et al., 2008). This effect has been interpreted as an adaptive response to nutrient limitation, whereby animals reduce investment in reproduction and instead invest their resources in somatic maintenance so as to outlive the period of famine (Holliday, 1989; Kirkwood & Shanley, 2005; Speakman & Mitchell, 2011). Yet, it remains unclear whether dietary protein restriction would have effects of similar strength or even direction under the more stressful conditions experienced by natural populations. Dietary protein enhances an animal's capacity to respond to a variety of stresses and challenges, such as pathogens, injuries and temperature variation (Carrillo & Flouris, 2011; Dirks & Leeuwenburg, 2006; Johnson, Murray, Young, & Landsberg, 1982; Kristan, 2008). Because the capacity to respond to such challenges could be an important determinant of fitness in natural populations, but probably has much less importance under benign laboratory conditions, protein restriction could have very different consequences for fitness in natural versus captive insect populations (and, for similar reasons, mutants that redirect resources from such defensive and stress response functions to somatic maintenance might exhibit extended life spans in the laboratory but not in the wild; Briga & Verhulst, 2015). If dietary nutrients have dramatically different effects in wild animals, then the evolutionary interpretation of effects observed in the laboratory must be reconsidered as well (Adler & Bonduriansky, 2014). Very little experimental work on the effects of dietary nutrients on life span and senescence has been carried out in natural populations (but see Mautz, Rode, Bonduriansky, & Rundle, 2019). Generally, we also know little about natural variation in resource availability and accessibility. More knowledge about these species- and population-specific parameters could inform the selection of experimental protocols of dietary restriction in the laboratory and could potentially also inform predictions for the evolution of senescence patterns and responses to nutrient restriction. The latter is a field with large potential for future research, where experimental evolution in the laboratory and maybe even in natural populations could be employed.

2.2 | Selection on senescence

Life-history theory treats ageing as a key cost of reproduction, resulting in a loss of fitness through reduced probability of survival and reproduction in old age, and this trade-off between the maintenance of physiological state and survival on the one hand and reproduction on the other hand is assumed to shape the evolution of life histories (Kirkwood, 1977; Kirkwood & Rose, 1991; Lemaître et al., 2015; Lemaître, Gaillard, Pemberton, Clutton-Brock, & Nussey, 2014; Stearns, 1992; Williams, 1957). Yet, paradoxically, it was widely believed until quite recently that very few individuals in natural populations of insects and other short-lived animals survived long enough to express senescence (Comfort, 1979; Medawar, 1952; Roach & Carey, 2014). While we now know that senescence occurs and can exact substantial fitness costs in natural populations of even very short-lived animals (e.g. Bonduriansky & Brassil, 2002), we still know little about the patterns and fitness costs of senescence in such taxa. Accumulating evidence shows that senescence occurs and can impose fitness costs in wild insects such as antler flies, damselflies, dragonflies, butterflies, mosquitoes and crickets (Table 1). However, it remains unclear how important senescence is in wild insects, or how patterns of senescence vary among taxa or in response to environmental conditions in the wild. Indeed, some studies have failed to detect senescence in wild insects (e.g. see Hassall, Sherratt, Watts, & Thompson, 2015; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al., 2019; Table 1), or in one sex (Kawasaki et al., 2008; Table 1), suggesting that its costs could be strongly environment-dependent or could vary markedly among species or between sexes. By contrast, senescence is almost universally detected in laboratory studies (Flatt & Partridge, 2018). This dearth of knowledge of senescence in natural insect populations therefore represents a major gap in understanding of the evolution of life histories in insects and other short-lived animals.

