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EDITORIAL

Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history

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Abstract

This introduction to the topical collection on *Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology, and life history* provides an overview of conceptual, theoretical, methodological, and empirical progress in research on pace-of-life syndromes (POLSs) over the last decade. The topical collection has two main goals. First, we briefly describe the history of POLS research and provide a refined definition of POLS that is applicable to various key levels of variation (genetic, individual, population, species). Second, we summarise the main lessons learned from current POLS research included in this topical collection. Based on an assessment of the current state of the theoretical foundations and the empirical support of the POLS hypothesis, we propose (i) conceptual refinements of theory, particularly with respect to the role of ecology in the evolution of (sexual dimorphism in) POLS, and (ii) methodological and statistical approaches to the study of POLS at all major levels of variation. This topical collection further holds (iii) key empirical examples demonstrating how POLS structures may be studied in wild populations of (non)human animals, and (iv) a modelling paper predicting POLS under various ecological conditions. Future POLS research will profit from the development of more explicit theoretical models and stringent empirical tests of model assumptions and predictions, increased focus on how ecology shapes (sex-specific) POLS structures at multiple hierarchical levels, and the usage of appropriate statistical tests and study designs.

Significance statement

As an introduction to the topical collection, we summarise current conceptual, theoretical, methodological and empirical progress in research on pace-of-life syndromes (POLSs), a framework for the adaptive integration of behaviour, physiology and life history at multiple hierarchical levels of variation (genetic, individual, population, species). Mixed empirical support of POLSs, particularly at the within-species level, calls for an evaluation and refinement of the hypothesis. We provide a refined definition of POLSs facilitating testable predictions. Future research on POLSs will profit from the development of more explicit theoretical models and stringent empirical tests of model assumptions and predictions, increased focus on how ecology shapes (sex-specific) POLSs structures at multiple hierarchical levels and the usage of appropriate statistical tests and study designs.

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Introduction

Life-history theory is one of the most influential and comprehensive frameworks in contemporary organismal biology (Roff 1992, 1997; Stearns 1992). Life-history theory is based on the idea that the combination of natural selection and trade-offs in resource allocation to different biological functions (maintenance, growth, reproduction) can jointly maintain variation at the phenotypic and the genetic level, within populations, between populations within species and between species. Traditionally, life-history research has mainly focused on traits such as longevity, age and size at first reproduction and number and size of offspring. Under limiting resources, the trade-off between resource allocation to current versus future reproduction or survival can generate patterns of covariation between life-history traits resulting in a slow-fast life-history continuum (Stearns 1983), paralleling r- versus K-selection ideas (MacArthur and Wilson 1967; Pianka 1970). As supported by comparative analyses in mammals (Promislow and Harvey 1990; Oli 2004; Bielby et al. 2007), birds (Saether 1988), reptiles (Clobert et al. 1988; Bauwens and Diaz-Uriarte 1997), fish (Winemiller and Rose 1992), insects (Johansson 2000) and plants (Franco and Silvertown 1996; Salguero-Gómez et al. 2016), species at the fast end of this continuum show early reproductive maturity and short lives, whereas those at the slow end take more time to reach reproductive maturity and live longer.

More recently, several researchers proposed an organismal biological approach by suggesting that life-history characteristics and suites of physiological traits have coevolved in response to environmental conditions forming a *pace-of-life syndrome* (POLS) (Ricklefs and Wikelski 2002; Wikelski et al. 2003). This concept is based on the observation that ecological conditions favour certain life-history strategies and thereby a whole set of physiological traits such as hormonal, metabolic and immunological traits. Populations or species living in resource-limited environments should have lower metabolic rates and a slower pace of life, i.e. later maturation, fewer offspring of higher quality and a longer lifespan, compared to species living in richer environments. Correlational selection is a potential mechanism leading to this functional integration among multiple phenotypic traits. Converging evidence from several comparative studies has confirmed the existence of links between physiology and life history as predicted by the POLS hypothesis. For example, closely related mammals inhabiting different environments differ in suites of physiological and life-history traits (Lovegrove 2003), and congeneric *Peromyscus* mice have higher metabolic rates in more productive habitats (Mueller and Diamond 2001). In contrast, tropical birds are characterised by a slow pace of life and reduced metabolic rates (Tieleman et al. 2005; Wiersma et al. 2007). In stonechats (*Saxicola torquata*), metabolic rate was, for instance, intrinsically lower in tropical sedentary than in migrating temperate populations (Wikelski et al. 2003).

