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Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes

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ABSTRACT

We present a novel perspective on life-history evolution that combines recent theoretical advances in fluctuating density-dependent selection with the notion of pace-of-life syndromes (POLSs) in behavioural ecology. These ideas posit phenotypic co-variation in life-history, physiological, morphological and behavioural traits as a continuum from the highly fecund, short-lived, bold, aggressive and highly dispersive ‘fast’ types at one end of the POLS to the less fecund, long-lived, cautious, shy, plastic and socially responsive ‘slow’ types at the other. We propose that such variation in life histories and the associated individual differences in behaviour can be explained through their eco-evolutionary dynamics with population density – a single and ubiquitous selective factor that is present in all biological systems. Contrasting regimes of environmental stochasticity are expected to affect population density in time and space and create differing patterns of fluctuating density-dependent selection, which generates variation in fast *versus* slow life histories within and among populations. We therefore predict that a major axis of phenotypic co-variation in life-history, physiological, morphological and behavioural traits (i.e. the POLS) should align with these stochastic fluctuations in the multivariate fitness landscape created by variation in density-dependent selection. Phenotypic plasticity and/or genetic (co-)variation oriented along this major POLS axis are thus expected to facilitate rapid and adaptively integrated changes in various aspects of life histories within and among populations and/or species. The fluctuating density-dependent selection POLS framework presented here therefore provides a series of clear testable predictions, the investigation of which should further our fundamental understanding of life-history evolution and thus our ability to predict natural population dynamics.

Key words: fluctuating selection, frequency-dependent selection, environmental stochasticity, eco-evolutionary dynamics, animal personality, behavioural syndromes, correlational selection, plasticity, phenotypic integration, bet-hedging.

CONTENTS

I. INTRODUCTION

Understanding the evolution of life histories represents one of the biggest challenges in biology (Stearns, 1992; Roff, 2002). This is because life-history traits, such as reproductive rates and lifespan, feed directly back into the ecological dynamics of the populations within which those life histories evolve (see Sæther *et al.*, 2016 and references therein). The reciprocal nature of the ecological and evolutionary dynamics involved in life histories is therefore central to the problem of predicting and managing population changes, especially in the face of (human-induced) environmental change (Moritz & Agudo, 2013). For example, in fisheries the harvesting of larger older individuals not only reduces the population size, but it imposes selection favouring the evolution of smaller individuals that reproduce earlier in life (Law, 2000). Smaller faster-reproducing individuals will tend to respond differently to changes in population density as compared with the original larger slower reproducers, thereby potentially creating more volatile population dynamics and a greater probability of stochastic extinction as an unintended consequence of harvesting. The evolution of such *slow* versus *fast* life histories, or differences in the 'pace of life' (Ricklefs & Wikelski, 2002) arising *via* the fundamental trade-off between current *versus* future reproduction, depends critically upon their contrasting responses to increases in population density (Fig. 1). Individuals with fast rates of reproduction will do best in newly founded and low-density populations, but as populations increase in size and approach carrying capacity it is the slower-reproducing types that will instead be favoured because of their ability to resist the negative fitness effects of greater intra-specific competition.

These contrasting selective pressures generated by local demographic conditions have long been part of theoretical treatments of life-history evolution. In one of the earliest treatments, MacArthur (1962) and MacArthur & Wilson (1967) argued that high intrinsic (density-independent) rates of reproduction and short lifespans should be favoured in new or small populations (r-selection), whereas at large population sizes there should be density-dependent selection for competitive ability and resilience to any detrimental effects of high population densities, favouring life histories that increase the population carrying capacity (K-selection) (see Fig. 1D). In order for density-dependent selection to produce fast *versus* slow pace-of-life types, a negative trade-off is assumed to exist between intrinsic rates of reproduction (r_0) and the ability to cope with the negative effects of competition (γ) arising from increases in population density (Engen, Lande & Sæther, 2013; see Fig. 1D). It is important to note that density-dependent selection may *increase* the carrying capacity (K), as envisioned by MacArthur & Wilson's (1967) original theory. For example, K-selected types may avoid the costs of competition by being more efficient in their use of resources, more cooperative and resolving contests without recourse to costly fighting, and thus maintain larger populations at carrying capacity than would r-selected types (e.g. Duckworth, Belloni & Anderson, 2015). However, density-dependent selection could also *decrease* the carrying capacity (K), because the competitive advantage in contests to individuals that invest more in aggression, costly fighting and/or larger body sizes, etc. will result in less-efficient populations with lower carrying capacities (see Boyce, 1984; Mueller, 1997). Such density-dependent selection for individuals with larger body sizes for the purposes of contest competition then has important implications for the ecological differences observed among species due to allometric and metabolic scaling that drive many important biological processes shaping the pace of life in different species (see Marquet, Navarette & Castilla, 1995; West, Brown & Enquist, 1997; Brown *et al*., 2004; Banavar *et al*., 2010). Hence, many species with a slower pace of life tend to have smaller population sizes than those with a faster pace of life, despite existing in more stable populations closer to their carrying capacity (K), explicitly because density-dependent selection has favoured larger bodies that are more competitive under conditions of contest competition (Boyce, 1984). These arguments for density-dependent selection for efficiency and cooperation as opposed to the inefficiency of contest competition and larger body sizes are also not necessarily mutually exclusive, and phenotypic plasticity provides an obvious middle ground between the two. For example, plasticity in reproductive effort may efficiently reduce the costs of contest competition in years with high-density populations, but such plasticity is likely to come at a cost that is only worth paying if individuals also increase their somatic investment to achieve longer lifespans within which to carry out any deferred reproduction (see Section IV.1 below).

Despite criticisms of earlier versions of density-dependent selection in the form of r- *versus* K-selection theory (see Boyce, 1984; Stearns, 1992; Reznick, Bryant & Bashey, 2002), density-dependent regulation of natural populations appears to be ubiquitous (Brook & Bradshaw, 2006) and thus density-dependent selection must play a substantial role in the eco-evolutionary dynamics of life-history evolution (MacArthur, 1962; Charlesworth, 1994), whether it promotes greater social efficiency, increased plasticity, and/or increased contest-competitive ability in the form of increases in aggression and/or body size, etc. Likewise, despite the earlier and much-criticized simplistic categorization of species on an r/K continuum by Pianka (1970), it seems clear that the majority of life histories are amenable to characterization along a more general fast *versus* slow 'pace-of-life' continuum. For example, the pace-of-life continuum has now been confirmed as a major axis of phenotypic (co-)variation in key life-history traits (e.g. reproductive rate, lifespan, age of first reproduction, generation time) representing an important determinant for population dynamics in birds (Sæther, 1987; Sæther & Bakke, 2000), mammals (Gaillard *et al.*, 2005; Oli, 2004; Bielby *et al.*, 2007), fish (Goodwin *et al.*, 2006; Bjørkvoll *et al.*, 2012), reptiles (Bauwens & Diaz-Uriarte, 1997) and insects (Johansson, 2000), and more recently in plants (Adler *et al.*, 2014; Salguero *et al.*, 2015). Unfortunately, we currently lack a unified approach to the study of life-history variation that combines the eco-evolutionary dynamics of density-dependent selection with the multivariate evolution of these different life-history traits comprising the fast *versus* slow pace-of-life continuum observed among populations and species.

This brings us to the other major challenge in understanding life-history evolution, which is that it normally involves selection for suites of multiple coevolving traits, such as those implicated in comparative studies of a pace-of-life continuum (see above). Predicting the evolution of multiple co-varying traits within a population is complex (Armbruster *et al.*, 2014), because it necessarily involves the evolution of genetic correlations and integration of (developmental) plasticity across multiple traits (Lande, 1982; Lande & Arnold, 1983; Schlichting, 1989; Pigliucci & Preston, 2004). Such genetic and environmental sources of life-history trait (co-)variation within populations would appear to be crucial in explaining the specific trait combinations we observe in pace-of-life differences among species and populations, as well as any deviations from this single axis of life-history variation.

The first studies to consider such trait covariances beyond just life-history characters explored co-adaptations between life history and physiology in particular (Ricklefs & Wikelski, 2002). Such physiology and life-history comparisons identified 'slow' *versus* 'fast' populations and species according to immunological (see Tieleman, 2018) and metabolic traits linked to metabolic scaling (see Brown *et al*., 2004; Banavar *et al*., 2010). More recently, individual variation in the tempo of life histories (i.e. the pace of life within populations) has been linked to wider patterns of phenotypic covariance commonly observed across a wide range of physiological, morphological and behavioural traits, a phenomenon that has therefore been termed a 'pace-of-life syndrome' (POLS; Careau *et al*., 2008; Réale *et al*., 2010*b*; Dammhahn *et al*., 2018). The position of individuals within a population along the POLS continuum, from fast-reproducing short-lived, bold, aggressive types at one end to slow-reproducing long-lived, cautious, shy types at the other, appears to provide a general explanation for repeatable individual differences in behaviour ('animal personality') and their covariation as part of 'behavioural syndromes' (Réale *et al*., 2010*a*; Carere & Maestripieri, 2013). Behavioural ecologists have thus developed various models predicting the adaptive integration of life history, physiology, body condition, structural size, metabolism and behaviour as part of POLSs within single populations (see Biro & Stamps, 2010; Houston, 2010; Luttbeg & Sih, 2010; Salzmann *et al*., 2018). There is also clear evidence for this integration demonstrating that behaviourally 'fast' individuals are larger and have higher metabolic rates (e.g. Careau *et al*., 2008; Le Galliard *et al*., 2013; Niemelä & Dingemanse, 2017, and that such 'fast' types also have higher annual reproductive output (see Biro & Stamps, 2008; Smith & Blumstein, 2008). However, if such POLSs within populations are a product of the same processes that cause variation in pace of life among populations and species, we need to identify a general evolutionary mechanism that operates across a wide variety of ecological situations and taxa.

