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ORIGINAL ARTICLE

# The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum

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## Abstract

The pace-of-life syndrome (i.e., POLS) hypothesis posits that behavioral and physiological traits mediate the trade-off between current and future reproduction. This hypothesis predicts that life history, behavioral, and physiological traits will covary under clearly defined conditions. Empirical tests are equivocal and suggest that the conditions necessary for the POLS to emerge are not always met. We nuance and expand the POLS hypothesis to consider alternative relationships among behavior, physiology, and life history. These relationships will vary with the nature of predation risk, the challenges posed by resource acquisition, and the energy management strategies of organisms. We also discuss how the plastic response of behavior, physiology, and life history to changes in ecological conditions and variation in resource acquisition among individuals determine our ability to detect a fast-slow pace of life in the first place or associations among these traits. Future empirical studies will provide most insights on the coevolution among behavior, physiology, and life history by investigating these traits both at the genetic and phenotypic levels in varying types of predation regimes and levels of resource abundance.

## Significance statement

We revisit the pace-of-life syndrome hypothesis, suggesting that behaviors involving a risk of death or injury should coevolve with higher metabolic rates, higher fecundity, faster growth, and heightened mortality rates. Empirical support for this hypothesis is mixed. We show how relaxing some of the assumptions underlying the pace-of-life syndrome hypothesis allows us to consider alternative relationships among behavior, physiology, and life history, and why we fail to meet the predictions posed by the pace-of-life syndrome hypothesis in some populations. Our discussion emphasizes the need to re-integrate the role of the species' natural history, ecological conditions, and phenotypic plasticity in shaping relationships among behavior, physiology, and life history.

**Keywords** Behavior · Immunity · Life history strategies · Metabolism · Personality · Trait interaction

## Introduction

Organisms must decide how much time or energy to invest in reproduction relative to maintenance and survival (Stearns 1992). Depending on how they negotiate this trade-off, populations or species are positioned along a fast-slow life history continuum. This continuum ranges from organisms that prioritize reproduction over survival (i.e., a fast life history) to those that prioritize survival over reproduction (i.e., a slow life history, Stearns 1983, 1989; Promislow and Harvey 1990). Differences in life history strategies among species or populations are associated with differences in physiology such as metabolic rate or stress reactivity (Wikelski and Ricklefs 2001; Ricklefs and Wikelski 2002).

Behavior might play a functional role in the fast-slow life history continuum and thus covary predictably with life

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history traits such as fecundity, survival, or growth (the pace-of-life syndrome hypothesis, POLS thereafter, Stamps 2007; Biro and Stamps 2008; Réale et al. 2010). The POLS hypothesis predicts that if some behavioral traits such as high boldness, exploration, aggressiveness, or activity increase acquisition of resources at an expense of survival, then individuals expressing these traits should also have a faster life history (Wolf et al. 2007; Réale et al. 2010). Species, populations, or individuals with a faster pace of life should also invest less resources in their immunological defenses (Tieleman et al. 2005; Martin et al. 2006). Réale et al. (2010) initially invoked correlational selection to explain the evolution of such associations between life history, physiology, and behavior, but feedbacks between behavior and state could also explain why we observe these associations at the individual level (Luttbeg and Sih 2010; Dingemanse and Wolf 2013).

Since the initial publications (Stamps 2007; Biro and Stamps 2008; Réale et al. 2010), multiple studies have investigated the relationships between behavior, physiology, and life history within populations (Dammhahn et al. 2018). Several of them have examined the relationships between boldness, exploration, activity, or aggressiveness, and metabolism (e.g., Careau et al. 2009, 2011; Timonin et al. 2011; Gifford et al. 2014; Royauté et al. 2015; Binder et al. 2016; White et al. 2016) or immunological functions (e.g., Niemelä et al. 2013; Zylberberg et al. 2014; Dosmann et al. 2015). Others have tested for and quantified the relationships between behavioral traits and age at maturity (e.g., Réale et al. 2000; Niemelä et al. 2013; Müller and Müller 2015; Urszán et al. 2015), fecundity (e.g., Réale et al. 2000; Kontiainen et al. 2009; Brommer et al. 2014; Montiglio et al. 2014; Bridger et al. 2015), survival (e.g., Réale and Festa-Bianchet 2003; Réale et al. 2009; Bergeron et al. 2013), and growth (e.g., Hoogenboom et al. 2013; Biro et al. 2014; White et al. 2016). Some studies support the initial predictions made by the POLS hypothesis in its strict sense, but others have failed to find such support (reviewed in Royauté et al. 2018, topical collection on Pace-of-life syndromes).