The POLS hypothesis was originally coined to explain population or species differences in suites of life-history and physiological traits, implying that this variation emerged because of population or species differences in ecology (Ricklefs and Wikelski 2002). More recently, it has been argued that behaviour should also be included in POLS research (called the "extended" POLS hypothesis; Careau et al. 2008; Réale et al. 2010a) because behavioural traits, particularly risk-taking behaviours, play a functional role in mediating life-history trade-offs (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008). The integration of behaviour in POLS research has particularly led to a focus on variation in life-history strategies *among* individuals *within* populations; POLS concepts are therefore also increasingly applied to this hierarchical level of variation (Réale et al. 2010a). For example, consistently more active and bold genotypes or individuals should also mature faster, live shorter and invest less in immune defence compared to less active and bold individuals within the same population.

This extended POLS hypothesis has recently generated much research interest (Fig. 1), particularly because of its connection with adaptive "animal personality" research (Réale et al. 2010b), with increasing amount of citations to the two key publications on POLS every year. Empirical evidence nevertheless remains ambiguous (meta-analysis: Royauté et al. 2018, topical collection on Pace-of-life syndromes). It is thus timely to encourage reflection on the topic and to provide a tribune of opinions on different topics related to the POLS hypothesis to trigger the development of new research directions.

This introduction to a topical collection of *Behavioral Ecology and Sociobiology* on *Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history* clarifies the definition of the POLS hypothesis and its underlying assumptions and places the contributions to the topical collection in context. We review POLS research with two main objectives. First, we aimed to provide a refined definition of POLS applicable to different hierarchical levels of variation (genetic, individual, population, species). Second, by summarising the contributions to the topical issue, we aimed to extract and integrate the main lessons that could be learned from the most recent work in this field. Based on an assessment of the current state of the theoretical foundations and the empirical support of the POLS hypothesis, we propose (i) conceptual refinements, particularly for POLS as an ecological adaptation and for the evolution of sexual dimorphism in POLS, and (ii) methodological and statistical approaches to the study of POLS at all key levels of variation.

We further highlight (iii) empirical studies estimating POLS structures in wild populations of (non)human animals, as well as (iv) novel modelling approaches placing POLS evolution in an ecological context.

Defining pace-of-life syndromes

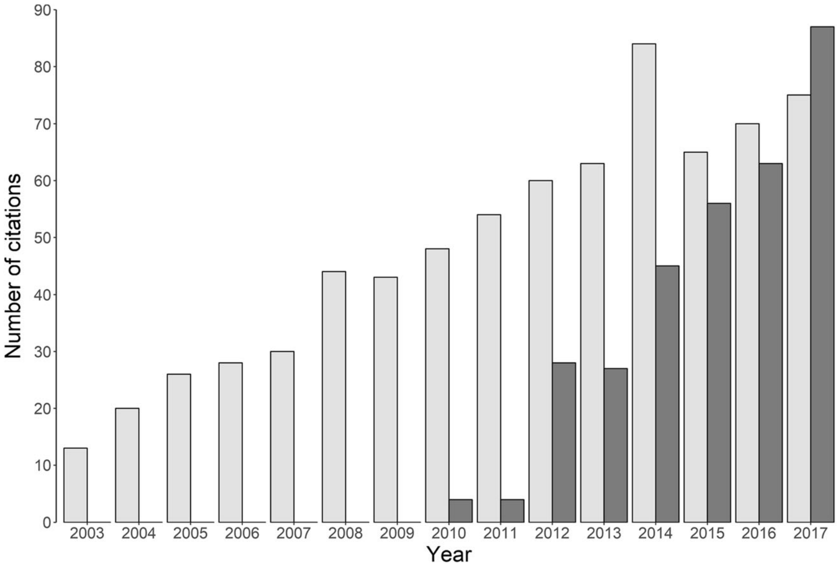
There is a considerable debate on how POLS research should best be embedded in contemporary evolutionary ecology research, while there is also considerable confusion about the definition of POLS. We therefore provide (i) a brief history of the development of the ideas in POLS research and (ii) a refined definition of the POLS hypothesis.