Heterogeneous or fluctuating selection in time or space has been suggested as a possible mechanism for maintaining phenotypic variation within populations (see Frank & Slatkin, 1990), and such processes have also been identified as possible causes of animal personalities (reviewed by Dingemanse & Réale, 2013). Fluctuating selection on life histories due to stochastic variation in population densities has the potential to provide an explanation for POLSs (e.g. Nicolaus *et al*., 2016). Environmental stochasticity and density dependence are general features of almost all biological systems and have eco-evolutionary consequences for life-history evolution (MacArthur, 1962; Tuljapurkar, 1990; Charlesworth, 1994; Tuljapurkar, Gaillard & Coulson, 2009). In low-density populations (i.e. those kept low by environmental stochasticity) the nature of density-dependent selection will differ from that in high-density populations (i.e. those allowed to grow due to less environmental stochasticity) (see Engen *et al*., 2013). Therefore, our contention is that variation from low to high density-dependent selection has the potential to explain much of the variation we see in the pace of life across populations and species, and that 'fluctuating density-dependent selection' caused by environmentally induced temporal variation in population density may explain the variation in life-history and other traits associated with POLSs within populations.

In making a detailed case for the role of fluctuating density-dependent selection on life-history evolution and the associated suite of co-varying traits in POLSs, this review brings together previously disparate approaches to the study of life histories from population ecology, behavioural ecology, quantitative genetics and evolutionary biology. Our aim is to promote the development of a unified eco-evolutionary framework for the effective study of life-history evolution in natural populations, and the persistence of individual differences across a wide range of phenotypic traits within these populations.

II. ADVANCES IN DENSITY-DEPENDENT SELECTION THEORY

Recent theoretical developments of MacArthur & Wilson's (1967) long-standing idea of *r*-*versus K*-selection have successfully incorporated stochastic environmentally induced variation in population size into models of the ecological and evolutionary dynamics along a single axis of life-history variation (Lande, Engen & Sæther, 2009, 2017; Engen *et al*., 2013; Engen & Sæther, 2016*a*,*b*). These studies confirm the prediction that density-independent rates of reproduction (r_0) should be maximized in small populations, but in larger populations r_0 should be traded off against the ability to reduce the negative density-dependent effects of intra-specific competition on reproduction (γ). Hence, at different population sizes life histories evolve the combination of values of r_0 and γ that best maximize Malthusian fitness (see Fig. 1D). A recent study on great tits (*Parus major*) has confirmed many of these predictions, showing that females laying the largest clutch sizes at small population sizes were also the ones that experienced the greatest density-dependent reductions in fitness at large population sizes (Sæther *et al*., 2016). As noted above, exactly how density-dependent selection mitigates the detrimental effects of intra-specific competition on fitness (i.e. the slope γ, see Fig. 1D) will depend upon the particular species and life history concerned. It is mostly likely to involve selection for increased contest-competitive ability in the form of a larger body size at the costs of greater somatic effort, extended parental care and a longer lifespan, and all of the allometric and metabolic scaling implications that this entails (Marquet *et al*., 1995; West *et al*., 1997; Brown *et al*., 2004; Banavar *et al*., 2010). However, density-dependent selection for increased social efficiency and plasticity may provide more efficient ways to mitigate some of the detrimental effects on fitness of high population densities (see Section IV.1 below, e.g. Duckworth *et al*., 2015).

Therefore, the suggestion here is that populations kept low by repeated stochastic environmental events represent conditions that favour fast types of individuals, because their high rates of reproduction at low population densities (r_0) allow them to contribute disproportionately to any population growth when it does happen. Conversely, high-density populations experiencing few such stochastic events end up approaching carrying capacity, where slow types are favoured because of their insensitivity to negative fitness effects of density-dependent intra-specific competition (low values of γ), thereby allowing them to contribute disproportionately more offspring to the next generation in dense populations. Contrasting regimes of stochasticity in population size should therefore lead to population-specific levels of low *versus* high fluctuating density-dependent selection, and thus to predictable variation in pace of life of life histories among populations and species.

The maximization of Malthusian fitness shown in Fig. 1D thus reflects the cumulative effect across generations of the trade-off between current *versus* future reproduction, which is manifest at the individual level as the trade-off between reproductive effort per breeding attempt *versus* lifespan (see Fig. 1A–C). In essence, slow types with their lower rates of reproduction per attempt achieve greater fitness than fast types at higher population densities because they live for longer and achieve a greater number of breeding attempts per lifetime under such competitive conditions. As suggested by the Sæther *et al*. (2016) example above, there might also be density-dependent effects on reproductive output per breeding attempt, which should disproportionately affect fast as compared with slow types (not shown for simplicity in Fig. 1A). It is these effects on lifespan and/or reproductive output that produce the negative relationship (i.e. the life-history trade-off) between high values of r_0 *versus* low values of γ, and represent a key assumption of density-dependent selection theory (Fig. 1D; Engen *et al*., 2013). Thus, investment by fast types in a high r_0 reflects investment in current over future reproduction, whilst investment by slow types in a low γ reflects investment in future over current reproduction and the kinds of competitive advantages that will insulate the individual from density-dependent effects on their reproduction and survival.

Based upon these arguments, we expect populations kept small and lacking intra-specific competition for resources due to high levels of environmental disruption, such as a series of severe winters and/or those in more generally stochastic environments, to contain more fast types with life histories emphasising current over future reproduction (towards the fast end of the POLS), because of low density-dependent selection (favouring high individual values of r_0 and γ, Fig. 1D). The larger fluctuations between relatively low *versus* relatively high density-dependent selection in such disrupted and more stochastically varying population densities may also result in greater within-population variation among different individual life histories – i.e. a greater range of coexisting pace-of-life types. By contrast, larger populations closer to carrying capacity (K) that, for example, experience only mild winters and less stochastic environmental conditions will be under consistently high density-dependent selection and thus characterized by slow types of life histories giving prominence to future over current reproduction (favouring low individual values of r_0 and low γ, Fig. 1D). These slow types of populations may also show less among-individual variation in life histories – i.e. a narrower range of coexisting pace-of-life types. The difference in pace of life among populations or species should thus reflect differences in average long-term local population dynamics (i.e. how far below carrying capacity the average population is), whereas the extent of within-population variation in the range of pace-of-life types should be indicative of the degree of fluctuating selection on life histories.

III. ANIMAL PERSONALITIES, SOCIAL BEHAVIOUR AND FREQUENCY DEPENDENCE

We suggest that fluctuating density-dependent selection in time and space arising from stochastic variation in population size may represent a key factor in generating within-population variation in the tempo of individual life histories. It is therefore the trade-off between r_0 versus γ, and thus also between current *versus* future reproduction, that could provide a root cause of POLSs and the phenotypic covariance commonly observed across a range of physiological, morphological and behavioural traits associated with life-history variation (see Réale *et al*., 2010*b*; Biro & Stamps, 2008; Smith & Blumstein, 2008; Dammhahn *et al*., 2018; Salzmann *et al*., 2018; Royauté *et al*., 2018). The fluctuating density-dependent selection framework presented above thus provides a general eco-evolutionary explanation for the repeatable individual differences in behaviour seen within populations, which we suggest arise as a result of the evolution of a POLS. It is important to note that our suggestion here is completely consistent with the recent theoretical treatments of 'adaptive' animal personality variation arising due to state dependence and asset protection (e.g. McElreath & Strimling, 2006; Wolf *et al*., 2007; Wolf, van Doorn & Weissing, 2008; Luttbeg & Sih, 2010; Wolf & Weissing, 2010; Dingemanse & Wolf, 2010; Sih *et al*., 2015). Indeed, the individual differences in behaviour produced by these models (e.g. boldness in foraging under threat of predation) only arise because of a pace of life trade-off that is assumed to exist between current *versus* future fitness. In addition, stochastic variation in population densities causing fluctuating density-dependent selection could provide a continuous ubiquitous source of individual variation in offspring state (e.g. *via* temporal or spatial variation in resources available to their parents), which has been suggested as a driving force behind the emergence of animal personality in such models.

Individuals from different positions within the POLS continuum are predicted to show characteristic patterns of morphology, physiology and behaviour, based upon their values of r_0 (density-independent reproduction) *versus* γ (the negative effects on fitness of increasing population density). For example, activity in open-field assays has been found to be positively related to dispersal (e.g. Dingemanse *et al*., 2003), as has sociability (e.g. Cote *et al*., 2009). This could be because such individuals possess adaptive combinations of high rates of activity, social aggression and dispersal (e.g. Duckworth & Badyaev, 2007). Such fast-type individuals with high intrinsic rates of reproduction (high r_0) benefit more from dispersal because this allows them to settle in low-density environments, where they can then do well. By contrast, dispersal is less useful for slow-reproducing, less-active and less-aggressive slow types that do well by staying in established populations because they experience fewer negative effects of increasing density on fitness (i.e. a low γ). The costs of suitable fast-type phenotypes for dispersal to lower density habitats will in turn drive various life-history trade-offs leading to syndrome-like covariation between dispersal and other life-history traits at the individual, population and species levels (Bonte *et al*., 2011; Clobert, 2012). Similarly, the commonly observed aggression–boldness syndrome (see Garamszegi, Marko & Herczeg, 2012) could well be a product of fast-type individuals (expecting high average mortality as a result of environmental stochasticity) having adaptively high levels of aggression and boldness in the face of predation threats (Abbey-Lee, Mathot & Dingemanse, 2016). Such fast types thus explore their environment more superficially and/or are less sensitive to environmental change, as compared with the less-aggressive, more-cautious, slower exploring slow types at the other end of the POLS continuum (Nicolaus *et al*., 2014). Therefore, the current animal personality literature already incorporates components consistent with the suggestion of POLSs and the notion that fluctuating density-dependent selection drives, and is in turn influenced by, repeatable individual differences in behaviour commonly found in naturally varying wild populations.

