Environmental effects on the covariation among pace-of-life traits

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1. Introduction

Much life-history variation falls along a slow-fast continuum, with a low reproductive rate, slow development and long lifespan at the slow end of the continuum and opposing traits at the fast end. Variation in these life-history strategies is commonly referred to as the pace-of-life (POL) (Ricklefs & Wikelski, 2002). Environmental variability is thought to play a major role in the evolution of such life-history variation (Hastings & Caswell, 1979; Koons, Pavard, Baudisch, & Metcalf, 2009; Metcalf & Koons, 2007) by determining the optimal allocation of resources into reproductive investment relative to self-maintenance. Consequently, the variance and covariance of different life-history traits depends on the environmental variation (Sgrò & Hoffmann, 2004; Via & Lande, 1987). The same ecological selective pressures may lead to the emergence of suites of physiological and behavioural traits that maximize fitness by facilitating optimal reproduction-survival allocation under certain environmental conditions (Ricklefs & Wikelski, 2002). Appropriate behavioural tendencies could be important for matching the life-history pace to the environmental conditions because behavioural responses to novel conditions can facilitate faster adaptation. The pace-of-life syndrome (POLS) hypothesis has been proposed as an integrative framework to explain the resulting patterns of trait covariation (Réale et al., 2010).

The POLS framework predicts that a high investment in current reproduction is paired with risk-prone behaviours such as high activity and aggression at the fast end of the continuum and that high investment into later reproduction is coupled with risk-averse behaviours at the slow end of the continuum (Réale et al., 2010). Behavioural traits could mediate life-history trade-offs through correlative selection or genetic and/ or hormonal pleiotropy acting on behavioural, physiological and life-history traits (Réale et al., 2010; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007).

Environmental conditions can be presumed to play a critical role in generating and maintaining (co)variation in traits closely associated with life-history trade-offs. Many studies testing the POLS hypothesis to date have lacked an appropriate environmental context, which could contribute to the equivocal empirical evidence for trait associations conforming to the predictions of pace-of-life syndromes (Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018; Royauté, Berdal, Garrison, & Dochtermann, 2018; Tieleman, 2018).

The effects of the environment on the phenotype are complex. They depend on the specific ways in which certain environmental characteristics affect different types of organisms at different life stages. Despite this complexity, general scenarios can be derived from the typical effects of specific ecological conditions on life history and behavioural traits to structure the testing of hypotheses on POLS. Here, we generated a set of testable hypotheses on the environmental effects on covariances of behavioural and life-history traits and evaluated support for these hypotheses in the literature (description of a systematic review in the Supplementary material). We highlight knowledge gaps and promising directions for future research into POLS in the environmental context.

2. Hypotheses on the effects of environmental conditions on trait covariances (POLS) and evidence from the literature

We provide a framework for addressing the broad effects of the environment on POLS trait covariances in Table 1, with each of the hypotheses developed in more detail below. We focus on the overall predictability and harshness of the environment and life-stage at which environmental cues or constraints should have profound effects and evaluate how salient features of the study organism could influence the outcome for the detection of predictable associations between behavioural and life-history traits. We outline findings from empirical work on the POLS-environment interactions to evaluate support for each hypothesis, summarized in Table 2. We then highlight knowledge gaps that at present limit the full testing of our hypotheses.

Table 1. Hypotheses on the effects of ecological factors and intrinsic organizing mechanism that might affect POLS structure.

	Ecological or organizational factor:	**Hypothesis:**
H1	Environmental harshness	POLS only emerges under harsh environmental conditions.
H2	Environmental predictability	POLS may be more likely to emerge in stable or predictably fluctuating environments; in unpredictable, stochastic environments, reversible plasticity may be favoured over a fixed strategy, reducing selection for POLS.
H3	Life stage	Environmental conditions can alter POLS when experienced in early life but not in adulthood, because irreversible plasticity generally acts in early life, during (pre- or early post-natal) developmental sensitive periods.
H4	Type of organism	Effects of specific environmental factors on POLS depend on whether the study species is endotherm vs. ectotherm or invertebrate vs. vertebrate, as the life-history strategies and primary physiological/behavioural mechanisms differ.

H1: Environmental harshness.

Hypothesis: POLS should primarily be detected under unfavourable environmental conditions.

Environmental favourability vs. harshness can be expected to influence trait covariances between life history and behaviour, with favourability defined broadly as the degree of average fitness effect or energetic demands posed by the condition. Recent theory suggests that unfavourable environments will increase phenotypic trait variances and that individuals with a higher condition-dependence should be affected more by increasing environmental unfavourability (O’Dea, Noble, Johnson, Hesselson, & Nakagawa, 2016). For example, risk-prone, fast-paced individuals are usually expected to outcompete risk-averse, slow-paced individuals in growth and reproduction at the expense of survival. However, risk-taking may only influence survival in harsh or risky environments, such as under high predation pressure. Hence, a correlation between survival and risk-taking may be masked under benign, low-risk environments where risk avoidance does not bring a survival advantage (Dammhahn et al., 2018; Piquet, López-Darias, van der Marel, Nogales, & Waterman, 2018; Salzman, Mclaughlin, Westneat, & Crowley, 2018). Condition-dependence might, thus, also be higher in “fast-paced” individuals because they usually depend more strongly on access to resources for rapid growth and fast reproduction (Biro & Stamps, 2008; Stamps, 2007).

Resource acquisition constraints can have adverse effects on traits such as growth, metabolic rates or developmental time, while simultaneously amplifying their associations with correlated behavioural traits (Campos-Candela, Palmer, Balle, Álvarez, & Alós, 2019; Careau, Buttemer, & Buchanan, 2014; Dirienzo & Montiglio, 2016). More broadly, exposure to moderate environmental stressors tends to amplify or reveal hidden trait correlations (Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013). Together, the theoretical and empirical work suggests that POLS should be stronger in unfavourable environments.

