Current perspectives and future directions in animal life history evolution

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October 4, 2023

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Article type: Review

Keywords: comparative demography, phenotypic plasticity, reproduction, senescence, strategies

Word count: 7,119 (excluding author contributions, acknowledgments and references)

Number of Figures: 4;

Number of References: 190

ABSTRACT

1. A life history strategy, the collection of actions, timings and characteristics individuals employ to optimize fitness, represents the evolutionary answer to a species' ecological problems. From the fatally reproductive salmon to the seemingly immortal jellyfish *Turritopsis dohrnii*, different species have found vastly different answers to their ecological problems, generating the vast suite of life histories observed across the animal kingdom. To explain this variation, life history theorists have generated and tested specific hypotheses to describe this variance and define what drives it.
2. Since Stearns (1992) and Roff (2002), animal life history evolution has pushed new frontiers. Specifically, insights from theoretical modelling, experiments, fieldwork and comparative studies have elucidated: how to describe life histories, what drives variance in life histories and what are the mechanisms that underlie life history traits. However, despite this progress, gaps in knowledge still remain.
3. In turn, here we review current perspectives, developed over the past 20 years, that support much of life history research today. These perspectives include: (1) the two-axes framework to describe life histories across taxa, (2) three different types of variance that impact life history evolution (*i.e.*, variance within time-steps, across time-steps and variance in life history outcomes) and (3) the utility of integrating ultimate and proximate modes of research to understand life history evolution. Subsequently, we outline future directions that represent new frontiers in animal life history evolution. These future directions are targeted at specific gaps in knowledge that offer timely insights for the broader ecology and evolutionary biology community: (1) where does selection act in a

life history, (2) a new representation of life histories in variable environments and (3) dealing with time in life history evolution.

4. In summary, this review provides a holistic perspective (from molecules to selection gradients) on *how* life histories are studied and *why* life history research requires interdisciplinarity. The further discussion of current perspectives and future directions provides a cross-section of animal life history research today: where we are, how we got here and where we are likely heading.

INTRODUCTION

Life history theory is a field of research focused on describing the rich diversity of strategies species use to pass their genes across generations. Specifically, a life history is the sequence of events and timings in an individual's lifespan, governed by underlying vital rates (*e.g.*, survival, growth, reproduction), that contribute to both individual fitness and broader population dynamics (Roff, 2002; Stearns, 1992). Such events and timings that constitute a life history are referred to as life history traits – here defined as phenotypes constructed from vital rates that describe fitness components (*e.g.*, generation time, expected lifespan and lifetime reproductive output). Collectively, these life history traits are often referred to as a life history strategy – the combination of life history traits that has evolved for the population to persist.

Across the animal kingdom, there is enormous variation in life history strategies (Jones et al., 2014). The Greenland shark takes a protracted period of 150 years to eventually reach sexual maturity (Nielsen et al., 2016). The aphid *Rhopalosiphum prunifolia* condenses the time it takes for necessary resource acquisition, development and reproductive output to have a generation time of just 4.7 days (at 25°C; Noda, 1960). The Chinook salmon populations that support coastal ecosystems and economies on the west coast of North America take the perilous journey upstream to reproduce and immediately perish in the waters they struggled so hard to reach (Groot & Margolis, 1991). This broad heterogeneity in animal life histories has pushed researchers to explain: (1) how we can describe these differences, and (2) what drives their evolution in a changing world.

Animal life history research is highly interdisciplinary. For example, imagine four researchers from different fields that are interested in studying the life history of "man's best friend" (*i.e.*, the dog, Fig. 1). The comparative demographer may be interested in characterizing the major axes of variance in life history strategies across all dog breeds (Healy et al., 2019; Salguero-Gómez et al., 2017). The evolutionary biologist may be interested in characterizing life history trade-offs (*i.e.*, negative covariances between life history traits) individual dog breeds exhibit in response to different diets (Stearns, 1989; Zera & Harshman, 2001; Zera & Zhao, 2006). The organismal biologist may be interested in the genetic, cellular and physiological pathways that initiate the timings associated with life history traits (*e.g.*, age at sexual maturity) (Jimenez, 2016). The population ecologist may be interested in characterizing the sources of variation (*e.g.*, genetic, environmental, luck) in life history traits within a population (Careau et al., 2010). All these research programmes, whilst completely within the interdisciplinary field of life history theory, test very different hypotheses using very different methods Hence, over the past twenty years, researchers have pushed new frontiers and posed new questions from a variety of different approaches.