Thus far we have made an argument for behavioural phenotypic variation within the POLS simply being the result of fluctuating density-dependent selection among individuals. However, there are obviously other, non-mutually exclusive, evolutionary mechanisms that can generate behavioural variation among individuals within populations, such as frequency-dependent selection (Frank & Slatkin, 1990; Dingemanse & Réale, 2013). Indeed, gametheoretical predictions suggest that almost any intraspecific social interaction has the potential to result in negative frequency-dependent selection, which would then favour a mix of different types within a POLS (see Novak & Sigmund, 2004). Hence, it is negative frequency-dependent selection (sometimes instantiated *via* type-specific density dependence), rather than fluctuating selection, that is used to maintain among-individual variation in behaviour in almost all existing formal models of animal personalities, including those involving links to individual differences in life histories (Wolf *et al*., 2007, 2008; Wolf, van Doorn & Weissing, 2011; Wolf & McNamara, 2012). Within the POLS fluctuating density-dependent selection scenario we propose, frequency-dependent social effects could arise as an additional process from the mixes of specific types at the different population densities. For example, too many fast aggressive types from the fast end of the POLS might interact to their mutual detriment at higher population densities (e.g. Duckworth *et al*., 2015). Greater frequencies of extra-pair paternity are also seen in bird populations at higher population densities (Araya-Ajoy, Dingemanse & Kempenaers, 2016*a*), and it seems that it is the fast types that lose a greater share of their paternity (Duckworth, 2006; Araya-Ajoy *et al*., 2016*b*). Such processes will allow fast types to be more quickly replaced by slow types whenever intraspecific competition intensifies as the population density approaches carrying capacity. Such negative frequency-dependent selection has previously been suggested to explain the eco-evolutionary dynamics of small mammal population cycles (Chitty, 1960; Krebs, 2013). Conversely, we might predict positive frequency dependence amongst slow types at high population densities, if they are more phenotypically plastic (see Section IV.1 below) in terms of their social responsiveness (see Wolf *et al*., 2008, 2011), because this would allow slow types to mitigate the worst fitness effects of intraspecific competition when interacting with other slow types, but not fast types, in dense populations (e.g. improved coordination in social foraging or collective anti-predator behaviours; Giraldeau & Caraco, 2000). In line with this notion, in great tits slow explorers experience increased annual survival rates under high densities (Nicolaus *et al*., 2016), in bluebirds (*Sialia mexicana*) less-aggressive individuals have higher reproductive success at high population densities (Duckworth, 2006), and in common lizards (*Lacerta vivipara*) more-sociable individuals survive better at high population densities (Cote & Clobert, 2007; Cote, Dreiss & Clobert, 2008). We can therefore easily envisage fluctuating density-dependent selection on individual pace of life being supplemented by frequency-dependent selection on certain social behaviours at one or both ends of the POLS within populations.

Frequency dependence will affect the details of how density dependence impacts the population dynamics of the system (e.g. Mougeot *et al*., 2003), because we expect a dynamic interaction between density- and frequency-dependent fitness effects on POLSs within populations. Indeed, the ‘adaptive dynamics’ approach to the theoretical modelling of eco-evolutionary feedbacks is explicitly based upon the effects of density-dependent and frequency-dependent selection (see Waxman & Gavrilets, 2005). However, we currently lack life-history models involving frequency-dependent selection plus fluctuating density-dependent selection. Empirical evidence is also needed to identify the specific social behavioural mechanisms involved in any frequency dependence and to determine their generality across different systems. Without suitable mathematical treatments and more data on this topic, it is difficult at this stage to predict the role of frequency-dependent selection in further shaping POLSs within populations. We are primarily interested here in the possibility that variation in density-dependent selection in general explains the pace of life continuum observed among populations and species, and that fluctuating density-dependent selection specifically creates POLSs within populations. Therefore, we will now discuss further the implications of fluctuating density-dependent selection on POLS evolution at these different levels, for the moment without the additional complication of frequency-dependent selection within populations.

IV. LIFE-HISTORY VARIATION AND POLS COVARIATION AT DIFFERENT LEVELS

The theoretical framework presented here combines recent advances in density-dependent selection theory with behavioural research on animal personalities and POLSs to explain the continuum of fast to slow types within and among populations. Such phenotypic differences in types can result from genetic differences, from among-individual differences in development (irreversible plasticity), and/or from within-individual reversible plasticity in response to current conditions (i.e. the local population density in the case of density-dependent selection). This detail is important given the role of environmental stochasticity and fluctuating selection in density-dependent selection theory, because it is the time scale and predictability of these fluctuations that will determine whether or not the optimum life history can be tracked by evolutionary change in gene frequencies, and whether or not adaptive irreversible or reversible plasticity will evolve (Botero *et al.*, 2015; Tufto, 2015). In addition, even though our focus here is on phenotypic (co-)variances within the POLS, key evolutionary trade-offs in fast *versus* slow life histories, such as in survival *versus* reproduction or the number *versus* quality of young, are expected to involve genetic covariances (Partridge, 1992; Reznick, 1992). The assumption that individual phenotypic differences in life histories reflect underlying genetic variation and covariation (e.g. Hadfield *et al.*, 2007; Brommer, 2013) is called the 'phenotypic gambit' in behavioural ecology (Grafen, 1984) and 'Cheverud's conjecture' in evolutionary biology (Cheverud, 1988). Given that this key assumption may often not be valid (see Hadfield *et al.*, 2007; Dochtermann, 2011; Araya-Ajoy *et al.*, 2016*b*), it is nearly always important to distinguish between the genetic *versus* environmental sources of trait (co-)variation (Lande, 1979; Lande & Arnold, 1983).

As part of any discussion of POLS and the continuum from slow to fast pace-of-life types, it is therefore of interest to clearly distinguish between genetic (G) *versus* permanent environmental (PE, including developmental plasticity) or current environment (E) causes of the phenotypic variation (see Dingemanse *et al*., 2010; Niemelä & Dingemanse, 2017. PE effects are thus any among-individual differences (I) not attributable to additive genetic sources of variation. At first sight, the within-individual effects of E (i.e. reversible plasticity) might not seem important for the evolution of POLSs, which are based upon among-individual phenotypic differences. However, consistent individual differences in responsiveness to E (i.e. I×E, and hence possible PE×E and G×E effects) would imply that different 'types' of individuals differ in their levels of reversible plasticity, which adds an important aspect to any POLS (see Section IV.1 below).

In addition, Santostefano *et al*. (2017) demonstrate that in field crickets (*Gryllus bimaculatus*) the G *versus* PE correlations between life-history and behavioural traits involved in POLS operate in the opposite direction. Therefore, covariation among phenotypic traits in any POLS should also be decomposed into its different components, where it is usually quantified in symmetrical matrices with trait variances as diagonal elements and trait covariance as off-diagonal elements. The variance–covariance **D**-matrix captures among population/species POLSs, while the **P**-matrix describes the within-population POLS. As with the variances, the phenotypic **P**-matrix is often then decomposed into the genetic component **G**-matrix and a permanent environmental component **PE**-matrix, and when repeated measures for individuals exist, a within-individual component **E**-matrix describing the variance–covariances of different events (e.g. breeding attempts) within a lifetime. The **PE**-matrix thus includes effects of integrated developmental plasticity among lifetimes, whilst the **E**-matrix reflects integrated reversible plasticity in response to the current environment at different times within the lifetime. A last residual **R**-matrix describes any remaining trait variance–covariances, which is usually due to measurement error (but see Westneat, Wright & Dingemanse, 2015). In the following sections, we detail how variation in fluctuating density-dependent selection on the pace of life might lead to the trait variance–covariance observed along the POLS axis at these different levels of organization.

(1) Irreversible and reversible plasticity (PE- and E-matrix POLSs)

A crucial issue is the degree to which phenotypic plasticity in life histories is responsible for the existence of pace of life variation among populations or species, and POLSs within populations. Adaptively, it would make more sense under fluctuating density-dependent selection for individuals phenotypically to track any predictable variation in population size *via* developmental plasticity (Botero *et al*., 2015; Tufto, 2015). For example, population-density effects on offspring rearing conditions could be used by parents to create adaptive modifications in offspring development and their subsequent pace of life, provided that there is sufficient temporal autocorrelation in population sizes across generations to make any environmental effects predictable on the scale of more than an individual lifetime (West-Eberhard, 2003; Botero *et al*., 2015). In such cases, we therefore see that mean offspring life-history phenotypes will plastically track predictable variation in local population densities and/or resource availability (Stearns, 1992; Lindstrom, 1999; Beckerman *et al*., 2002). However, for many iteroparus species under fluctuating density-dependent selection, population densities may well vary substantially within lifetimes with little temporal autocorrelation (e.g. between breeding seasons). If this variation is sufficiently predictable, for example using environmental or social cues immediately prior to breeding, then we might expect adaptive reversible plasticity to evolve in individual reproductive effort across breeding attempts (Gabriel *et al*., 2005; Hämäläinen *et al*., 2017). In this way, occasionally harsh competitive conditions could be more effectively dealt with by more plastic types of individual *via* customized levels of reproduction per breeding attempt over a longer lifetime for which the costs of plasticity are worth paying (Fig. 2). A key question is therefore whether individuals are able to adjust phenotypic traits associated with different POLS types in order adaptively to match changes in environmental conditions, such as population density. For example, slower-exploring great tits survive better in years with higher population densities, but apparently this is not because of adaptive density-dependent plasticity, perhaps because population densities are difficult for the birds to predict in this system (Nicolaus *et al*., 2016). In such cases, observations therefore have to be made over a sufficient range of environmental conditions to distinguish plastic from non-plastic strategies, because when viewed under only benign conditions the life histories of non-plastic fast types and plastic slow types could appear the same (Fig. 2A, B; e.g. Hämäläinen *et al*., 2017).