Furthermore, environmental parameters could determine how natural selection acts on senescence. Classic theory predicts that elevated adult mortality rate should select for faster ageing (Williams, 1957). However, both theory (Abrams, 1993; Caswell, 2007; Charlesworth, 1994; Moorad, Promislow, & Silvertown, 2019; Wensink, Caswell, & Baudisch, 2017) and empirical evidence from nematode worms, *Daphnia* and guppies (Chen & Maklakov, 2012; Reznick, Bryant, Roff, Ghalambor, & Ghalambor, 2004; Walsh, Whittington, & Walsh, 2014), suggest that the classic prediction can be negated or even reversed if mortality is strongly condition-dependent. This suggests that the evolution of senescence could be strongly dependent on the nature of mortality sources (Ronget et al., 2017; Williams & Day, 2003) and the stage of life when the organism is most vulnerable to these risks (Moorad et al., 2019). Theory also suggests that the effect of elevated mortality rate could depend on environmental parameters such as the abundance of food and the costs of mating, as well as the consequences of extrinsic mortality for population demography (Shokhirev & Johnson, 2014). Because potentially condition-dependent sources of mortality (such as predators) are lacking in typical laboratory settings, and numerous environmental factors differ between these environments, tests of theory on the evolution of senescence could yield different results in laboratory versus natural populations. To avoid artefacts, studies endeavouring to carry out such tests in the laboratory need to recreate key environmental conditions (such as condition-dependent mortality) experienced by natural populations, and doing so requires an understanding of the progression and environment dependence of senescence in similar animals in the wild.

2.3 | Genetics and epigenetics of senescence

Much research on senescence in *Drosophila melanogaster* (and other key model species, such as *Mus musculus*, *Caenorhabditis elegans* and *Saccharomyces cerevisiae*) has focused on testing genetic models

of the evolution of senescence such as the antagonistic pleiotropy model, and identifying the genes involved in senescence and its associated trade-offs (Austad & Hoffman, 2018; Hughes, 2010; Kimber & Chippindale, 2013; Nussey et al., 2013). However, allelic effects on life-history traits tend to be highly sensitive to environmental conditions (Nylin & Gotthard, 1998), and there is a great deal of evidence that environmental factors such as diet and stress can alter the expression of genes that affect life span (Kenyon, 2005). Similarly, recent evidence from several species shows that epigenetic (DNA methylation) patterns across the genome undergo consistent changes with age, perhaps causing some of the phenotypic manifestations of senescence, and this 'epigenetic clock' can be accelerated by environmental factors such as high-fat diet and stress (Horvath & Raj, 2018). Indeed, there is evidence that subjecting organisms to more natural conditions can have profound effects on their life-history traits and can modulate or even reverse genetic effects relative to standard laboratory conditions (Briga & Verhulst, 2015). Establishing the roles of candidate genes and mutant alleles for life span and senescence, such as genes that are part of the insulin/insulin-like growth factor signalling (*IIS*) pathway that is involved in growth, reproduction and senescence (e.g. chico, Clancy et al., 2001; foxo, Hwangbo, Gersham, Tu, Palmer, & Tatar, 2004), therefore requires quantifying effects in ecologically relevant environments. For example, naturally occurring (epi)mutants or genetic knockouts can be studied in natural populations and their life histories compared with wild-type individuals. While obtaining longitudinal data on natural populations of nematodes and yeast is likely to remain impractical, insects offer opportunities for such research. Once the key differences between laboratory and natural environments are better understood, it may also be possible to recreate more realistic environments in the laboratory (Briga & Verhulst, 2015).

Inference from laboratory studies is also complicated by the use of laboratory-adapted populations. Many widely used lines of *D. melanogaster* and other insect model species have been maintained over hundreds of generations in standardized laboratory environments of comparatively low complexity (such as identical dietary environments during development and adulthood, constant temperature and humidity, and low spatial heterogeneity and complexity). It has been argued that these laboratory-adapted populations are near or at evolutionary equilibrium and that they are therefore well suited for the estimation of quantitative genetic parameters, compared with wild-caught flies whose phenotypes are more likely to be affected by difficult-to-predict genotype by environment (G × E) interactions (Service & Rose, 1985; Clark, 1987; for a relevant experimental comparison, see Sgro & Partridge, 2000). Such interactions are ubiquitous and can be very strong (Kenyon, 2010; de Magalhaes, Wuttke, Wood, Plank, & Vora, 2012). It is certainly true that some species can rapidly adapt to new environments, as shown in numerous artificial selection and experimental evolution studies (Simões, Santos, & Matos, 2009), and there is some evidence that wild-derived populations react in similar ways to the same novel environment (Metaxakis & Partridge, 2013). However, it is not clear in most cases to what degree specific allelic variation under these conditions is beneficial in natural environments, which involve highly complex and dynamic ecological networks and direct and indirect effects of variable abiotic factors (Chown & Terblanche, 2006). In vertebrates, it is increasingly possible to reconcile the study of senescence in the wild with environmental heterogeneity and quantitative genetics (e.g. Brommer, Wilson, & Gustafsson, 2007; Wilson, Charmantier, & Hadfield, 2008). By contrast, in insects, the similarities of the genetic mechanisms governing life span and senescence in the wild compared with the laboratory remain poorly understood. This is illustrated by the failure of many long-lived mutants identified in laboratory studies to achieve extended survival under more natural conditions (e.g. chico, mth, indy206 in *D. melanogaster*, reviewed in Briga & Verhulst, 2015).