Studies could fail to support the POLS hypothesis because they characterize boldness, exploration, or activity with too diverse methodologies (Royauté et al. 2018, topical collection on Pace-of-life syndromes). These methodologies could vary in their sensitivity to detect individual differences, or measure different aspects of an animal's behavior. Alternatively, assumptions made by Wolf et al. (2007) or Réale et al. (2010) may be too strict to fit all the possible associations between behavior, physiology, and life history (we refer to these models as predicting a POLS sensu stricto). Indeed, any trait improving resources acquisition and current reproduction, at the expense of survival or future reproduction, could coevolve with an organism's pace of life. Alternatively, traits such as exploration, aggressiveness, or activity do not automatically improve resources acquisition.

Ecological conditions might also lead to varying degrees of association between behavior, physiology, and life history depending on the population studied (Dammhahn et al. 2018, topical collection on Pace-of-life syndromes). Hence, we might need to reconsider the strict definition used in the formulation of the POLS hypothesis to account for the role of ecological conditions. All these points were discussed in the initial papers (e.g., Réale et al. 2010) and in others (Adriaenssens and Johnsson 2009; Mathot and Dingemanse 2015), but we still lack a clear framework for predicting whether a syndrome should emerge and what relationships between behavior, life history, and physiology we should observe.

In this paper, we outline elements of such a framework to explain variation in syndromes across systems and ecological conditions. Our aim is to switch the focus from testing whether the POLS structure suggested by Réale et al. (2010) is observed or not to investigating how ecological conditions (predation risk, resource acquisition) shape relationships between life history, physiology, and behavior at the genetic and phenotypic levels. We consider several ways in which we can nuance the predictions on the POLS sensu stricto. We extend the initial logic underlying the POLS hypothesis (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Réale et al. 2010) to consider alternative structures of relationships among behavior, physiology, and life history. We first consider how relaxing the assumptions about the functional role of behavior and physiology (see Table 1) in supporting the life history of organisms along the fast-slow continuum generates alternative hypotheses and predictions on the links among behavior, physiology, and life history. Second, we consider how phenotypic plasticity of behavior, physiology, and life history could shape POLS.

## Behavior and physiology can have different roles within the pace-of-life syndrome

The POLS hypothesis assumes that particular behaviors increase the risk of predation and the acquisition of resources such as food, partners, or territories (Stamps 2007; Wolf et al. 2007; Réale et al. 2010). The POLS hypothesis also assumes that metabolism is the pacemaker of an organism's pace of life or life history productivity (Careau et al. 2008; Biro and Stamps 2010; Réale et al. 2010). Relaxing these assumptions allows us to focus on predicting which behavioral and physiological adaptions should be favored by a particular set of environmental conditions. Below we discuss how the role of behavior and physiology can vary within a POLS exhibited within a species or population.

**Table 1** Assumptions at the basis of the evolution of a pace-of-life syndrome sensu stricto within populations and reasons why these assumptions might not be met

| Assumptions to be tested | Reasons why these assumptions may not be met |
|---|---|
| There is a trade-off between early-life reproduction, and survival or late-life reproduction. | A large variance in resource acquisition among individuals can hide the trade-off in the allocation of resources between early-life and survival or late-life reproduction.<br>Plastic responses to environmental changes and uncontrolled environmental conditions may blur the detection of the pace-of-life syndrome in a population. |
| A trait associated to the pace of life (i.e., a behavioral or physiological trait[a]) should play a functional role for each of the life history traits. | The studied trait does not have any functional role on either early reproduction or survival.<br>The studied trait is weakly repeatable, lowering its association with life history traits or our statistical power to detect this association.<br>Strict assumptions about the functional link between behavior and both survival and reproduction (i.e., sensu Wolf et al. 2007; Réale et al. 2010) might not be met. Relaxing these assumptions (i.e., pace-of-life syndrome sensu *lato*) may permit us to consider situations in which the direction of the association between behavior and life history is contrary to what is expected in the POLS hypothesis sensu stricto.<br>Although two traits may independently affect reproduction and survival, they may not be linked with each other. Therefore, we may not expect that a behavioral trait may be systematically linked to metabolism, even though they both affect survival and reproduction. |
| Correlational selection should favor some combinations of behavioral/physiological and life history traits. | The correlation between traits provides no fitness benefit but is rather the results of constraints to their independent expression. |

[a] Note that these traits need to be repeatable to show consistent links with life history traits. Highly labile traits cannot be linked to any stable life history strategy. Traits can be repeatable because it is heritable or developmentally plastic (i.e., early life conditions or parental effects)