Within-individual reversible plasticity in reproductive effort should result in a pace of life more similar to slow-type than fast-type individuals, both in the reproductive effort per breeding attempt and the number of breeding attempts per lifetime (Fig. 2). Indeed, the greater somatic investment in competitive abilities usually associated with longer density-dependent selected lifespans and a slow pace of life (e.g. small mammals; Chitty, 1960; Krebs, 2013) might also involve greater adaptive investment in the costs of plasticity, such as in the acquisition of information (e.g. about forthcoming competitive conditions) and in the ability to exhibit more plastic reproductive strategies. Plasticity is also more likely to be effective for slow-type individuals in populations with high density-dependent selection that on average experience more predictable and less stochastically variable environments. By contrast, in populations experiencing low density-dependent selection it would perhaps be more beneficial for fast types to be inflexible, save on the costs of plasticity and information gathering if most population variation is stochastic, and simply be fast reproducing all of the time given the rarity of any detrimental effects of density dependence that could be avoided using plasticity. Animals that have a short life span or a short remaining lifespan should be generally less likely to be plastic or to use learning (Kokko & Sutherland, 2001). For example, more-aggressive male great tits tend to be consistently less plastic (Araya-Ajoy & Dingemanse 2017). Therefore, within a single population POLS, fast non-plastic types will have been selected for at times and in places where environmental stochasticity made those low population densities more variable but less predictable. By contrast, slow plastic types will have been selected for when and where high population densities varied less but any variation was more predictable and thus favoured the evolution of reversible plasticity. Interestingly, these expected differences in plasticity between fast *versus* slow types within a POLS correspond very well with observations published in the animal personality literature, because among-individual differences in behaviour appear to be associated with individual differences in plasticity (Mathot *et al*., 2012). For example, more-aggressive individuals tend to be less socially responsive to the levels of aggression in others (see Koolhaas *et al*., 1999), and slow-exploring great tits better match their clutch size to local environmental conditions in the wild (Nicolaus *et al*., 2014). Fast types within a POLS may therefore not only be more active and aggressive and disperse further, but they should also be more proactive superficial explorers and less phenotypically plastic in response to physical and social environmental change (e.g. Duckworth & Badyaev, 2007; Nicolaus *et al*., 2014). This is in contrast to more phenotypically flexible and faster learning slow types that gather more information from more detailed exploration of their more predictable environments, as well as being less aggressive and more socially responsive in their interactions with conspecifics (Sih & Del Giudice, 2012; Mathot *et al*., 2012; Nicolaus *et al*., 2014). We therefore have good reason to expect a greater role for adaptive within-individual phenotypic plasticity in life histories (e.g. in response to local population densities) towards the slow-type end of any POLS.

Any POLS generated in whole or in part by phenotypic plasticity will necessarily involve multiple traits that co-vary together so that each of them is more-or-less aligned with the major POLS axis of phenotypic variation. We therefore expect any irreversible or reversible plasticity to be integrated across traits (i.e. 'integration of plasticity' *sensu* Schlichting, 1989) in order to produce a coherent and functional phenotype. The **PE**-matrix and **E**-matrix should therefore describe similar variance–covariance patterns of these integrated POLS phenotypic responses to any predictable environmental variation at different temporal scales. The phenotypic plasticity and its integration in response to environmental variation in population density can therefore be quantified, both in terms of irreversibly plastic traits (e.g. body size) and reversibly plastic traits (e.g. clutch size, behaviour) (Nicolaus *et al*., 2013, 2016). In this way, we can determine the part played by genetic *versus* environmental sources in life-history variation, and thus the role of integrated plasticity in creating and structuring the POLS. As detailed in Section IV.3 below, our arguments here predict that the direction of the major axis of trait (co-)variation will be similar for both the different genetic (**G**-matrix) and the environmental (**PE**- and **E**-matrix) sources of phenotypic variance and covariance (both among and within individuals), largely reflecting the adaptive alignment of the POLS axis with the orientation of fluctuating density-dependent selection.

Following the arguments above for greater individual plasticity at the slower end of the POLS, we might also expect that integrated irreversible and/or reversible plasticity explains a higher proportion of life-history (co-)variation in populations or species with a history of high (as opposed to low) density-dependent selection in their pace of life. This prevalence of plasticity might explain the low heritabilities recorded for many life-history traits (e.g. clutch size and laying date in birds; Stirling, Réale & Roff, 2002), and we would predict that this lack of heritability is more prevalent for life-history traits in slow types and in populations or species that have experienced high density-dependent selection. We therefore need studies that compare population-specific levels of additive genetic *versus* phenotypic (co-)variance caused by irreversible (i.e. developmental) or reversible plasticity in different aspects of life histories. In this way, the degree of plasticity within the POLS for different populations or species can be compared against the degree of low *versus* high density-dependent selection. Such plasticity in life histories can also have consequences for the eco-evolutionary dynamics of the system (e.g. Benton & Beckerman, 2005). More stable populations should become even more stable as a result of high density-dependent selection for greater integrated plasticity, because any density-dependent adjustments by slow pace-of-life individuals will occur *via* plasticity in reproductive effort (Fig. 2). Conversely, more environmentally unstable populations that give rise to greater selection for a faster pace of life might be expected to be regulated more by mortality of fast pace-of-life individuals, which will further contribute to the demographic instability of the system. These contrasting patterns should also be seen within populations at the different ends of the POLS, but it is only among populations or species that we might expect to see such eco-evolutionary feedbacks that exaggerate the effects of low *versus* high density-dependent selection.

(2) Bet-hedging (a special case of a PE-matrix POLS)

Over evolutionary time, we predict that stochastic environmental effects on population density will produce population- and species-specific patterns of fluctuating density-dependent selection that shape life-history evolution in the form of the pace of life, with or without irreversible and reversible plasticity playing a role. However, we might also expect additional life-history adaptations to the immediate and detrimental effects of such stochastic events on fitness in the form of bet-hedging (see Simons, 2011; Starrfelt & Kokko, 2012). The most commonly discussed form of bet-hedging is a strategy of 'diversification' that spreads the risk of a catastrophic loss of fitness due to unpredictable events in a single environment by producing (random developmental) phenotypic variation in offspring so that they occupy different environments in time and/or space (e.g. within-family phenotypic variation in timing of seed germination in plants; Simons & Johnston, 2006). However, there are also 'conservative' bet-hedging strategies that provide protection and insure against unpredictable loss within any single environment (e.g. early diapause in copepods in case of unpredictably early onset of seasonal fish predation; Hairston & Munns, 1984). In essence, bet-hedging involves any number of a range of phenotypic strategies that achieve an adaptive reduction of fitness variation among individuals or generations in order to maximize long-term geometric mean fitness. It should be noted that this is exactly what is achieved by using Malthusian fitness in Fig. 1D and formal models of fluctuating density-dependent selection (e.g. Engen *et al*., 2013), because the continuous time measure of genotype Malthusian fitness is the equivalent of log[W] when measured in discrete time (under the assumption of weak selection), where W is arithmetic mean fitness (Crow & Kimura, 1970; Orr, 2009). So, the arguments above for the evolution of individual values for density-independent reproduction (r_0) and the slope of the negative effects of population density on fitness (γ) in the face of stochastic population variation involve the maximization of the appropriate measure of geometric mean fitness that is negatively affected by stochastic variation in fitness.

The point here is that bet-hedging theory leads us to expect additional adaptive modification of life-history traits within the POLS driven by the stochasticity of fluctuating density-dependent selection that would strategically further reduce fitness variance in ways beyond simply optimizing values of r_0 and γ (Fig. 1D). For example, the threat of extinction in small populations may be expected to promote diversification bet-hedging in fast-type individuals, perhaps in the form of greater and more varied rates of dispersal within families, if there is sufficient spatial variation in stochastic environmental events. Conversely, minor stochastic variation in larger more stable populations may favour conservative bet-hedging in slow-type individuals (e.g. ‘sub-optimal’ clutch sizes in birds; Boyce & Perrins, 1987), because more cautious reproduction and even longer lifespans enable lineages to withstand more easily the worst effects of temporal variation in stochastic environmental events. Therefore, contrasting regimes of environmental stochasticity should not only affect mean population sizes and thus the nature of density-dependent selection (Fig. 1D), but they should also result in the differential evolution of diversification and/or conservative bet-hedging strategies that maximize overall Malthusian fitness in each type of population.

Perhaps of more general interest here is the possibility that adaptive diversification bet-hedging might play a role in the generation of individual phenotypic life-history variation along the POLS. Unpredictable fluctuations in population sizes and thus low *versus* high density-dependent selection could be met by individual parents creating a range of fast *versus* slow offspring phenotypes with the aim of at least some of them always being suitable for the prevailing conditions in the next generation. We might also expect greater levels of diversification bet-hedging and a larger range of fast *versus* slow offspring phenotypes to be produced per parent in more stochastically fluctuating populations, where offspring might experience a wider range of possible environmental conditions as adults. The required level of within-parent variation in offspring phenotypes could be achieved by varying the resources provided to different offspring during development (e.g. food intake during development *via* brood hierarchies in birds). Adaptive individual strategies of asset-protection could then maintain these repeatable phenotypic differences among offspring throughout their lifetimes (*sensu* Luttbeg & Sih, 2010). One consequence here would be that POLSs will not necessarily involve sizable systematic genetic differences between fast *versus* slow phenotypes within the same population. This is because selection for diversification bet-hedging has the potential to generate much of the phenotypic variation between fast *versus* slow types *via* developmental (i.e. PE) effects within families. Indeed, one consistent result from studies of animal personality is that as much as half of the individual variation we see in behaviours appears to come from PE effects (see Dochtermann, Schwab & Sih, 2015), and this proportion can increase even further when behaviours are measured in the wild (e.g. Nicolaus *et al*., 2012). Therefore, much of the POLS phenotypic variation observed within populations may be the result of integration of developmental plasticity across the different traits due to adaptive diversification bet-hedging producing individually variable life histories, as opposed to evolved genetic differences in those life histories within populations.

Fig. 3 shows in more detail exactly how randomly fluctuating selection for different trait values affects the shape of the overall arithmetic and geometric mean fitness functions. Diversification bet-hedging in POLSs is thus an adaptive response that allows a genotype's range of phenotypes to follow the broad peak or ridge in arithmetic mean fitness experienced per generation as a result of fluctuating density-dependent selection (Fig. 3). Environmental (PE) phenotypic variation introduced *via* development into life-history trait values would allow a diversification bet-hedging genotype to occupy at least one of the many possible fitness peaks experienced per generation and thus avoid extinction in the long term (Bull, 1987). Fig. 3 also suggests that spatially varying selection results in a broad peak or ridge in (arithmetic mean) fitness experienced by a genotype (or a whole population) when spread across a range of different environments at any one moment in time. This is because whilst fitness accumulates multiplicatively over time (i.e. geometrically – see above), it combines additively across space (Levins, 1962). Hence, spatially varying selection on pace of life would favour diversification bet-hedging in the form of even greater rates of dispersal beyond the individually adaptive optimum (*sensu* Delgado, Ratikainen & Kokko, 2011). Instead of the bet-hedging genotype spreading its individuals out among different phenotypes, by increasing rates of dispersal in random directions and distances it spreads its individuals out among different environments thereby reducing individual fitness variation and thus maximizing long-term geometric mean fitness.

