



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

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3 **Life-history evolution under fluctuating density-dependent**
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6 **selection and the adaptive alignment of pace-of-life syndromes**
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46
47 2 ABSTRACT
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49 3 We present a novel perspective on life-history evolution that combines recent theoretical
50 4 advances in fluctuating density-dependent selection with the notion of pace-of-life syndromes
51 5 (POLSSs) in behavioural ecology. These ideas posit phenotypic co-variation in life-history,
52 6 physiological, morphological and behavioural traits as a continuum from the highly fecund,
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3 7 short-lived, bold, aggressive and highly dispersive ‘fast’ types at one end of the POLS to the
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5 8 less fecund, long-lived, cautious, shy, plastic and socially responsive ‘slow’ types at the other.
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7 9 We propose that such variation in life histories and the associated individual differences in
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9 10 behaviour can be explained through their eco-evolutionary dynamics with population density
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11 11 – a single and ubiquitous selective factor that is present in all biological systems. Contrasting
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13 12 regimes of environmental stochasticity are expected to affect population density in time and
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15 13 space and create differing patterns of fluctuating density-dependent selection, which generates
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17 14 variation in fast *versus* slow life histories within and among populations. We therefore predict
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19 15 that a major axis of phenotypic co-variation in life-history, physiological, morphological and
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21 16 behavioural traits (i.e. the POLS) should align with these stochastic fluctuations in the
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23 17 multivariate fitness landscape created by variation in density-dependent selection. Phenotypic
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25 18 plasticity and/or genetic (co-)variation oriented along this major POLS axis are thus expected
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27 19 to facilitate rapid and adaptively integrated changes in various aspects of life histories within
28
29 20 and among populations and/or species. The fluctuating density-dependent selection POLS
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31 21 framework presented here therefore provides a series of clear testable predictions, the
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33 22 investigation of which should further our fundamental understanding of life-history evolution
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35 23 and thus our ability to predict natural population dynamics.
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42 25 *Key words:* fluctuating selection, frequency-dependent selection, environmental stochasticity,
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44 26 eco-evolutionary dynamics, animal personality, behavioural syndromes, correlational
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46 27 selection, plasticity, phenotypic integration, bet-hedging.
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29 43 **I. INTRODUCTION**

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31 44 Understanding the evolution of life histories represents one of the biggest challenges in
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33 45 biology (Stearns, 1992; Roff, 2002). This is because life-history traits, such as reproductive
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35 46 rates and lifespan, feed directly back into the ecological dynamics of the populations within
36
37 47 which those life histories evolve (see Sæther *et al.*, 2016 and references therein). The
38
39 48 reciprocal nature of the ecological and evolutionary dynamics involved in life histories is
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41 49 therefore central to the problem of predicting and managing population changes, especially in
42
43 50 the face of (human-induced) environmental change (Moritz & Agudo, 2013). For example, in
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45 51 fisheries the harvesting of larger older individuals not only reduces the population size, but it
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47 52 imposes selection favouring the evolution of smaller individuals that reproduce earlier in life
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49 53 (Law, 2000). Smaller faster-reproducing individuals will tend to respond differently to
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51 54 changes in population density as compared with the original larger slower reproducers,
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53 55 thereby potentially creating more volatile population dynamics and a greater probability of
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3 56 stochastic extinction as an unintended consequence of harvesting. The evolution of such *slow*
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5 57 versus *fast* life histories, or differences in the ‘pace of life’ (Ricklefs & Wikelski, 2002)
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7 58 arising *via* the fundamental trade-off between current *versus* future reproduction, depends
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9 59 critically upon their contrasting responses to increases in population density (Fig. 1).
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11 60 Individuals with fast rates of reproduction will do best in newly founded and low-density
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13 61 populations, but as populations increase in size and approach carrying capacity it is the
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15 62 slower-reproducing types that will instead be favoured because of their ability to resist the
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17 63 negative fitness effects of greater intra-specific competition.
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19 64 These contrasting selective pressures generated by local demographic conditions have long
20
21 65 been part of theoretical treatments of life-history evolution. In one of the earliest treatments,
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23 66 MacArthur (1962) and MacArthur & Wilson (1967) argued that high intrinsic (density-
24
25 67 independent) rates of reproduction and short lifespans should be favoured in new or small
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27 68 populations (*r*-selection), whereas at large population sizes there should be density-dependent
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29 69 selection for competitive ability and resilience to any detrimental effects of high population
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31 70 densities, favouring life histories that increase the population carrying capacity (*K*-selection)
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33 71 (see Fig. 1D). In order for density-dependent selection to produce fast *versus* slow pace-of-
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35 72 life types, a negative trade-off is assumed to exist between intrinsic rates of reproduction (r_0)
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37 73 and the ability to cope with the negative effects of competition (γ) arising from increases in
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39 74 population density (Engen, Lande & Sæther, 2013; see Fig. 1D). It is important to note that
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41 75 density-dependent selection may *increase* the carrying capacity (*K*), as envisioned by
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43 76 MacArthur & Wilson’s (1967) original theory. For example, *K*-selected types may avoid the
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45 77 costs of competition by being more efficient in their use of resources, more cooperative and
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47 78 resolving contests without recourse to costly fighting, and thus maintain larger populations at
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49 79 carrying capacity than would *r*-selected types (e.g. Duckworth, Belloni & Anderson, 2015).
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51 80 However, density-dependent selection could also *decrease* the carrying capacity (*K*), because
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3 81 the competitive advantage in contests to individuals that invest more in aggression, costly
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5 82 fighting and/or larger body sizes, etc. will result in less-efficient populations with lower
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7 83 carrying capacities (see Boyce, 1984; Mueller, 1997). Such density-dependent selection for
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9 84 individuals with larger body sizes for the purposes of contest competition then has important
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11 85 implications for the ecological differences observed among species due to allometric and
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13 86 metabolic scaling that drive many important biological processes shaping the pace of life in
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15 87 different species (see Marquet, Navarette & Castilla, 1995; West, Brown & Enquist, 1997;
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17 88 Brown *et al.*, 2004; Banavar *et al.*, 2010). Hence, many species with a slower pace of life tend
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19 89 to have smaller population sizes than those with a faster pace of life, despite existing in more
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21 90 stable populations closer to their carrying capacity (K), explicitly because density-dependent
22
23 91 selection has favoured larger bodies that are more competitive under conditions of contest
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25 92 competition (Boyce, 1984). These arguments for density-dependent selection for efficiency
26
27 93 and cooperation as opposed to the inefficiency of contest competition and larger body sizes
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29 94 are also not necessarily mutually exclusive, and phenotypic plasticity provides an obvious
30
31 95 middle ground between the two. For example, plasticity in reproductive effort may efficiently
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33 96 reduce the costs of contest competition in years with high-density populations, but such
34
35 97 plasticity is likely to come at a cost that is only worth paying if individuals also increase their
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37 98 somatic investment to achieve longer lifespans within which to carry out any deferred
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39 99 reproduction (see Section IV.1 below).
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43 100 Despite criticisms of earlier versions of density-dependent selection in the form of *r-* versus
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45 101 *K*-selection theory (see Boyce, 1984; Stearns, 1992; Reznick, Bryant & Bashey, 2002),
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47 102 density-dependent regulation of natural populations appears to be ubiquitous (Brook &
48
49 103 Bradshaw, 2006) and thus density-dependent selection must play a substantial role in the eco-
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51 104 evolutionary dynamics of life-history evolution (MacArthur, 1962; Charlesworth, 1994),
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53 105 whether it promotes greater social efficiency, increased plasticity, and/or increased contest-
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3 106 competitive ability in the form of increases in aggression and/or body size, etc. Likewise,
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5 107 despite the earlier and much-criticized simplistic categorization of species on an r/K
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7 108 continuum by Pianka (1970), it seems clear that the majority of life histories are amenable to
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9 109 characterization along a more general fast *versus* slow ‘pace-of-life’ continuum. For example,
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11 110 the pace-of-life continuum has now been confirmed as a major axis of phenotypic (co-
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13 111)variation in key life-history traits (e.g. reproductive rate, lifespan, age of first reproduction,
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15 112 generation time) representing an important determinant for population dynamics in birds
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17 113 (Sæther, 1987; Sæther & Bakke, 2000), mammals (Gaillard *et al.*, 2005; Oli, 2004; Bielby *et*
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19 114 *al.*, 2007), fish (Goodwin *et al.*, 2006; Bjørkvoll *et al.*, 2012), reptiles (Bauwens & Diaz-
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21 115 Uriarte, 1997) and insects (Johansson, 2000), and more recently in plants (Adler *et al.*, 2014;
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23 116 Salguero *et al.*, 2015). Unfortunately, we currently lack a unified approach to the study of
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25 117 life-history variation that combines the eco-evolutionary dynamics of density-dependent
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27 118 selection with the multivariate evolution of these different life-history traits comprising the
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29 119 fast *versus* slow pace-of-life continuum observed among populations and species.
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31 120 This brings us to the other major challenge in understanding life-history evolution, which is
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33 121 that it normally involves selection for suites of multiple coevolving traits, such as those
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35 122 implicated in comparative studies of a pace-of-life continuum (see above). Predicting the
36
37 123 evolution of multiple co-varying traits within a population is complex (Armbruster *et al.*,
38
39 124 2014), because it necessarily involves the evolution of genetic correlations and integration of
40
41 125 (developmental) plasticity across multiple traits (Lande, 1982; Lande & Arnold, 1983;
42
43 126 Schlichting, 1989; Pigliucci & Preston, 2004). Such genetic and environmental sources of
44
45 127 life-history trait (co-)variation within populations would appear to be crucial in explaining the
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47 128 specific trait combinations we observe in pace-of-life differences among species and
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49 129 populations, as well as any deviations from this single axis of life-history variation.
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3 130 The first studies to consider such trait covariances beyond just life-history characters explored
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5 131 co-adaptations between life history and physiology in particular (Ricklefs & Wikelski, 2002).
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7 132 Such physiology and life-history comparisons identified ‘slow’ *versus* ‘fast’ populations and
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9 133 species according to immunological (see Tieleman, 2018) and metabolic traits linked to
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11 134 metabolic scaling (see Brown *et al.*, 2004; Banavar *et al.*, 2010). More recently, individual
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13 135 variation in the tempo of life histories (i.e. the pace of life within populations) has been linked
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15 136 to wider patterns of phenotypic covariance commonly observed across a wide range of
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17 137 physiological, morphological and behavioural traits, a phenomenon that has therefore been
18
19 138 termed a ‘pace-of-life syndrome’ (POLS; Careau *et al.*, 2008; Réale *et al.*, 2010*b*; Dammhahn
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21 139 *et al.*, 2018). The position of individuals within a population along the POLS continuum, from
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23 140 fast-reproducing short-lived, bold, aggressive types at one end to slow-reproducing long-
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25 141 lived, cautious, shy types at the other, appears to provide a general explanation for repeatable
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27 142 individual differences in behaviour (‘animal personality’) and their covariation as part of
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29 143 ‘behavioural syndromes’ (Réale *et al.*, 2010*a*; Carere & Maestriperi, 2013). Behavioural
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31 144 ecologists have thus developed various models predicting the adaptive integration of life
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33 145 history, physiology, body condition, structural size, metabolism and behaviour as part of
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35 146 POLSs within single populations (see Biro & Stamps, 2010; Houston, 2010; Luttbeg & Sih,
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37 147 2010; Salzmann *et al.*, 2018). There is also clear evidence for this integration demonstrating
38
39 148 that behaviourally ‘fast’ individuals are larger and have higher metabolic rates (e.g. Careau *et*
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41 149 *al.*, 2008; Le Galliard *et al.*, 2013; Niemelä & Dingemanse, 2017, and that such ‘fast’ types
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43 150 also have higher annual reproductive output (see Biro & Stamps, 2008; Smith & Blumstein,
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45 151 2008). However, if such POLSs within populations are a product of the same processes that
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47 152 cause variation in pace of life among populations and species, we need to identify a general
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49 153 evolutionary mechanism that operates across a wide variety of ecological situations and taxa.
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3 154 Heterogeneous or fluctuating selection in time or space has been suggested as a possible
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5 155 mechanism for maintaining phenotypic variation within populations (see Frank & Slatkin,
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7 156 1990), and such processes have also been identified as possible causes of animal personalities
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9 157 (reviewed by Dingemanse & Réale, 2013). Fluctuating selection on life histories due to
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11 158 stochastic variation in population densities has the potential to provide an explanation for
12
13 159 POLSs (e.g. Nicolaus *et al.*, 2016). Environmental stochasticity and density dependence are
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15 160 general features of almost all biological systems and have eco-evolutionary consequences for
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17 161 life-history evolution (MacArthur, 1962; Tuljapurkar, 1990; Charlesworth, 1994; Tuljapurkar,
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19 162 Gaillard & Coulson, 2009). In low-density populations (i.e. those kept low by environmental
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21 163 stochasticity) the nature of density-dependent selection will differ from that in high-density
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23 164 populations (i.e. those allowed to grow due to less environmental stochasticity) (see Engen *et*
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25 165 *al.*, 2013). Therefore, our contention is that variation from low to high density-dependent
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27 166 selection has the potential to explain much of the variation we see in the pace of life across
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29 167 populations and species, and that ‘fluctuating density-dependent selection’ caused by
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31 168 environmentally induced temporal variation in population density may explain the variation in
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33 169 life-history and other traits associated with POLSs within populations.
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37 170 In making a detailed case for the role of fluctuating density-dependent selection on life-
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39 171 history evolution and the associated suite of co-varying traits in POLSs, this review brings
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41 172 together previously disparate approaches to the study of life histories from population
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43 173 ecology, behavioural ecology, quantitative genetics and evolutionary biology. Our aim is to
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45 174 promote the development of a unified eco-evolutionary framework for the effective study of
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47 175 life-history evolution in natural populations, and the persistence of individual differences
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49 176 across a wide range of phenotypic traits within these populations.
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178 **II. ADVANCES IN DENSITY-DEPENDENT SELECTION THEORY**

