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

Anni M. Hämäläinen[1,2,3,†], Anja Guenther[4,5], Samantha C. Patrick[6], Wiebke Schuett[7,8]

[1] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada
[2] Institute of Environmental Science, Jagiellonian University, Kraków, Poland
[3] Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
[4] Department of Evolutionary Biology, Bielefeld University, Bielefeld, Germany
[5] Department of Evolutionary Genetics, Max Planck Institute for Evolutionary Biology, Plön, Germany
[6] School of Environmental Sciences, University of Liverpool, Liverpool, UK
[7] Institute of Zoology, Universität Hamburg, Hamburg, Germany
[8] School of Life Sciences, University of Sussex, Brighton, UK

[†] Correspondence: Anni Hämäläinen, Institute of Environmental Science, Jagiellonian University,
ul. Gronostajowa 7, 30-387 Kraków, Poland.
Email: anni.m.hamalainen@gmail.com
ORCID: 0000-0001-9260-8299

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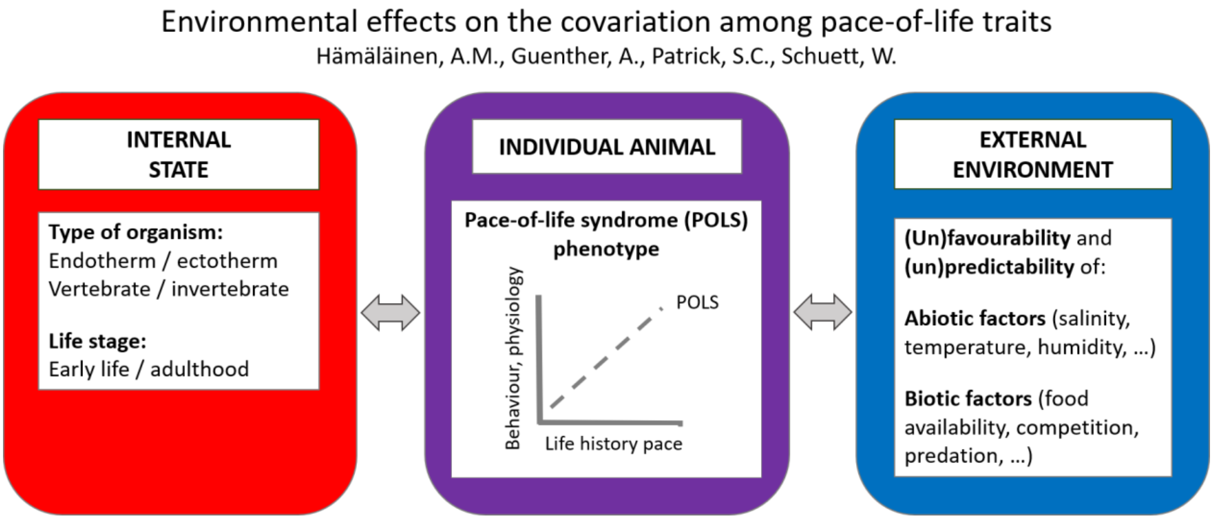
Abstract

Pace-of-life syndromes (POLSs) are suites of life-history, physiological and behavioral traits that arise due to trade-offs between allocation to current and future reproduction. Traits generally show covariation that can arise from genetic and environmental influences on phenotypes and constrain the independent evolution of traits, resulting in fitness consequences and impacts on population dynamics. The notion that correlations among traits may vary among populations along environmental gradients suggests an important role for the environment in shaping and maintaining POLS. However, no synthesis has been attempted of the myriad ways in which environmental factors should influence POLS. Here, we formulate a series of hypotheses targeting the critical interfaces of the environment and life history-behaviour associations across different organisms. We discuss the hypotheses in light of findings from a systematic review of studies that measured changes in the association between behavior and life-history traits as a function of environmental conditions. The review revealed that POLS is often shaped by environmental variation, where harshness of the environment in early life has the most consistent effects on POLS. However, only partial or no effects of environmental variation were found in a number of studies, which may result from the highly variable study systems, traits, and environments studied. We highlight promising directions arising from the available studies and identify knowledge gaps that, if unaddressed, will impede progress in the field.