(3) Evolution of genetic (co-)variation (G-matrix POLSs)

While fluctuating density-dependent selection has the potential to generate a POLS *via* adaptive plasticity or *via* increased phenotypic variation due to diversification bet hedging (see above), the expected effect of fluctuating selection in increasing genetic variation along a POLS is less clear. In general, stronger stabilizing selection selects for lower phenotypic and genetic variance in a trait (Layzer, 1980; Lande & Arnold, 1983). However, additive genetic variance can increase, decrease or be left unchanged by fluctuating selection, depending upon its periodicity and amplitude, the shape of the fitness function and the effect sizes of underlying loci (Bürger, 1999; Bürger & Gimelfarb, 2002; Le Rouzic, Alvarez-Castro & Hansen, 2013). Interestingly, for a Gaussian-shaped fitness function there should be no effect at all of fluctuating selection on the selection experienced by the population and therefore on the amount of additive genetic variance in the population (see Fig. 3). The results in Fig. 3 are derived using non-overlapping generations, whilst fluctuating selection in combination with overlapping generations generally selects for increased genetic variation (Ellner & Hairston, 1994).

The actual relationship between patterns of selection and changes in genetic variation is, however, likely to be even more complex since it also depends upon the particular genetic architecture (Bürger, 2000; Hermisson, Hansen & Wagner, 2003; Carter, Hermisson & Hansen, 2005). In fact, models that include non-additive (epistatic) genetic effects show that increasing levels of fluctuating selection lead to increasingly de-canalized genotypes (i.e. larger mutational effects due to less canalizing epistasis), and hence to increased additive genetic variance (Kawecki, 2000; Le Rouzic *et al*., 2013). Interestingly, Le Rouzic *et al.* (2013) do not interpret this increase in genetic variance as an adaptation to fluctuating environments, even when it is favourable for the population in terms of greater evolvability along the line of the fluctuations in selection. Instead, they interpret the fluctuations as a disruptive force on normally adaptive genetic canalization that arises from stabilizing selection towards the peak of a stationary fitness function. In an artificial selection experiment over 20 generations, Pélabon *et al.* (2010) showed that both stabilizing and fluctuating selection slightly decreased genetic variation relative to control populations. However, because we do not expect genetic canalization to evolve on the timescales of such artificial selection experiments this is could still be seen as consistent with theoretical predictions. Therefore, we expect long-term fluctuating density-dependent selection to result in the genetic de-canalization of life-history traits, and it is this process that would create the expected major axis of genetic (co-)variation along the POLS in multivariate trait space, as illustrated in Fig.4. Again, this process is predicted to be greater in fast-type populations that have experienced greater long-term stochastic fluctuations in population density, and we might therefore expect greater genetic variance along POLSs in fast-type populations or species.

An important consideration for the types of comparisons in Fig. 4 at the within-population level is that genetic correlations among life-history traits due to trade-offs can often be masked at the phenotypic level because individuals differ in resource acquisition (van Noordwijk & de Jong, 1986; Houle, 1991; Stearns, 1992; Reznick, Nunney & Tessier, 2000). The predicted among-individual covariation between r_0 and γ or other pairs of life-history traits underlying the POLS (see Fig. 4), might therefore only be apparent once individual differences in resource acquisition have been statistically controlled [e.g. Santostefano *et al.* (2017) in the context of POLS research]. For example, it might be possible to use within-population variation in lifetime reproductive success (*LRS*) as a proxy for individual resource acquisition. Among species (see below, Fig. 5), however, this second axis of variation is less of an issue, as we expect differences in resource acquisition to be minimal at the species level. Wagner (1996) suggested that pleiotropic links between functional traits evolve through a combination of fluctuating directional selection and stabilizing selection in order to accommodate the independent evolution of each trait combination or 'module'. This verbal model suggests the evolution of pleiotropy within a POLS module composed of all the traits affected by fluctuating low *versus* high density-dependent selection. From this, we expect the **G**-matrix to reflect this pleiotropy as a high degree of genetic covariance in multivariate trait space (Fig. 4). Following the arguments above regarding plasticity, we might also expect a greater role for pleiotropy as captured by the **G**-matrix towards the fast-type end of any POLS within populations, and thus genetic (co)variance to play more of a role in POLSs in more fast-type populations as a whole. This is because of the relatively greater role predicted for integrated plasticity and the **PE**- and **E**-matrices towards the slow-type end of any POLS within and among populations or species. As Fig. 4 illustrates, we expect high genetic and phenotypic variation along the ridge in arithmetic mean fitness created by fluctuating density-dependent selection. The genetic variation generated by fluctuating density-dependent selection, plus any phenotypic plasticity and diversification bet-hedging (see Section IV.2), is expected to facilitate rapid and adaptively coordinated changes along the POLS major axis in life-history trait co-variation within and among populations and/or species (Figs 4 & 5). However, only in the case of POLS driven by plasticity and diversification bet-hedging (see Sections IV.1 and IV.2 above) could the increased speed of this phenotypic change be considered 'adaptive' at the individual level (*sensu* Le Rouzic *et al*., 2013).

(4) Evolution among species/populations (the D-matrix POLS)

The POLS fluctuating density-dependent selection hypothesis further predicts that phenotypic and genetic variation among populations (or species) will be arranged according to the distribution of fitness peaks for the different populations along this same major axis of fluctuating low *versus* high density-dependent selection. Variation in the nature of density-dependent selection among populations or species will create a distribution of fitness peaks along a line (not necessarily linear) in multivariate trait space, because populations/species will differ in their optimum combinations of r_0 and γ, and therefore in trait means that are favoured depending on their average level of low *versus* high density-dependent selection (Fig. 5). Population or species means will evolve towards these optima and thereby create a pace of life axis of variation among populations/species along this dimension (Fig. 5), thus explaining the results of the many comparative studies showing a pace-of-life continuum for various taxa [birds (Sæther, 1987; Sæther & Bakke, 2000), mammals (Gaillard *et al*., 2005; Oli, 2004; Bielby *et al*., 2007), fish (Goodwin *et al*., 2006; Bjørkvoll *et al*., 2012), reptiles (Bauwens & Diaz-Uriarte, 1997), insects (Johansson, 2000) and plants (Adler *et al*., 2014; Salguero-Gómez *et al*., 2015)]. Increased genetic variation along the pace-of-life axis due to fluctuating selection (see above) would facilitate such among-population divergence. In effect, we would expect a generally similar alignment of the pace-of-life continuum among species/populations to the POLS axes at the within-population level. However, on shorter timescales any POLS evolution within populations and any population divergence will be strongly affected by the specific pattern of genetic variances and covariances in the **G**-matrix (Lande, 1979; Schluter, 1996; Bolstad *et al*., 2014).

Different populations (or species) at different places along a pace-of-life continuum should also experience different patterns in eco-evolutionary feedbacks. For fast-type populations or species with high intrinsic rates of reproduction (r_0) there will be consequences of any predicted greater rates of dispersal. Assuming for simplicity that such dispersal is essentially random and undirected, and does not involve habitat matching (*sensu* Edelaar, Siepielski & Clobert, 2008), meta-populations (such as that illustrated in Fig. 5) containing greater proportions of fast-type sub-populations might be expected to be more connected genetically and demographically in space, but any local adaptation at the sub-population level will be slowed by the degree of spatial variation in selection pressures. Conversely, the meta-population dynamic feedbacks for collections of slow-type sub-populations will be reduced in scale by lower rates of dispersal in favour of reproductive plasticity and the strategy of waiting until conditions improve, facilitated by potentially longer lifespans. Meta-populations containing more of the less-dispersive slow types may therefore be less connected genetically and demographically in space, and so should evolve faster to their local optima (in plasticities as well as mean character values) due also to the dampening of random temporal fluctuations in population sizes and selection pressures *via* greater phenotypic plasticity, conservative bet-hedging and more cooperative social structures.

V. TESTING THE PREDICTIONS

The arguments made above have been accompanied in most cases by a considerable amount of circumstantial evidence from a range of fields in support of the idea that fluctuating density-dependent selection is responsible for generating the POLSs we observe within and among populations/species. However, relatively few studies have yet directly to address the types of research questions that critically test the main ideas presented herein. For example, there is very little literature assessing whether the behavioural or physiological position of fast- *versus* slow-type individuals along a POLS is linked with the kinds of negative effects experienced in density-dependent competition (i.e. γ). Three studies (cited repeatedly above) are extremely relevant here because they have most clearly investigated this question using observational data from wild populations of bluebirds (Duckworth, 2006, 2008; Duckworth &

Badyaev, 2007; Duckworth & Kruuk, 2009; Duckworth *et al*., 2015) and great tits (Nicolaus *et al*., 2013, 2014, 2016; Araya-Ajoy *et al*., 2016*a*,*b*) or experimental manipulations under semi-wild conditions of common lizards (Cote & Clobert, 2007; Cote *et al*., 2008). Specifically, the notion that sociable individuals do best under high densities because they are more socially responsive and efficiently cooperative is implied by the results from bluebirds (Duckworth *et al*., 2015). This model system also provides some of the best evidence that aggressive individuals are more dispersive, do best in low-density environments but do very poorly in high-density environments, because they are poor parents that are easily outcompeted by unaggressive phenotypes (Duckworth, 2006, 2008; Duckworth & Badyaev, 2007; Duckworth & Kruuk, 2009; Duckworth *et al*., 2015). As predicted, slow less-aggressive types of great tits explore their environment more slowly and are therefore more plastic and sensitive to environmental conditions when adjusting their clutch size in the wild (Nicolaus *et al*., 2013, 2014). These slow explorers also experience increased annual survival rates under high densities (Nicolaus *et al*., 2016), whilst aggressive fast-type males lose more paternity when competition for extra-pair paternity increases in high-density populations (Araya-Ajoy *et al*., 2016*a*,*b*). In addition, Cote & Clobert (2007), and Cote *et al*. (2008) show that 'social' common lizards that like to be with others (as opposed to 'asocial' individuals that prefer being alone) are favoured (*via* survival selection) under high (*versus* low) population densities, and that these types also prefer to disperse into high- (*versus* low-)density populations. All of which suggests that when we do have access to information concerning density-dependent selection on suites of relevant traits they seem to conform to the predictions of the fluctuating density-dependent selection POLS hypothesis.