Current evidence

The effect of environmental favourability on the emergence or strength of POLS has been tested in multiple studies. “Unfavourable” environments studied include high temperature (Goulet, Ingley, Scharf, & Pruitt, 2016), pesticide exposure (Debecker, Sanmartín-Villar, de Guinea-Luengo, Cordero-Rivera, & Stoks, 2016), and inter-group conflict (Međedović, 2018), resource acquisition constraints and predation risk (see below). While studies have often reported an effect of favourability, no overarching patterns have emerged (Table 2).

Food abundance affected POLS in two studies: Liu & Fu (2017) found growth rate to correlate with boldness under low but not under high food availability and Závorka, Aldvén, Näslund, Hjesjö, & Johnsson (2015) found the association between growth rate and activity to depend on home range size, a proxy of resource abundance. The level of resource competition often increases with increasing population density, potentially with stronger effects on fast-paced individuals (Begon, Mortimer, & Thompson, 1996; Gurevitch, Morrison, & Hedges, 2000). When tested directly, population density influenced POLS in one study (Le Galliard, Paquet, & Mugabo, 2015), but no effect was found in another (Závorka et al., 2015).

Predation can act as a selective force that simultaneously influences the behaviour, physiology and life-history traits of individuals (e.g. Creel & Christianson (2008). Furthermore, behavioural trade-offs between avoiding predation and acquiring resources are strong candidates for inducing changes in POLS (Biro & Stamps, 2008; Stamps, 2007) as risk-prone behaviours may allow individuals to acquire many resources but simultaneously increase predation risk (Wilson, Clark, Coleman, & Dearstyne, 1994, but see Harris, Ramnarine, Smith, & Pettersson, 2010). The evidence for an effect of predation risk on POLS, however, remains inconclusive. An effect of the immediate predator environment on POLS was suggested by an association between dispersal, boldness and sociability of mosquitofish that was found only when fish encountered a predator cue (Cote, Fogarty, Tymen, Sih, & Brodin, 2013). However, the study did not address possible selective mortality due to predation or whether the treatment induced stable changes in behaviour. In contrast, Fu, Fu, Wu, & Cao (2017) found no indication that the likelihood of predation during development influenced trait associations. Similarly, Schuett et al. (2015) found no direct effect of the predator presence on any traits measured, or trait covariances in pea aphids, *Acyrthosiphon pisum*. Yet, aphid color morphs differed in the link between behaviour (escape response) and life-history. Links were only present in the red morph that is more susceptible to predation (Harmon, Losey, & Ives, 1998; Losey, Ives, Harmon, Ballantyne, & Brown, 1997), and experience stronger life-history trade-offs between early reproduction and lifespan (Schuett et al., 2015). Committing to a predictable POLS might thus pay off when there are strong life-history trade-offs induced by environmental conditions experienced by the individual (i.e. for red aphids).

Although several studies found POLS to be influenced by environmental favourability, it remains unclear whether POLS is more likely to be observed under favourable or unfavourable conditions. In line with our prediction, four studies found evidence for trait correlations between life history and behaviour only under harsh environmental conditions. In contrast, two studies found evidence for POLS only under benign conditions and one study found no effect of the environment on trait correlations. Finally, two studies found diverging patterns of environmental impact on bold vs. shy individuals or morphs differing in predator susceptibility. The presence of POLS presumably depends on the environmental history of the population, the potential to avoid unfavourable environments for example via dispersal, diapause, eclosion or hibernation, or the temporal scale of the environmental perturbation (e.g. Wang & Bradburd, 2014, see also Montiglio et al., 2018), which present promising avenues for further investigation.

H2: Environmental predictability.

Hypothesis: POLS is more likely to emerge in stable or predictably fluctuating environments.

The predictability and variability of the environment have been proposed as important determinants of life history as well as POLS (Hoogenboom, Armstrong, Groothuis, & Metcalfe, 2013; Langenhof & Komdeur, 2018; Padilla & Adolph, 1996; Reed, Waples, Schindler, Hard, & Kinnison, 2010; Tuljapurkar, Gaillard, & Coulson, 2009; Wright, Bolstad, Araya-Ajoy, & Dingemanse, 2019). In predictable environments, behaviours associated with resource monopolization such as high activity and high aggressiveness may be correlated with a fast life history and high metabolism. This is because the ability to monopolize food resources should increase energy intake, which can compensate for the higher maintenance costs (Alvarez & Nicieza, 2005). In unpredictable environments, however, lower activity may have a selective advantage through the better survival of slower-growing individuals (Biro, Abrahams, Post, & Parkinson, 2006, 2004) and trait correlations may break down because an inflexible, energy-expensive strategy could impair fitness. Thus, we predict that, in stochastic or unpredictable environments, reversible plasticity may be favoured over a fixed strategy, reducing selection for POLS.

Environmental predictability should also largely determine the adaptive value of adjustments in early life (Kuijper & Hoyle, 2015; Reed et al., 2010), and whether certain adaptations should be genetically fixed, plastic (permanent environment effects), or flexible (reversible plasticity) in the short term. As such, the temporal scale of environmental predictability should influence POLS (see e.g. Hoogenboom et al., 2013 for food availability). The effects of temporal variability of environmental conditions on POLS likely depend on the level of predictability and magnitude of variation relative to generation time. When extrinsic conditions persist for several generations, the phenotype may become genetically encoded through selection (genetic assimilation; Lande, 2009)). Correlated traits and pleiotropic effects such as expected in the POLS framework could either slow down or speed up adaptation (Chevin, 2013; Russell Lande & Arnold, 1983; Sikkink, Reynolds, Cresko, & Phillips, 2015) in interaction with the temporal fluctuations in the environmental selective pressures.