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

Hämäläinen, A.M., Guenther, A., Patrick, S.C., Schuett, W.

1. Introduction

Much of 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; Stearns, 1992) by determining the strategy for optimal allocation of resources into reproductive investment relative to self-maintenance (or trade-offs between current vs. future reproduction). 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). The emerging trait combinations are referred to as pace of life syndromes (POLSs).

The POLS hypothesis was originally developed to explain variation in life history and related physiological traits across species or populations (Ricklefs & Wikelski, 2002). Réale et al. (2010) extended this framework also to the among-individual level (within populations) and incorporated behavioural traits into the framework (Careau et al., 2008, Réale et al., 2010, Dammhahn et al., 2018). The extended POLS hypothesis is typically applied at the population-level, where behavioural and life history traits have been quantified at the individual level (Dammhahn et al., 2018), and this level is also our focus in this study. It is noteworthy, however, that the patterns of covariation may differ when examining the syndromes among and within populations and species (e.g. Debecker et al., 2016; Debecker & Stoks, 2019; Delahaie et al. 2018; see also Raffard, Cucherousset, Prunier, Loot, Santoul, & Blanchet, 2019) due to adaptive or random processes (Raffard et al., 2019). The application of the predictions of the POLS framework at different hierarchical level (across species/populations, within populations) have been discussed in detail elsewhere (Araya-Ajoy, Bolstad, Brommer, Careau, Dingemanse, & Wright 2018; see also Mathot & Frankenhuis, 2018).

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. 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). The POLS framework (sensu Réale et al 2010) 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 POL continuum and that high investment into later reproduction is coupled with risk-averse behaviours at the slow end of the POL continuum (Réale et al., 2010, Biro & Stamps, 2008, Mathot & Frankenhuis, 2008). This could come about, for example, if risk-taking or other consistent behaviors lead to improvements in acquisition of resources or mates at the expense of survival.

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 (e.g. van Noordwijk & de Jong, 1986). 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 the POLS hypothesis (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. Associations between life-history and physiological traits have been intensively investigated already since the seminal work of Ricklefs and Wikelski (2002), whereas studies focusing on the association of behavioural and life history traits in an environmental context are still scarce and often lack testable hypotheses. Here, we therefore focus on studies investigating primarily behaviour- life history covariance within populations.

Despite the complexity of environmental effects on phenotypes, 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 on the life-stage at which environmental cues or constraints should have profound effects. We also 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. The empirical findings on the trait associations, along with their relevance to the hypotheses, are summarized in Table 2. We then highlight knowledge gaps that at present limit the full testing of our hypotheses.

We did not come across studies that would directly assess trade-offs between current and future reproduction or between reproduction and survival (for a discussion on quantifying this trade-off see e.g. Mathot & Frankenhuis, 2018) in association with behaviour and environmental variation (but see Schuett et al., 2015). Therefore, we also included in our review studies that measured any life history trait considered directly relevant to survival or reproductive investment (i.e. linked to POL, *sensu* Realé et al. 2010) and that provide partial support for the POLS hypothesis. This was a necessary compromise to find studies that evaluated the association of POLS with distinct environmental conditions.

H1: Environmental harshness.

Hypothesis: POLSs 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 here defined broadly as the degree of average fitness effect or energetic demands posed by the environmental condition (e.g. Ebensberger et al., 2014; Chesson & Huntly, 1997). Recent theory suggests that unfavourable environments will increase phenotypic trait variances and that individuals whose body condition (i.e. energy reserves) depend more on external environmental conditions 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 (Wilson, Clark, Coleman, & Dearstyne, 1994, but see Harris, Ramnarine, Smith, & Pettersson, 2010). 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).

Environmental constraints on the acquisition of resources 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 for H1

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 negatively with activity 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 (see Table 2). In contrast, no significant associations were found between activity or aggression with life history (age at first reproduction or longevity) in red squirrels regardless of experiencing a resource pulse (Haines et al., 2020). 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; but see Haines et al., 2020). 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). As suggested by Wright et al. (2019), effects of population density on POLSs might depend on density-dependent selection patterns and environmental stochasticity, as discussed in more detail in hypothesis 2.