As mentioned briefly above, Ricklefs and Wikelski (2002) postulated that life-history characteristics and a suite of physiological traits have coevolved as a function of species- or population-specific environmental conditions. Their paper briefly mentions the existence of "a syndrome of a slow pace of life in tropical passerines" (Box 3, p. 466). The first mentioning of the term "pace of life" outside of the human literature is found in Wikelski et al. (2003) (for an integration of the POLS hypothesis with the human literature see Lehmann et al. 2018, topical collection on Pace-of-life syndromes). In this paper, a pace of life (POL) corresponds to the position along the slow-fast continuum of particular populations of stonechat (*Saxicola torquata*) living at different latitudes. Later, this concept was referred to as the pace-of-life syndrome, which "specifies that closely related species or populations experiencing different ecological conditions should differ in a suite of metabolic, hormonal and immunity traits that have coevolved with the life-history particularities related to these conditions" (Réale et al. 2010a, p. 4051). Moreover, the concept was "extended" to include among-individual differences in suites of traits *within* populations, with a focus on integrating repeatable differences in behaviour (i.e. "animal personality"). Thus, the extended POLS hypothesis posits that "consistent behavioural differences among individuals, or personality, covary with life history and physiological differences at the within-population, inter-population and inter-specific levels." (Réale et al. 2010a, p. 4051). The pace-of-life *syndrome* refers to the correlations among POLS-related traits at any hierarchical level of variation and should be clearly distinguished from the "pace of life", which represents the position of a unit (individual, population or species) in the syndrome (Fig. 2). For example, the positive correlation between longevity, age at first reproduction and shyness represents the syndrome, but a shy, late-reproducing and long-lived individual exhibits a particular pace of life within the syndrome.

The POLS hypothesis *sensu stricto* (Montiglio et al. 2018, topical collection on Pace-of-life syndromes) makes predictions on the specific direction of relationships (Fig. 1 in Réale et al. 2010a), largely borrowing from conclusions drawn by a modelling study (Wolf et al. 2007) and conceptual ideas viewing metabolism as a key pacemaker of POL (Careau et al. 2008). Specifically, life-history theory predicts that individuals differ in how they trade-off their investment in current versus future reproduction (Stearns 1983), resulting in individual differences in POL. Aggressive, fast-exploring, bold individuals should therefore have a fast POL, characterised by fast growth, early reproduction and short longevity and *vice versa* (Stamps 2007). Most empirical studies testing POLS applied this strict definition.

There is concern in the field that this definition is too restrictive to appropriately embrace the full range of potential associations between behavioural, physiological and life-history traits. We therefore propose to define POLS more broadly as the suite of phenotypic characters associated with the life-

Fig. 1 Temporal trends in the number of citations of the two early key publications on pace-of-life syndromes (dark grey: Ricklefs and Wikelski 2002; light grey: Réale et al. 2010a); numbers based on a query in ISI web of science on January 8th, 2018