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3 179 Recent theoretical developments of MacArthur & Wilson's (1967) long-standing idea of *r*-
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5 180 *versus* *K*-selection have successfully incorporated stochastic environmentally induced
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7 181 variation in population size into models of the ecological and evolutionary dynamics along a
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9 182 single axis of life-history variation (Lande, Engen & Sæther, 2009, 2017; Engen *et al.*, 2013;
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11 183 Engen & Sæther, 2016*a,b*). These studies confirm the prediction that density-independent
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13 184 rates of reproduction (r_0) should be maximized in small populations, but in larger populations
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15 185 r_0 should be traded off against the ability to reduce the negative density-dependent effects of
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17 186 intra-specific competition on reproduction (γ). Hence, at different population sizes life
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19 187 histories evolve the combination of values of r_0 and γ that best maximize Malthusian fitness
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21 188 (see Fig. 1D). A recent study on great tits (*Parus major*) has confirmed many of these
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23 189 predictions, showing that females laying the largest clutch sizes at small population sizes were
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25 190 also the ones that experienced the greatest density-dependent reductions in fitness at large
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27 191 population sizes (Sæther *et al.*, 2016). As noted above, exactly how density-dependent
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29 192 selection mitigates the detrimental effects of intra-specific competition on fitness (i.e. the
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31 193 slope γ , see Fig. 1D) will depend upon the particular species and life history concerned. It is
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33 194 mostly likely to involve selection for increased contest-competitive ability in the form of a
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35 195 larger body size at the costs of greater somatic effort, extended parental care and a longer
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37 196 lifespan, and all of the allometric and metabolic scaling implications that this entails (Marquet
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39 197 *et al.*, 1995; West *et al.*, 1997; Brown *et al.*, 2004; Banavar *et al.*, 2010). However, density-
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41 198 dependent selection for increased social efficiency and plasticity may provide more efficient
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43 199 ways to mitigate some of the detrimental effects on fitness of high population densities (see
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45 200 Section IV.1 below, e.g. Duckworth *et al.*, 2015).
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51 201 Therefore, the suggestion here is that populations kept low by repeated stochastic
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53 202 environmental events represent conditions that favour fast types of individuals, because their
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55 203 high rates of reproduction at low population densities (r_0) allow them to contribute
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3 204 disproportionately to any population growth when it does happen. Conversely, high-density
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5 205 populations experiencing few such stochastic events end up approaching carrying capacity,
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7 206 where slow types are favoured because of their insensitivity to negative fitness effects of
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9 207 density-dependent intra-specific competition (low values of γ), thereby allowing them to
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11 208 contribute disproportionately more offspring to the next generation in dense populations.
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13 209 Contrasting regimes of stochasticity in population size should therefore lead to population-
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15 210 specific levels of low *versus* high fluctuating density-dependent selection, and thus to
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17 211 predictable variation in pace of life of life histories among populations and species.
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19 212 The maximization of Malthusian fitness shown in Fig. 1D thus reflects the cumulative effect
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21 213 across generations of the trade-off between current *versus* future reproduction, which is
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23 214 manifest at the individual level as the trade-off between reproductive effort per breeding
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25 215 attempt *versus* lifespan (see Fig. 1A–C). In essence, slow types with their lower rates of
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27 216 reproduction per attempt achieve greater fitness than fast types at higher population densities
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29 217 because they live for longer and achieve a greater number of breeding attempts per lifetime
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31 218 under such competitive conditions. As suggested by the Sæther *et al.* (2016) example above,
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33 219 there might also be density-dependent effects on reproductive output per breeding attempt,
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35 220 which should disproportionately affect fast as compared with slow types (not shown for
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37 221 simplicity in Fig. 1A). It is these effects on lifespan and/or reproductive output that produce
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39 222 the negative relationship (i.e. the life-history trade-off) between high values of r_0 *versus* low
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41 223 values of γ , and represent a key assumption of density-dependent selection theory (Fig. 1D;
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43 224 Engen *et al.*, 2013). Thus, investment by fast types in a high r_0 reflects investment in current
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45 225 over future reproduction, whilst investment by slow types in a low γ reflects investment in
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47 226 future over current reproduction and the kinds of competitive advantages that will insulate the
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49 227 individual from density-dependent effects on their reproduction and survival.
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3 228 Based upon these arguments, we expect populations kept small and lacking intra-specific
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5 229 competition for resources due to high levels of environmental disruption, such as a series of
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7 230 severe winters and/or those in more generally stochastic environments, to contain more fast
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9 231 types with life histories emphasising current over future reproduction (towards the fast end of
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11 232 the POLS), because of low density-dependent selection (favouring high individual values of
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13 233 r_0 and γ , Fig. 1D). The larger fluctuations between relatively low *versus* relatively high
14
15 234 density-dependent selection in such disrupted and more stochastically varying population
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17 235 densities may also result in greater within-population variation among different individual life
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19 236 histories – i.e. a greater range of coexisting pace-of-life types. By contrast, larger populations
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21 237 closer to carrying capacity (K) that, for example, experience only mild winters and less
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23 238 stochastic environmental conditions will be under consistently high density-dependent
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25 239 selection and thus characterized by slow types of life histories giving prominence to future
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27 240 over current reproduction (favouring low individual values of r_0 and low γ , Fig. 1D). These
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29 241 slow types of populations may also show less among-individual variation in life histories –
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31 242 i.e. a narrower range of coexisting pace-of-life types. The difference in pace of life among
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33 243 populations or species should thus reflect differences in average long-term local population
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35 244 dynamics (i.e. how far below carrying capacity the average population is), whereas the extent
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37 245 of within-population variation in the range of pace-of-life types should be indicative of the
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39 246 degree of fluctuating selection on life histories.
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248 **III. ANIMAL PERSONALITIES, SOCIAL BEHAVIOUR AND FREQUENCY**