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). 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 high dispersal tendency (considered as a life history trait by the authors, as suggested also by Réale et al., 2010), high boldness and low 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, a positive association between risk taking and fast POL (rapid growth and reduced survival) was observed in juvenile lemon sharks only in a population with low predation pressure and not in another population with a high predation pressure (Dhellemmes, Finger, Smukall, Gruber, Guttridge, Laskowski, & Krause, 2020). Finally, Fu, Fu, Wu, & Cao (2017) found no indication that the likelihood of predation during development influenced trait associations between boldness, activity, and growth rate. 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). Trait associations conforming to those predicted in the POLS framework 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).

Two studies have investigated the effects of pesticide exposure/ metal pollution on trait associations (Debecker et al. 2016; Debecker and Stocks, 2019), after a broader role of contaminants in shaping trait associations has been suggested (Killen et al. 2013). Both examples found only little support for the role of contaminants in shaping POLSs. While Debecker et al. (2016) found a positive association between life history and risk-taking to emerge after a pesticide treatment, this effect was limited to one out of four tested species. The second example found no effect of zinc pollution on POLS in the tested species (Debecker and Stocks, 2019).

Although several studies found POLSs to be influenced by environmental favourability, it remains unclear whether POLSs are 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 three studies found no effect of the environment on trait correlations. Finally, at least two studies have 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 (Padilla & Adolph, 1996; Reed, Waples, Schindler, Hard, & Kinnison, 2010; Tuljapurkar, Gaillard, & Coulson, 2009) as well as POLS (Hoogenboom, Armstrong, Groothuis, & Metcalfe, 2013; 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. Along the same lines, Wright et al. (2019) proposed that fluctuating environmental effects act on POLSs through fluctuating, density-dependent selection and their effects on population density. A trade-off between intrinsic rates of reproduction and the ability to cope with negative effects of competition in high density populations is assumed to produce fast versus slow POL-types. Here, we predict that, in stochastic or unpredictable environments, reversible plasticity may be favoured over a fixed strategy, reducing selection for POLS.

Environmental stochasticity and density-dependent selection should also largely determine the adaptive value of phenotypic development in early life (Kuijper & Hoyle, 2015; Reed et al., 2010; Wright et al., 2019), and whether certain developmental 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 for H2

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. In contrast, no POLS was observed in any population of the Turquoise killifish *Nothobranchius furzeri* regardless of the predictability (pond permanence) of their origin (no formal test of the effect of pond permanence on the trait covariances was reported; Thoré, Grégoir, Adriaenssens, Philippe, Stoks, Brendonck, & Pinceel, 2019). The lack of studies assessing effects of environmental predictability on POLS do not allow us to draw general conclusions based on empirical studies but results by Polverino et al. (2018) or Hoogenboom et al. (2013) suggest this may be a potential fruitful avenue for future studies.

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.

Trait covariance structures suggestive of POLS should primarily be determined by 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; 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 for H3

Several studies supported our prediction that only environmental factors acting during early developmental stages affect POLSs, but some studies found that environmental conditions also affected the POLS structure in adult individuals (Table 2). Very few studies examined both juvenile and adult phases in the same system, limiting the potential to directly compare the magnitude of the effects.

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; 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 (proxy for reproductive investment) in male sticklebacks (*Gasterosteus aculeatus*), although being raised under warm conditions significantly reduced the coloration. Additionally, early-life pesticide exposure changed a weak negative correlation between boldness and life-history traits under control conditions to a positive correlation in the damselfly *I. pumilio*. In the same study, however, no POLS was observed in the other three tested damselfly species under either environmental condition (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; Diaz Pauli, Edeline, & Evangelista, 2020; Haines et al., 2020; 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 POLSs 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 conditions experienced early in life (including the prenatal period and egg stage) could 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).

In contrast, 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. Differences in POLSs might, nonetheless, be observed also later in life under certain conditions. Bold individuals may, for example, face higher extrinsic mortality risks (Dugatkin, 1992), leading to altered trait covariance patterns in older individuals even in the absence of consistent trait associations in younger animals (e.g. Bell & Sih, 2007). Personality-dependent responses to predation pressure may additionally affect reproductive decisions, as observed for laying date in great tits (Abbey-Lee & Dingemanse, 2019). Even if such associations are reversible, strong correlations may emerge among behavioural and life-history traits in adults. As such, transient changes in reproductive investment or selective disappearance of certain phenotypes in a given environment could lead to the observation of POLS emerging only later in life.