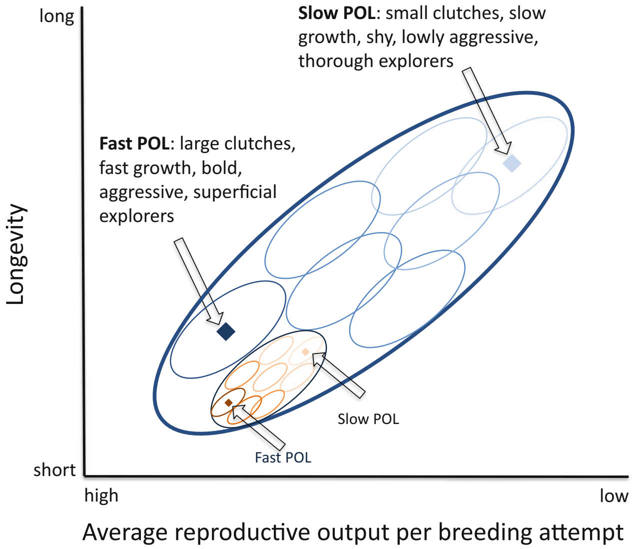


Fig. 2 A Russian doll view of the pace-of-life syndrome. Here we consider a situation where the POLS exists at all biological hierarchical levels. For illustrational reasons only, two main traits are depicted to characterise the slow-fast life-history continuum, average reproductive output per breeding attempt and longevity. The largest ellipse (dark blue) represents the pace-of-life syndrome POLS or a set of life-history, behavioural and physiological traits that are correlated with each other and along the fast-slow continuum. Within this large ellipse, each smaller ellipse (light blue) represents a species, itself characterised by a mean for each trait and a (co)variance between traits. Slow species start reproducing late and live long (i.e. have a slow POL), whereas fast species reproduce relatively early and live shorter (i.e. have a fast POL). Thus, a POL represents the position of a species along the POLS characterised by all the species studied. Each species is also characterised by a POLS and regroups populations that can either show a fast or a slow POL, within the species (smallest ellipses in red shades). Note that the POL is always relative to the level of analysis in which it is studied: a population with a slow POL relative to other populations of the same species can show a fast POL relative to other species. In turn, within each population, individuals may differ in their POLs (not shown here), and some of the traits involved in the pace-of-life syndrome can also covary within an individual as a result of plastic changes throughout its life

history trade-off between current and future reproduction, where phenotypic characters may represent behavioural, morphological, physiological or other characters adhering to this definition. This broad definition facilitates the independent development of multiple hypotheses concerning its evolutionary origin: some phenotypic characters may have coevolved as adaptations to how organisms resolve the trade-off between current and future reproduction. For example, assuming that a risky behaviour mediates the trade-off between investment in current and future reproduction, the specific prediction here is that risky behaviour increases resource acquisition at the expense of survival (Wolf et al. 2007; Réale et al. 2010a). Other phenotypic characters may instead be quasi-independent (sensu Araya-Ajoy and Dingemanse 2014) because they have instead coevolved as adaptations to other, associated, trade-offs such as the one between number and quality of offspring per reproductive event and therefore are associated to some but not other life-history traits involved in the trade-off between current and future reproduction (for an empirical example, see Santostefano et al. 2017). This topical collection refines the extended POLS hypothesis, positing that natural selection has favoured the adaptive integration of syndromes of life-history, behavioural and physiological traits.

Contributions to and insights from the topical collection

The topical collection of articles we present here includes (1) reviews (Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes; Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Tieleman 2018, topical collection on Pace-of-life syndromes) and meta-analyses of empirical literature (Royauté et al. 2018, topical collection on Pace-of-life syndromes; Tarka et al. 2018, topical collection on Pace-of-life syndromes) that draw a portrait of the current state of knowledge on the topic and propose conceptual advancements predicting the ecological conditions favouring POLSs, as well as sex-specific POLSs (Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes; Immonen et al. 2018, topical collection on Pace-of-life syndromes; Tarka et al. 2018, topical collection on Pace-of-life syndromes), (2) a novel simulation model predicting relationships between traits involved in POLSs under different environmental conditions (Salzman et al. 2018, topical collection on Pace-of-life syndromes), (3) novel statistical methodologies (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes), and (4) empirical quantifications of POLSs at multiple levels of biological organisation (Bengston in review; Delahaie et al. 2018, topical collection on Pace-of-life syndromes; Jablonszky et al. 2018, topical collection on Pace-of-life syndromes; Lehmann et al. 2018, topical collection on Pace-of-life syndromes; Sol et al. 2018, topical collection on Pace-of-life syndromes). Here, we briefly summarise the main conclusions that can be drawn from these contributions.