Current evidence

The effects of predictability or stochasticity of the environment on POLS has not been directly addressed, but some evidence indicates a potential for unpredictability to contribute to the effects of an unfavourable environment. Polverino, Santostefano, Díaz-Gil, & Mehner (2018) found distinctly different POLS-trait covariance structures in lab-reared mosquitofish that originated from a stable (possibly more favourable) habitat, relative to fish from a harsher, unpredictable source habitat. While the study supports the hypothesis in that POLS was found only under the more predictable environment, the direction of the trait correlations were opposite to those predicted: the fish sourced from the more predictable environment expressed a slower POL relative to fish from the unpredictable habitat, but their slower POL was associated with higher metabolic maintenance costs, higher activity and boldness. The fish originating from the unstable source habitat had a relatively faster POL, but no POLS was found in those fish.

H3: Life stage.

Hypothesis: Environmental conditions can alter POLS when experienced in early life but not in adulthood because irreversible developmental plasticity acts in early life.

A change in POLS should primarily arise as a consequence of environmental differences in early life. POLS theory predicts correlations between life-history and behaviour caused by genetic effects or as result of irreversible developmental plasticity (Dammhahn et al., 2018). There are some indications that early-life stress may increase the correlations between and within traits (i.e. repeatability) (Briffa, 2013; Burton, Killen, Armstrong, & Metcalfe, 2011; Guenther, Groothuis, Krüger, & Goerlich-Jansson, 2018; Han & Dingemanse, 2017; Jenkins, 2011; Merrill

& Grindstaff, 2018; Reid, Armstrong, & Metcalfe, 2011; Royauté, Greenlee, Baldwin, & Dochtermann, 2015). Irreversible plasticity generally acts in early life, during (pre- or early post-natal) developmental sensitive periods (Mousseau & Fox, 1998). As the scope for developmental plasticity decreases during ontogeny, a change of environment for adult individuals should not result in a change of POLS. Thus, the life stage at which the environmental factor is experienced might be crucial in shaping POLS.

Current evidence

Several studies supported our prediction that only environmental factors acting during early developmental stages affect POLS but some studies found that environmental conditions also affected the POLS structure in adult individuals (Table 2).

Different juvenile environments (population density; birth cohort; food availability and intergroup conflict exposure) had clear effects on the life history – behavioural trait correlations later in life in different taxa (Le Galliard et al., 2015; Liu & Fu, 2017; Međedović, 2018; P. Montiglio, Garant, Bergeron, Messier, & Réale, 2014). In contrast, Kim & Velando (2016) found no indication that growing up in unusually warm or normal winter conditions would affect the relationship between shoaling behaviour and red coloration in male sticklebacks (*Gasterosteus aculeatus*), although being raised under warm conditions significantly reduced the coloration. Additionally, early-life pesticide exposure influenced the correlation between boldness and life-history traits in the damselfly *I. pumilio*, but in the same study, no POLS was observed in the other three tested damselfly species under any environmental conditions (Debecker et al., 2016).

Several studies of adult individuals found no effect of the environmental factor on life history-behaviour correlations (Bergeron et al., 2013; Goulet et al., 2016; Schuett et al., 2015; Yli-Renko, Pettay, & Vesakoski, 2018), conforming to our prediction. In one study, however, adult individuals showed differences in POLS due to environmental effects. Goulet et al. (2016) found temperature to be negatively correlated with survival in aggressive female spiders (*Anelosimus studiosus*) while docile individuals exhibited the opposite pattern. In addition, docile individuals produced more egg cases with increasing temperatures while aggressive individuals had higher reproductive rates at low temperatures.

Although inconclusive, these results suggest that environmental changes experienced during early life stages could have a higher potential to change POLS compared to environmental changes later in life. Environmental effects experienced in adulthood usually exert reversible, short-term influences (e.g. via transient changes in multiple traits through hormonal control; Ketterson & Nolan, 1999) and should therefore not have evolutionary implications. Environmental conditions experienced early in life (including the prenatal period and egg stage) are more likely to shape POLS traits via either developmental constraints or parental effects (Mousseau & Fox, 1998). “Predictive parental effects” may be adaptive if they result in a phenotype that is better fitted to the environment the individual is likely to experience as an adult (Bateson & Gluckman, 2011; Gluckman, Hanson, & Spencer, 2005). Differences in POLS might be observed later in life if selective disappearance of individuals follows from a changing environment. Bold individuals may, for example, face higher extrinsic mortality risks (Dugatkin, 1992). Indeed, Bell & Sih (2007) found that predation generated correlations between boldness and aggressiveness mainly because bold fish were predated more heavily than shy fish.

H4: Type of organism.

Hypothesis: Effects of specific environmental factors on POLS depend on whether the study species is endotherm vs. ectotherm or invertebrate vs. vertebrate.

The same ecological conditions can have distinct effects on the type of organism depending on the life-history patterns and primary physiological/behavioural mechanisms employed to cope with environmental challenges. A recent theoretical framework proposes that the vulnerability of a species to changing environmental conditions depends on the species' exposure and sensitivity to environmental change, its resilience to perturbations, and its potential to adapt to change (Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). As such, coping mechanisms may include an ability to escape adverse conditions spatially or temporally; adaptive adjustments within sensitive periods of certain developmental pathways; and physiological pathways or dominant hormones that coordinate integrated phenotypic responses to environmental constraints. The environmental sensitivities of certain taxonomic groups likely differ substantially.

The sensitivity and resilience of endotherm vs. ectotherm species against different biotic and abiotic environmental characteristics is likely very different, considering their special physiological and behavioural adaptations (Pough, 1980; Shine, 2005). For example, in endotherm vs. ectotherm vertebrates ambient temperature may have different effects on life history (e.g. maturation time), behaviour and physiology (Kralj-Fišer & Schuett, 2014; Mathot, Dingemanse, & Nakagawa, 2018; Montiglio et al., 2018). Metabolism and behaviour tend to be associated with one another more strongly in ectotherms (Mathot et al., 2018). Associated differences in thermal physiology affect how organisms interact with the environment (Huey et al., 2012). We consequently expect abiotic factors, especially climatic effects such as temperature, salinity or moisture, to affect ectotherms more strongly than endotherms.