## Behavior

Several behavioral traits can affect resource acquisition and the risk of predation (Fig. 1), but their relative importance varies with the type of interaction between an organism and its predators (Lima and Dill 1990) and with the characteristics of the resources consumed. As a result, the type of resources an organism acquires and the foraging behavior of its predators can affect which behavioral traits most likely support the pace of life. For example, when an organism's vulnerability to predation depends strongly on its ability to avoid encounters with predators, we expect activity and exploration to covary with the slow-fast life history continuum (Fig. 1). Alternatively, when vulnerability to predation depends more strongly on being detected by predators or increasing chances of escapes following an attack, then we expect freezing behavior or flight initiation distance to covary with the pace of life (Ydenberg and Dill 1986). Situations where predation risk can be lowered by increasing the detection of potential predators by the prey, vigilance, rather than activity or freezing, should covary with pace of life of organisms (Lima and Dill 1990).

Investigating the relationships between the chances of encounter with predators, the probability of being detected by them, and the probability of detecting predators could also explain why these traits can be correlated with each other in some cases and not in others. Furthermore, predators exhibit a diversity of foraging tactics, from sit-and-wait to active pursuit, varying both among individuals and among species (Schmitz et al. 2004; Pruitt and Ferrari 2011; Miller et al. 2014). Hence, the type of hunting strategy of the predator or the distribution of food patches in the environment should affect which behaviors are most likely to be associated with life history.

The exact constraints placed on resource acquisition can also affect which behavior covaries with life history. Activity and exploration are more likely to impact resource acquisition in organisms foraging on clumped and ephemeral food sources than in organisms foraging on abundant and homogeneously distributed resources (Macarthur and Pianka

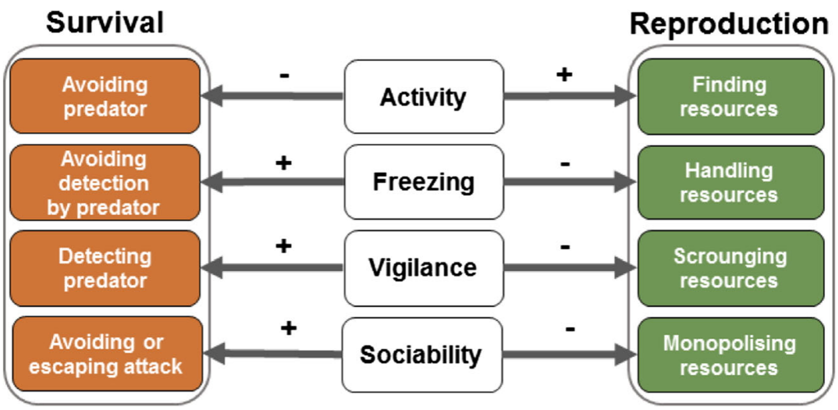

**Fig. 1** Behaviors mediate the trade-off between current and future reproduction through their effects on various components of resources acquisition and risk of predation. Individuals can increase their survival by decreasing the rate of encounter with predators, by decreasing their chances of being detected, by increasing predator detection before an attack, or by improving the probability of escaping or surviving following an attack by a predator, respectively (orange boxes). To acquire resources and fuel their reproduction, individuals must search for, find, and handle food items. In some systems, resource acquisition involves scrounging from or defending food items against conspecifics (green boxes). The behavior most likely to mediate the trade-off between mortality risk and resource acquisition (black arrows and signs) is expected to vary across species depending on their different natural histories and on the relative importance of the various components of predation risk and resource acquisition. For example, we can expect that, in species where survival and resource acquisition depend more strongly on the rate of encounter with a predator and on time spent searching for resources, respectively, active individuals will trade their survival for higher current reproduction. In contrast, in species where survival and resource acquisition depend more strongly on detecting a predator and handling resources, individuals that invest more in reproduction rather than in survival will be less vigilant (but not necessarily more active). Note that some of the behaviors represented here could affect more than one component of predation risk or resource acquisition and that several other trade-offs could shape the evolution of a pace-of-life syndrome

1966; Heads 1986; Dixon and Baker 1987; see also Fraser and Gilliam 1987). Vigilance or freezing behavior is instead more likely to covary with the pace of life when organisms rely on food items requiring long bouts of handling (Krebs 1980; Lima 1988). Alternatively, aggressiveness might covary with the pace of life when contest/interference competition is associated with resource acquisition (Wolf et al. 2007; Bergmüller and Taborsky 2010; Montiglio et al. 2013).