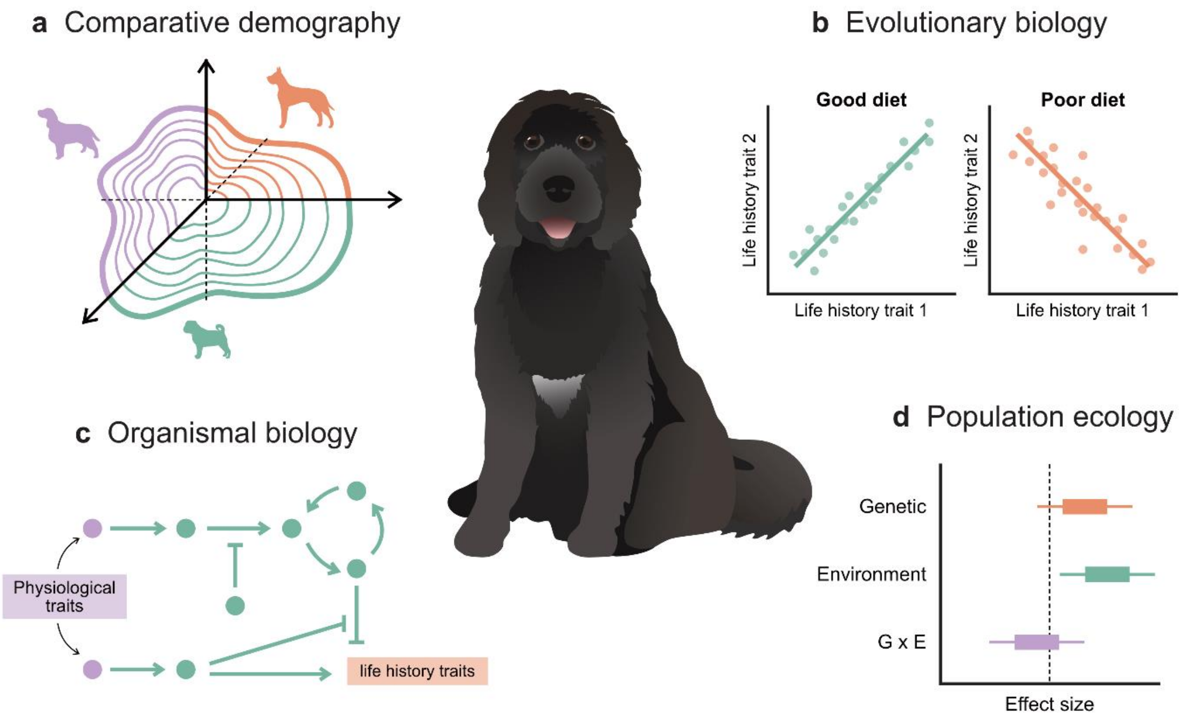

Figure 1. The many ways to study life histories. Here, we outline four distinct strategies to study the life histories of dogs. (a) Comparative demography may involve using dimension reduction methods (*e.g.*, phylogenetically controlled principal component analyses (Revell, 2009)) to identify the primary axes of dog life history variation. (b) Evolutionary biology may involve identifying the causes and constraints that lead to life history trait covariances (*e.g.*, how diet can alter the presence of trade-offs). (c) Organismal biology may involve studying the physiological pathways (*e.g.*, insulin/insulin-like growth factor signalling (Jimenez, 2016)) that mediate the generation of life history traits. (d) Population ecology may involve partitioning the variance in life history traits by their contributions from genes, the environment and their interaction.

Life history theory can greatly benefit from an integration of the different approaches researchers use to study animal life history evolution. To aid this integration, here we review current-perspectives and future directions in life history theory from across ecology and evolution. The current perspectives outlined in this paper represent step changes in thinking in life history research since Stearns (1992) and Roff (2002). Subsequently, we discuss future directions that represent new frontiers for life history researchers to explore, and potentially generate new perspectives in the years to come.

CURRENT PERSPECTIVES

Here, we outline current perspectives in animal life history research that have progressed significantly in the past 20 years. Whilst not exhaustive, these three sections act as a primer summarizing research programmes that have pushed the field forward and bolster much of life history research today. These sections progressively zoom in, in terms of scale, on recent findings in life history research: from comparative approaches across species, to variance decomposition approaches within species to the drivers of individual life history traits.

Describing life histories across the animal kingdom

Ecologists have long been interested in answering the question, how do life histories differ? The first attempt to characterize life histories was Robert MacArthur and E. O. Wilson's r vs. K-continuum (MacArthur & Wilson, 1967). Built on the logistic growth equation $\left(\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)\right)$, the r vs. K-continuum differentiates life histories based on the term under strongest selection; notably, this was also swiftly connected to the observation of survivorship curves which were also first formulated at this time (Van Valen, 1973). Whilst generalizable across taxa, the r vs. K-continuum does not account for major life history traits and their tendency to covary. For example, generation time, mean life expectancy and age at sexual maturity vary greatly across the animal kingdom (from the aphid to the Greenland shark) and, furthermore, covary to a significant degree

– to the degree of becoming a *syndrome*. As a consequence, the second attempt to characterize life histories came when Stephen Stearns framed life history variation in terms of a *pace-of-life syndrome* (Stearns, 1983). Some life histories are *slow* (long generation time, higher mean life expectancy and later age at sexual maturity) whilst others are *fast* (short generation time, lower mean life expectancy and earlier age at sexual maturity). Until recently, this fast-slow continuum was the primary method to explain the variation in life histories across the animal kingdom.

Currently, animal life histories are characterized across two axes of life history variation. To empirically quantify the primary axes of life history variation in animals, Healy et al. (2018) used a body mass and phylogenetically corrected principal component analysis (PCA) of life history traits from 121 species. This PCA identified two axes that collectively explain 71% of the variance in life history traits. These axes include pace-of-life syndrome and the distribution of age-specific reproduction and mortality – this follows Salguero-Gómez et al. (2017) finding a similar pattern in plants. Identifying these two axes of animal life history variation was immediately impactful for two reasons. First, this result shows that the distribution of demographic processes, such as survival and reproduction, is orthogonal to pace-of-life syndrome. Therefore, selection for the evenness (*e.g.*, constant survival, iteroparity) or skew (*e.g.*, varied survival, semelparity) of demographic rates across a life history can arise in both slow and fast life histories. Second, this result connects directly to the Euler-Lotka equation ($1 = \sum_{x=1}^{\omega} \lambda^{-x} l_x m_x$), another fundamental equation in demography, which defines survivorship (l_x) and reproduction (m_x) as vectors that constrain the mathematical space of possible life histories.

After Healy et al. (2018), the two-axes framework for animal life histories has fostered new findings. Some examples include:

1. The sensitivity and resilience of a population to temporal autocorrelation and demographic disturbance is strongly correlated with pace-of-life syndrome (temporal autocorrelation: Paniw et al., 2018; demographic disturbance: Capdevila et al., 2022).
2. Both terrestrial and aquatic life histories inhabit the same two-axes of life history variation, but with key differences in their diversity (Capdevila et al., 2020).
3. Populations can harbour high degrees of interindividual life history variation that differ across species whilst allowing for high intraspecific variation not described by the axes (Van De Walle et al., 2023).
4. The two-axes framework aids in predicting the conservation status of various species in response to anthropogenic disturbance and climate change (Indo-Pacific fishes: Wang et al., 2020; chelonians and crocodilians: Rodríguez-Caro et al., 2023; the gray mouse lemur: Ozgul et al., 2023).

Whilst these findings have made new connections between life history theory and multiple areas of ecology, the two-axes framework is not without its flaws. The two-axes framework of animal life histories is data and, more specifically, model hungry. To perform the analysis, life history traits from across the animal kingdom must be derived. The life history traits are often derived from structured population models – many of which are stored in open-access databases (Jasilioniene et al., 2015; Levin et al., 2022; Marques et al., 2018; Salguero-Gómez et al., 2016; Wilmoth et al., 2007). Whilst these models sometimes contain errors (Che-Castaldo et al., 2020; Gascoigne, Rolph, et al., 2023; Kendall et al., 2019), there has been a push for standardizing research practices around the dissemination of models (Gascoigne, Rolph, et al., 2023; Simmonds & Jones, 2023). Thankfully, there has also been a recent push for standardizing the traits used within the two-axes framework (Stott et al., 2023). This standardization, across model construction, communication and the comparative inference drawn from them, represents a necessary next step for reproducibility in research using the two-axes framework (Salguero-Gómez et al., 2021).

Characterizing variance in life histories within populations

Life histories are not static. Yet, much of the canonical life history literature, from Pearl (1925) to Charlesworth (1994), and the comparative approaches detailed above have focused on the expression of *average* life histories in populations. Currently, the exploration of *variance* in life histories within a population is just as, if not more, exciting and relevant to understand life histories in a changing world.