249 **DEPENDENCE**

50 250 We suggest that fluctuating density-dependent selection in time and space arising from
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52 251 stochastic variation in population size may represent a key factor in generating within-
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54 252 population variation in the tempo of individual life histories. It is therefore the trade-off
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3 253 between r_0 versus γ , and thus also between current *versus* future reproduction, that could
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5 254 provide a root cause of POLSs and the phenotypic covariance commonly observed across a
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7 255 range of physiological, morphological and behavioural traits associated with life-history
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9 256 variation (see Réale *et al.*, 2010*b*; Biro & Stamps, 2008; Smith & Blumstein, 2008;
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11 257 Dammhahn *et al.*, 2018; Salzman *et al.*, 2018; Royauté *et al.*, 2018). The fluctuating density-
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13 258 dependent selection framework presented above thus provides a general eco-evolutionary
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15 259 explanation for the repeatable individual differences in behaviour seen within populations,
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17 260 which we suggest arise as a result of the evolution of a POLS. It is important to note that our
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19 261 suggestion here is completely consistent with the recent theoretical treatments of ‘adaptive’
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21 262 animal personality variation arising due to state dependence and asset protection (e.g.
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23 263 McElreath & Strimling, 2006; Wolf *et al.*, 2007; Wolf, van Doorn & Weissing, 2008; Luttbeg
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25 264 & Sih, 2010; Wolf & Weissing, 2010; Dingemanse & Wolf, 2010; Sih *et al.*, 2015). Indeed,
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27 265 the individual differences in behaviour produced by these models (e.g. boldness in foraging
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29 266 under threat of predation) only arise because of a pace of life trade-off that is assumed to exist
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31 267 between current *versus* future fitness. In addition, stochastic variation in population densities
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33 268 causing fluctuating density-dependent selection could provide a continuous ubiquitous source
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35 269 of individual variation in offspring state (e.g. *via* temporal or spatial variation in resources
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37 270 available to their parents), which has been suggested as a driving force behind the emergence
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39 271 of animal personality in such models.
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43 272 Individuals from different positions within the POLS continuum are predicted to show
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45 273 characteristic patterns of morphology, physiology and behaviour, based upon their values of
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47 274 r_0 (density-independent reproduction) *versus* γ (the negative effects on fitness of increasing
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49 275 population density). For example, activity in open-field assays has been found to be positively
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51 276 related to dispersal (e.g. Dingemanse *et al.*, 2003), as has sociability (e.g. Cote *et al.*, 2009).
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54 277 This could be because such individuals possess adaptive combinations of high rates of
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3 278 activity, social aggression and dispersal (e.g. Duckworth & Badyaev, 2007). Such fast-type
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5 279 individuals with high intrinsic rates of reproduction (high r_0) benefit more from dispersal
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7 280 because this allows them to settle in low-density environments, where they can then do well.
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9 281 By contrast, dispersal is less useful for slow-reproducing, less-active and less-aggressive slow
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11 282 types that do well by staying in established populations because they experience fewer
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13 283 negative effects of increasing density on fitness (i.e. a low γ). The costs of suitable fast-type
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15 284 phenotypes for dispersal to lower density habitats will in turn drive various life-history trade-
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17 285 offs leading to syndrome-like covariation between dispersal and other life-history traits at the
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19 286 individual, population and species levels (Bonte *et al.*, 2011; Clobert, 2012). Similarly, the
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21 287 commonly observed aggression–boldness syndrome (see Garamszegi, Marko & Herczeg,
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23 288 2012) could well be a product of fast-type individuals (expecting high average mortality as a
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25 289 result of environmental stochasticity) having adaptively high levels of aggression and
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27 290 boldness in the face of predation threats (Abbey-Lee, Mathot & Dingemanse, 2016). Such fast
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29 291 types thus explore their environment more superficially and/or are less sensitive to
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31 292 environmental change, as compared with the less-aggressive, more-cautious, slower exploring
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33 293 slow types at the other end of the POLS continuum (Nicolaus *et al.*, 2014). Therefore, the
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35 294 current animal personality literature already incorporates components consistent with the
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37 295 suggestion of POLSs and the notion that fluctuating density-dependent selection drives, and is
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39 296 in turn influenced by, repeatable individual differences in behaviour commonly found in
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41 297 naturally varying wild populations.
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44 298 Thus far we have made an argument for behavioural phenotypic variation within the POLS
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46 299 simply being the result of fluctuating density-dependent selection among individuals.
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48
49 300 However, there are obviously other, non-mutually exclusive, evolutionary mechanisms that
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51 301 can generate behavioural variation among individuals within populations, such as frequency-
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53 302 dependent selection (Frank & Slatkin, 1990; Dingemanse & Réale, 2013). Indeed, game-

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3 303 theoretical predictions suggest that almost any intraspecific social interaction has the potential
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5 304 to result in negative frequency-dependent selection, which would then favour a mix of
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7 305 different types within a POLS (see Novak & Sigmund, 2004). Hence, it is negative frequency-
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9 306 dependent selection (sometimes instantiated *via* type-specific density dependence), rather than
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11 307 fluctuating selection, that is used to maintain among-individual variation in behaviour in
12
13 308 almost all existing formal models of animal personalities, including those involving links to
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15 309 individual differences in life histories (Wolf *et al.*, 2007, 2008; Wolf, van Doorn & Weissing,
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17 310 2011; Wolf & McNamara, 2012). Within the POLS fluctuating density-dependent selection
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19 311 scenario we propose, frequency-dependent social effects could arise as an additional process
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21 312 from the mixes of specific types at the different population densities. For example, too many
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23 313 fast aggressive types from the fast end of the POLS might interact to their mutual detriment at
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25 314 higher population densities (e.g. Duckworth *et al.*, 2015). Greater frequencies of extra-pair
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27 315 paternity are also seen in bird populations at higher population densities (Araya-Ajoy,
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29 316 Dingemanse & Kempenaers, 2016a), and it seems that it is the fast types that lose a greater
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31 317 share of their paternity (Duckworth, 2006; Araya-Ajoy *et al.*, 2016b). Such processes will
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33 318 allow fast types to be more quickly replaced by slow types whenever intraspecific
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35 319 competition intensifies as the population density approaches carrying capacity. Such negative
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37 320 frequency-dependent selection has previously been suggested to explain the eco-evolutionary
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39 321 dynamics of small mammal population cycles (Chitty, 1960; Krebs, 2013). Conversely, we
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41 322 might predict positive frequency dependence amongst slow types at high population densities,
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43 323 if they are more phenotypically plastic (see Section IV.1 below) in terms of their social
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45 324 responsiveness (see Wolf *et al.*, 2008, 2011), because this would allow slow types to mitigate
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47 325 the worst fitness effects of intraspecific competition when interacting with other slow types,
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49 326 but not fast types, in dense populations (e.g. improved coordination in social foraging or
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51 327 collective anti-predator behaviours; Giraldeau & Caraco, 2000). In line with this notion, in
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328 great tits slow explorers experience increased annual survival rates under high densities
329 (Nicolaus *et al.*, 2016), in bluebirds (*Sialia mexicana*) less-aggressive individuals have higher
330 reproductive success at high population densities (Duckworth, 2006), and in common lizards
331 (*Lacerta vivipara*) more-social individuals survive better at high population densities (Cote
332 & Clobert, 2007; Cote, Dreiss & Clobert, 2008). We can therefore easily envisage fluctuating
333 density-dependent selection on individual pace of life being supplemented by frequency-
334 dependent selection on certain social behaviours at one or both ends of the POLS within
335 populations.
336 Frequency dependence will affect the details of how density dependence impacts the
337 population dynamics of the system (e.g. Mougeot *et al.*, 2003), because we expect a dynamic
338 interaction between density- and frequency-dependent fitness effects on POLSs within
339 populations. Indeed, the ‘adaptive dynamics’ approach to the theoretical modelling of eco-
340 evolutionary feedbacks is explicitly based upon the effects of density-dependent and
341 frequency-dependent selection (see Waxman & Gavrillets, 2005). However, we currently lack
342 life-history models involving frequency-dependent selection plus fluctuating density-
343 dependent selection. Empirical evidence is also needed to identify the specific social
344 behavioural mechanisms involved in any frequency dependence and to determine their
345 generality across different systems. Without suitable mathematical treatments and more data
346 on this topic, it is difficult at this stage to predict the role of frequency-dependent selection in
347 further shaping POLSs within populations. We are primarily interested here in the possibility
348 that variation in density-dependent selection in general explains the pace of life continuum
349 observed among populations and species, and that fluctuating density-dependent selection
350 specifically creates POLSs within populations. Therefore, we will now discuss further the
351 implications of fluctuating density-dependent selection on POLS evolution at these different

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3 352 levels, for the moment without the additional complication of frequency-dependent selection
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5 353 within populations.
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9 355 **IV. LIFE-HISTORY VARIATION AND POLS COVARIATION AT DIFFERENT**
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11 356 **LEVELS**

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13 357 The theoretical framework presented here combines recent advances in density-dependent
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15 358 selection theory with behavioural research on animal personalities and POLSs to explain the
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17 359 continuum of fast to slow types within and among populations. Such phenotypic differences
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19 360 in types can result from genetic differences, from among-individual differences in
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21 361 development (irreversible plasticity), and/or from within-individual reversible plasticity in
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23 362 response to current conditions (i.e. the local population density in the case of density-
24
25 363 dependent selection). This detail is important given the role of environmental stochasticity
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27 364 and fluctuating selection in density-dependent selection theory, because it is the time scale
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29 365 and predictability of these fluctuations that will determine whether or not the optimum life
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31 366 history can be tracked by evolutionary change in gene frequencies, and whether or not
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33 367 adaptive irreversible or reversible plasticity will evolve (Botero *et al.*, 2015; Tufto, 2015). In
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35 368 addition, even though our focus here is on phenotypic (co-)variances within the POLS, key
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37 369 evolutionary trade-offs in fast *versus* slow life histories, such as in survival *versus*
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39 370 reproduction or the number *versus* quality of young, are expected to involve genetic
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41 371 covariances (Partridge, 1992; Reznick, 1992). The assumption that individual phenotypic
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43 372 differences in life histories reflect underlying genetic variation and covariation (e.g. Hadfield
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45 373 *et al.*, 2007; Brommer, 2013) is called the ‘phenotypic gambit’ in behavioural ecology
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47 374 (Grafen, 1984) and ‘Cheverud’s conjecture’ in evolutionary biology (Cheverud, 1988). Given
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49 375 that this key assumption may often not be valid (see Hadfield *et al.*, 2007; Dochtermann,
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51 376 2011; Araya-Ajoy *et al.*, 2016b), it is nearly always important to distinguish between the
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377 genetic *versus* environmental sources of trait (co-)variation (Lande, 1979; Lande & Arnold,
378 1983).