While very few studies have investigated selection on life span and senescence in natural insect populations, comparisons of laboratory-adapted versus wild-adapted lines suggest that laboratory culturing procedures can have substantial consequences for the evolution of life span and senescence (Partridge & Gems, 2007). For example, Linnen, Tatar, and Promislow (2001) reported nearly identical life span of a wild-derived *Drosophila* population and a population that had been selected for long life for many years, whereas laboratory control lines showed much shorter life span. These findings suggest that standard laboratory culturing exerts negative selection on life span.

3 | THE CHALLENGES OF RESEARCH ON SENESCENCE IN WILD INSECTS

Insects are understudied in natural environments because their small size makes them more difficult to locate in their natural habitat than larger-bodied organisms, and poses challenges to capturing, handling and marking. Moreover, there is a high risk of introducing bias in capturing (McDermott & Mullens, 2017) as a result of individual variation in exploratory behaviour, activity, condition or size, and in the effects of handling and marking, since larger or high-condition individuals might cope better with the induced stresses. Highly mobile species (e.g. flying insects or species with generally high dispersal rate) may be very hard to track, making it difficult to obtain longitudinal data on individuals. The difficulties of resighting or recapturing marked individuals can pose especially serious challenges in the estimation of mortality rates, since a low resighting or recapture probability could lead to an over-estimation of mortality rate and under-estimation of life span.

For any insect species, environmental fluctuations, such as the presence or absence of predators, can lead to spurious results and might either obscure patterns of senescence in the wild or create patterns that only resemble ageing. For example, the survival of butterflies can be highly dependent on the presence and activity of dragonflies, a main predator (Sang & Teder, 2011). Changes in the distribution or performance of predators might lead to apparent age-dependent changes in mortality rate of prey, and such changes could be erroneously interpreted as actuarial senescence. Climate

patterns also strongly influence insect survival and senescence and therefore pose difficulties for longitudinal field research on insects. In general, uncontrolled variation in environmental parameters such as weather, predators, parasites or competitors could obscure or confound estimates of life span and both actuarial and reproductive senescence in the wild through non-senescent changes in mortality, dispersal rate or reproductive output. If most focal individuals belong to a single, synchronized cohort, such a change can generate a pattern resembling an age-dependent increase in mortality rate or decrease in reproductive rate that could be misinterpreted as actuarial or reproductive senescence. For example, the WildCrickets project (www.wildcrickets.org) has collected data for individually tracked and continuously video-recorded population of field crickets (*Gryllus campestris*) over 12 years (Fisher, David, Rodríguez-Muñoz, & Tregenza, 2018; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al., 2019; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al., 2019; Rodriguez-Munoz, Bretman, Slate, Walling, & Tregenza, 2010). These data have shown high variation in mortality rates and demographic ageing patterns between years (Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al., 2019).

4 | MODEL INSECT SPECIES FOR FIELD RESEARCH

The choice of the preferred model system depends on the research question, the aforementioned challenges and specific trait combinations that make a species amenable for studies of senescence in the wild. Unfortunately, the features that make certain species amenable for longitudinal field research could also introduce a phenotypic bias (e.g. towards larger body size, philopatry, low mobility and ease of access; see, e.g., Table 1). Previously studied species in which senescence has been detected in the wild are predominantly highly philopatric and terrestrial as adults (see Table 1, including antler flies, *Protopiophila litigata*, Bonduriansky & Brassil, 2002; Bonduriansky & Brassil, 2005; Mautz et al., 2019), neriid flies, *Telostylinus angusticollis* (Kawasaki et al., 2008), the crickets *Teleogryllus commodus* and *Gryllus campestris* (Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al., 2019; Zajitschek, Brassil, Bonduriansky, & Brooks, 2009), dragonflies and damselflies (Carroll & Sherratt, 2017; Sherratt, Hassall, Laird, Thompson, & Cordero-Rivera, 2011; Sherratt et al., 2010) and mosquitoes (Ryan, Ben-Horin, & Johnson, 2015). If the practical challenges could be overcome, it would also be very interesting to investigate senescence and life span in natural populations of highly motile insect species, such as migratory or widely dispersing dragonflies, butterflies or orthopterans. This could reveal whether investment in migration and dispersal trades off against investment in somatic maintenance, or whether dispersal imposes strongly condition-dependent selection that actually slows senescence and prolongs life. It would also be interesting to investigate how senescence progresses at the somatic level and affects various aspects of physiology and performance, in natural populations of very short-lived insects, in which substantial physiological changes could occur over the course of a few days or hours. This could reveal whether evidence of 'programmed' senescence from laboratory studies holds up under natural conditions. Likewise, research on highly cryptic species such as stick insects could reveal whether effective camouflage can promote the evolution of slow ageing and long life by reducing adult mortality risk.