Defining the role of behavioral traits in mediating life history trade-offs allows us to nuance our predictions on the behaviors that are more likely to covary with the pace of life of an organism. Considering the ecology of predation risk and foraging of the individuals can change the predictions one could derive from the POLS hypothesis. Furthermore, it generates richer and more specific predictions to on the link between ecology of species and the type of POLS they exhibit. Of course, it is also possible that behavior does not mediate any life history trade-off in some systems. Studies simultaneously reporting a clear trade-off between current reproduction and future reproduction or survival, and no relationship between life history and behavior, are rare. Such studies would be the strongest and clearest challenges to the POLS hypothesis.

## Physiology

The original POLS hypothesis posits that metabolism is the pacemaker of life (Ricklefs and Wikelski 2002). Supporting this view, individuals with a higher resting metabolic rate also show the highest daily energy expenditure in many endotherms (Careau and Garland 2012). At the within-species level, individuals with a higher metabolic rate could potentially afford a faster pace of life, because a higher metabolic rate allows them to mobilize the energy needed to express a high level of activity, a fast exploration, or high aggressiveness (Careau et al. 2008; Biro and Stamps 2010; Réale et al. 2010).

Energy allocation, acquisition, and expenses might be linked in several different ways (Careau et al. 2008; Careau and Garland 2012; Mathot and Dingemanse 2015). For example, daily energy expenditure can be independent of basal metabolic rate (i.e., the allocation model, Speakman 1997). In this case, individuals spending a lot of energy on maintenance (expressed as basal metabolic rate) have less energy available for energetically costly behaviors. Alternatively, a greater capacity to produce and mobilize energy (reflected by basal metabolic rate) could lead to a higher daily energy expenditure (i.e., the performance model, Speakman 1997). In this case, behaviors that both increase energy gain and energy expenditure are predicted to scale positively with basal metabolic rate, because individuals with a fast running metabolic machinery also have to fuel it and must mobilize more energy for energetically costly behaviors (Mathot and Dingemanse 2015). Finally, daily energy expenditure and basal metabolic rate could also be unrelated (independent model) and only behaviors increasing energy gain might scale positively with basal metabolic rate (Mathot and Dingemanse 2015). Thus, predicting the direction of among-individual correlations between metabolic, behavioral, and life history traits requires a priori knowledge of the underlying relationships between metabolic rate and energy expenditure in a given species (see also Mathot and Dingemanse 2015).

The relationship between metabolic rate and energy expenditure could also vary with a species' natural history. For example, endotherms and ectotherms are likely to show different relationships between metabolic rate and energy expenditure, given their fundamental differences in physiology. Several studies on species of fish demonstrated that proactive individuals have higher standard metabolic rates, thereby supporting predictions of the performance model (e.g., Cutts et al. 1998; Lahti et al. 2012). In contrast, studies on birds and mammals tend to provide support for the allocation model (e.g., Wiersma and Verhulst 2005; Vaanholt et al. 2007; but see Careau et al. 2013). Future comparative research should clarify whether this is indeed a general pattern and whether the differential metabolic maintenance costs of these very different ways of life can explain such a pattern.

The relationships between metabolism and pace of life should not only differ among species as a function of their energy management strategy but should also vary with the position of the organism in its life cycle. For example, endothermic animals can exhibit tremendous reductions in metabolic rate during some phases of their life cycle (up to 99% reduction in metabolic rate, e.g., Thomas et al. 1990). The main feature of these strategies is to lower the running costs of the metabolic engine for short (daily torpor) or long (hibernation) periods of time by controlled reduction of body temperature (i.e., heterothermy). Thus, heterothermy is an important adaptation to fluctuating environmental conditions and has important life history consequences, such as extended longevity and slow life histories (Turbill et al. 2011). Individuals within species differ in their energy-saving strategies (Vuarin et al. 2013), and this affects their survival and reproductive success (Dammhahn et al. 2017). Analyzing such differences among individuals can surely help us understand the relationships between physiology and life history (see also Glazier 2015).

## The pace of life can be apparent or hidden

The previous section detailed how different behaviors and physiological traits can covary with an organism's pace of life. Such a view assumes that there is a life history trade-off and that populations or species exhibit variation in the position of their individuals along the fast-slow pace-of-life continuum. However, the actual fast-slow pace-of-life continuum is not always present in a population or species. In what follows, we discuss when individuals should or should not vary over a fast-slow pace-of-life continuum.