Variance in life histories can take many different forms. Variance may arise by relatively complicated mechanisms such as strength of frequency dependence on demographic processes (Potter et al., 2023) or heterogeneity in parental care in a population (Pape Møller & Thornhill, 1998). However, the emergent variance in life histories can be simply categorized into three types: variance within time-steps, variance across time-steps and variance in life history outcomes (*e.g.*, lifespan, reproductive output).

Variance within time-steps alludes to the heterogeneity within a population at time *t*. This heterogeneity, also called individual variability, may arise due to life history explicit factors. For example, individuals in a population may vary by genotype, sex, ontogenetically (*e.g.*, juvenile or adult), by a separate state (*e.g.*, dormancy or dispersal) or by strategy (*e.g.*, sneakers vs. guarders in *Onthophagus* beetles: Emlen, 1997). This heterogeneity is necessary to understand the relative fitness of individuals in a population. To quantify this relative fitness, researchers often use *reproductive value*: the discounted contribution of an individual to future offspring (for a thorough explanation, see: Barton & Etheridge, 2011 and Grafen, 2006). Using reproductive value, researchers are able to build hypotheses as to the evolution of life history strategies in structured populations (*e.g.*, senescence in age-structured populations (Newton & Rothery, 1997; Roper et al., 2021), the evolution of sociality (Roper et al., 2023), bet-hedging (Grafen, 1999) and parasitism (Andersson, 2017)).

Variance across time-steps, often called *environmental stochasticity*, refers to the difference in life history outcomes over time (*e.g.*, from time *t* to *t*+1). To illustrate this concept, imagine a researcher interested in modelling the life histories of a charismatic opossum population in the Brazilian rainforest (Kajin et al., 2008). In year *t*, the opossum population is exposed to a favourable environment full of resources and habitat. As a consequence, at time *t*, individuals with a large body size and reproductive capacity had a relatively higher fitness than smaller individuals with delayed age at sexual maturity. However, in year *t*+1, a fire passes through the rainforest reducing habitat area and resource availability. In turn, at time *t*+1, smaller individuals that were able to delay their age at sexual maturity, and not reproduce during the fire, were able to disproportionately contribute to the new offspring – and thereby have a higher fitness that their larger conspecifics. This switch between the relative fitness of life history strategies across timesteps poses a problem to the researcher who asks: “Which life history is characteristic of the population?” The truth is, both are. To study life histories in response to environmental stochasticity, researchers often use the tools of stochastic demography (Tuljapurkar, 1990). This set of tools allows researchers to quantify the impact of variance across timesteps on life histories. Using these tools, researchers have identified the demographic mechanisms that drive the emergence of life history strategies – some of whom were previously thought non-adaptive (e.g., Jongejans et al., 2010; Koons et al., 2008, 2009; Tuljapurkar, Gaillard, et al., 2009).

Variance in life history outcomes is a relatively new area of study within life history evolution. Researchers in this field are interested in quantifying (1) the variance in life history outcomes and (2) what drives this variance. To quantify the variance in life history outcomes, researchers use structured population models to calculate the expected variance in a life history outcome given a set of demographic processes. This variance is often referred to as *dynamic heterogeneity* (Tuljapurkar, Steiner, et al., 2009) or *individual stochasticity* (Caswell, 2009), but confusion about definitions exists (Forsythe et al., 2021). Research into dynamic heterogeneity has been able to uncouple: genetic, environmental, gene by environment (*i.e.*, phenotypic plasticity) and demographic stochastic components and further provide quantitative estimates of dynamic (neutral) heterogeneity in life courses that can serve as null models (Snyder & Ellner, 2018, 2022; Steiner et al., 2021; van Daalen & Caswell, 2017, 2020a). Ideas about dynamic heterogeneity have been perceived with criticism (Cam et al., 2016) as deterministic perspectives are deeply rooted in our biological thinking – life history theory in particular. However, both empirical and theoretical research have illustrated how purely deterministic explanations fall short (Fay, Authier, et al., 2022; Snyder & Ellner, 2022; Varas Enríquez et al., 2022). Individual stochasticity, even though neutral in itself, slows adaptation (Steiner & Tuljapurkar, 2012) and selective forces might act in favour of, against, or be close to neutral of the generating processes that drive the level of individual stochasticity (Steiner & Tuljapurkar, 2023). Such diversity is not surprising as increased variance in mortality and reproduction can increase individual stochasticity while reducing fixed heterogeneity but can also increase both components in some systems (van Daalen & Caswell, 2020b). Variance in reproduction associated to individual stochasticity is high within and between populations across species and such variance explains the variation in life history strategies amongst animals and plants to a similar if not larger degree than mean differences (Varas Enríquez et al., 2022).

Ultimate vs. proximate explanations of life history evolution

In the past, research into animal life history evolution has focused on ultimate (evolutionary) modes of research. Why has selection not resulted in the evolution of solely semelparous species (Cole's paradox: Cole, 1954)? What are the necessary conditions for dormancy/diapause/torpor to be the dominant strategy in a population (Tuljapurkar & Istock, 1993)? This focus on ultimate rather than proximate (mechanistic) research questions arose due to a widely held sentiment that evolutionary biology was the ideal home for life history theory.

> The connection between genotype and phenotype has traditionally been provided by developmental biology and physiology, fields which have become increasingly molecular. . . We cannot afford to wait until the molecular analysis of development and physiology has delivered a few mature summary statements relevant to individual variation in fitness, for that will take centuries – if it ever happens at all. We must make our own hypotheses and hope that the molecular connection will come at a later date.
>
> \- Stearns (1992, p. 10)

Thankfully, this "molecular connection" is now being well explored.

The molecular underpinnings of life history traits are central to life history research. Over the past 20 years, researchers have uncovered the molecular mechanisms of senescence – the deterioration of homeostatic mechanisms with age (López-Otín et al., 2013). From telomere shortening (Haussmann & Vleck, 2002; Henriques & Ferreira, 2012) to dysregulated physiological pathways (e.g., hyperfunction theory: Blagosklonny, 2006, 2021), and from too much protein (Fanson et al., 2012) to differential resource allocation (Adler & Bonduriansky, 2014), researchers have identified many proximate explanations for senescence across the animal kingdom (López-Otín et al., 2013). Furthermore, mechanisms have also been fleshed out for the other side of life histories - fertility. All periods of reproduction, from pre-copulation to copulation to post-copulation, contain candidate proximate mechanisms that influence the variation in life histories: including endogenous insulin/insulin-life growth factor signalling (IIS) (Lind et al., 2019; Regan et al., 2020; Sepil et al., 2020), target of rapamycin signalling (Alves et al., 2022), sperm traits (Ni et al., 2016; Sanghvi et al., 2023) and seminal fluid proteins (Hopkins et al., 2019; Sepil et al., 2020; Wigby et al., 2020) – just to name a few.