The main aim of this review is to encourage further studies of this type and more specifically into the role of fluctuating density-dependent selection in generating POLSs by outlining this specific hypothesis, its various predictions and the methods that could be used to assess them critically. Table 1 outlines a series of falsifiable predictions arising from the hypothesis that fluctuating density-dependent selection drives the evolution of POLSs within populations and pace-of-life continuums among species. We now provide an overview of methods that can be used to test critically several of these predictions.

Our main prediction is that the variation in trait optima caused by variation in low *versus* high density-dependent selection within or among populations and species will have generated an axis in trait space with large amounts of variation at all levels (Table 1). To test this prediction, we first need to identify the axis in trait space where we expect increased variation due to greater variation in density-dependent selection. Second, we need to measure the variation along this axis and compare it to other axes of trait variation. The axis of interest is the direction in multivariate trait space from the optimal phenotype under selection for fast types to the optimal phenotype under selection for slow types given by

$$\Delta\theta = \theta_K - \theta_r$$

where $\theta_K = [z_1, z_2, \ldots, z_n]$ is a vector of trait values optimal at the slow end of the POLS axis, and θ_r is an optimal trait vector at the fast end of the POLS axis.

Among populations and species, optimal trait values can be found by using the ‘optimal regression’ (Hansen, Pienaar & Orzack, 2008) with differences among taxa in the nature of density-dependent selection as the explanatory variable, or by using standard linear regression (if there is little phylogenetic signal in the residuals). Differences among taxa in the nature of density-dependent selection can be quantified by using their mean population size relative to *K* (carrying capacity). However, accurate estimates of *K* are often lacking, particularly for taxa with low population densities (i.e. that are further from *K*) and thus under low density-independent selection for fast types. In such cases, we suggest that the relative scale of any stochastic fluctuations in population size can be used as a proxy measure of the nature of density-dependent selection from low to high, because populations with more or greater fluctuations will be subjected to more low density-dependent selection (Engen *et al.*, 2013). For POLSs within populations, there are numerous statistical methods for finding optimal trait values using fitness regressions (e.g. Lande & Arnold, 1983; Schluter, 1988; Morrissey, 2014; Chevin, Visser & Tufto, 2015). These methods have to be carried out at a range of different population densities, or modified to include an interaction between population density and trait values, to estimate optimal trait values at different population densities (e.g. the elegant statistical method to estimate optimal clutch sizes as a function of population density in great tits used by Sæther *et al.*, 2016). However, in many systems it may prove challenging to identify optimal trait values using the methods cited above, particularly for a high number of traits. Hence, a comparative method using 'optimal regression' among populations may be more powerful for obtaining $\Delta\theta$. This seems to be a good substitute, but requires the critical assumption that the distribution of optima created by fluctuations from low to high density-dependent selection within populations and the differences in average level of density-dependent selection among populations are aligned, as predicted by our POLS fluctuating density-dependent selection hypothesis, or that any heterogeneity among populations needs to be estimated as part of the model and taken into account.

Once a direction of optimum variation ($\Delta\theta$) is established, we can estimate the amount of variance in this direction as part of any variance–covariance matrix and compare its magnitude to the variance in other directions (e.g. minimum, maximum, and mean variance) using the method proposed by Hansen & Houle (2008). These analyses can be performed using available software like the *evolvability* R-package (Bolstad *et al.*, 2014). This can be carried out on variance–covariance matrices describing variation at all the different levels discussed here (**D**, **P**, **G**, **PE**, and **E**), and in this way the level of variation due to $\Delta\theta$ and fluctuating density-dependent selection can be compared relative to other directions among these matrices.

A second prediction is that phenotypic variation along the POLS axis is expected to be lower in more slow-type populations or species compared with more fast-type ones, due to differences in the scale of stochastic fluctuations in population density (Table 1). In other words, the POLS is expected to be more pronounced in fast- than slow-type populations or species. This prediction can be tested by comparing the variances along $\Delta\theta$ in **P**-matrices among populations/species experiencing different levels of density-dependent selection. One issue here concerns the contribution of differences in genetic *versus* environmental variation to this effect among population or species, because it is often difficult to know the rate of evolution for **G**, **P**, **PE** or **E** matrices. This effect might therefore only be apparent in cases of long-term evolutionary differences in low *versus* high density-dependent selection among populations or species (see Section IV.3 above). Therefore, comparisons of populations within the same species may not provide the predicted patterns if the populations are likely to have shifted relatively recently between different regimes of low *versus* high density-dependent selection differing in background levels of environmental stochasticity.

A third prediction is that POLS fast-type individuals will have higher r_0 values and higher γ values compared with slow-type individuals from within the same population (Table 1). We already know that behaviourally fast types tend to show greater reproductive output per breeding attempt, presumably reflecting higher r_0 values (Biro & Stamps, 2008; Smith & Blumstein, 2008). However, the link between r_0 values and the corresponding γ values is less often quantified (but see the three main example systems discussed above). This can be tested using the same regression techniques as above, and by including an interaction term among trait values and population density. This is because each trait value combination will be associated with a particular r_0 and γ in such a model, and the optimal trait values at low and high population densities will also be apparent. Sæther *et al.* (2016) confirmed this prediction in that fast-type female great tits laying large clutch sizes had higher r_0 and a subsequently higher γ. In systems where it is possible to collect repeated measures of reproductive success, individual estimates of r_0 and γ will be possible to obtain. One can then statistically decompose variation in r_0 and γ into the respective **G-**, **PE-** and **E-**matrices, and then investigate the relationship between different life-history, behavioural, physiological and morphological traits and r_0 and γ at these different levels using path analyses (see Fig. 6). Because of the trade-off between r_0 and γ, we expect these different traits to contribute in the opposite direction to r_0 than γ (i.e. a negative effect on one and a positive effect on the other; see Fig. 6). Again, because of individual differences in resource acquisition, this trade-off may be masked unless variation in resources can be controlled – see above (van Noordwijk & de Jong, 1986; Houle, 1991; Stearns, 1992; Reznick *et al.*, 2000).

VI. CONCLUSIONS

(1) We argue that observed patterns of variation in fast *versus* slow life histories within and among species are the result of fluctuations in low *versus* high density-dependent selection. Such patterns of selection in turn cause a particular pattern of covariation, or pace-of-life syndrome (POLS), involving covariances among life history, morphological, physiological and behavioural traits. POLSs are expected at different levels of the demographic hierarchy: among species, among populations within species, and among (geno)types or individuals within populations.

(2) Species and populations experiencing higher levels of stochastic variation in population densities and lower density-dependence should evolve a faster pace of life in order to maximize Malthusian fitness. Threat of extinction in such small fast-type populations may

also favour diversification bet-hedging in the form of increased dispersal, ensuring genotype survival by spreading offspring out among different environments.

(3) Among and within species and populations, the orientation of the major axis of phenotypic (co-)variation (the POLS) is predicted to align with the multivariate fitness landscape created by stochastic fluctuations in population density and low *versus* high density-dependent selection.

(4) Within populations, POLSs are expected to reflect genetic differences in life histories, as they do among populations or species. However, POLS within populations could also result from the integration of developmental plasticity producing adaptive variation in individual life histories in response to both predictable and unpredictable variation in population densities.

(5) Within individual lifetimes, predictable variation in population densities should result in adaptive reversible plasticity in individual density-dependent reproductive expenditure during different breeding attempts. Such integrated reversible plasticity in multiple traits will thus move individuals around during their lifetime within the POLS. This phenomenon of a POLS driven by within-individual phenotypic variation is expected to be more prevalent at the slow-selected end of the POLS and in species with a slow pace of life, where investment in the costs of plasticity and acquisition of information is expected to be of more use during longer lifespans spent in more predictable environments.

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874

875 **Table 1.** A list of falsifiable predictions arising from the fluctuating density-dependent 876 selection pace-of-life syndrome (POLS) framework for the evolution of life histories and 877 associated phenotypic traits, and the section(s) within which they are discussed in this 878 review.

Predictions	Section
1. A major fast–slow axis of variation in life histories and associated traits within and among populations/species will align with fluctuations in the nature of density-dependent selection	Bet-hedging, **PE**- & **E**-matrix, **G**-matrix POLS, Fig. 4 **D**-matrix POLS, Fig. 5
2. Greater phenotypic (and perhaps genotypic) variation along the POLS axis in fast-type populations/species compared with slow-type populations	Bet-hedging, **PE**- & **E**-matrix **G**-matrix POLS, Fig. 4
3. Fast-type individuals and populations/species will have higher r_0 values and higher γ values compared with slow types	Bet-hedging, **PE**- & **E**-matrix, **G**-matrix POLS, Fig. 4 **D**-matrix POLS, Fig. 5
4. Greater plasticity within individuals/populations/species towards the slow-type end of any POLS, but a greater role for genetic pleiotropy towards the fast-type end	**PE**- & **E**-matrix, Fig. 3 **G**-matrix POLS, Fig. 4
5. More diversification bet-hedging in the form of dispersal in fast types, but more conservative bet-hedging (e.g. 'sub-optimal' clutch sizes in birds) in slow types	Bet-hedging **PE**-matrix
6. Greater connectivity and less population stability within fast-type meta-populations, more population stability from plasticity and more local adaptation in slow-type ones	**PE**- & **E**-matrix **D**-matrix POLS

Figure Legends

Fig. 1. A simple hypothetical representation of a pace-of-life continuum in life-history variation across species or populations. In (A) reproductive rates (e.g. per breeding attempt) decline in all types more-or-less equally (for simplicity) with population density (N); with (B) subsequent negative effects on lifespan of these different type-specific reproductive rates mediated by differential effects of N; and (C) the resultant pace of life (POL) negative trade-off between (current) reproductive rate and (future) lifespan. Predicted lines are shown for fast (orange), medium (brown) and slow (green) types, with coloured circles indicating phenotypic values (filled to indicate values of highest fitness). In (D) Malthusian fitness is shown as a function of N for only the fast-selected and slow-selected types. Fast types have higher intrinsic reproduction (high r_0), but suffer from more density-dependent effects (γ_{fast}), giving them greater fitness (r_0-γN) at lower mean population densities (μ_{low}). Slow types have lower intrinsic reproduction (low r_0), but fewer density-dependent effects (γ_{slow}), giving them higher total fitness at higher mean population densities (μ_{high}) closer to the population carrying capacity (K). See text for further explanation and Engen *et al.* (2013).