### Local ecological conditions can drive or hide life history trade-offs

Survival and reproduction can covary positively, negatively, or not at all, depending on the variation in resources acquired among individuals (van Noordwijk and de Jong 1986; Roff and Fairbairn 2007). Failure to detect the predicted link between behavior and life history could thus be explained by a failure to detect a fast-slow pace-of-life continuum in the first place. To fully validate or reject the assumptions underlying the POLS hypothesis, we need to study the relationships between life history, physiology, and behavior over gradients of resource abundance or predation risk (see Table 1). Yet very few studies have achieved this level of insights. Changing ecological conditions, for example, yearly fluctuations in predation pressure, could change the role played by some behaviors in the POLS. In other cases, there may be no clear trade-off between early and late reproduction (Martin and Festa-Bianchet 2011; Jablonszky et al. 2018 in press, topical collection on Pace-of-life syndromes), potentially because of selection eroding the variation in allocation strategies within population, thereby making it impossible to detect a link between behavior, physiology, and life history (Réale et al. 2009).

### Fixed or plastic pace-of-life syndromes?

The POLS hypothesis assumes that the plasticity of behavior is constrained by metabolic organs (Biro and Stamps 2010; see Bijleveld et al. 2014 for an empirical study challenging this assumption). Yet, temporal or spatial variation in environmental conditions can induce a change in an individual's morphology, life history, or behavior (Walther et al. 2002; Réale and Festa-Bianchet 2003; Charmantier et al. 2008; Pfennig et al. 2010; Montiglio et al. 2014; Niemelä and Dingemanse 2017). Ecological conditions determine our ability to identify a life history trade-off at the phenotypic level and thus our ability to detect a link between behavior, physiology, and life history (Nicolaus et al. 2012; Montiglio et al. 2014).

When environmental variation occurs within at the same spatial scale as the dispersal of individuals, individuals are likely to encounter different types of conditions during their life. Selection should favor reversible plasticity for the traits involved in the POLS (Sultan and Spencer 2002). Such short-term reversible plastic changes are not considered to be part of the syndrome (Dingemanse et al. 2012b), but they can hide or affect the relationships we observe among the traits. We thus need to account for reversible plastic changes in behavior and physiology to detect POLS at the population level.

When environmental variation is strong and predictable, selection should favor developmental (i.e., irreversible) phenotypic plasticity (Scheiner 1993; West-Eberhard 2003; Pigliucci 2005; Fitzpatrick 2012). In this case, we should expect the evolution of an integrated developmental plasticity in the pace of life of an organism (Nicolaus et al. 2012; Montiglio et al. 2014). Changes in life history trajectory, behavior, and physiology may depend on early life conditions or parental effects (Ellis et al. 2013). The environmental conditions encountered by an organism early in life could be used to anticipate future conditions and adjust its development accordingly (i.e., the predictive adaptive response hypothesis; Gluckman et al. 2005; Monaghan 2008) or instead constrain its ability to cope with future conditions (i.e., the silver spoon effect; Monaghan 2008). Developmental plasticity complicates our task of detecting an association between the life history of an organism and its behavior or physiology. For example, differences in behavior and life history between three populations of Corsican blue tits (*Cyanistes caeruleus*) suggest the existence of a POLS in some years but not in others (Dubuc Messier et al. 2016). This probably occurs because of plastic adjustments of both life history and behavior traits that affect the mean position of each population along the pace-of-life continuum (Dubuc Messier et al. 2016). It is thus necessary to compare the traits across populations over several years to be able to detect potential differences in pace of life between them.

Finally, when the variation in ecological conditions occurs at larger spatial scales, selection should favor the evolution of locally adapted traits (Wang and Bradburd 2014) and thus maintain some genetic polymorphism for traits along the POLS (Dubuc Messier et al. 2016; GDM et al. unpublished). The maintenance of some genetic polymorphism in POLS traits can also be considered through the trade-off between life history strategies involved in the POLS. The evolution of plastic POLS traits does not preclude genetic associations between them (Brommer and Kluen 2012; Fitzpatrick 2012; Santostefano et al. 2017). The relative importance of fixed polymorphism and developmental plasticity in generating associations among traits involved in a syndrome will depend on the fitness costs of this developmental plasticity, on the strength of the genetic correlations among traits, and on the predictability and magnitude of variation in ecological conditions (Scheiner 1993; West-Eberhard 2003; Fitzpatrick 2012).

## Conclusion: What should future studies on the pace-of-life syndrome look like?

We can develop and nuance the initial POLS hypothesis by considering a wider range of relationships between behavior, physiology, and life history strategy. These relationships can also emerge from genetic polymorphism and developmental plasticity and be obscured by reversible plastic changes in the traits. While we did not discuss this option extensively, it is important that we consider the possibility that life history, physiology, and behavior do not form a syndrome in some systems. Studying such systems will be useful to illuminate when we should expect the emergence of a pace-of-life syndrome and when we should not.