The primary physiological mechanisms and ways of different taxa to respond to abiotic and biotic conditions could also have bearing on the emerging POLS. We hypothesize that the type of environmental factor including the physical or chemical (abiotic) and biological (biotic) environment may determine the physiological pathway by which these factors are perceived, transduced and dealt with in the downstream response (Feder, 1999; Sørensen, Kristensen, & Loeschcke, 2003; Wingfield, 2008, 2013; Wingfield et al., 2011; Wingfield, Kelley, & Angelier, 2011), with consequences for POLS. For example, physiological and life-history responses to abiotic stressors may be directly regulated by molecular chaperones, such as heat shock proteins that are present in most life forms to protect protein integrity in cells (e.g. Feder, 1999; Sørensen et al., 2003). These proteins may skew the current vs. future reproduction through costly investment in self-maintenance in response to (abiotic) threats without necessarily inducing behavioural changes (i.e., no POLS), although notably these proteins can also interact with the endocrine stress response (Iwama, Vijayan, Forsyth, & Ackerman, 1999).

Endocrine systems are physiological mechanisms by which organisms can flexibly adjust behavioural, physiological and morphological traits to variation in environmental conditions (Nelson, 2011). As the dominant hormones differ among taxa, their role in the integration of

POLS-traits may also differ. In invertebrates, the juvenile hormone is responsible for a number of organizational functions from development to investment in parental care and (sexual) behaviours (see reviews in Flatt, 2005; Immonen, Hämäläinen, Schuett, & Tarka, 2018; Schal, Holbrook, Bachmann, & Sevala, 1997; Trumbo, 2002). Across vertebrate taxa, there is strong evidence that glucocorticoid hormones mediate environmental stressors through pleiotropic effects on multiple neurological, physiological and behavioural traits (reviewed in Hau, Casagrande, Ouyang, & Baugh, 2016). Experimental work indicates potential for glucocorticoids to alter associations between life history, physiological and behavioural traits (Guenther et al., 2018; Merrill & Grindstaff, 2018). Glucocorticoids may be particularly meaningful in responding to changes in energy demands as they help adjust energy balance according to current needs by coordinating responses to regular but also to acute, unpredictable circumstances (Sapolsky, Romero, & Munck, 2000; Wingfield, 2013). However, coping mechanisms of vertebrates involve also other hormonal suites (Sapolsky et al., 2000). The reaction to biotic environmental factors, especially social effects, may be strongly influenced by oxytocin and vasopressin in vertebrates (Churchland & Winkielman, 2012; Neumann, 2008). As such, we might expect different effects of certain abiotic and biotic factors on POLS in different taxonomic groups, because of their different environmental sensitivities, coping methods and organizational mechanisms. This may extend to the traits that form the integrated POLS phenotype in different taxa.

Current evidence

The paucity of relevant studies limits evaluating support for our hypothesis about the responses of endotherms vs. ectotherms to different types of abiotic and biotic ecological conditions. Even within taxonomic group, the patterns may be contradictory: in ectotherm species, temperature influenced POLS in one study (Goulet et al., 2016) but not in the other (Kim & Velando, 2016). Studies on endotherm species (two on chipmunks, human, blue tit) simply compared cohorts or populations inhabiting different natural environments (temporal or spatial comparisons) rather than testing the effect of a single, distinct environmental gradient on POLS, making comparisons with ectotherms challenging.

In addition to the distinction between endotherms and ectotherms, there may be more general differences among vertebrates and invertebrates due to their different life histories as well as their organizational characteristics and associated environmental sensitivities. We found some indications of such effects, as abiotic conditions had some significant effects on the life history-behaviour association in two studies of abiotic environmental conditions of invertebrates (Debecker et al., 2016; Goulet et al., 2016), whereas no effect of biotic conditions was found in the two studies examining invertebrates under a biotic environment (Schuett et al., 2015; Yli-Renko et al., 2018). In contrast, in vertebrates, biotic conditions influenced the life history-behaviour association in all five studies that tested it (Cote et al., 2013; Fu et al., 2017; Le Galliard et al., 2015; Liu & Fu, 2017; Mededovic, 2018), whereas the one study of a clearly defined abiotic condition had no effect (Kim & Velando, 2016). Spatiotemporal gradients had unclear effects: two studies found effects on some but not all associations (Bergeron et al., 2013; Ward-Fear et al., 2018), another found sex-specific trends (Montiglio, Garant, Bergeron, Messier, & Réale, 2014). The extent to which these differences result from the different physiological/organizational mechanisms present in endotherms vs. ectotherms or invertebrates vs. vertebrates and under abiotic vs. biotic conditions is currently unclear.

Our literature search identified no studies that directly addressed the effect of the organizational mechanism on the environmental effects on POLS (but see Mathot et al., 2018). Coping mechanisms that improve fitness may differ among types of organisms and environments. For example, flexible behavioural adjustments may be most adaptive in certain environmental conditions; altered developmental trajectory or physiological profile in others. While we predicted that responses to abiotic and biotic environmental gradients may differ because of the different primary physiological mechanism employed (e.g. response involving heat shock proteins and no behavioural response, vs. endocrine mechanisms with a strong behavioural component), this prediction cannot be addressed at present in the complete absence of studies testing consistent behavioural traits associated with physiological mechanisms such as heat shock proteins.

Table 2. Support from empirical studies for our proposed hypotheses. Tax.: denotes the taxon (A, arachnid; C, crustacean, F, fish; I, insect; M, mammal; R, reptile). B refers to behavioural traits, LH refers to life-history traits. Details on the choice of studies, behavioural and life-history traits and environmental conditions are provided in the Supplement.