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

390 In addition, Santostefano *et al.* (2017) demonstrate that in field crickets (*Gryllus bimaculatus*)
391 the G *versus* PE correlations between life-history and behavioural traits involved in POLS
392 operate in the opposite direction. Therefore, covariation among phenotypic traits in any POLS
393 should also be decomposed into its different components, where it is usually quantified in
394 symmetrical matrices with trait variances as diagonal elements and trait covariance as off-
395 diagonal elements. The variance–covariance **D**-matrix captures among population/species
396 POLSs, while the **P**-matrix describes the within-population POLS. As with the variances, the
397 phenotypic **P**-matrix is often then decomposed into the genetic component **G**-matrix and a
398 permanent environmental component **PE**-matrix, and when repeated measures for individuals
399 exist, a within-individual component **E**-matrix describing the variance–covariances of
400 different events (e.g. breeding attempts) within a lifetime. The **PE**-matrix thus includes
401 effects of integrated developmental plasticity among lifetimes, whilst the **E**-matrix reflects

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3 402 integrated reversible plasticity in response to the current environment at different times within
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5 403 the lifetime. A last residual **R**-matrix describes any remaining trait variance–covariances,
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7 404 which is usually due to measurement error (but see Westneat, Wright & Dingemanse, 2015).
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9 405 In the following sections, we detail how variation in fluctuating density-dependent selection
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11 406 on the pace of life might lead to the trait variance–covariance observed along the POLS axis
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13 407 at these different levels of organization.
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18 409 **(1) Irreversible and reversible plasticity (PE- and E-matrix POLSs)**

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20 410 A crucial issue is the degree to which phenotypic plasticity in life histories is responsible for
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22 411 the existence of pace of life variation among populations or species, and POLSs within
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24 412 populations. Adaptively, it would make more sense under fluctuating density-dependent
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26 413 selection for individuals phenotypically to track any predictable variation in population size
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28 414 *via* developmental plasticity (Botero *et al.*, 2015; Tufto, 2015). For example, population-
29
30 415 density effects on offspring rearing conditions could be used by parents to create adaptive
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32 416 modifications in offspring development and their subsequent pace of life, provided that there
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34 417 is sufficient temporal autocorrelation in population sizes across generations to make any
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36 418 environmental effects predictable on the scale of more than an individual lifetime (West-
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38 419 Eberhard, 2003; Botero *et al.*, 2015). In such cases, we therefore see that mean offspring life-
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40 420 history phenotypes will plastically track predictable variation in local population densities
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42 421 and/or resource availability (Stearns, 1992; Lindstrom, 1999; Beckerman *et al.*, 2002).
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44 422 However, for many iteroparus species under fluctuating density-dependent selection,
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46 423 population densities may well vary substantially within lifetimes with little temporal
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48 424 autocorrelation (e.g. between breeding seasons). If this variation is sufficiently predictable,
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50 425 for example using environmental or social cues immediately prior to breeding, then we might
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52 426 expect adaptive reversible plasticity to evolve in individual reproductive effort across
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3 427 breeding attempts (Gabriel *et al.*, 2005; Hämäläinen *et al.*, 2017). In this way, occasionally
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5 428 harsh competitive conditions could be more effectively dealt with by more plastic types of
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7 429 individual *via* customized levels of reproduction per breeding attempt over a longer lifetime
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9 430 for which the costs of plasticity are worth paying (Fig. 2). A key question is therefore whether
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11 431 individuals are able to adjust phenotypic traits associated with different POLS types in order
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13 432 adaptively to match changes in environmental conditions, such as population density. For
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15 433 example, slower-exploring great tits survive better in years with higher population densities,
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17 434 but apparently this is not because of adaptive density-dependent plasticity, perhaps because
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19 435 population densities are difficult for the birds to predict in this system (Nicolaus *et al.*, 2016).
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21 436 In such cases, observations therefore have to be made over a sufficient range of environmental
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23 437 conditions to distinguish plastic from non-plastic strategies, because when viewed under only
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25 438 benign conditions the life histories of non-plastic fast types and plastic slow types could
26
27 439 appear the same (Fig. 2A, B; e.g. Hämäläinen *et al.*, 2017).
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29 440 Within-individual reversible plasticity in reproductive effort should result in a pace of life
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31 441 more similar to slow-type than fast-type individuals, both in the reproductive effort per
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33 442 breeding attempt and the number of breeding attempts per lifetime (Fig. 2). Indeed, the
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35 443 greater somatic investment in competitive abilities usually associated with longer density-
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37 444 dependent selected lifespans and a slow pace of life (e.g. small mammals; Chitty, 1960;
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39 445 Krebs, 2013) might also involve greater adaptive investment in the costs of plasticity, such as
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41 446 in the acquisition of information (e.g. about forthcoming competitive conditions) and in the
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43 447 ability to exhibit more plastic reproductive strategies. Plasticity is also more likely to be
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45 448 effective for slow-type individuals in populations with high density-dependent selection that
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47 449 on average experience more predictable and less stochastically variable environments. By
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49 450 contrast, in populations experiencing low density-dependent selection it would perhaps be
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51 451 more beneficial for fast types to be inflexible, save on the costs of plasticity and information
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3 452 gathering if most population variation is stochastic, and simply be fast reproducing all of the
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5 453 time given the rarity of any detrimental effects of density dependence that could be avoided
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7 454 using plasticity. Animals that have a short life span or a short remaining lifespan should be
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9 455 generally less likely to be plastic or to use learning (Kokko & Sutherland, 2001). For
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11 456 example, more-aggressive male great tits tend to be consistently less plastic (Araya-Ajoy &
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13 457 Dingemanse 2017). Therefore, within a single population POLS, fast non-plastic types will
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15 458 have been selected for at times and in places where environmental stochasticity made those
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17 459 low population densities more variable but less predictable. By contrast, slow plastic types
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19 460 will have been selected for when and where high population densities varied less but any
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21 461 variation was more predictable and thus favoured the evolution of reversible plasticity.
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23 462 Interestingly, these expected differences in plasticity between fast *versus* slow types within a
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25 463 POLS correspond very well with observations published in the animal personality literature,
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27 464 because among-individual differences in behaviour appear to be associated with individual
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29 465 differences in plasticity (Mathot *et al.*, 2012). For example, more-aggressive individuals tend
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31 466 to be less socially responsive to the levels of aggression in others (see Koolhaas *et al.*, 1999),
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33 467 and slow-exploring great tits better match their clutch size to local environmental conditions
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35 468 in the wild (Nicolaus *et al.*, 2014). Fast types within a POLS may therefore not only be more
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37 469 active and aggressive and disperse further, but they should also be more proactive superficial
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39 470 explorers and less phenotypically plastic in response to physical and social environmental
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41 471 change (e.g. Duckworth & Badyaev, 2007; Nicolaus *et al.*, 2014). This is in contrast to more
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43 472 phenotypically flexible and faster learning slow types that gather more information from more
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45 473 detailed exploration of their more predictable environments, as well as being less aggressive
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47 474 and more socially responsive in their interactions with conspecifics (Sih & Del Giudice, 2012;
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49 475 Mathot *et al.*, 2012; Nicolaus *et al.*, 2014). We therefore have good reason to expect a greater
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476 role for adaptive within-individual phenotypic plasticity in life histories (e.g. in response to
477 local population densities) towards the slow-type end of any POLS.

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

495 Following the arguments above for greater individual plasticity at the slower end of the
496 POLS, we might also expect that integrated irreversible and/or reversible plasticity explains a
497 higher proportion of life-history (co-)variation in populations or species with a history of high
498 (as opposed to low) density-dependent selection in their pace of life. This prevalence of
499 plasticity might explain the low heritabilities recorded for many life-history traits (e.g. clutch
500 size and laying date in birds; Stirling, Réale & Roff, 2002), and we would predict that this

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3 501 lack of heritability is more prevalent for life-history traits in slow types and in populations or
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5 502 species that have experienced high density-dependent selection. We therefore need studies
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7 503 that compare population-specific levels of additive genetic *versus* phenotypic (co-)variance
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9 504 caused by irreversible (i.e. developmental) or reversible plasticity in different aspects of life
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11 505 histories. In this way, the degree of plasticity within the POLS for different populations or
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13 506 species can be compared against the degree of low *versus* high density-dependent selection.
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15 507 Such plasticity in life histories can also have consequences for the eco-evolutionary dynamics
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17 508 of the system (e.g. Benton & Beckerman, 2005). More stable populations should become even
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19 509 more stable as a result of high density-dependent selection for greater integrated plasticity,
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21 510 because any density-dependent adjustments by slow pace-of-life individuals will occur *via*
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23 511 plasticity in reproductive effort (Fig. 2). Conversely, more environmentally unstable
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25 512 populations that give rise to greater selection for a faster pace of life might be expected to be
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27 513 regulated more by mortality of fast pace-of-life individuals, which will further contribute to
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29 514 the demographic instability of the system. These contrasting patterns should also be seen
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31 515 within populations at the different ends of the POLS, but it is only among populations or
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33 516 species that we might expect to see such eco-evolutionary feedbacks that exaggerate the
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35 517 effects of low *versus* high density-dependent selection.
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519 **(2) Bet-hedging (a special case of a PE-matrix POLS)**

520 Over evolutionary time, we predict that stochastic environmental effects on population
521 density will produce population- and species-specific patterns of fluctuating density-
522 dependent selection that shape life-history evolution in the form of the pace of life, with or
523 without irreversible and reversible plasticity playing a role. However, we might also expect
524 additional life-history adaptations to the immediate and detrimental effects of such stochastic
525 events on fitness in the form of bet-hedging (see Simons, 2011; Starrfelt & Kokko, 2012). The