Future studies on the POLS hypothesis will move forward if they analyze the relationships between life history, physiology, and behavior over ecological gradients of predation risk, resource abundance and distribution, or population density. This challenging goal will perhaps be achieved most effectively by long-term studies monitoring free-ranging individuals over several generations (Dingemanse et al. 2004; Kontiainen et al. 2009; Réale et al. 2009; Quinn et al. 2011; Montiglio et al. 2014; Jablonszky et al. 2018, topical collection on Pace-of-life syndromes) or by experiments manipulating ecological conditions (Mathot et al. 2011, 2012; Dingemanse et al. 2012a; Nicolaus et al. 2012a; Guenther and Trillmich 2013). A multivariate quantitative genetic framework and a reaction norms approach will be key in analyzing such complex datasets (Robinson et al. 2009; Husby et al. 2010; Brommer 2013). We are aware that such studies will be challenging. They will require repeated measurements on multiple traits across different levels of predation pressure or resource abundance for several individuals of known relatedness or pedigree (Nussey et al. 2007; Husby et al. 2010; Brommer 2013). Nevertheless, as data on behavioral traits in long-term study programs are accumulating, this type of analysis could be soon within reach for a greater number of study systems (Niemelä and Dingemanse 2017; for examples, see Santostefano et al. 2017).

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## Compliance with ethical standards

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

## References

Adriaenssens B, Johnsson JI (2009) Personality and life-history productivity: consistent or variable associations? Trends Ecol Evol 24:179–180

Bergeron P, Montiglio P-O, Réale D, Humphries MM, Gimenez O, Garant D (2013) Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. J Evol Biol 26:766–774

Bergmüller R, Taborsky M (2010) Animal personality due to social niche specialisation. Trends Ecol Evol 25:504–511

Bijleveld AI, Massourakis G, van der Marel A, Dekinga A, Spaans B, van Gils JA, Piersma T (2014) Personality drives physiological adjustments and is not related to survival. Proc R Soc Lond B 281: 20133135

Binder TR, Wilson ADM, Wilson SM, Suskic SD, Godin J-G, Cooke SJ (2016) Is there a pace-of-life syndrome linking boldness and metabolic capacity for locomotion in bluegill sunfish? Anim Behav 121: 175–183

Biro PA, Adriaenssens B, Sampson P (2014) Individual and sex-specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. J Anim Ecol 83:1186–1195

Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? Trends Ecol Evol 23:361–368

Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol 25:653–659

Bridger D, Bonner SJ, Briffa M (2015) Individual quality and personality: bolder males are less fecund in the hermit crab Pagurus bernhardus. Proc R Soc Lond B 282:20142492

Brommer JE (2013) On between-individual and residual (co)variances in the study of animal personality: are you willing to take the “individual gambit”? Behav Ecol Sociobiol 67:1027–1032

Brommer JE, Karell P, Ahola K, Karstinen T (2014) Residual correlations, and not individual properties, determine a nest defense boldness syndrome. Behav Ecol 25:802–812

Brommer JE, Kluen E (2012) Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. Ecol Evol 2:3032–3044

Careau V, Bininda ORP, Thomas DW, Réale D, Humphries MM (2009) Exploration strategies map along fast-slow metabolic and life-history continua in muroid rodents. Funct Ecol 23:150–156

Careau V, Garland T (2012) Performance, personality, and energetics: correlation, causation, and mechanism. Physiol Biochem Zool 85: 543–571

Careau V, Réale D, Garant D, Pelletier F, Speakman JR, Humphries MM (2013) Context-dependent correlation between resting metabolic rate and daily energy expenditure in wild chipmunks. J Exp Biol 216:418–426

Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. Oikos 117:641–653

Careau V, Thomas D, Pelletier F, Turki L, Landry F, Garant D, Réale D (2011) Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (*Peromyscus maniculatus*). J Evol Biol 24:2153–2163

Charmantier A, Mccleery RH, Cole LR, Perrins C, Kruuk LEB (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–804

Cutts CJ, Metcalfe NB, Taylor AC (1998) Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. J Fish Biol 52:1026–1037

Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D (2018) Pace-of-life syndromes : a framework for the adaptive integration of behaviour, physiology and life history. Behav Ecol Sociobiol 72:62–70

Dammhahn M, Landry-cuerrier M, Réale D, Garant D, Humphries MM (2017) Individual variation in energy-saving heterothermy affects survival and reproductive success. Funct Ecol 31:866–875