Support hypothesis	Contradict hypothesis	Findings	Tax.
H1: POLS only emerges under harsh environmental conditions.			
	(Cote et al., 2013)	Shy, asocial individuals were more likely to disperse than bold, social individuals when predation was absent while no association between personality and dispersal was found under predation threat.	F
(Debecker et al., 2016)	(Debecker et al., 2016)	Pesticide exposure reversed a weak negative association between boldness and LH to a stronger positive association in *I. pumilo*. The covariation between boldness and LH (POLS) was only present in 1 out of 4 species.	I
	(Fu et al., 2017)	Correlations between survival, activity and boldness did not differ depending on whether fish grew up in a low or high predation environment	F
(Goulet et al., 2016)		Survival and egg production of aggressive females suffered more from high temperatures than that of docile individuals.	A
	(Kim & Velando, 2016)	A negative association between male sexual ornamentation and sociability was present in benign and control temperatures.	F
	(Le Galliard et al., 2015)	High social densities diminished the association between activity and survival and between growth rates and female breeding frequency.	R
(Liu & Fu, 2017)		Growth rate was negatively correlated with activity under low but not under high food availability.	F
(Mededovic, 2018)		Individuals with high extraversion and low emotionality had higher mating success when exposed to inter-group conflict while no such correlations existed in the control group.	M
(Schuett et al., 2015)	(Schuett et al., 2015)	Predator escape behaviour was associated with LH only in a colour morph with high susceptibility to predation in pea aphids. However, the immediate presence of a predator did not affect the association.	I
(Závorka et al., 2015)	(Závorka et al., 2015)	Active individuals showed reduced growth with increasing home range size (home range assumed to be an estimate for resource abundance by the authors) whereas less active individuals showed slightly increased growth with increasing home range. Population density however had no effect.	F
H2: POLS may be more likely to emerge in stable or predictably fluctuating environments.			
Direct evidence unavailable in the absence of targeted studies, but see text.			
H3: Environmental conditions can alter POLS when experienced in early life but not in adulthood.			
(Bergeron et al., 2013)		The prevailing season did not affect the association between LH and exploration in adults.	M
(Debecker et al.,	(Debecker et	Rearing individuals under pesticide exposure affected LH and B. The covariation between boldness and LH	I

2016)	al., 2016)	(POLS) was only present in 1 out of 4 species and affected by treatment in the damselfly *I. pumilo*.	
	(Goulet et al., 2016)	Temperature affected the association between reproduction and aggressiveness/ docility in adult females.	A
	(Kim & Velando, 2016)	Rearing in warm temperatures decreased reproduction in females and sexual coloration in males. The negative association between sociability and coloration in males was not affected by treatment.	F
(Le Galliard et al., 2015)		Rearing in different social densities affected growth. While growth was correlated with sociability under low density, the association vanished with increasing density.	R
(Liu & Fu, 2017)		Growth rate was negatively correlated with activity in individuals reared under low food availability while no association was found under high food availability.	F
(Mededovic, 2018)		Environmental harshness during childhood does alter the association between sexual activity and personality traits.	M
(Yli-Renko et al., 2018)		No effect on LH-B association after manipulating shelter types in adults.	C
H4: Effects of specific environmental factors on POLS depend on whether the study species is endotherm vs. ectotherm or invertebrate/vertebrate.			
Direct evidence unavailable in the absence of targeted studies, but see text.			

3. Environmental effects on POLS: emerging patterns, knowledge gaps and outlook

Although the extended POLS hypothesis (sensu Réale et al., 2010) is an intriguing explanation for the frequently observed behavioural differences among individuals, there is little consensus on the strength and direction of the correlations of behavioural traits with physiological or life-history traits in general. The environmental context may have a profound effect on the observed trait correlations, but the interaction of ecological conditions and POLS is complex. We proposed four hypotheses targeting the critical interfaces of the environment and life history-behaviour associations to synthesize research findings to date. These involved general characteristics of the environment (harshness and predictability), characteristics of the organism (taxonomic group and life stage) and possible physiological mechanisms connecting these.

By reviewing evidence for each of the proposed hypotheses, we found suggestive evidence that environmental characteristics can have significant influences on POLS-traits and their covariances. We were able to identify two themes for which tentative conclusions emerge at this early stage: (1) The presence of POLS frequently depends on the harshness or favourability of the environment (Hypothesis 1); and (2) Variability in the environmental sensitivity of POLS frequently depends on the life-history stage at which the relevant environmental cue is experienced (Hypothesis 3). Obvious knowledge gaps include the effects of environmental predictability (Hypothesis 2) and the significance of (physiological) organizational mechanisms and specific environmental factors across different types of organisms (Hypothesis 4).

Despite relatively broad evidence of environment-POLS interactions, the primary conclusion is that such effects are not generalizable across a wide range of environmental conditions and organisms. This is likely as much a consequence of the strength of local adaptations, as of the wide variety of species, (potentially flexible) phenotypic traits and ecological conditions studied. Furthermore, the natural environment of any species is multidimensional; ecological factors covary and interact; and no environment is static in time or space. The relevant components of our hypotheses (type of organism; partially shared and partially distinct physiological mechanisms of the types of organisms; different abiotic and biotic gradients) are also likely to interact, creating complex patterns such that their simultaneous effects cannot be thoroughly assessed with the small number of studies available. Decomposing the independent and interacting effects of these factors is undoubtedly the most important future challenge for determining the effects of the environment on POLS and its evolution.

Addressing the knowledge gaps that we identified would require testing the responses of different types of organisms to similar (abiotic and biotic) environmental conditions in similar experimental setups and by comparing multiple populations of the same species across environmental gradients. Once this basic comparison has been accomplished, it would be beneficial to examine the physiological mechanisms involved in the different organisms, the sensitive life stages, and the effect of the predictability of the environmental cue to begin to decipher the complexities of these interacting effects. A way forward may be experimental treatments to quantify the effects of specific environmental gradients on trait covariations. Gaining biologically relevant information also requires an extensive understanding of the species' natural life history, behaviour, and selective pressures these evolved under.