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3 526 most commonly discussed form of bet-hedging is a strategy of ‘diversification’ that spreads
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5 527 the risk of a catastrophic loss of fitness due to unpredictable events in a single environment by
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7 528 producing (random developmental) phenotypic variation in offspring so that they occupy
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9 529 different environments in time and/or space (e.g. within-family phenotypic variation in timing
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11 530 of seed germination in plants; Simons & Johnston, 2006). However, there are also
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13 531 ‘conservative’ bet-hedging strategies that provide protection and insure against unpredictable
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15 532 loss within any single environment (e.g. early diapause in copepods in case of unpredictably
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17 533 early onset of seasonal fish predation; Hairston & Munns, 1984). In essence, bet-hedging
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19 534 involves any number of a range of phenotypic strategies that achieve an adaptive reduction of
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21 535 fitness variation among individuals or generations in order to maximize long-term geometric
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23 536 mean fitness. It should be noted that this is exactly what is achieved by using Malthusian
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25 537 fitness in Fig. 1D and formal models of fluctuating density-dependent selection (e.g. Engen *et*
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27 538 *al.*, 2013), because the continuous time measure of genotype Malthusian fitness is the
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29 539 equivalent of $\log[W]$ when measured in discrete time (under the assumption of weak
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31 540 selection), where W is arithmetic mean fitness (Crow & Kimura, 1970; Orr, 2009). So, the
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33 541 arguments above for the evolution of individual values for density-independent reproduction
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35 542 (r_0) and the slope of the negative effects of population density on fitness (γ) in the face of
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37 543 stochastic population variation involve the maximization of the appropriate measure of
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39 544 geometric mean fitness that is negatively affected by stochastic variation in fitness.
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43 545 The point here is that bet-hedging theory leads us to expect additional adaptive modification
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45 546 of life-history traits within the POLS driven by the stochasticity of fluctuating density-
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47 547 dependent selection that would strategically further reduce fitness variance in ways beyond
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49 548 simply optimizing values of r_0 and γ (Fig. 1D). For example, the threat of extinction in small
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51 549 populations may be expected to promote diversification bet-hedging in fast-type individuals,
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53 550 perhaps in the form of greater and more varied rates of dispersal within families, if there is
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3 551 sufficient spatial variation in stochastic environmental events. Conversely, minor stochastic
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5 552 variation in larger more stable populations may favour conservative bet-hedging in slow-type
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7 553 individuals (e.g. ‘sub-optimal’ clutch sizes in birds; Boyce & Perrins, 1987), because more
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9 554 cautious reproduction and even longer lifespans enable lineages to withstand more easily the
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11 555 worst effects of temporal variation in stochastic environmental events. Therefore, contrasting
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13 556 regimes of environmental stochasticity should not only affect mean population sizes and thus
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15 557 the nature of density-dependent selection (Fig. 1D), but they should also result in the
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17 558 differential evolution of diversification and/or conservative bet-hedging strategies that
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19 559 maximize overall Malthusian fitness in each type of population.
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22 560 Perhaps of more general interest here is the possibility that adaptive diversification bet-
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24 561 hedging might play a role in the generation of individual phenotypic life-history variation
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26 562 along the POLS. Unpredictable fluctuations in population sizes and thus low *versus* high
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28 563 density-dependent selection could be met by individual parents creating a range of fast *versus*
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30 564 slow offspring phenotypes with the aim of at least some of them always being suitable for the
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32 565 prevailing conditions in the next generation. We might also expect greater levels of
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34 566 diversification bet-hedging and a larger range of fast *versus* slow offspring phenotypes to be
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36 567 produced per parent in more stochastically fluctuating populations, where offspring might
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38 568 experience a wider range of possible environmental conditions as adults. The required level of
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40 569 within-parent variation in offspring phenotypes could be achieved by varying the resources
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42 570 provided to different offspring during development (e.g. food intake during development *via*
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44 571 brood hierarchies in birds). Adaptive individual strategies of asset-protection could then
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46 572 maintain these repeatable phenotypic differences among offspring throughout their lifetimes
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48 573 (*sensu* Luttbeg & Sih, 2010). One consequence here would be that POLSs will not necessarily
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50 574 involve sizable systematic genetic differences between fast *versus* slow phenotypes within the
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52 575 same population. This is because selection for diversification bet-hedging has the potential to
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3 576 generate much of the phenotypic variation between fast *versus* slow types *via* developmental
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5 577 (i.e. PE) effects within families. Indeed, one consistent result from studies of animal
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7 578 personality is that as much as half of the individual variation we see in behaviours appears to
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9 579 come from PE effects (see Dochtermann, Schwab & Sih, 2015), and this proportion can
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11 580 increase even further when behaviours are measured in the wild (e.g. Nicolaus *et al.*, 2012).
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13 581 Therefore, much of the POLS phenotypic variation observed within populations may be the
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15 582 result of integration of developmental plasticity across the different traits due to adaptive
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17 583 diversification bet-hedging producing individually variable life histories, as opposed to
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19 584 evolved genetic differences in those life histories within populations.
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22 585 Fig. 3 shows in more detail exactly how randomly fluctuating selection for different trait
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24 586 values affects the shape of the overall arithmetic and geometric mean fitness functions.
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26 587 Diversification bet-hedging in POLSs is thus an adaptive response that allows a genotype's
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28 588 range of phenotypes to follow the broad peak or ridge in arithmetic mean fitness experienced
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30 589 per generation as a result of fluctuating density-dependent selection (Fig. 3). Environmental
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32 590 (PE) phenotypic variation introduced *via* development into life-history trait values would
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34 591 allow a diversification bet-hedging genotype to occupy at least one of the many possible
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36 592 fitness peaks experienced per generation and thus avoid extinction in the long term (Bull,
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38 593 1987). Fig. 3 also suggests that spatially varying selection results in a broad peak or ridge in
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40 594 (arithmetic mean) fitness experienced by a genotype (or a whole population) when spread
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42 595 across a range of different environments at any one moment in time. This is because whilst
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44 596 fitness accumulates multiplicatively over time (i.e. geometrically – see above), it combines
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46 597 additively across space (Levins, 1962). Hence, spatially varying selection on pace of life
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48 598 would favour diversification bet-hedging in the form of even greater rates of dispersal beyond
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50 599 the individually adaptive optimum (*sensu* Delgado, Ratikainen & Kokko, 2011). Instead of
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52 600 the bet-hedging genotype spreading its individuals out among different phenotypes, by
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3 601 increasing rates of dispersal in random directions and distances it spreads its individuals out
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5 602 among different environments thereby reducing individual fitness variation and thus
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7 603 maximizing long-term geometric mean fitness.
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10 11 12 604 **(3) Evolution of genetic (co-)variation (G-matrix POLSs)**

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14 605 While fluctuating density-dependent selection has the potential to generate a POLS *via*
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16 606 adaptive plasticity or *via* increased phenotypic variation due to diversification bet hedging
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18 607 (see above), the expected effect of fluctuating selection in increasing genetic variation along a
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20 608 POLS is less clear. In general, stronger stabilizing selection selects for lower phenotypic and
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22 609 genetic variance in a trait (Layzer, 1980; Lande & Arnold, 1983). However, additive genetic
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24 610 variance can increase, decrease or be left unchanged by fluctuating selection, depending upon
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26 611 its periodicity and amplitude, the shape of the fitness function and the effect sizes of
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28 612 underlying loci (Bürger, 1999; Bürger & Gimelfarb, 2002; Le Rouzic, Alvarez-Castro &
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30 613 Hansen, 2013). Interestingly, for a Gaussian-shaped fitness function there should be no effect
31
32 614 at all of fluctuating selection on the selection experienced by the population and therefore on
33
34 615 the amount of additive genetic variance in the population (see Fig. 3). The results in Fig. 3 are
35
36 616 derived using non-overlapping generations, whilst fluctuating selection in combination with
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38 617 overlapping generations generally selects for increased genetic variation (Ellner & Hairston,
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40 618 1994).

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44 619 The actual relationship between patterns of selection and changes in genetic variation is,
45
46 620 however, likely to be even more complex since it also depends upon the particular genetic
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48 621 architecture (Bürger, 2000; Hermisson, Hansen & Wagner, 2003; Carter, Hermisson &
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50 622 Hansen, 2005). In fact, models that include non-additive (epistatic) genetic effects show that
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52 623 increasing levels of fluctuating selection lead to increasingly de-canalized genotypes (i.e.
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54 624 larger mutational effects due to less canalizing epistasis), and hence to increased additive
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3 625 genetic variance (Kawecki, 2000; Le Rouzic *et al.*, 2013). Interestingly, Le Rouzic *et al.*
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5 626 (2013) do not interpret this increase in genetic variance as an adaptation to fluctuating
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7 627 environments, even when it is favourable for the population in terms of greater evolvability
8
9 628 along the line of the fluctuations in selection. Instead, they interpret the fluctuations as a
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11 629 disruptive force on normally adaptive genetic canalization that arises from stabilizing
12
13 630 selection towards the peak of a stationary fitness function. In an artificial selection experiment
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15 631 over 20 generations, Pélabon *et al.* (2010) showed that both stabilizing and fluctuating
16
17 632 selection slightly decreased genetic variation relative to control populations. However,
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19 633 because we do not expect genetic canalization to evolve on the timescales of such artificial
20
21 634 selection experiments this is could still be seen as consistent with theoretical predictions.
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23
24 635 Therefore, we expect long-term fluctuating density-dependent selection to result in the genetic
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26 636 de-canalization of life-history traits, and it is this process that would create the expected major
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28 637 axis of genetic (co-)variation along the POLS in multivariate trait space, as illustrated in
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30
31 638 Fig.4. Again, this process is predicted to be greater in fast-type populations that have
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33 639 experienced greater long-term stochastic fluctuations in population density, and we might
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35 640 therefore expect greater genetic variance along POLSs in fast-type populations or species.
36
37 641 An important consideration for the types of comparisons in Fig. 4 at the within-population
38
39 642 level is that genetic correlations among life-history traits due to trade-offs can often be
40
41 643 masked at the phenotypic level because individuals differ in resource acquisition (van
42
43 644 Noordwijk & de Jong, 1986; Houle, 1991; Stearns, 1992; Reznick, Nunney & Tessier, 2000).
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45
46 645 The predicted among-individual covariation between r_0 and γ or other pairs of life-history
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48 646 traits underlying the POLS (see Fig. 4), might therefore only be apparent once individual
49
50 647 differences in resource acquisition have been statistically controlled [e.g. Santostefano *et al.*
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52 648 (2017) in the context of POLS research]. For example, it might be possible to use within-
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54 649 population variation in lifetime reproductive success (*LRS*) as a proxy for individual resource
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3 650 acquisition. Among species (see below, Fig. 5), however, this second axis of variation is less
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5 651 of an issue, as we expect differences in resource acquisition to be minimal at the species level.
6
7 652 Wagner (1996) suggested that pleiotropic links between functional traits evolve through a
8
9 653 combination of fluctuating directional selection and stabilizing selection in order to
10
11 654 accommodate the independent evolution of each trait combination or ‘module’. This verbal
12
13 655 model suggests the evolution of pleiotropy within a POLS module composed of all the traits
14
15 656 affected by fluctuating low *versus* high density-dependent selection. From this, we expect the
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17 657 **G**-matrix to reflect this pleiotropy as a high degree of genetic covariance in multivariate trait
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19 658 space (Fig. 4). Following the arguments above regarding plasticity, we might also expect a
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21 659 greater role for pleiotropy as captured by the **G**-matrix towards the fast-type end of any POLS
22
23 660 within populations, and thus genetic (co)variance to play more of a role in POLSs in more
24
25 661 fast-type populations as a whole. This is because of the relatively greater role predicted for
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27 662 integrated plasticity and the **PE**- and **E**-matrices towards the slow-type end of any POLS
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29 663 within and among populations or species. As Fig. 4 illustrates, we expect high genetic and
30
31 664 phenotypic variation along the ridge in arithmetic mean fitness created by fluctuating density-
32
33 665 dependent selection. The genetic variation generated by fluctuating density-dependent
34
35 666 selection, plus any phenotypic plasticity and diversification bet-hedging (see Section IV.2), is
36
37 667 expected to facilitate rapid and adaptively coordinated changes along the POLS major axis in
38
39 668 life-history trait co-variation within and among populations and/or species (Figs 4 & 5).
40
41 669 However, only in the case of POLS driven by plasticity and diversification bet-hedging (see
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43 670 Sections IV.1 and IV.2 above) could the increased speed of this phenotypic change be
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45 671 considered ‘adaptive’ at the individual level (*sensu* Le Rouzic *et al.*, 2013).
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673 (4) Evolution among species/populations (the **D**-matrix POLS)