A general finding of the meta-analyses and reviews of the topical collection is that the empirical evidence for POLS, particularly at the within-species level, is ambiguous (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes; Tieleman 2018, topical collection on Pace-of-life syndromes); these papers therefore challenge the validity of the POLS hypothesis. An efficient theory, notably, posits a conceptual representation of the phenomenon it seeks to explain, and failure to empirically confirm a theory, rather than provoking its rejection in block, should be followed by attempts to refine the theory by further examining potential important processes that have been missed in the previous model (Marquet et al. 2014). This process requires interactions and feedback between theoreticians and empiricists to understand the biological world. Here we identify some potential causes for this mixed empirical support.

First, the extended POLS hypothesis is built upon two fundamental assumptions, namely the existence of a trade-off between current and future reproduction and the functional role of behavioural/physiological traits on life-history decisions (Stamps 2007; Wolf et al. 2007; Réale et al. 2010a; see definition above). Although these two assumptions are simple, Réale et al. (2010a) did not make them explicit, and one reason for some empirical studies failing to support the POLS hypothesis may be that these assumptions are simply not met (Montiglio et al. 2018, topical collection on Pace-of-life syndromes). The majority of published studies included in the meta-analysis by Royauté et al. (2018), topical collection on Pace-of-life syndromes did not mention whether such key assumptions were met; in lieu of this information, the magnitude of this problem therefore cannot yet be assessed. Furthermore, not all life-history traits are equally indicative of the relative investment in current versus future reproduction (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes). This difficulty of selecting the "right" set of traits to appropriately test theoretical predictions also pertains to physiology and might have partly hampered a full integration of immune function into contemporary POLS research (Tieleman 2018, topical collection on Pace-of-life syndromes). Here, we stress that the predictions of the POLS hypothesis should be tested using a stepwise approach, where these two major assumptions (i.e. trade-off between current and future reproduction and the role of behaviour/physiology in life-history decisions) are validated prior to testing further predictions (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; see also Montiglio et al. 2014).

Second, despite strong theoretical bases for the evolution of life-history traits (Roff 1992, 1997; Stearns 1992) and the existence of a formal theoretical model linking individual behaviour with life history (Wolf et al. 2007), there is a general paucity of theoretical models predicting POLS evolution; this lack of theory hampers progress in testing of theory by empiricists (Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes). Rigorously reviewing the theoretical basis of POLS, Mathot and Frankenhuis (2018), topical collection on Pace-of-life syndromes evaluated theoretical models providing adaptive explanations for the covariation between POLS-traits while assuming a trade-off between current and future reproduction. Based on their critical evaluation, only very few models generate specific testable predictions on the covariation between life-history and behavioural and/or physiological traits. Furthermore, ecological processes are the presumed drivers of coevolution among the traits involved in the POLS (Ricklefs and Wikelski 2002), but the effects of specific ecological conditions on the functional role of behavioural or physiological traits on fitness and on the strength of the trade-offs between life-history traits are unspecified in the theoretical models that are currently available to guide empirical testing.