Social insects such as bees (Dukas, 2008b), for which senescence in foraging performance and survival has also been reported in natural populations (Dukas, 2008a, 2008b) and ants (Parker & Parker, 2006), are additional suitable systems for studies on senescence in the wild, although most direct estimates of life span for queen ants have been reported from laboratory nests (Keller, 1998). It is of particular interest to investigate caste systems, where individuals have the same genome but display highly divergent life spans. Moreover, interspecific variation in social organization may allow for interesting comparisons (e.g. Keller & Genoud, 1997). Insects featuring relatively easy-to-spot phenotypes such as butterflies also have potential to produce high-quality longitudinal data in natural populations (Molleman, Zwaan, Brakefield, & Carey, 2007). Other systems with high potential to successfully study senescence in the wild, due to being characterized by a combination of above-mentioned suitable traits, include stink bugs (Hemiptera: Pentatomidae, Venugopal et al., 2016), assassin bugs (Hemiptera: Reduviidae, Jackson, Salm, & Nelson, 2010), Soapberry bugs (Hemiptera: Rhopalidae, *Jadera haematoloma*, Carroll, 1991), fungus beetles (Coleoptera: Tenebrionidae, *Bolitotherus cornutus*, Conner, 1988), burying beetles (Coleoptera: Silphidae, *Nicrophorus* spp., Scott, 1998), flesh flies (Diptera: Sarcophagidae, *Sarcophaga crassipalpis*, Hawley, Simpson, & Wilder, 2015) and flightless stick and leaf insects (Phasmatodea). In addition, a number of pest species are naturally adapted to human agricultural practices, such that the laboratory environment can be assumed to mimic the conditions experienced by at least some natural populations for many generations (as in the cowpea weevil, *Callosobruchus maculatus*, a bruchid beetle that occurs in human stores of grain legumes). Many such pests have the potential to be further developed as models for research on senescence under natural or semi-natural conditions. Another approach with great potential to bridge the laboratory and the natural environment is the use of artificial metapopulations, involving large, interconnected, semi-natural enclosures (Legrand et al., 2012).

5 | WHICH TRAITS CAN AND SHOULD BE MEASURED?

5.1 | Population ecology and biodemography

Currently, there is a scarcity of knowledge on population ecology and biodemography of insects in the wild, despite calls for assigning higher priority to these fields of research (e.g. see Wachter, 2008). Such data are especially valuable given recent reports of declining

insect populations in both disturbed and relatively pristine habitats (Sánchez-Bayoa & Wyckhuys, 2019). To understand population dynamics, it is necessary to include measurements of births, deaths, emigration and immigration, and investigate abiotic and biotic factors that affect these traits and processes. Population size and density, predation pressures and rates, as well as resource availability, are important factors that need to be taken into account. Importantly, measures of sex ratios will be relevant for estimates of effective population sizes, and sex-specific survival should be measured.

On the level of the individual, it is necessary to obtain longitudinal data on individual insects in order to construct intra-individual trajectories of age-dependent changes in phenotype and performance. Such data will yield estimates of senescence in key components of fitness, including reproductive potential ('reproductive senescence') and survival probability ('actuarial senescence'). A great deal could also be gained by collecting detailed data on phenotypic changes that accompany and perhaps mediate the observed changes in performance with age. For example, it would be useful to obtain data on the integrity and functionality of morphological structures (such as legs, wings, and exoskeletons), measures of physiological and metabolic performance (such as metabolic rate and wound healing), measures of immune and anti-parasite defences, and performance in behavioural tasks such as locomotion, anti-predator defences or escape responses, combat and sexual display. While a number of studies have demonstrated senescence in wild insects (Table 1), few of these studies have quantified reproductive senescence, and none have quantified accompanying phenotypic changes. Such data would help to uncover the proximate causes of age-related decline in performance, as well as reveal the potential for consistent individual differences in life-history strategies within populations (see, e.g., the pace-of-life syndrome, Reale et al., 2010; Fisher et al., 2018).