One takeaway from this plethora of proximate mechanisms is the lack of generality. For every life history trait, there is one or many physiological mechanisms that impact the generation of the life history trait phenotype. Whilst these mechanisms have offered a great deal of relevance to developmental biology (Davidson et al., 2023; Emlen & Nijhout, 2001; Kapali et al., 2022; McDonald et al., 2018; Shingleton et al., 2007; Simmons & Emlen, 2006) and evolutionary medicine (Stearns & Medzhitov, 2015), proximate mechanisms alone do not implicate the evolutionary drivers that shape life histories. To gain this generality, current research programs have linked the proximate with the ultimate to offer direct links between the two modes of research. Examples of this integrative approach to life history theory include:

1. Wolves in North America – In Cubaynes et al. (2022), the authors test the hypothesis that canine distemper virus (CDV) drives the latitudinal distribution of coat colour in the wolves of North America (*i.e.*, the increased frequency of black coats in higher latitudes). The authors use a combination of genetics and demographic models to show that CDV creates a selective pressure for disassortative mating, due to heterozygous

advantage. In turn, Cubaynes et al. (2022) demonstrate how strength of selection on reproductive strategies can be moderated by genetically determined pathogen resistance.

2. *Drosophila melanogaster* and insulin across latitudes – In the lab, researchers have demonstrated the broad impacts of insulin/insulin-like growth factor signalling (IIS) on development (Parker & Shingleton, 2011; Shingleton et al., 2005, 2007), nutrient sensing (McDonald et al., 2021), environmental cues (Kapali et al., 2022; Regan et al., 2020; Snell-Rood & Moczek, 2012) and life histories (Giannakou & Partridge, 2007; Sepil et al., 2020) in *Drosophila melanogaster*. However, there was no evidence that these lab-based findings were related to the already known impacts of latitudinal clines on *Drosophila* life histories (James et al., 1997). To fill this gap in knowledge, Fabian et al., (2012) explored genome-wide patterns in latitudinal differentiation in *Drosophila melanogaster* across the east coast of North America. Interestingly, they found IIS associated genes (*e.g.*, *FOXO* and *InR*) that differentiated across the latitudinal cline. In turn, genome-wide tools of natural populations are able to connect lab-based findings to real world life history phenomena.
3. Guppies in Trinidad – In Potter et al. (2023), the authors explore the possible mechanisms that maintain variance in male colouration in a population of guppies. The authors use a combination of a pedigree (spanning 10 generations), spatial data and demographic rates to show that variance in male colouration and the long discussed genetic mechanisms that underpin them (Houde, 1994; Hughes et al., 2005; Paris et al., 2022) are maintained via female preference for rarity. This female preference is adaptive due to an indirect benefit on the fitness of their “sexy sons.” In turn Potter et al. (2023) show that female preference is sufficient to promote variance in genetically determined male secondary sexual signals – also see (Kvalnes et al., 2022) for a similar, but density-dependent, case in barn owls.

These examples demonstrate how ultimate and proximate questions can be integrated to advance our understanding of life history evolution. Admittedly, these studies are built on great deals of hard-fought longitudinal data, making the scaling of this inference across taxa especially challenging. Thankfully, developments in the ways we model populations are making this obstacle progressively smaller (Bocedi et al., 2021; Coulson, 2021; Wilson et al., 2010).

FUTURE DIRECTIONS

Here, we outline future directions in animal life history evolution, each of which targets a specific gap in knowledge. Since these are future directions – and the work has not been done yet – we first describe the gap in knowledge and then outline research programs that may address these gaps and, possibly, offer new insights.

Where does selection act in a life history?

Currently, research on life history evolution has a problem – a problem specifically linked to the *evolution* part of life history evolution. To illustrate this problem, let us imagine a young budding ecologist, called Willow, enjoying her undergraduate courses in ecology and evolution. In these courses, Willow learns there are three requirements for evolution by natural selection:

- First, the trait must have an impact on fitness.
- Second, there must be variance in the trait across the population.
- Third, the variance in the trait must be heritable to some degree.

After completing her undergrad, Willow is excited to begin her graduate studies focused on life history evolution. However, after perusing through the literature, Willow is shocked. The majority of papers on the evolution of life histories focus solely on the first criterion for evolution by natural selection (Barraquand & Yoccoz, 2013; Benton & Grant, 1996; Hilde et al., 2020; Jaggi et al., 2023; Koons et al., 2009; Le Coeur et al., 2022; J. L. McDonald et al., 2017; Morris et al., 2008; Pfister, 1998; Tuljapurkar, Gaillard, et al., 2009). Why is this the case?

There are two reasons why studying the evolution of life histories remains difficult.

First, defining fitness is problematic (Smith, 1983). In theory, fitness is easy to determine: the genetic contribution of an individual to successive generations relative to other individuals in the population. However, in the real world, fitness is harder to quantify. This difficulty is partly due to the multi-faceted nature of fitness. The fitness of an individual is determined by multiple components – *e.g.*, offspring number, offspring quality, parental care, social status. Each of these components combines to generate the sum total fitness we, as life history theorists, are interested in. Out of practicality, researchers often use life history traits as proxies of fitness (see Fig. 2). The basis for this approximate approach is in both ease and phenotypic correlations often being reasonable proxies for genetic correlations (see Cheverud's conjecture: Cheverud, 1988). Unfortunately, this approximation may lead to bias and misrepresent the fitness profile of individuals in a population (Pick, 2023).

Second, modelling the evolution of life histories is difficult. Reverting back to the definition, a life history is the sequence of events and timings in an individual's lifespan, governed by underlying vital rates, that contribute both to individual fitness and broader population dynamics. Of this series of events and timings, researchers can only capture a subset in a demographic model or a lab-based study. For example, demographic models rarely, if ever, include mate choice mechanisms (despite their abundance: Westneat et al., 2000), the impact of transgenerational effects (despite their abundance: Crean & Bonduriansky, 2014; Skinner, 2016)) and behaviours that have direct impacts on individual fitness (*e.g.*, the Bogert effect: Bogert, 1949).