Fig. 2. Reversibly plastic individual phenotypes (in purple) introduced into a simple within-population version of the hypothetical among species or population pace of life representation in Fig. 1A–C, showing: (A) reproductive rates (e.g. per breeding attempt) with an optimal plastic response to population density (N) and reproduction uniformly decreased by costs of plasticity (red arrows – note that in this particular scenario energetic costs of plasticity simply decrease reproduction and are scaled to provide no overall fitness advantage over non-plastic life histories); (B) lifespan differences and the lack of an effect of N on plastic types due to their perfectly adjusted reproductive effort per attempt; and (C) the pace of life (POL) negative trade-off between lifespan *versus* reproductive rate at the mean population density

(μ). Predicted lines are shown for fast (orange), plastic (dashed purple) and slow (green) types (i.e. three different genotypes or classes of individual sharing the same life-history phenotype), with points indicating mean values along what would actually be a pace-of-life continuum. See text for further explanation.

Fig. 3 Illustrations of fluctuating Gaussian selection (in black) on hypothetical trait values, and the resulting arithmetic (in red) and geometric (in blue) mean fitness functions for non-overlapping generations. The top panels show examples with more widely spaced fluctuations. Patterns in absolute fitness are shown on the left and relative fitness on the right. While both the maximum and width of the arithmetic mean fitness function are affected by the fluctuations, only the maximum absolute geometric mean fitness is affected. The width of the geometric mean fitness function (in blue) is the same as the fluctuating fitness functions themselves (in black). Therefore, the relative geometric mean fitness function (scaled by maximum fitness) is exactly equal to the fluctuating fitness function itself.

Fig. 4 Illustration of covariation and correlated selection between two of the expected multiple life history (morphological, physiological or behavioural) traits ($\mathbf{z}_1$ and $\mathbf{z}_2$), which could also represent r_0 and γ from Fig. 1D. (A) Fluctuations in the position of Gaussian fitness surfaces (grey) create a ridge of arithmetic mean fitness surface (red), but do not affect the geometric mean fitness surface (blue) – see Fig. 3 – producing a potential pace-of-life syndrome (POLS) dashed two-headed arrow varying from fast types resulting from low density-dependent selection (orange) to slow types resulting from high density-dependent selection (green), plus possible frequency-dependent selection. (B) Imposed on A, individual phenotypes (open blue squares), with the purple two-headed arrow indicating the major axis of phenotypic trait covariation ($\mathbf{P}_{\max}$), and the black two-headed arrow the major axis of genetic covariance ($\mathbf{G}_{\max}$). POLS, pace-of-life syndrome. See text for more detail.

Fig. 5. The within- and among-population (or species) covariation and correlated selection between two of the expected multiple life-history (morphological, physiological or behavioural) traits ($\mathbf{z}_1$ and $\mathbf{z}_2$), which could also represent r_0 and γ. Separate populations (or species) are shown with fitness contours, as in Fig. 3, with solid two-headed arrows representing within-population pace-of-life syndromes (POLSs) from fast (orange) to slow (green). The overall among-population pace-of-life continuum is shown as the dashed two-headed arrow from fast types resulting from low density-dependent selection (orange) to slow types resulting from high density-dependent selection (green). Fluctuations in the nature of density-dependent selection within- and among-population thus structure the variation in POLSs at different hierarchical levels. See text for more detail.

Fig. 6. Diagram showing how different measured traits (dashed boxes) affect individual variation in density-independent reproduction (r_0) and detrimental effects of population density (γ), and hence fitness (w), in a hypothetical bird species (positive effects shown as solid arrows, negative effects shown as dashed arrows). A proper path analyses of these relationships could be parameterized as a set of mixed-effect models (see Morrissey, 2014), using animal models (Lynch & Walsh, 1998) to partition genetic and environmental variance in r_0 and γ due to the different POLS traits.

Figure 1

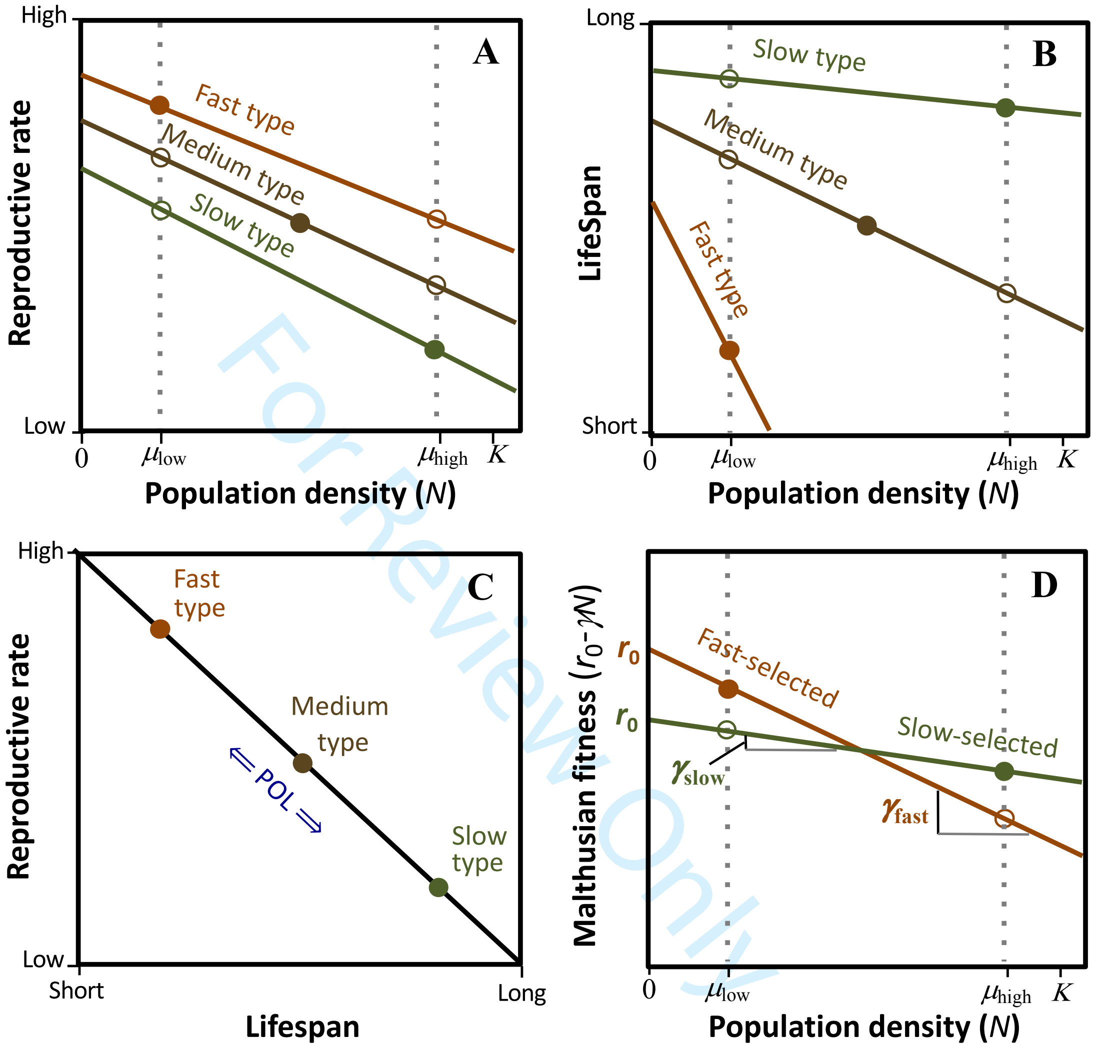

A
High
Low
Reproductive rate
Fast type
Medium type
Slow type
0
μ_{low}
μ_{high}
K
Population density (N)
B
Long
Short
LifeSpan
Slow type
Medium type
Fast type
0
μ_{low}
μ_{high}
K
Population density (N)
C
High
Low
Reproductive rate
Fast type
Medium type
⇐ POL ⇒
Slow type
Short
Long
Lifespan
D
Malthusian fitness ($r_0 - \gamma N$)
r_0
r_0
Fast-selected
Slow-selected
γ_{slow}
γ_{fast}
0
μ_{low}
μ_{high}
K
Population density (N)