In recent years, molecular biology has begun to provide a bridge between laboratory and field studies (see, e.g., Crow, 2017). Ten years ago, Flatt and Schmidt (2009) called for a better integration of molecular and evolutionary genetics, highlighting the role in natural populations of 'longevity genes' identified in the laboratory as one of the paramount unresolved questions in the biology of ageing (see also Flatt & Partridge, 2018). As mentioned before, there is strong support for the regulatory effects of genes in nutrient signalling pathways (IIS and TOR) on senescence (Flatt et al., 2013). However, several *Drosophila* studies based on populations capturing naturally occurring genetic variation failed to find genes in these pathways as the major contributors to life span and senescence (Durham, Magwire, Stone, & Leips, 2014; Flatt, 2004; Remolina, Chang, Leips, Nuzhdin, & Hughes, 2012; Stanley, Ng'oma, O'Day, & King, 2017), and these results need corroboration from studies in more natural environments. To this end, individuals of known age or senescence status from natural populations could be sampled for genome and transcriptome sequencing, and the results could be compared with individuals of similar age or senescence status from laboratory populations.

6 | METHODS AND TECHNIQUES FOR RESEARCH ON SENESCENCE IN WILD INSECTS

Research on animals *from* natural populations is not the same as research *in* natural populations. One way of studying genetic variation that segregates in natural populations is to sample live individuals from natural populations, transfer them to the laboratory and either make phenotypic measurements on the captured individuals directly, or measure offspring produced in the laboratory by captured females that were inseminated in the wild. While this can be a convenient way of characterizing genetic and genomic variation, problems arise when genetic data have to be associated with phenotypic traits, especially fitness components to study evolutionary processes (see above).

Technical limitations are likely to preclude longitudinal field research on many insect species but, as we noted above, a number of tractable model species are available (Table 1). In contrast to birds and mammals, radiotracking is not suitable for most invertebrates because of their small body size and the need to track large numbers of individuals. However, capture–mark–recapture (CMR) and mark–release–recapture (MRR) methods can be used to investigate actuarial and reproductive senescence (and associated phenotypic changes) in insects with suitable ecological and behavioural traits, such as strong philopatry or site fidelity, and ease of detection (Table 1). Data collected in such studies can be analysed using established methods (classic CMR, as implemented, e.g., in the software MARK, White & Burnham, 1999; and, more recently, Bayesian survival analysis, as implemented in the R package BaSTA, Colchero & Clark, 2012), or the deconvolution model – a method that uses the post-capture life span, as measured in captivity, with the risk of introducing a certain level of G × E interaction, which can affect survival estimates (Muller, Wang, Yu, Delaigle, & Carey, 2007). Marking can be accomplished with paint or colour pigments (external and subcuticular), stickers, anatomical alterations (wing clipping, burn marks), electronic tagging (external), all of which should be examined for aversive effects in the laboratory first (see Bonduriansky & Brooks, 1997; Hagler & Jackson, 2001).

One of the challenges that needs to be dealt with is the loss of marking, which could become more likely with advancing age. Chronological age of individuals can also be estimated by CMR (based on probability of recapture and on time between first and last capture, of individuals of known age or unknown age at first release). Other morphological, biochemical or genetic biomarkers for physiological age that correlate with chronological age might be possible to employ, but may be difficult to calibrate, are potentially more invasive or harmful and may have low accuracy (Wang et al., 2013) or become unreliable at later ages (Aw & Ballard, 2013; Kay, Ryan, Quick-miles, & Hugo, 2014). Such methods include measuring age-dependent tissue reflectance spectra with near-infrared spectroscopy (NIRS, Sikulu-Lord et al., 2016), quantification of fluorescing pigments that accumulate with age in cells (lipofuscin in post-mitotic cells, Fonseca, Brancato, Prior, Shelton, & Sheehy, 2005; pteridine in insect eyes,