All in all, this leaves the researcher with a dilemma: What events and timings are necessary to include when modelling a life history? Is there such a thing as a model that is too complex, or not complex enough? Currently, researchers have not defined the criteria for the inclusion of a variable in a life history model; however, there are strong arguments against the inclusion of anything and everything (Borges, 1999; Caswell, 2019, p.6).

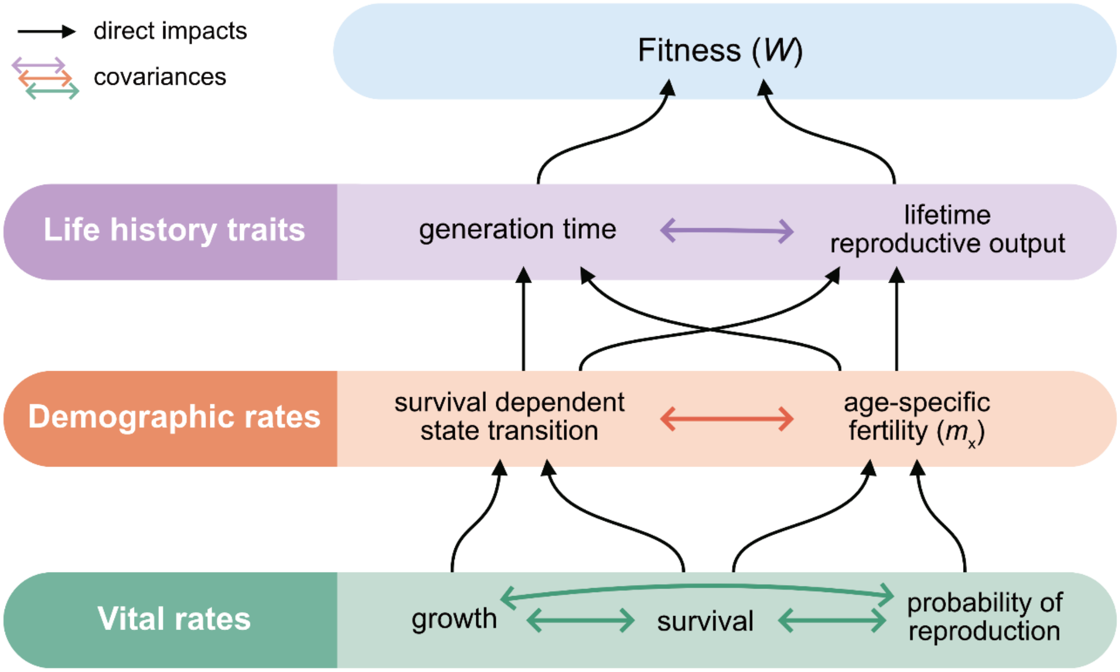

Figure 2. The complexities of life history evolution. Here, we show how the current toolbox of demographic methods reveal the inherent complexity of life history evolution. Life history traits, often used as proxies of fitness (*W*), have both direct (black arrows) and indirect (coloured arrows, *i.e.*, via covariances/trade-offs with other life history traits) impacts on fitness. Furthermore, life history traits themselves are constructed by underlying demographic rates and, at a deeper level, vital rates, which exhibit the same nested complexities of direct and indirect impacts on fitness. We note that, whilst this shows the apparent complexity of life history evolution, there are levels below vital rates (*e.g.*, resource availability) that can further complicate the expression of life history traits and their covariance structure (De Jong & Van Noordwijk, 1992; Metcalf, 2016; Noordwijk & de Jong, 1986).

To address these difficulties, we recommend two approaches. First, we recommend a trait-based approach as presented in Coulson (2021). In this approach, life histories can be viewed through one focal life history trait (*i.e.* body size) using an integral projection model (Easterling et al., 2000; Ellner et al., 2016). Within this framework, a series of resource accrual traits are selected upon to optimize body size given a set of eco-evolutionary feedback loops. By using body size as the metric of interest, Coulson (2021) shows how perturbation analyses can be used to define the eco-evolutionary determinants of body size. This modelling approach (also see Coulson et al., 2021), whilst scalable, loses the complexities offered by previous demographic approaches. In turn, we also recommend a second approach which involves variance decomposition. Both population ecologists and population geneticists have developed variance decomposition techniques to identify the drivers of system-wide behaviour through demographic rates or allele frequencies, respectively. These methods are life table response experiments (Caswell, 1996, 2010; Hernández et al., 2023) and quantitative trait loci (QTL)/genome-wide association studies (GWAS) (e.g., Ivanov et al., 2015). Whilst methods exist to knit together structured demographic models and genetic structure (de Vries & Caswell, 2019; Steiner et al., 2021), researchers currently do not have a tool to explore the genetic underpinnings of life history traits without a known link between a gene and a life history trait *a priori*. To build and test these models, we recommend using tractable model systems, such as *Drosophila melanogaster* and *Caenorhabditis elegans*, due to the readily available tools for GWAS/QTL studies and the easily modelled life history due to discrete ontogenetic stages. These models would thus represent ideal avenues for research programmes focussed on integrating ultimate and proximate understandings of life history evolution.

A phase diagram of life histories in variable environments

The impact of variable environments on life histories is a key topic in life history evolution and population dynamics (Sutherland et al., 2013). The reason for this is, in addition to being interesting, global climate change is predicted to change environment variability (a key driver of variance in life history processes (Jackson et al., 2022)) across the globe – posing an imminent threat to biodiversity (Bathiany et al., 2018; Drake, 2005; Masson-Delmotte et al., 2021; Vasseur et al., 2014).

Much of our current understanding around life histories in variable environments is centred around Tuljapurkar's approximation (Tuljapurkar, 1989, Eq. 1).

(Eq. 1) $\log(\lambda_s) \approx \log(\lambda_1) - \frac{\sigma^2+\tau}{2\lambda_1^2} + \frac{\theta}{\lambda_1^2}$

Here, the logarithmic long-run stochastic population growth rate ($\log(\lambda_s)$) can be approximated via the population growth rate associated with the mean environment (λ_1) with contributions from demographic rate variances (σ^2), covariances (τ) and temporal autocorrelation (θ). In studies of life histories in variable environments, $\log(\lambda_s)$ is often used as a measure of fitness associated with a specific life history strategy (Cubaynes et al., 2022). In turn, researchers have been interested in the ways by which life histories can optimize $\log(\lambda_s)$ given the terms on the right-hand side of the equation.