Figure 2

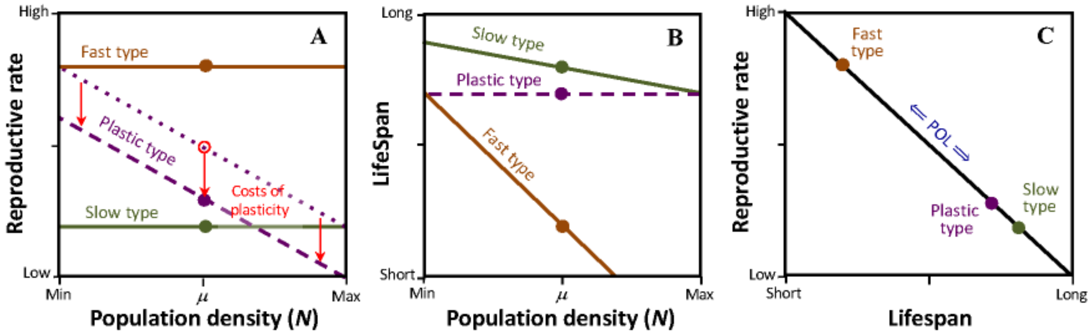

High
Low
Reproductive rate
Fast type
Plastic type
Costs of plasticity
Slow type
A
Min
μ
Max
Population density (N)
Long
Short
LifeSpan
Slow type
Plastic type
Fast type
B
Min
μ
Max
Population density (N)
High
Low
Reproductive rate
Fast type
⇐ POL ⇒
Slow type
Plastic type
C
Short
Long
Lifespan

Figure 3

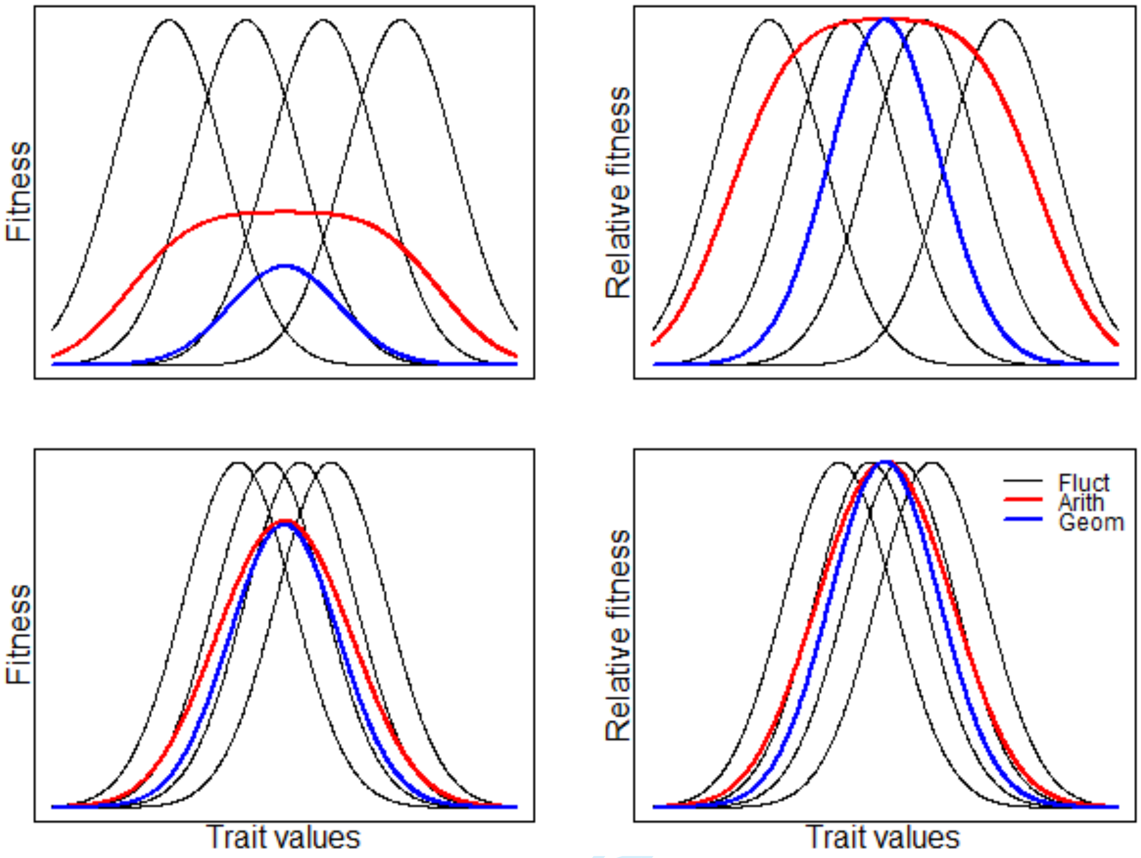

Fitness
Relative fitness
Fitness
Relative fitness
Fluct
Arith
Geom
Trait values
Trait values

Figure 4

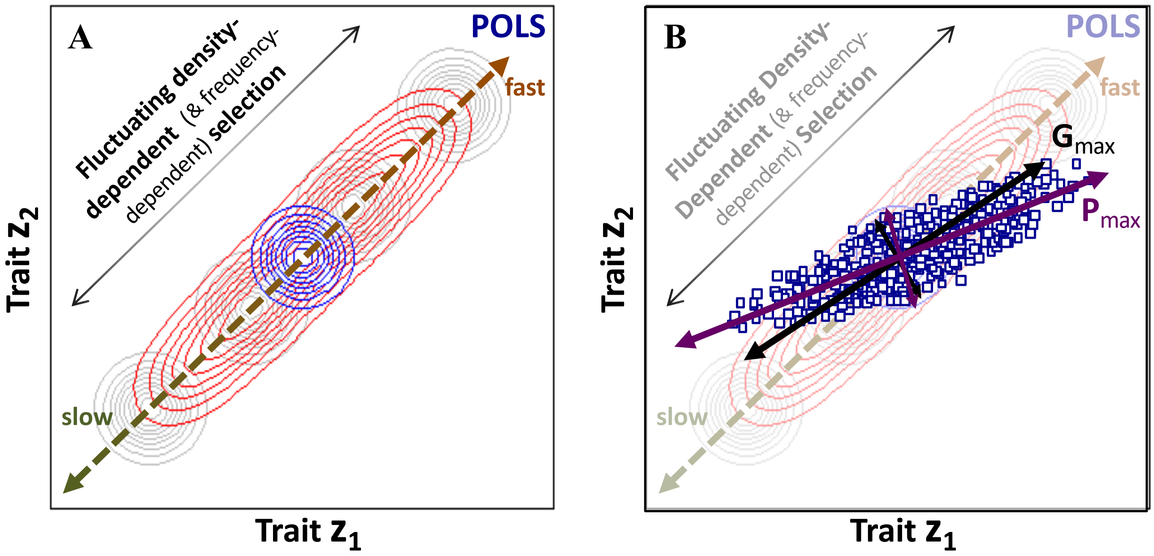

A
POLS
Fluctuating density-dependent (& frequency-dependent) selection
fast
slow
Trait Z_2
Trait Z_1
B
POLS
Fluctuating Density-Dependent (& frequency-dependent) Selection
fast
G_{max}
P_{max}
slow
Trait Z_2
Trait Z_1

Figure 5

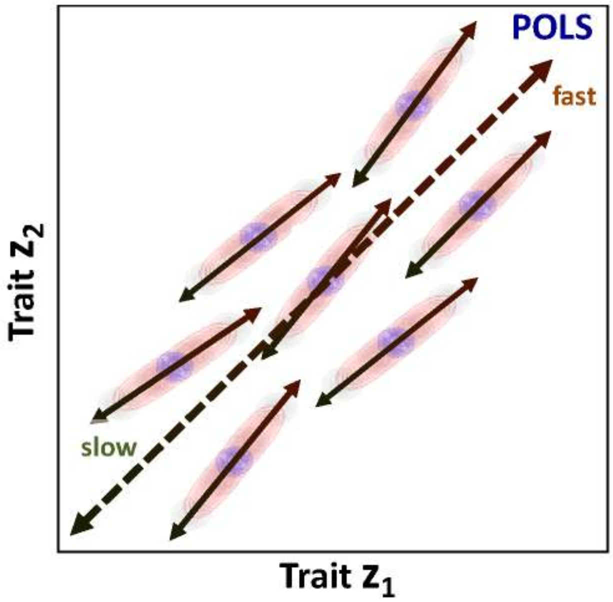
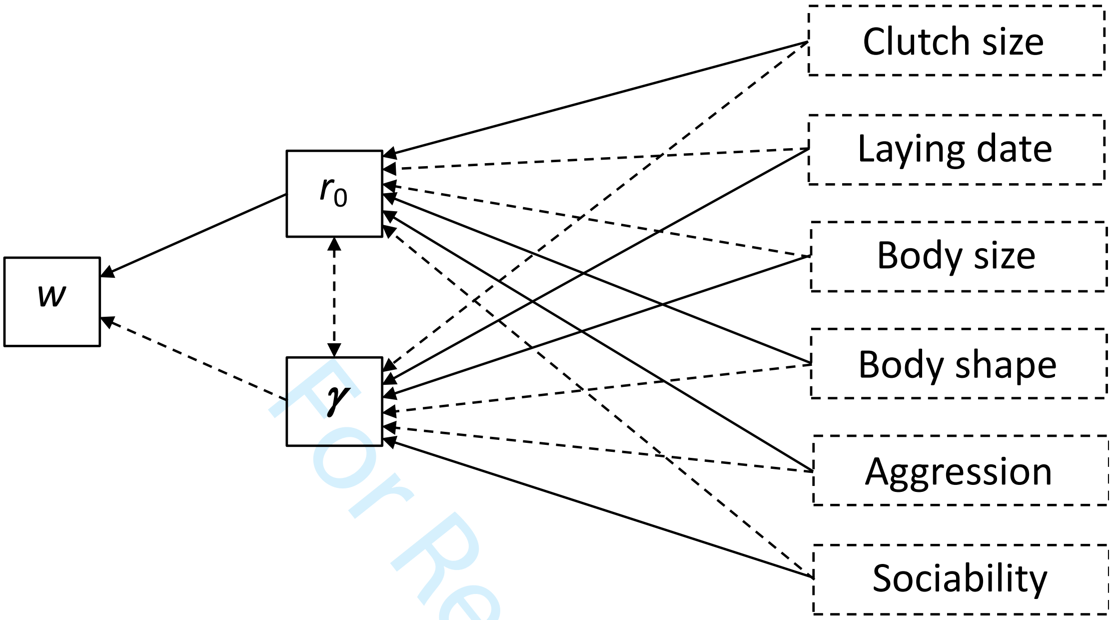


Figure 6


Clutch size
Laying date
Body size
Body shape
Aggression
Sociability
r_0
w
γ