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3 674 The POLS fluctuating density-dependent selection hypothesis further predicts that phenotypic
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5 675 and genetic variation among populations (or species) will be arranged according to the
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7 676 distribution of fitness peaks for the different populations along this same major axis of
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9 677 fluctuating low *versus* high density-dependent selection. Variation in the nature of density-
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11 678 dependent selection among populations or species will create a distribution of fitness peaks
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13 679 along a line (not necessarily linear) in multivariate trait space, because populations/species
14
15 680 will differ in their optimum combinations of r_0 and γ , and therefore in trait means that are
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17 681 favoured depending on their average level of low *versus* high density-dependent selection
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19 682 (Fig. 5). Population or species means will evolve towards these optima and thereby create a
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21 683 pace of life axis of variation among populations/species along this dimension (Fig. 5), thus
22
23 684 explaining the results of the many comparative studies showing a pace-of-life continuum for
24
25 685 various taxa [birds (Sæther, 1987; Sæther & Bakke, 2000), mammals (Gaillard *et al.*, 2005;
26
27 686 Oli, 2004; Bielby *et al.*, 2007), fish (Goodwin *et al.*, 2006; Bjørkvoll *et al.*, 2012), reptiles
28
29 687 (Bauwens & Diaz-Uriarte, 1997), insects (Johansson, 2000) and plants (Adler *et al.*, 2014;
30
31 688 Salguero-Gómez *et al.*, 2015)]. Increased genetic variation along the pace-of-life axis due to
32
33 689 fluctuating selection (see above) would facilitate such among-population divergence. In
34
35 690 effect, we would expect a generally similar alignment of the pace-of-life continuum among
36
37 691 species/populations to the POLS axes at the within-population level. However, on shorter
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39 692 timescales any POLS evolution within populations and any population divergence will be
40
41 693 strongly affected by the specific pattern of genetic variances and covariances in the **G**-matrix
42
43 694 (Lande, 1979; Schluter, 1996; Bolstad *et al.*, 2014).
44
45 695 Different populations (or species) at different places along a pace-of-life continuum should
46
47 696 also experience different patterns in eco-evolutionary feedbacks. For fast-type populations or
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49 697 species with high intrinsic rates of reproduction (r_0) there will be consequences of any
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51 698 predicted greater rates of dispersal. Assuming for simplicity that such dispersal is essentially
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3 699 random and undirected, and does not involve habitat matching (*sensu* Edelaar, Siepielski &
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5 700 Clobert, 2008), meta-populations (such as that illustrated in Fig. 5) containing greater
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7 701 proportions of fast-type sub-populations might be expected to be more connected genetically
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9 702 and demographically in space, but any local adaptation at the sub-population level will be
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11 703 slowed by the degree of spatial variation in selection pressures. Conversely, the meta-
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13 704 population dynamic feedbacks for collections of slow-type sub-populations will be reduced in
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15 705 scale by lower rates of dispersal in favour of reproductive plasticity and the strategy of
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17 706 waiting until conditions improve, facilitated by potentially longer lifespans. Meta-populations
18
19 707 containing more of the less-dispersive slow types may therefore be less connected genetically
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21 708 and demographically in space, and so should evolve faster to their local optima (in plasticities
22
23 709 as well as mean character values) due also to the dampening of random temporal fluctuations
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25 710 in population sizes and selection pressures *via* greater phenotypic plasticity, conservative bet-
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27 711 hedging and more cooperative social structures.
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33 713 **V. TESTING THE PREDICTIONS**

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35 714 The arguments made above have been accompanied in most cases by a considerable amount
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37 715 of circumstantial evidence from a range of fields in support of the idea that fluctuating
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39 716 density-dependent selection is responsible for generating the POLSs we observe within and
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41 717 among populations/species. However, relatively few studies have yet directly to address the
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43 718 types of research questions that critically test the main ideas presented herein. For example,
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45 719 there is very little literature assessing whether the behavioural or physiological position of
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47 720 fast- *versus* slow-type individuals along a POLS is linked with the kinds of negative effects
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49 721 experienced in density-dependent competition (i.e. γ). Three studies (cited repeatedly above)
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51 722 are extremely relevant here because they have most clearly investigated this question using
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53 723 observational data from wild populations of bluebirds (Duckworth, 2006, 2008; Duckworth &
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3 724 Badyaev, 2007; Duckworth & Kruuk, 2009; Duckworth *et al.*, 2015) and great tits (Nicolaus
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5 725 *et al.*, 2013, 2014, 2016; Araya-Ajoy *et al.*, 2016*a,b*) or experimental manipulations under
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7 726 semi-wild conditions of common lizards (Cote & Clobert, 2007; Cote *et al.*, 2008).
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9 727 Specifically, the notion that sociable individuals do best under high densities because they are
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11 728 more socially responsive and efficiently cooperative is implied by the results from bluebirds
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13 729 (Duckworth *et al.*, 2015). This model system also provides some of the best evidence that
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15 730 aggressive individuals are more dispersive, do best in low-density environments but do very
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17 731 poorly in high-density environments, because they are poor parents that are easily
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19 732 outcompeted by unaggressive phenotypes (Duckworth, 2006, 2008; Duckworth & Badyaev,
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21 733 2007; Duckworth & Kruuk, 2009; Duckworth *et al.*, 2015). As predicted, slow less-aggressive
22
23 734 types of great tits explore their environment more slowly and are therefore more plastic and
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25 735 sensitive to environmental conditions when adjusting their clutch size in the wild (Nicolaus *et*
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27 736 *al.*, 2013, 2014). These slow explorers also experience increased annual survival rates under
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29 737 high densities (Nicolaus *et al.*, 2016), whilst aggressive fast-type males lose more paternity
30
31 738 when competition for extra-pair paternity increases in high-density populations (Araya-Ajoy
32
33 739 *et al.*, 2016*a,b*). In addition, Cote & Clobert (2007), and Cote *et al.* (2008) show that ‘social’
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35 740 common lizards that like to be with others (as opposed to ‘asocial’ individuals that prefer
36
37 741 being alone) are favoured (*via* survival selection) under high (*versus* low) population
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39 742 densities, and that these types also prefer to disperse into high- (*versus* low-)density
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41 743 populations. All of which suggests that when we do have access to information concerning
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43 744 density-dependent selection on suites of relevant traits they seem to conform to the
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45 745 predictions of the fluctuating density-dependent selection POLS hypothesis.
46
47 746 The main aim of this review is to encourage further studies of this type and more specifically
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49 747 into the role of fluctuating density-dependent selection in generating POLSs by outlining this
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51 748 specific hypothesis, its various predictions and the methods that could be used to assess them
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3 749 critically. Table 1 outlines a series of falsifiable predictions arising from the hypothesis that
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5 750 fluctuating density-dependent selection drives the evolution of POLSs within populations and
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7 751 pace-of-life continuums among species. We now provide an overview of methods that can be
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9 752 used to test critically several of these predictions.

10
11 753 Our main prediction is that the variation in trait optima caused by variation in low *versus* high
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13 754 density-dependent selection within or among populations and species will have generated an
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15 755 axis in trait space with large amounts of variation at all levels (Table 1). To test this
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17 756 prediction, we first need to identify the axis in trait space where we expect increased variation
18
19 757 due to greater variation in density-dependent selection. Second, we need to measure the
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21 758 variation along this axis and compare it to other axes of trait variation. The axis of interest is
22
23 759 the direction in multivariate trait space from the optimal phenotype under selection for fast
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25 760 types to the optimal phenotype under selection for slow types given by

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

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31 761 where $\theta_K = [z_1, z_2, \dots, z_n]$ is a vector of trait values optimal at the slow end of the POLS axis,
32
33 762 and θ_r is an optimal trait vector at the fast end of the POLS axis.

34
35 763 Among populations and species, optimal trait values can be found by using the ‘optimal
36
37 764 regression’ (Hansen, Pienaar & Orzack, 2008) with differences among taxa in the nature of
38
39 765 density-dependent selection as the explanatory variable, or by using standard linear regression
40
41 766 (if there is little phylogenetic signal in the residuals). Differences among taxa in the nature of
42
43 767 density-dependent selection can be quantified by using their mean population size relative to
44
45 768 K (carrying capacity). However, accurate estimates of K are often lacking, particularly for
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47 769 taxa with low population densities (i.e. that are further from K) and thus under low density-
48
49 770 independent selection for fast types. In such cases, we suggest that the relative scale of any
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51 771 stochastic fluctuations in population size can be used as a proxy measure of the nature of
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772 density-dependent selection from low to high, because populations with more or greater
773 fluctuations will be subjected to more low density-dependent selection (Engen *et al.*, 2013).
774 For POLSs within populations, there are numerous statistical methods for finding optimal trait
775 values using fitness regressions (e.g. Lande & Arnold, 1983; Schluter, 1988; Morrissey, 2014;
776 Chevin, Visser & Tufto, 2015). These methods have to be carried out at a range of different
777 population densities, or modified to include an interaction between population density and
778 trait values, to estimate optimal trait values at different population densities (e.g. the elegant
779 statistical method to estimate optimal clutch sizes as a function of population density in great
780 tits used by Sæther *et al.*, 2016). However, in many systems it may prove challenging to
781 identify optimal trait values using the methods cited above, particularly for a high number of
782 traits. Hence, a comparative method using ‘optimal regression’ among populations may be
783 more powerful for obtaining $\Delta\theta$. This seems to be a good substitute, but requires the critical
784 assumption that the distribution of optima created by fluctuations from low to high density-
785 dependent selection within populations and the differences in average level of density-
786 dependent selection among populations are aligned, as predicted by our POLS fluctuating
787 density-dependent selection hypothesis, or that any heterogeneity among populations needs to
788 be estimated as part of the model and taken into account.