Third, correlations between traits within a population are a function of genetic correlations but also vary due to long- or short-term environmental effects on multiple phenotypic traits; genetic and environmental correlations between components of POLS often differ in sign and magnitude (e.g. Santostefano et al. 2017). Thus, the negative relationship between current and future reproduction (trade-off) or the expected correlation between life history and other traits may not be found because it may be hidden due to environmental effects. This is a classical issue in the study of trade-offs or costs of reproduction (van Noordwijk and de Jong 1986; Cheverud 1988; Roff 1995; Reznick et al. 2000), but it can be extended to the study of any type of association or syndrome (Dingemanse and Dochtermann 2013; Santostefano et al. 2017). For example, Jablonszky et al. (2018), topical collection on Pace-of-life syndromes showed in their empirical study of POLS in collared flycatchers, *Ficedula albicollis*, that although risk-taking behaviour was negatively related to survival and positively to reproductive investment, high-quality individuals would still survive better and invest more into reproduction. Thus, within-species individual quality might mask life-history trade-offs (van Noordwijk and de Jong 1986), hindering the detection of POLS at this level of variation. Both study design and statistical tools applied in the available studies are often not suitable to properly decompose (co)variation of variables included in POLS to the different levels (within-individual, among-individual). Indeed, a recent meta-analysis showed that nearly 80% of studies claiming to test individual-level associations between behaviour and metabolic rate, hormone levels, body mass and body size were not actually doing so (Niemelä and Dingemanse 2018). POLS theory predicts patterns of among-individual covariance caused by genetic correlations and/or the integration of developmental (i.e. irreversible) plasticity; it is not concerned with patterns of within-individual covariance caused by the integration of reversible plasticity. A forceful demonstration of a POLS requires a repeated measures design, where both traits are repeatedly assayed across years within the same set of individuals, such that multi-level statistical approaches (e.g. bivariate mixed-effects models; Dingemanse and Dochtermann 2013) can be used to estimate the among-individual correlation of interest from the phenotypic data or a pedigree design to separate the genetic from the environmental component of the correlation between the traits (Niemelä et al. 2013; Santostefano et al. 2017).

Fourth, a lack of a single comparable POL measure to quantify POLS at different hierarchical levels (genetic, individual, population, species) has hampered empirical progress (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes). Various papers included in this topical collection address the question of whether a heuristic metric may exist that measures an individual's POL, such as age at first reproduction, average clutch size per breeding attempt, age of peak reproduction or longevity. Araya-Ajoy et al. (2018), topical collection on Pace-of-life syndromes demonstrate that metrics based on repeated observations (e.g. average clutch size over multiple breeding attempts) more closely correlate with POL because within-individual (biological or measurement) error might aggregate at the within-individual level. As a consequence, an individual's merit for clutch size may represent a more precise estimate of POL compared to a metric measured only once (e.g. age of first reproduction or longevity). However, metrics best measuring POL therefore also depend on the longevity of the species (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes). Considerable caution is thus required when planning a study design to test hypotheses concerning POL and POLSs. Moreover, failures to confirm theoretical predictions (e.g. meta-analysis by Royauté et al. 2018, topical collection on Pace-of-life syndromes) may thus also stem from biases caused by the inappropriate choice of life-history metrics used to measure POL.

Fifth, although POLS is presumed to represent an ecological adaptation, ecology is often treated as a black box, particularly at the within-species level (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Tieleman 2018, topical collection on Pace-of-life syndromes). To better understand when POLSs exist and what form they take, requires studies firmly placing the study of phenotypes into appropriate ecological contexts of variation in risks and resources (Montiglio et al. 2018, topical collection on Pace-of-life syndromes). For example, variation in predation risk in the environment might hamper our ability to detect POLS (as discussed above)—a bold and explorative individual might acquire more resources to fuel a faster life history but might only have a higher chance to die than a less bold and explorative individual, in high-predation risk environments. One of the leading themes of many contributions to the topical collection is that ecology matters. In her review on the integration of immune function into POLS in birds, Tieleman (2018), topical collection on Pace-of-life syndromes identified environmental and ecological conditions as the main drivers of variation in various immune traits, potentially overriding correlations between immune function and life history. Several empirical studies, each focussing on different hierarchical levels of variation, provide worked examples for taxon-specific considerations of ecological contexts. For example, using phylogenetically controlled comparative analyses, Sol et al. (2018), topical collection on Pace-of-life syndromes found predicted relationships between slow life-history and risk-taking behaviour, but only under rural environmental conditions and not under the changed predation risk of urban environments. In blue tits, *Cyanistes caeruleus*, POLS-relationships within populations were only present under certain environmental conditions of resource availability, but existed at the among-population level (Delahaie et al. 2018, topical collection on Pace-of-life syndromes). Also, a common-garden experiment with eusocial *Temnothorax* ants revealed differences in energy allocation to current versus future reproduction among colonies from two populations originating from different ecological conditions (Bengston in review, topical collection on Pace-of-life syndromes). Additionally, modelling approaches further stressed the importance of environmental variation. Taking an optimality modelling approach, Salzman et al. (2018), topical collection on Pace-of-life syndromes showed that strength and direction of correlations between metabolic and behavioural POLS traits depended on variation in resource availability and mortality risk. Furthermore, predicting an individual's POL based on various life-history measures was also highly affected by environmental stochasticity in simulations run with species at various positions along the slow-fast life-history continuum (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes). Thus, one important lesson to take from these studies is that a POLS can result from ecological processes, also those at the metapopulation level (Delahaie et al. 2018, topical collection on Pace-of-life syndromes; Sol et al. 2018, topical collection on Pace-of-life syndromes), and that further studies are needed to understand how the interactions between these processes facilitate or constrain the emergence of POLS at different levels of variation.