To assess the general significance of environmental variation in generating and maintaining variation in POLS, we argue that it is meaningful to evaluate associations between behavioural and life-history traits only within the context of the defining features of the environment (favourability and predictability) and of the study organism. We renew the call of Réale et al. (2010) for a rigorous testing of alternative hypotheses on the effects of the environmental characteristics on trait covariance structures. Our proposed hypotheses provide a scaffold for designing meaningful tests by isolating the broadly relevant and widely comparable aspects of animals and their environment.

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Supplementary material

Methods and general summary of the literature review

To identify studies that investigated POLS in the context of varying environmental conditions, we initially conducted a systematic literature search on 16.4.2018 (we later supplemented this with more recent publications). We selected all peer-reviewed articles that had cited two seminal papers on the POLS phenomenon: Réale et al. (2010); and Ricklefs & Wikelski (2002) in Web of Science (Core Collection; Thomson Reuters). In addition, we conducted a search on Web of Science with the search terms “POLS” and “behavio(u)r” or "pace-of-life syndrome" and “behavio(u)r”. After removal of duplicates, 1035 studies remained.

From those, we selected all studies that had measured at least one life-history and one behavioral trait for the same individuals, as well as an environmental variable. Because few studies directly assessed a trade-off between current and future reproduction, we chose studies that examined life-history traits relevant to the slow-fast POL continuum: onset of breeding (e.g. age and size at maturity and/or first reproduction), growth, offspring production (e.g. timing and rate of breeding, fecundity, size and number of offspring, and offspring growth rate), parental care, survival/lifespan, dispersal/migration, and onset/rate of senescence. For behavioral traits, we included the five broad categories proposed by Réale, Reader, Sol, Mcdougall, & Dingemanse (2007): activity, aggression, exploration, boldness, and sociability. Behaviors not falling into these categories were assigned as “other”. We categorized behaviors as labelled by the authors unless otherwise indicated. We chose here to exclude studies that only quantified behaviors strictly associated with parental care, migration, or foraging, because these behaviors are easily confounded with life-history strategies and studies rarely account for this possible confounding effect.

We considered as an environmental variable any condition extrinsic to the studied individuals that varied either naturally or experimentally among individuals of the population, with potential to generate consistent differences among individuals (see Dammhahn et al. 2018). Thus, we excluded, for instance, studies that only measured acute changes in response to short-term treatments. For each study, we also recorded the taxonomic group and demographic group studied, as these variables can have bearing on the traits measured and potentially, the effect of the environment on them.

Thirty-seven out of the 1035 studies fulfilled our criteria (Tables S1 and S2). While all 37 studies measured phenotypic traits and their covariances, none evaluated trait covariances at the genetic level. Nineteen studies measured at least one physiological trait in addition to a behavioral and a life-history trait. Thirteen of the 37 studies directly analyzed the effect of an environmental gradient on phenotypic correlations among life-history traits and behavior (i.e. LH-B[E]; findings summarized in Table S1).

Table S1. Summary of studies investigating effects of the environment (E) on life-history (LH), behavioral (B) and physiological (P) traits.

Reference	**Species (taxon)**	**Details**	**E**	**LH**	**B**	**P**	**LH-B**	**LH-P**	**LH-E**	**B-E**	**P-E**	**B-P**	**LH-B [E]**	**LH-P [E]**	**B-P [E]**
(Bergeron et al., 2013)	*Tamias striatus* (M)	cor/wild/ juv- ad/f,m	temporal: season (2)	growth; survival	expl	immun	*/ns [b]	ns	*	NA	NA	ns	ns	NA	NA
(Cote et al., 2013)	*Gambusia affinis* (F)	man/lab/ ad?/f,m	biotic: predation, density (2x2)	dispersal	activ; bold; expl; sociab		*	NA	*	NA	NA	NA	*	NA	NA
(Debecker et al. 2016)	4 *Ischnura* spp. (I)	man/lab/ juv-ad/f,m	abiotic; human impact: pesticide (2)	PCA: growth; matur; other; survival	activ; bold		*/ns [c]	NA	*/ns	ns	NA	NA	*/ns	NA	NA
(Fu et al., 2017)	*Parabramis pekinensis* (F)	man/lab/ juv – ad	biotic: predation	survival, growth	activ; bold; other	metabol	*	*	*	ns	*	*	*/ ns	*/*	*/ ns
(Goulet et al. 2016)	*Anelosimus studiosus* (A)	man/lab/ ad/f	abiotic; biotic: temperature, social E (6/2)	off prod; survival	aggr; sociab		*	NA	*	NA	NA	NA	*	NA	NA
(Kim & Velando, 2016)	*Gasterosteus aculeatus* (F)	man/lab/ juv/f,m	abiotic: winter temperature (2)	off prod; other	sociab		*/ns [c]	NA	*	NA	NA	NA	ns	NA	NA
(Le Galliard et al. 2015)	*Zootoca vivipara* (R)	man/semi-nat/ juv-ad/f,m	biotic: density (5)	growth; off prod; survival	activ; bold; sociab		*/ns	NA	*/ns [c, d]	NA	NA	NA	*/ns	NA	NA