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

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3 796 fluctuating density-dependent selection can be compared relative to other directions among
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5 797 these matrices.
6
7 798 A second prediction is that phenotypic variation along the POLS axis is expected to be lower
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9 799 in more slow-type populations or species compared with more fast-type ones, due to
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11 800 differences in the scale of stochastic fluctuations in population density (Table 1). In other
12
13 801 words, the POLS is expected to be more pronounced in fast- than slow-type populations or
14
15 802 species. This prediction can be tested by comparing the variances along $\Delta\theta$ in **P**-matrices
16
17 803 among populations/species experiencing different levels of density-dependent selection. One
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19 804 issue here concerns the contribution of differences in genetic *versus* environmental variation
20
21 805 to this effect among population or species, because it is often difficult to know the rate of
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23 806 evolution for **G**, **P**, **PE** or **E** matrices. This effect might therefore only be apparent in cases of
24
25 807 long-term evolutionary differences in low *versus* high density-dependent selection among
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27 808 populations or species (see Section IV.3 above). Therefore, comparisons of populations
28
29 809 within the same species may not provide the predicted patterns if the populations are likely to
30
31 810 have shifted relatively recently between different regimes of low *versus* high density-
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33 811 dependent selection differing in background levels of environmental stochasticity.
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36
37 812 A third prediction is that POLS fast-type individuals will have higher r_0 values and higher
38
39 813 γ values compared with slow-type individuals from within the same population (Table 1). We
40
41 814 already know that behaviourally fast types tend to show greater reproductive output per
42
43 815 breeding attempt, presumably reflecting higher r_0 values (Biro & Stamps, 2008; Smith &
44
45 816 Blumstein, 2008). However, the link between r_0 values and the corresponding γ values is less
46
47 817 often quantified (but see the three main example systems discussed above). This can be tested
48
49 818 using the same regression techniques as above, and by including an interaction term among
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51 819 trait values and population density. This is because each trait value combination will be
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53 820 associated with a particular r_0 and γ in such a model, and the optimal trait values at low and
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3 821 high population densities will also be apparent. Sæther *et al.* (2016) confirmed this prediction
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5 822 in that fast-type female great tits laying large clutch sizes had higher r_0 and a subsequently
6
7 823 higher γ . In systems where it is possible to collect repeated measures of reproductive success,
8
9 824 individual estimates of r_0 and γ will be possible to obtain. One can then statistically
10
11 825 decompose variation in r_0 and γ into the respective **G**-, **PE**- and **E**-matrices, and then
12
13 826 investigate the relationship between different life-history, behavioural, physiological and
14
15 827 morphological traits and r_0 and γ at these different levels using path analyses (see Fig. 6).
16
17 828 Because of the trade-off between r_0 and γ , we expect these different traits to contribute in the
18
19 829 opposite direction to r_0 than γ (i.e. a negative effect on one and a positive effect on the other;
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21 830 see Fig. 6). Again, because of individual differences in resource acquisition, this trade-off
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23 831 may be masked unless variation in resources can be controlled – see above (van Noordwijk &
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25 832 de Jong, 1986; Houle, 1991; Stearns, 1992; Reznick *et al.*, 2000).
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32 833 VI. CONCLUSIONS

33
34 834 (1) We argue that observed patterns of variation in fast *versus* slow life histories within and
35
36 835 among species are the result of fluctuations in low *versus* high density-dependent selection.
37
38 836 Such patterns of selection in turn cause a particular pattern of covariation, or pace-of-life
39
40 837 syndrome (POLS), involving covariances among life history, morphological, physiological
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42 838 and behavioural traits. POLSs are expected at different levels of the demographic hierarchy:
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44 839 among species, among populations within species, and among (geno)types or individuals
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46 840 within populations.
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48 841 (2) Species and populations experiencing higher levels of stochastic variation in population
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50 842 densities and lower density-dependence should evolve a faster pace of life in order to
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52 843 maximize Malthusian fitness. Threat of extinction in such small fast-type populations may
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3 844 also favour diversification bet-hedging in the form of increased dispersal, ensuring genotype
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5 845 survival by spreading offspring out among different environments.

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7 846 (3) Among and within species and populations, the orientation of the major axis of phenotypic
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9 847 (co-)variation (the POLS) is predicted to align with the multivariate fitness landscape created
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11 848 by stochastic fluctuations in population density and low *versus* high density-dependent
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13 849 selection.

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15 850 (4) Within populations, POLSs are expected to reflect genetic differences in life histories, as
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17 851 they do among populations or species. However, POLS within populations could also result
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19 852 from the integration of developmental plasticity producing adaptive variation in individual
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21 853 life histories in response to both predictable and unpredictable variation in population
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23 854 densities.

24
25 855 (5) Within individual lifetimes, predictable variation in population densities should result in
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27 856 adaptive reversible plasticity in individual density-dependent reproductive expenditure during
28
29 857 different breeding attempts. Such integrated reversible plasticity in multiple traits will thus
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31 858 move individuals around during their lifetime within the POLS. This phenomenon of a POLS
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33 859 driven by within-individual phenotypic variation is expected to be more prevalent at the slow-
34
35 860 selected end of the POLS and in species with a slow pace of life, where investment in the
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37 861 costs of plasticity and acquisition of information is expected to be of more use during longer
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39 862 lifespans spent in more predictable environments.

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24 **Table 1.** A list of falsifiable predictions arising from the fluctuating density-dependent
25
26 selection pace-of-life syndrome (POLS) framework for the evolution of life histories and
27
28 associated phenotypic traits, and the section(s) within which they are discussed in this
29
30 review.
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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

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60879 **Figure Legends**

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

894

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

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3 904 (μ). Predicted lines are shown for fast (orange), plastic (dashed purple) and slow (green) types
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5 905 (i.e. three different genotypes or classes of individual sharing the same life-history
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7 906 phenotype), with points indicating mean values along what would actually be a pace-of-life
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9 907 continuum. See text for further explanation.
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13 909 **Fig. 3** Illustrations of fluctuating Gaussian selection (in black) on hypothetical trait values,
14 910 and the resulting arithmetic (in red) and geometric (in blue) mean fitness functions for non-
15 911 overlapping generations. The top panels show examples with more widely spaced
16 912 fluctuations. Patterns in absolute fitness are shown on the left and relative fitness on the right.
17 913 While both the maximum and width of the arithmetic mean fitness function are affected by
18 914 the fluctuations, only the maximum absolute geometric mean fitness is affected. The width of
19 915 the geometric mean fitness function (in blue) is the same as the fluctuating fitness functions
20 916 themselves (in black). Therefore, the relative geometric mean fitness function (scaled by
21 917 maximum fitness) is exactly equal to the fluctuating fitness function itself.
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35 919 **Fig. 4** Illustration of covariation and correlated selection between two of the expected
36 920 multiple life history (morphological, physiological or behavioural) traits (z_1 and z_2), which
37 921 could also represent r_0 and γ from Fig. 1D. (A) Fluctuations in the position of Gaussian fitness
38 922 surfaces (grey) create a ridge of arithmetic mean fitness surface (red), but do not affect the
39 923 geometric mean fitness surface (blue) – see Fig. 3 – producing a potential pace-of-life
40 924 syndrome (POLS) dashed two-headed arrow varying from fast types resulting from low
41 925 density-dependent selection (orange) to slow types resulting from high density-dependent
42 926 selection (green), plus possible frequency-dependent selection. (B) Imposed on A, individual
43 927 phenotypes (open blue squares), with the purple two-headed arrow indicating the major axis
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928 of phenotypic trait covariation (\mathbf{P}_{\max}), and the black two-headed arrow the major axis of
929 genetic covariance (\mathbf{G}_{\max}). POLS, pace-of-life syndrome. See text for more detail.