Over the course of the past 25 years, may studies have explored the impact of demographic rate variances (σ^2: Doak et al., 2005; Engen et al., 1998; Foley, 1994; J. L. McDonald et al., 2017; Morris et al., 2008; Morris & Doak, 2004; Pfister, 1998; Sæther, 1997; Sæther et al., 1998) with relatively less focus on demographic rate covariances (Compagnoni et al., 2016; Fay, Hamel, et al., 2022) and environment autocorrelation (Evers et al., 2023; Gascoigne, Kajin, et al., 2023; Tuljapurkar & Haridas, 2006). Similarly, despite a large body of literature, little focus is given to the relationship between the most important term in Tuljapurkar's approximation, $\log(\lambda_1)$, and the variance components. This represents a key gap in knowledge as the simplest way for a life history strategy to improve its associated fitness is through changes in its mean demographic rates, not variance components. And unfortunately, shifts in mean life history strategies cannot be neatly uncoupled from variances as they confound one another. Therefore, we argue life history theory would benefit from a new perspective to probe life history evolution in variable environments.

To build this new perspective, we go back to using "man's best friend" in a thought experiment. Imagine an arachnophobic puppy named Hastings who has just come across a spider whilst on his morning walk. Given the behavioural ecology of the puppy, Hastings can respond in three ways. These responses include: *fight*, *flight* and *hide*. All of these responses are completely possible to deal with the approaching eight-legged threat. We relay this analogy to argue that life history strategies can also use these responses to deal with variable environments. Instead of a puppy, now imagine a population, and instead of a spider, now imagine environmental variability. In response to the threat of environmental variability, populations can evolve life history strategies whereby they can (Fig. 3a):

- persist (*fight*) via plasticity or adaptation to the variable environment.
- escape the environment (*flight*) via dispersal, migration or vagrancy.
- avoid the timestep (*hide*) via dormancy, torpor or hibernation.

These strategies are insightful as, in addition to being strategically distinct, their costs are broadly distinct as well (Fig. 3a):

- *fighting* involves the cost of environmental variability outlined in Tuljapurkar's approximation (*i.e.*, variance in demographic rates)
- *flight* often involves a cost to demographic rates (*i.e.*, reduced survival or reproductive output)
- *hiding* involves a cost directly to fitness in the form of extending generation time

From these costs we can build a visual representation of when and where each strategy should be selected for.

Here, we propose a phase diagram of life histories in variable environments (Fig. 3b). Taking inspiration from the 150-year-old concept of phase diagrams in physics and chemistry, we show a framework whereby different combinations of costs associated with dispersal/migration/vagrancy and dormancy/torpor/hibernation can evolve and, as a strategy, invade the population. We hypothesize this phase diagram will look very different for life histories with different ecologies (*e.g.*, Fig. 3c,d).

To test this phase diagram, we recommend a combination of theoretical modelling and experimental approaches. Modelling using two/multiple patch systems (Steiner et al., 2014; Sultan & Spencer, 2002) would allow a researcher to vary the cost of dispersal *a priori* – however we note the cost of dispersal can come in a variety of forms which should also be explicitly explored (Bonte et al., 2012). Furthermore, we recommend a modelling approach to explore a variety of life history archetypes to see how life histories shape the phase diagram (Takada et al., 2018). Analytical and individual-based eco-evolutionary models can be used to provide theoretical predictions on the evolution of, for example, dispersal vs. dormancy vs. *in situ* adaptation, under different combination of life histories, ecological conditions and relative costs of the different strategies (Gerber & Kokko, 2018; Travis et al., 2021; Vitalis et al., 2013).

Regarding experimental approaches, we recommend the use of insects with defined stages of development which also exhibit differential dispersal morphology (*e.g.*, the seed beetle *Callosobruchus maculatus* (Gascoigne et al., 2022; Sanghvi et al., 2021, 2022) with experimental evolution approaches (Lustenhouwer et al., 2023)). In seed beetles, multiple patch systems can be constructed to moderate the cost of dispersal, and temperature during juvenile development can be used to moderate cost of dormancy (here defined as prolonged development time).

We acknowledge that the costs associated with the *fight*, *flight* and *hide* strategies are not mutually exclusive. For example, it is quite likely that a cost of dispersal on demographic rates leads to a shift in generation time. However, we offer this phase diagram of life histories in variable environments as both a hypothesis and a heuristic to start testing life history evolution beyond variance components.