Sixth, potential sex specificity of POLS might add another, previously ignored, level of biological complexity. Drawing from sexual selection theory, Hämäläinen et al. (2018), topical collection on Pace-of-life syndromes developed a framework on what aspects of POLS might be sex-specific, based on which they suggest various ultimate mechanisms driving sex differences in mean trait expression and POLS-trait covariation and propose predictions on why and when we should expect to find sex-specific POLS. Immonen et al. (2018), topical collection on Pace-of-life syndromes outline potential mechanisms for the evolution of sex differences in POLS. Assessing and evaluating the current knowledge on the genetic basis of POLS-traits and their covariation, they discuss how a sex-specific genetic architecture might evolve and how hormonal and metabolic mechanisms might mediate sex differences proximately. In a meta-analysis of empirical studies, Tarka et al. (2018), topical collection on Pace-of-life syndromes found no general support for sex differences in mean and variances for POLS-related traits, but males tended to have a faster life history, particularly under wild conditions and in species with polygynous mating systems. Using data from a contemporary human population, Lehmann et al. (2018), topical collection on Pace-of-life syndromes showed that POLS relationships were similar for boys and girls, but that the sexes differed in the strength of trait associations. Thus, further empirical studies are needed to address sexual dimorphism in POLS; field studies conducted on species with high sex-specific selection pressures are most promising.

Conclusions

The contributions presented in this topical collection allow for a number of general conclusions to be drawn: (1) We need more and better POLS theory to further satisfactory progress in this area (Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes); (2) the environment matters; theoreticians and empiricists alike should include ecological variation (e.g. gradients of risks and resources) in their models and tests of POLS (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Salzman et al. 2018, topical collection on Pace-of-life syndromes; Tieleman 2018, topical collection on Pace-of-life syndromes); (3) given the fundamental differences in life history between males and females, aspects of POLS should be sex-specific (Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes; Immonen et al. 2018, topical collection on Pace-of-life syndromes; Lehmann et al. 2018, topical collection on Pace-of-life syndromes; Tarka et al. 2018, topical collection on Pace-of-life syndromes); (4) POLS can be studied at different levels of variation, but "raw" phenotypic correlations between POLS traits (the prevailing level at which data are currently analysed: Royauté et al. 2018, topical collection on Pace-of-life syndromes) alone seem relatively uninformative; (5) empirical studies should test the fundamental assumptions first (i.e. the trade-offs between life-history traits indicative of current versus future reproduction), use relevant traits (e.g. life-history traits indicative of reproductive investment and preferentially measured repeatedly and behavioural traits indicative of resource acquisition and risk-taking) and apply appropriate statistical approaches, such as variance partitioning and multivariate mixed models (Araya-Ajoy et al. 2018, topical collection on Pace-of-life syndromes; Montiglio et al. 2018, topical collection on Pace-of-life syndromes), and (6) given the limitations in the theoretical underpinning of POLS, the general explanatory power of the POLS hypothesis cannot be appropriately evaluated with the data currently at hand. We hope that this topical contribution will help readers to design new studies, whether conceptual or empirical in nature, allowing firmly future tests of the POLS hypothesis.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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