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

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

Figure 1

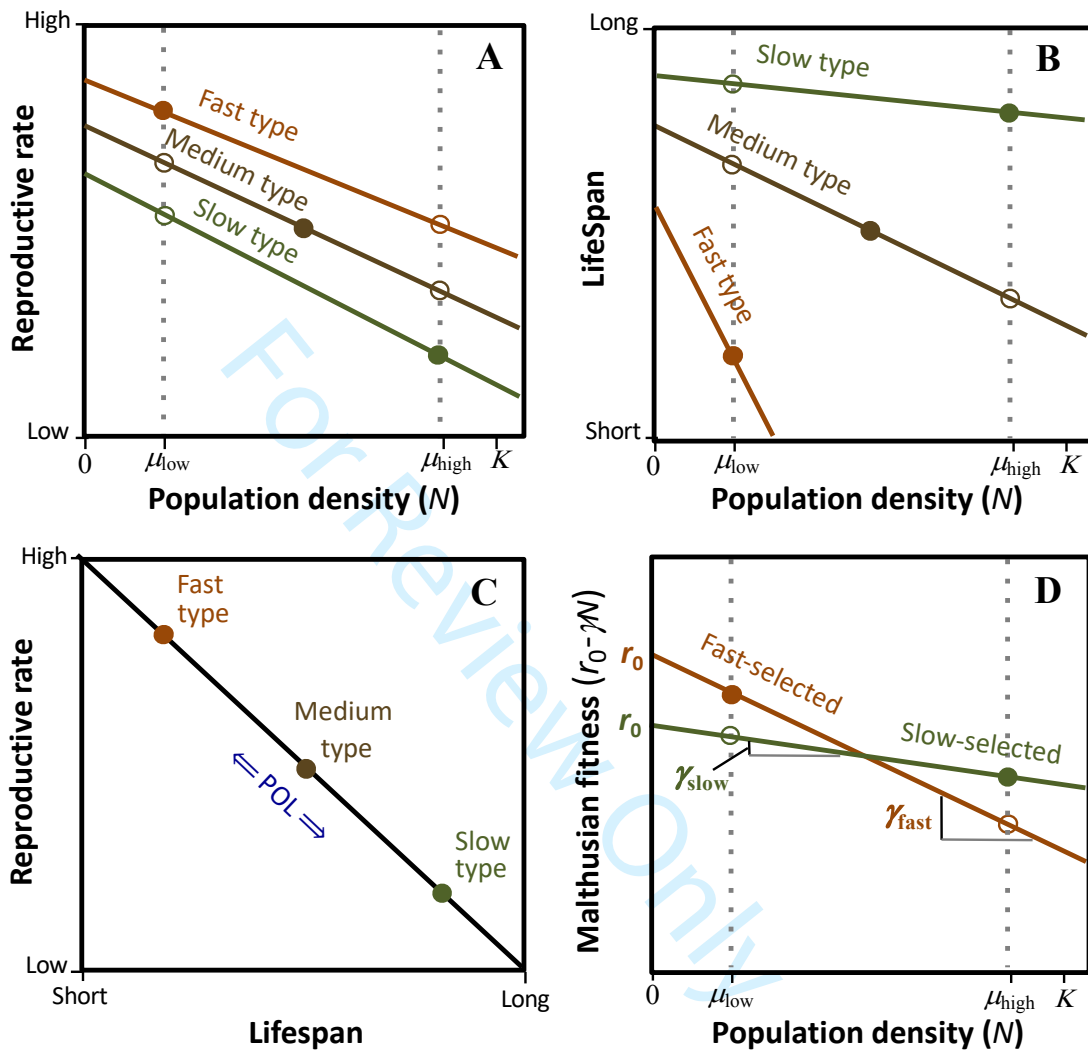
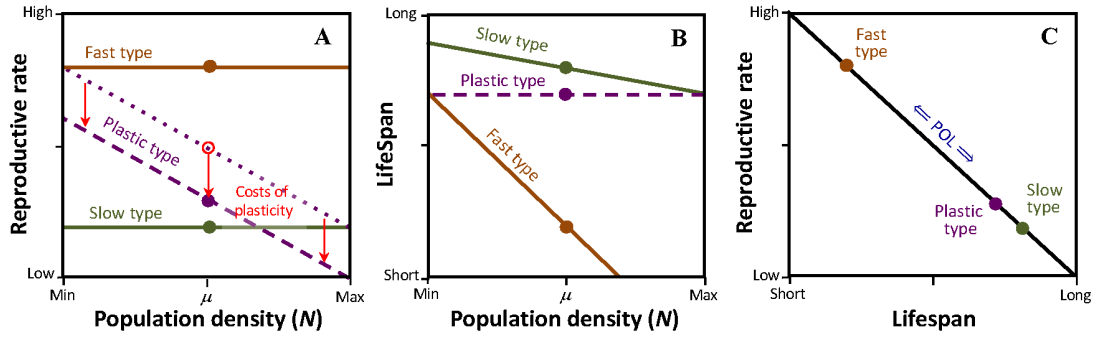
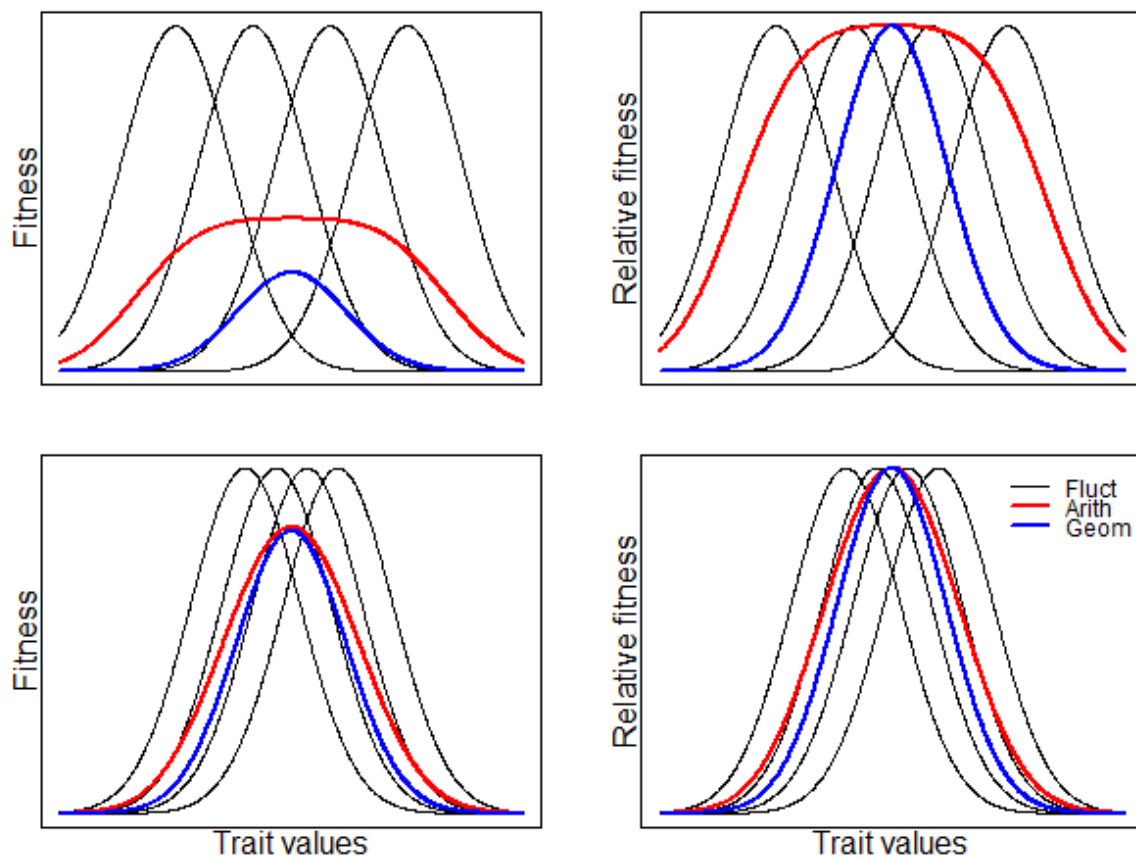


Figure 2



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Figure 3



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Figure 4

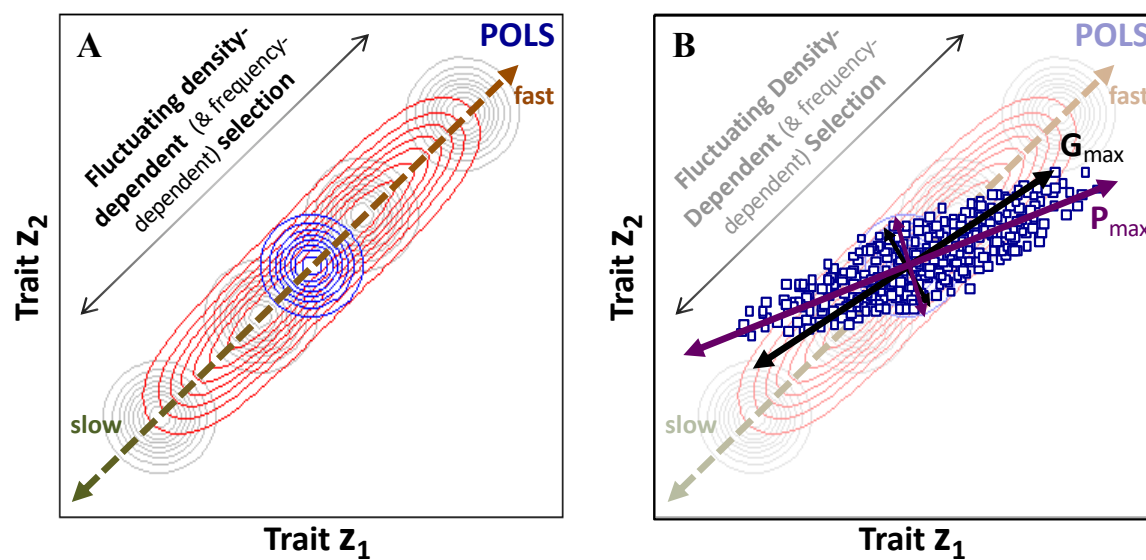


Figure 5

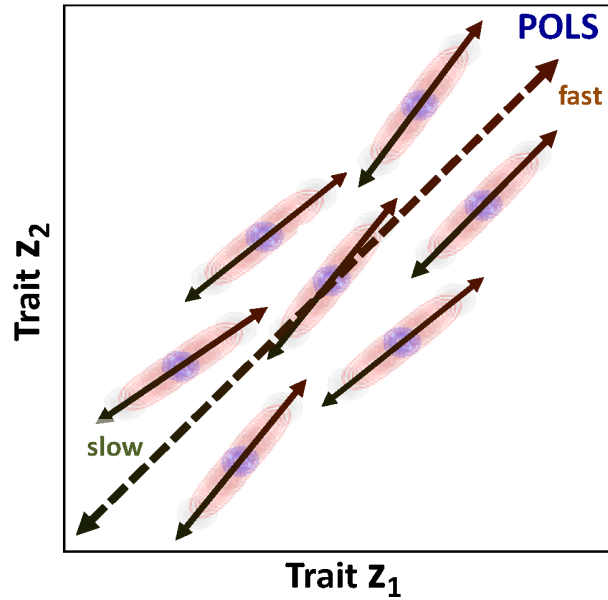
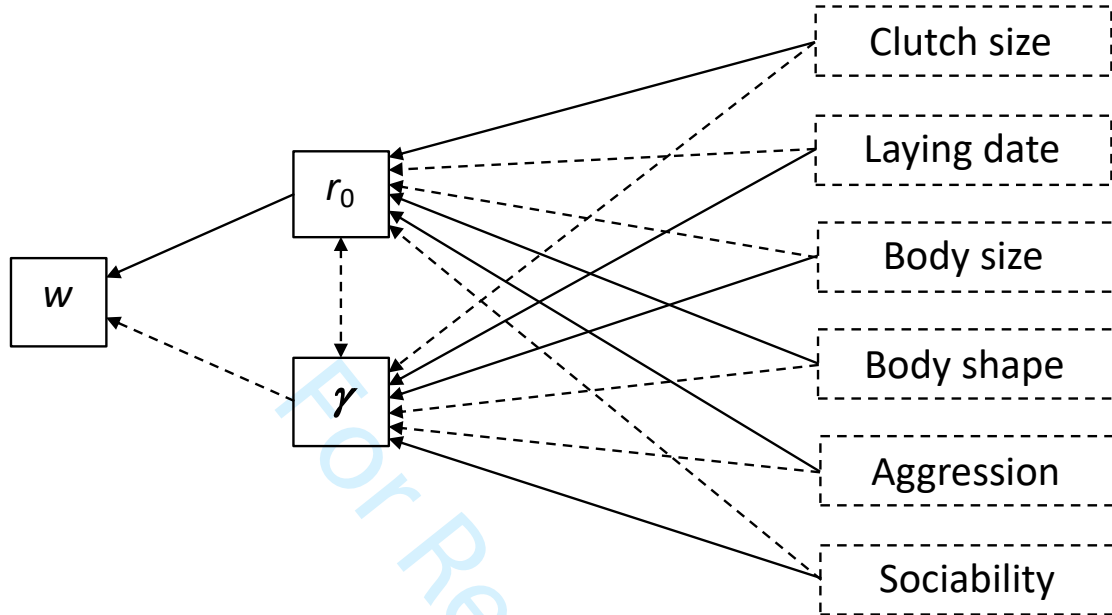


Figure 6



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