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. Proc R SocLond B 271:847–852

Dingemanse NJ, Bouwman KM, van de Pol M, van Overveld T, Patrick SC, Matthysen E, Quinn JL (2012a) Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. J Anim Ecol 81:116–126

Dingemanse NJ, Dochtermann NA, Nakagawa S (2012b) Defining behavioural syndromes and the role of “syndrome deviation” in understanding their evolution. Behav Ecol 66:1543–1548

Dingemanse NJ, Wolf M (2013) Between-individual differences in behavioural plasticity within populations: causes and consequences. Anim Behav 85:1031–1039

Dixon SM, Baker RL (1987) Effects of fish on feeding and growth of larval *Ischnura verticalis* (Coenagrionidae: Odonata). Can J Zool 65:2276–2279

Dosmann A, Brooks KC, Mateo JM (2015) Evidence for a mechanism of phenotypic integration of behaviour and innate immunity in a wild rodent: implications for animal personality and ecological immunology. Anim Behav 101:179–189

Dubuc Messier G, Réale D, Perret P, Charmantier A (2016) Environmental heterogeneity and population differences in blue tits personality traits. Behav Ecol 28:arw148

Ellis BJ, Del Giudice M, Shirtcliff EA (2013) Beyond allostatic load: The stress response system as a mechanism of conditional adaptation. Dev Psychopathol 26:1–20

Fitzpatrick BM Underappreciated consequences of phenotypic plasticity for ecological speciation. Int J Ecol 2012, 2012:32–37

Fraser DF, Gilliam JF (1987) Feeding under predation hazard: response of the guppy and Hart’s rivulus from sites with contrasting predation hazard. Behav Ecol Sociobiol 21:203–209

Gifford ME, Clay TA, Careau V (2014) Individual (co)variation in standard metabolic rate, feeding rate, and exploratory behavior in wild-caught semiaquatic salamanders. Physiol Biochem Zool 87:384–396

Glazier DS (2015) Is metabolic rate a universal “pacemaker” for biological processes? Biol Rev 90:377–407

Gluckman PD, Hanson MA, Spencer HG, Bateson P (2005) Environmental influences during development and their later consequences for health and disease: implications for the interpretation of empirical studies. Proc R Soc LondB 272:671–677

Guenther A, Trillmich F (2013) Photoperiod influences the behavioral and physiological phenotype during ontogeny. Behav Ecol 24: 402–411

Heads PA (1986) The costs of reduced feeding due to predator avoidance: potential effects on growth and fitness in *Ischnura elegans* larvae (Odonata: Zygoptera). Ecol Entomol 11:369–377

Hoogenboom MO, Armstrong JD, Groothuis TGG, Metcalfe NB (2013) The growth benefits of aggressive behavior vary with individual metabolism and resource predictability. Behav Ecol 24:253–261

Husby A, Nussey DH, Visser ME, Wilson AJ, Sheldon BC, Kruuk LE (2010) Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. Evolution 64:2221–2237

Jablonszky M, Szász E, Krenhardt K, Markó G, Hegyi G, Herényi M, Laczi M, Nagy G, Rosivall B, Szöllősi E, Török J, Garamszegi LZ (2018) Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndomes hypothesis using long-term data from a wild bird. Behav Ecol Sociobiol 72:52

Kontiainen P, Pietiäinen H, Huttunen K, Karell P, Kolunen H, Brommer JE (2009) Aggressive ural owl mothers recruit more offspring. Behav Ecol 20:789–796

Krebs JR (1980) Optimal foraging, predation risk and territory defense. Ardea 68:83–90

Lahti K, Huuskonen H, Laurila A, Piironen J (2012) Metabolic rate and aggressiveness between brown trout populations. Funct Ecol 16: 167–174

Lima SL (1988) Vigilance and diet selection: a simple example in the dark-eyed junco. Can J Zool 66:593–596

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Luttbeg B, Sih A (2010) Risk, resources and state-dependent adaptive behavioural syndromes. Phil Trans R Soc B 365:3977–3990

Macarthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Martin JGA, Festa-Bianchet M (2011) Age-independent and age-dependent decreases in reproduction of females. Ecol Lett 14:576–581

Martin LB II, Hasselquist D, Wikelski M (2006) Investment in immune defense is linked to pace of life in house sparrows. Oecologia 147: 565–575

Mathot KJ, Dingemanse NJ (2015) Energetics and behavior: unrequited needs and new directions. Trends Ecol Evol 30:199–206