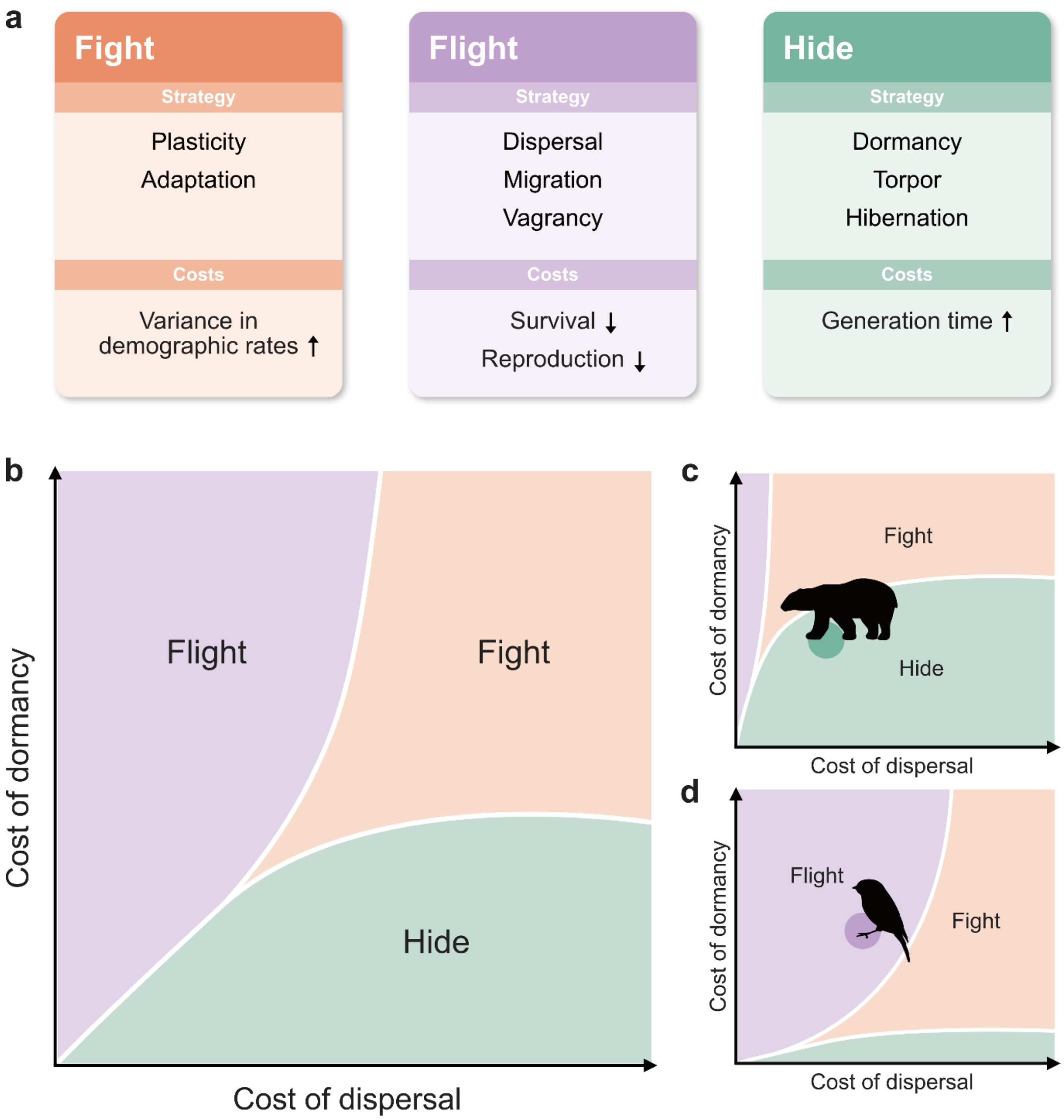

Figure 3. A phase diagram of life histories in variable environments. Here, we illustrate how life history evolution in variable environments can be represented by three different competing strategies: *fighting* (persisting in the face of environmental variability), *flight* (escaping the immediate threat of environmental variability) and *hiding* (avoid a time-step through dormancy/hibernation/torpor to reduce the impact of environmental variability. (a) The costs of each strategy are broadly independent and can, thus, be viewed as in competition with one another. To visualize this competition, we construct a phase diagram (b, resembling phase diagrams from physics and chemistry). Here, the *fight*, *flight* and *hide* strategies emerge at different combinations of costs associated with the *flight* and *hide* strategies. We use dispersal and dormancy to represent

the focal cost, but this could easily be migration/vagrancy or hibernation/torpor. We note that this space may look very different across species – shown by the polar bear (c) and the blue tit (d). The utility of this framework arises by the placing of a population on this phase diagram. To illustrate this, the polar is in the *hide* region – meaning the polar bear population could be successfully invaded by a life history strategy that has a relatively longer period of hibernation than the rest of the population. Likewise, the blue tit population in the *flight* region – meaning the blue tit population could be successfully invaded by a life history strategy that involves relatively more dispersal events across habitable patches than the rest of the population. We hypothesize that manipulating the costs along this space should predictably change the position of the population on the phase diagram.

The issue of time in studying life histories

Currently, life history evolution has not addressed the problem of time. Specifically, time is relative. Here, we are not talking about how animals perceive time (this is a topic we will leave to other fields (Roberts, 2002; Zentall, 2005)). Instead, we are discussing how time within the life history of an animal relates to the temporal pattern of events it senses in its environment.

Life histories and environments are temporally explicit processes. Whether we are discussing an age (e.g., Holmes & York, 2003), stage (e.g., Crouse et al., 1987) or size (e.g., Bassar et al., 2015) structured life history, individuals change state (*i.e.*, growth, progression, shrinkage, retrogression), stay in the same state (*i.e.*, stasis), reproduce or die across timesteps t to t+1. We note this would also work in the continuous case across dt. As a consequence of the temporal nature of life histories, many of the life history traits we derive are also temporally explicit (*e.g.*, generation time, age at sexual maturity, expected lifespan). In addition, environments are also temporally explicit. Whether we are discussing yearly (Hansen et al., 2019), monthly (Paniw et al., 2019), weekly (Wood et al., 2023) or even shorter timeframes (Jouvet et al., 2018), environment components are also structured across timesteps t to t+1, or dt. We outline these obvious facts as it is the combination of the life history and environment timeframes where life history research gets messy (Tuljapurkar, 2023).

Previous research analysing the role of environment components has been agnostic as to the mismatched timeframes of life histories and environment regimes. In other words, researchers estimate the impacts of environment components on life histories across timesteps relevant to an environment component (Vinton et al., 2022), not the life history in question (but see Park, 2019; Park & Post, 2022; Park & Wootton, 2021). This line of research is valuable from the point of view of conservation biologists as it is useful to estimate environment contributions toward broader population dynamics, however this does not allow us to interpret how life histories evolve. To illustrate this point, let us imagine two populations of interest, a mosquito population and an elephant population. Whilst El Niño and La Niña may have dramatic consequences on the size of the mosquito population at a certain point in time, a timeframe of two to seven years is not small enough to fit within a life history of a mosquito. For the elephant, however, a two-to-seven-year timeframe is sufficient to disrupt life histories to the point of altering life history outcomes (Li et al., 2015). To put the shoe on the other foot, daily predictable gusts of wind may have an impact on mosquito life history evolution (Endo & Eltahir, 2018; Wong & Jim, 2017) but likely does not impact the evolution of elephant life histories due to a timeframe disparity. In turn, whilst the impacts of environment regimes (agnostic of life history timeframes) on population dynamics is important, they do not necessarily inform the impacts of environment regimes on life history evolution.

To fill this gap in knowledge, we recommend accounting for generation time when analysing the impacts of environment components on life history evolution (Fig. 4a-d). We hypothesize that this standardization will demonstrate the degree to which life histories are able to accommodate environment components. We further hypothesize this will have important implications for the role of plastic/tracking vs. canalized/buffered strategies (Fig. 4e,f). Plastic strategies for life histories in variable environments have been discussed at length over the past twenty years (King & Hadfield, 2019; Koons et al., 2009; Snell-Rood, 2013; Sultan & Spencer, 2002; Vinton et al., 2022; West-Eberhard, 2003; Xue & Leibler, 2018), but, up until now, the impact of generation time has not been linked.

To test these hypotheses, we recommend a combination of comparative studies and theoretical modelling. Comparative analyses have brought great insights to animal life history evolution (Capdevila et al., 2020, 2022; Healy et al., 2019). A reanalysis of some of these results, accounting for generation time, may yield findings indicating how well populations deal with the environments *they* experience across their life history (Fig. 4a-d). In addition, we recommend modelling approaches of stochastic environments built on underlying spectra (*e.g.*, 1/f noise: Halley, 1996; Halley & Inchausti, 2004) to test the degree to which life histories evolve plastic or canalized strategies based on how environments contribute to the evolution of phenotypic plasticity (Dupont et al., 2023; Hoffmann & Bridle, 2022; Vinton et al., 2022, 2023).