Reference	**Species (taxon)**	**Details**	**E**	**LH**	**B**	**P**	**LH-B**	**LH-P**	**LH-E**	**B-E**	**P-E**	**B-P**	**LH-B [E]**	**LH-P [E]**	**B-P [E]**
(Liu & Fu, 2017)	triploid hybrid carp (F) [a]	man/lab/ juv/f,m	biotic: food availability (2)	growth	active; expl; bold; other	metabol	*/ns	NA	ns	ns	*	*/ns	*	*/ns	*
(Međedović, 2018)	*Homo sapiens* (M)	cor/human/ ad/f,m	biotic: intergroup conflict exposure (2)	off prod [e]	other		*/ ns	NA	*	*	NA	NA	*	NA	NA
(Montiglio et al. 2014)	*Tamias striatus* (M)	cor/wild/ juv- ad/f,m	temporal; food: birth cohort (2)	matur; off prod	expl		*/ns [c]	NA	ns	*/ns [c]	NA	NA	*/ns [c]	NA	NA
(Schuett et al., 2015)	*Acyrthosiphon pisum* (I)	man/lab/ juv-ad/f	biotic: predation risk (2)	growth; matur; off prod; survival	bold		ns	NA	ns	NA	NA	NA	ns	NA	NA
(Ward-Fear et al., 2018)	*Varanus panoptes (R)*	cor/wild/ juv-ad/f,m	temporal: season	growth; off prod; survival; other	bold		*/ns	NA	*/ns	NA	NA	NA	*/ns	NA	NA
(Yli-Renko et al. 2018)	*Idotea balthica* (C)	man/wild-caught lab/ juv/f,m	biotic: shelter plant/algae	survival	active		*/ ns [c]	NA	ns	ns	NA	NA	ns	NA	NA

Species (taxon): A, arachnid; B, bird; C: crustacean; F, fish; I, insect; M, mammal; R, reptile

Details: correlative (cor) vs. manipulative (man) study / wild vs. lab study vs. seminatural (semi-nat) / life stage of individuals: pre-reproductive or immature juvenile (juv), mature adult (ad) / sexes tested: females (f), males (m)

E, environment: broad category: type of gradient (number of levels of gradient; c, continuous); abiotic, abiotic state (e.g. chemical state, temperature); biotic, biotic state (e.g. predation, competition, density)

LH, life-history: matur, maturation, including age /size at maturation and onset of breeding; off, offspring; prod, production; provision, offspring provisioning; survival, including short-term survival or lifespan

B, behavior: activ, activity; aggr, aggression; bold, boldness; expl, exploration; other, other behaviors; sociab, sociability

P, physiology: horm, hormones; immun, immunology; metabol, metabolism; physiol state, physiological state

X-Z, Y-Z (LH-B, B-P etc.): indicate whether (*) or not (ns) significant relationships were found between the mentioned traits; B, behavior; E, environment; [E] indicates whether the found links differed for the environments; LH, life-history; P, physiology; empty cells denote that a link was not tested in the study; for simplicity, we did not differentiate whether some of the results were observed in interaction with an additional (non-POLS) variable, such as age or age^2, or depending on another variable (for exceptions, see footnotes)

[a] Latin name of species not mentioned in study

[b] a quadratic relationship LH-B^2 was significant, the linear LH-B was not significant

[c] at least some of the results in interaction with sex, or depending on sex, or analyzed separately for the sexes with different outcome

[d] at least some of the relationships were artefacts of other relationships through a third variable influencing both

[e] sexual promiscuity and extra-pair mating

Note that none of these studies assessed whether there was an interactive effect of physiology and behavior on life-history (LH-P*B).

Table S2: Studies that measured a relevant behavioral trait, life history trait, and environmental variable but did not explicitly test the effect of environmental variation on the behavior-life history association (i.e. LH-B [E]).

Reference	**Species (taxon)**	**Details**	**E**	**LH**	**B**	**P**	**LH-B**	**LH-P**	**LH-E**	**B-E**	**P-E**	**B-P**	**LH-P [E]**	**B-P [E]**
(Addis et al. 2017)	*Thamnophis elegans (R)*	wild/lab/man /F1/m/f	spatial/abiotic: elevation, temperature	survival; growth	feeding rates	IGF-conc.	NA[a]	*	*	*	*	*	NA	NA
(Atwell et al., 2014)	*Junco hyemalis* (B)	cor/wild,lab/ ad/m	spatial: geographic (2)	off care; off prod	aggr	hormones	NA	*	*/ns	*	*/ns	*/ns	ns	ns
(Blazek et al., 2017)	*Nothobranchius (F)*	man/lab/F1/ life/f,m	aridity; age (old-young)	off prod; survival	expl;bold;m-m agr	metab	NA	NA	*/ns	ns	ns	NA	NA	NA
(Careau et al. 2014)	*Taeniopygia guttata* (B)	man/lab /hatch-juv-ad/f	food: food treatment (2)	growth	activ	hormones; metab; phys state	NA	NA	*/ns[b]	ns	*/ns	NA	NA	NA
(Charmantier et al. 2016)	*Cyanistes caeruleus* (B)	review/wild /ad/f, m	spatial: deciduous-evergreen (2); mainland-island (2)	off care; off prod; survival	activ; aggr; other	NA	(*)	NA	*	*/ns	NA	NA	NA	NA
(Dirienzo & Montiglio, 2016)	*Latrodectus hesperus*(A)	man/lab/ immature-ad/f	food: food restriction (2)	matur	aggr; other	NA	NA	NA	*	*	NA	NA	NA	NA
(Dubuc-Messier et al. 2017)	*Cyanistes caeruleus (B)*	wild/cor/ adult/f,m	spatial: habitat type	off prod; survival	aggr, explor, other	heart rate	NA	NA	*	*/ns	*/ns	NA	NA	NA
(Finkemeier et al. 2016)	*Cavia aperea* (M)	man/lab/ juv-adolescent/f, m	temporal: photoperiod at birth & adolescence (4)	growth	bold; expl; other	metab	*/ns	*/ns.	*	*	*	*/ns	NA	NA