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 different organisms depending on the life-history patterns and primary physiological/behavioural mechanisms employed to cope with environmental challenges. A 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 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 potentially because ectotherms have fewer possibilities to reallocate energy as a consequence of lacking thermoregulation (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.

Differences in primary physiological responses to abiotic and biotic conditions among taxa could also have bearing on the emerging POLS. We hypothesize that the type of environmental factor may have consequences for POLS. This is because the physiological pathways used to perceive, transduce and react to the environment may differ for physical or chemical (abiotic) and biological (biotic) environmental factors (Feder, 1999; Sørensen, Kristensen, & Loeschcke, 2003; Wingfield, 2008, 2013; Wingfield et al., 2011; Wingfield, Kelley, & Angelier, 2011). 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). The relative significance of the molecular chaperones in adjusting to environmental conditions in different taxa remains unknown. However, it may be speculated that lifeforms that lack complex endocrine systems may use conserved mechanisms such as molecular chaperones as the primary means to respond to their environment. In such organisms, changes in the abiotic environment may elicit responses in POL, but with no observable extended POLS.

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). Beyond these mechanisms linking environmental conditions with POLS, for example telomere dynamics could play a role in species-specific responses to the environment and the resulting POLSs (Giraudeau, Angelier, & Sepp, 2019). 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 for H4

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 group, the patterns may be contradictory: in ectotherm species, temperature influenced POLS in one study on spiders (Goulet et al., 2016) but not in another on fish (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.

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. Very few studies have attempted to formally measure life-history trade-offs in the POLS-environment context, limiting the direct testability of these associations as envisioned by the verbal and formal models of POLS (Réale et al., 2010; Mathot & Frankenhuis, 2018). 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 considering each of the proposed hypotheses in light of findings from studies that measured changes in the association between behavior and life-history traits as a function of environmental conditions, we found suggestive evidence that environmental characteristics can influence 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 (e.g. with formal meta-analyses) 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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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.

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
	(Debecker & Stoks, 2019)	Neither latitude of population origin, temperature or zinc exposure affected the association structure between growth, survival, activity, exploration, feeding and several physiological parameters. Mean levels of both, behaviour and physiology were affected by temperature and zinc treatment.	I
	(Dhellemmes et al., 2020)	Exploration score was positively related to growth only in a population with low predator abundance but not in a population with high predator abundance. Exploration did not correlate with survival in either population.	F
	(Dial Pauli et al., 2020)	Contrasting results depending on analytic approach: Feeding rate, excretion rate, body elemental composition, somatic growth and boldness covaried but patterns did not differ between short-term environmental exposures (low vs. high light conditions and/or interspecific competitor). PCA score of covarying body composition, growth, and boldness was associated with POL and with interspecific competition and light intensity.	F
	(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
	(Haines et al., 2020)	No association of activity or aggression with age at first reproduction or longevity in males or females regardless of experiencing a resource pulse (favourable environment) in adulthood.	M

Support hypothesis	**Contradict hypothesis**	**Findings**	**Tax.**
	(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., 2016)	(Debecker et al., 2016)	Rearing individuals under pesticide exposure affected LH and B. The covariation between boldness and LH (POLS) was only present in 1 out of 4 species and affected by treatment in the damselfly *I. pumilo*.	I
	(Debecker & Stoks, 2019)	POLS was not affected by latitude of origin, rearing temperature or zinc treatment in the third instar.	I

Support hypothesis	**Contradict hypothesis**	**Findings**	**Tax.**
	(Goulet et al., 2016)	Temperature affected the association between reproduction and aggressiveness/ docility in adult females.	A
(Haines et al., 2020)		Experiencing a resource pulse in adulthood did not affect LH-B association in adults (no significant association in either condition).	M
	(Kim & Velando, 2016)	The negative association between sociability and adult coloration in males was not affected by treatment (rearing in warm temperatures)	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.			