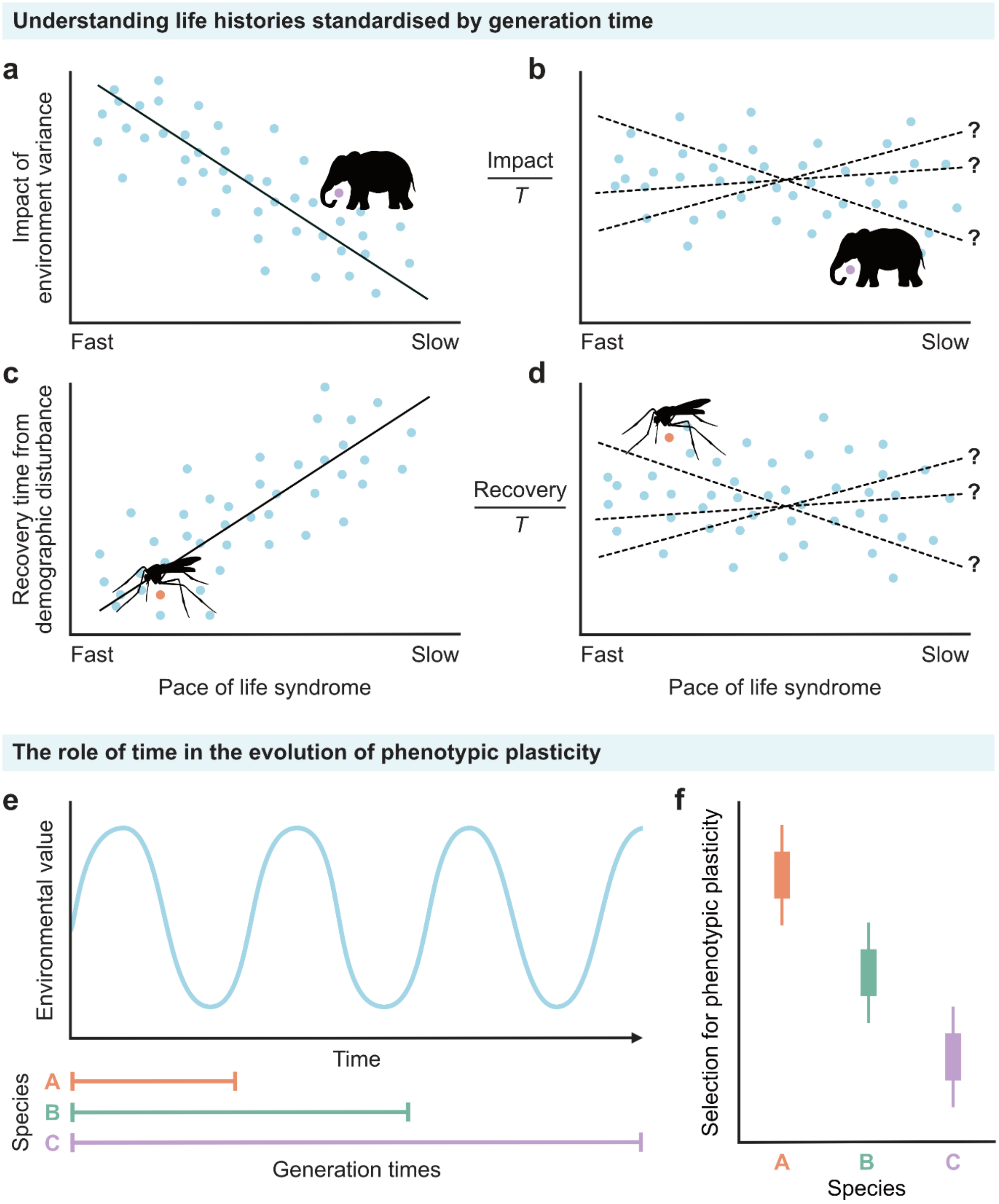

Figure 4. Accounting for time in both life histories and the environment in our understanding of life history evolution. Here, we show the impact of pace of life syndrome on inferences of life histories in variable environments. Previous research has shown broad relationships between the impact of environment variance (a, (Morris et al., 2008; Paniw et al., 2018)) and disturbance regimes (c, (Capdevila et al., 2022; Compagnoni et al., 2021)) across slow and fast life histories.

Whilst informative for conservation purposes, this approach does not account for the timeframe within which life histories take place – a necessary consideration to understand life history evolution in variable environments. In turn, we propose a new line of research measuring the impact of environment variability (b) and disturbance regimes (d) accounting for generation time (T). This analysis would indicate the degree to which a life history is responsive or stable in environmental regimes *relative* to the life history's timeframe. Furthermore, this approach has broad implications connecting life histories in variable environments to the evolution of phenotypic plasticity. (e) Depending on the timeframe within which the life history takes place, individuals may be exposed to relatively stable average environment values across generations (species A) or relatively unstable average environment values across generations (species C) – from the same environment. The differences only arise due to differences in generation time. The implications of this mismatch in generation time is that species A may evolve plasticity mechanisms that allow it to *track* its environment, more so than species B and C, due to generation time (also see Dupont et al., 2023; Hoffmann & Bridle, 2022; Vinton et al., 2023).

CONCLUDING REMARKS

Here, we offer a cross-section of the integrative field that is animal life history evolution. The current perspectives and future directions outlined in this manuscript are in no way exhaustive but are constructed as a resource to both review the current state-of-affairs in animal life history research and present frontiers for exploration. We fully expect the ideas relayed across this manuscript to develop, grow and maybe change as these frontiers are pushed – we leave this to the reader.

To close, we end with an important reminder. A life history is not a "thing"; one cannot physically grasp a life history. Instead, a life history is an abstraction used to define the life course of individuals, from birth to death, in an evolutionary context. It is important for researchers to remember this when relaying their findings. Within life history theory, results are always context-dependent and subject to deserved scrutiny. However, through a push for generality, we progress to understanding the truths by which organisms make their way from t to t+1.

AUTHOR CONTRIBUTIONS

SJLG conceived the initial ideas for this manuscript and wrote the first draft. SJLG and AR designed the figures which were subsequently built by AR. All authors contributed significantly to the ideas, structure and writing in this manuscript.

ACKNOWLEDGEMENTS

We would like to thank various friends and colleagues who have helped us, sometimes inadvertently, develop the ideas we present in this manuscript. Specifically, we would like to thank R. Salguero-Gómez, T. Coulson, J. Deere, C. Bernard, M. Kajin, A. Vinton, J. H. Watson and many of the attendees from the 8th meeting of the Evolutionary Demography Society in Paris, 2023.

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