Robson, Vickers, Blows, & Crozier, 2006) and, potentially, epigenetic clocks (based on DNA methylation changes, which have not yet been characterized in any insect, Bewick, Vogel, Moore, & Schmitz, 2017; Horvath & Raj, 2018). External wear and tear, for example mechanical damage to wings in crickets, flies (Vale, Hargrove, Jordan, Langley, & Mews, 1976) and Lepidoptera (Zimmerman & Madriñán, 1988), or other morphological structures (e.g. mandibles in Ground beetles, Butterfield, 1996) increase with advancing age. However, similar to other indirect age-estimation methods, this method hinges on how the function that correlates the measured trait to chronological age is affected by other traits, such as sex, sexual attractiveness, mating history, condition and social rank, that are often the target of research themselves and therefore unknown. It seems therefore essential to use a more direct way of age determination, such as marking of individuals of known age (e.g. at birth), sampling adults that eclose synchronously into adulthood, or employing specific probabilistic models that allow at least mortality rates to be estimated from CMR studies with individuals of unknown age at birth and death (Colchero & Clark, 2012; Zajitschek et al., 2009).

While correlational studies that quantify environmental parameters alongside the collection of longitudinal data can yield clues to environmental effects on life history, experimental approaches provide the most powerful and direct way to gauge the impact of key environmental factors such as diet or social environment on life span and senescence. Although challenging, experiments on wild insects are possible and could provide valuable data for the verification of laboratory findings. Dietary restriction is unlikely to be possible in natural populations because the foraging of wild animals is extremely difficult to control, and removal of food resources will usually lead to dispersal away from the study area. However, food supplementation experiments could be useful in gauging the effects of key nutrients such as protein on survival under natural conditions. Such studies would be especially useful if conducted in parallel in both natural and laboratory settings in genetically similar animals in order to directly measure the impact of laboratory conditions on experimental outcomes. To our knowledge, only one such study has been carried out to date (see Mautz et al., 2019). Likewise, it may be possible to manipulate the social environment by artificially adding or removing individuals from habitat patches. In some cases, it may also be possible to manipulate focal individuals themselves (e.g. by disabling certain functions, such as flight) to gauge effects on life span and senescence. No field experiments on life span and senescence in wild insects have been published so far, but such work has great potential to enhance understanding of the ecology and evolution of senescence in the wild.

7 | SOME QUESTIONS FOR FUTURE RESEARCH ON SENESCENCE IN WILD INSECTS

- How important are the fitness costs of senescence, and trade-offs between somatic maintenance and other life-history traits, in natural insect populations?
- How does the nature of variation in the rates, age of onset of senescence and fitness costs of senescence vary between species, and as a function of contrasting mating systems and life histories?
- How does the nature of variation in the rates, age of onset of senescence and fitness costs of senescence vary as a function of environmental conditions, and over time?
- What phenotypic changes accompany senescence in wild insects, and how do these phenotypic changes affect fitness?
- What genes are involved in variation in life span and senescence rates in natural insect populations, and do these genes have similar effects in the wild and in captivity?
- What are the key sources of mortality in natural insect populations, and how strongly do these mortality sources select on condition?
- Do the effects of nutrients on life span and senescence vary between laboratory and natural environments?
- Under what conditions does elevated adult mortality rate select for reduced somatic maintenance and accelerated senescence in natural insect populations?
- Do the sexes age differently in natural insect populations, and are these sex differences concordant with sex differences observed in the laboratory?
- What are the factors or conditions that cause senescence to be expressed differently in wild versus captive populations?

ACKNOWLEDGEMENTS

We would like to thank the special issue editors for the opportunity to contribute this review. Further, we would like to thank Jean-François Lemaître, Laurent Keller and an anonymous reviewer for insightful feedback on a previous version of the manuscript.

CONFLICT OF INTEREST

No conflicts to declare.

AUTHORS' CONTRIBUTIONS

All authors contributed to the conception, drafting and writing of the manuscript.

DATA AVAILABILITY STATEMENT

This manuscript does not use data.

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SUPPORTING INFORMATION

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How to cite this article: Zajitschek F, Zajitschek S, Bonduriansky R. Senescence in wild insects: Key questions and challenges. *Funct Ecol*. 2020;34:26–37. https://doi.org/10.1111/1365-2435.13399