Reference	**Species (taxon)**	**Details**	**E**	**LH**	**B**	**P**	**LH-B**	**LH-P**	**LH-E**	**B-E**	**P-E**	**B-P**	**LH-P [E]**	**B-P [E]**
(Guenther et al. 2014)	*Cavia aperea (M)*	man/lab/ juv-adolescent/f, m	temporal: photoperiod	growth	bold; expl; other	metab, hormones	ns	ns	ns	*/ns	*/*	*/ns	NA	NA
(Guenther & Trillmich, 2013)	*Cavia aperea* (M)	man/lab /juv-mat-ad/both	temporal: prenatal photoperiod (2)	matur	expl	hormones	NA	NA	*	*/ns [c]	*/ns [c]	NA	NA	NA
(Jacquin et al. 2012)	*feral pigeon*	man/lab, wild animals/ ad/f,m	food: food treatment (2)	off care; off prod	aggr	NA	NA	NA	*/ns [d]	ns	NA	NA	NA	NA
(Killen, 2014)	*Phoxinus phoxinus* (F)	man/lab, wild animals/ ?/?	food: food treatment (2)	growth	activ	metab	NA	NA	*	*	*	ns	NA	NA
(Kim & Velando, 2015)	*Larus michahellis* (B)	man/wild/ hatch/f,m	food: vitamin supplement (2)	growth	bold	oxidative damage/ telomere length	NA	*	ns	ns	ns	see B-P [E]	ns	*
(Krause et al. 2017)	*Taeniopygia guttata (B)*	man/lab /juv-ad/f,m	food: diet quality (2*2)	survival	activ, expl	NA	NA	NA	*/ns	*	NA	NA	NA	NA
(McCowan et al. 2015)	*Taeniopygia guttata* (B)	cor/wild/ ad/f,m	spatial: population (2)	off prod	expl; sociab	NA	ns	NA	*/ns	n.s	NA	NA	NA	NA
(Näslund et al. 2017)	*Salmo trutta (F)*	man/lab/wild/ juv/f,m	food:food restriction (2)	growth, survival	activ		*/ns	NA	*/ns	NA	NA	NA	NA	NA
(Nicolaus et al., 2014)	*Parus major* (B)	cor/man/ wild/ad/f	temporal: year (2)	off care, off prod, survival	expl	NA	*	NA	*	NA	NA	NA	NA	NA
(Niemelä et al. 2015)	*Gryllus campestris* (I)	cor/wild/ juv, a/f, m	abiotic: burrow temperature (c)	survival	activ; bold	NA	*/ns	NA	NA	(*) [e]	NA	NA	NA	NA
(Niemelä et al. 2012)	*Gryllus integer* (I)	cor/lab/ juv, ad/f, m	biotic: density (c)	matur	aggr; bold	immun	ns	*	*	NA	(*) [f]	ns	(*) [f]	NA

Reference	Species (taxon)	Details	E	LH	B	P	LH-B	LH-P	LH-E	B-E	P-E	B-P	LH-P [E]	B-P [E]
(Van Baaren et al. 2016)	*Asobara tabida* (I)	cor/lab, wild animals/ life/m	biotic/spatial: competition (2) [g]	off prod, survival	activ	metab; phys state	NA	NA	*	*	*/ns	NA	NA	NA
(Wengstrom et al., 2016)	*Salmo trutta* (F)	man/wild, (lab)/ yearl/?	temporal: parasite exposure (2)	growth	activ	immun	NA	ns	NA	NA	NA	*	NA	NA
(Woods et al. 2010)	*Eurycea spp* (RE)	man/lab/ juv-ad/f, m?	abiotic: oxygen level (3)	growth, survival	activ	metab	NA	NA	*/ns	*	*	*	NA	NA
(Závorka et al. 2015)	*Salmo trutta* (F)	man/lab-wild/ yearl/f,m?	biotic state: density (2)	growth, survival	activ	NA	ns	NA	NA	(ns)	NA	NA	NA	NA
(Zhao et al. 2016)	*Turdus rubrocanus* (B)	cor/wild/ ad/f, m	spatial; human impact; biotic; food: proximity to human use areas, nest density (c)	off prod	activ	NA [h]	ns	(*)/ns	*/ns	ns	*/ns	ns	NA	NA

Species (taxon): A, arachnid; B, bird; C: crustacean; F, fish; I, insect; M, mammal; R, reptile

Details: correlative (cor) vs. manipulative (man) study / wild vs. lab study vs. seminatural (semi-nat) / life stage of individuals: pre-reproductive or immature juvenile (juv), mature adult (ad) / sexes tested: females (f), males (m)

E, environment: broad category: type of gradient (number of levels of gradient; c, continuous); abiotic, abiotic state (e.g. chemical state, temperature); biotic, biotic state (e.g. predation, competition, density)

LH, life-history: matur, maturation, including age /size at maturation and onset of breeding; off, offspring; prod, production; provision, offspring provisioning; survival, including short-term survival or lifespan

B, behavior: activ, activity; aggr, aggression; bold, boldness; expl, exploration; other, other behaviors; sociab, sociability

P, physiology: horm, hormones; immun, immunology; metabol, metabolism; physiol state, physiological state

X-Z, Y-Z (LH-B, B-P etc.): indicate whether (*) or not (ns) significant relationships were found between the mentioned traits; B, behavior; E, environment; [E] indicates whether the found links differed for the environments; LH, life-history; P, physiology; empty cells denote that a link was not tested in the study; for simplicity, we did not differentiate whether some of the results were observed in interaction with an additional (non-POLS) variable, such as age or age^2, or depending on another variable (for exceptions, see footnotes)

a) The ecotype (elevation) and the rearing environment (temperature) affected all traits but correlations were not tested, except of arbitrary LH-B (growth correlates with feeding rate)

b) in interaction with quadratic age effect

c) in interaction with sex

d) partially in interaction with another term

e) Behavior changed within individuals with temperature

f) LH correlated with P, and apparent correlation P-E was caused by significant LH-E correlation

g) compares 2 strains originating from different areas, differences include interspecific competition

h) heart rate was taken as a measure of boldness (without reporting behavioral correlates) in the paper. For consistency, heart rate is here considered a physiological trait.

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