Mathot KJ, van den Hout PJ, Piersma T, Kempenaers B, Réale D, Dingemanse NJ (2011) Disentangling the roles of frequency-vs. state-dependence in generating individual differences in behavioural plasticity. Ecol Lett 14:1254–1262

Mathot KJ, Wright J, Kempenaers B, Dingemanse NJ (2012) Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. Oikos 121:1009–1020

Miller JRB, Ament JM, Schmitz OJ (2014) Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. J Anim Ecol 83:214–222

Monaghan P (2008) Early growth conditions, phenotypic development and environmental change. Phil Trans R Soc B 363:1635–1645

Montiglio P-O, Ferrari C, Réale D (2013) Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. Phil Trans R Soc B 368:20120343

Montiglio P-O, Garant D, Bergeron P, Dubuc Messier G, Réale D (2014) Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (*Tamias striatus*). J Anim Ecol 83:720–728

Müller T, Müller C (2015) Behavioural phenotypes over the lifetime of a holometabolous insect. Front Zool 12:S8

Nicolaus M, Tinbergen JM, Bouwman KM, Michler SP, Ubels R, Both C, Kempenaers B, Dingemanse NJ (2012) Experimental evidence for adaptive personalities in a wild passerine bird. Proc R Soc LondB 279:4885–4892

Niemelä PT, Dingemanse NJ (2017) Individual versus pseudo-repeatability in behaviour: lessons from translocation experiments in a wild insect. J Anim Ecol 86:1033–1043

Niemelä PT, Dingemanse NJ, Alioravainen N, Vainikka A, Kortet R (2013) Personality pace-of-life hypothesis: testing genetic associations among personality and life history. Behav Ecol 24:935–941

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol 20: 831–844

Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP (2010) Phenotypic plasticity's impacts on diversification and speciation. Trends Ecol Evol 25:459–467

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20:481–486

Promislow DEL, Harvey PH (1990) Living fast and dying young: a comparative analysis of life-history variation among mammals. J Zool 220:417–437

Pruitt J, Ferrari M (2011) Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. Ecology 92:1902–1908

Quinn JL, Cole EF, Patrick SC, Sheldon BC (2011) Scale and state dependence of the relationship between personality and dispersal in a great tit population. J Anim Ecol 80:918–928

Réale D, Festa-Bianchet M (2003) Predator-induced natural selection on temperament in bighorn ewes. Anim Behav 65:463–470

Réale D, Gallant BY, Leblanc M, Festa-Bianchet M (2000) Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim Behav 60:589–597

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. Phil Trans R Soc B 365: 4051–4063

Réale D, Martin J, Coltman DW, Poissant J, Festa-Bianchet M (2009) Male personality, life-history strategies and reproductive success in a promiscuous mammal. J Evol Biol 22:1599–1607

Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. Trends Ecol Evol 17:462–468

Robinson MR, Wilson AJ, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk LEB (2009) The impact of environmental heterogeneity on genetic architecture in a wild population of soay sheep. Genetics 181:1639–1648

Roff D, Fairbairn DJ (2007) The evolution of trade-offs: where are we? J Evol Biol 20:433–447

Royauté R, Berdal MA, Garrison CR, Dochtermann NA (2018) Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. Behav Ecol Sociobiol 72:64

Royauté R, Greenlee K, Baldwin M, Dochtermann NA (2015) Behaviour, metabolism and size: phenotypic modularity or integration in Acheta domesticus? Anim Behav 110:163–169

Santostefano F, Wilson AJ, Niemelä PT, Dingemanse NJ (2017) Behavioural mediators of genetic life-history trade-offs: a test of the pace-of-life syndrome hypothesis in field crickets. Proc R Soc Lond B 284:20171567

Scheiner SM (1993) Genetics and evolution of phenotypic plasticity. Annu Rev Ecol Syst 24:35–68

Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol Lett 7:153–163

Speakman JR (1997) Factors influencing the daily energy expenditure of small mammals. Proc Nutr Soc 56:119–1136

Stamps JA (2007) Growth-mortality tradeoffs and "personality traits" in animals. Ecol Lett 10:355–363

Stearns SC (1983) The influence of size and phylogeny on patterns of cavariation among life-history traits in the mammals. Oikos 41:173–187

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3:259–268

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York

Sultan SE, Spencer HG (2002) Metapopulation structure favors plasticity over local adaptation. Am Nat 160:271–283

Thomas DW, Dorais M, Bergeron J (1990) Winter energy budget and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. J Mammal 71:475–479

Tieleman B, Williams J, Ricklefs R, Klasing K (2005) Constitutive innate immunity is a component of the pace-of-life syndrome in tropical birds. Proc R Soc Lond B 272:1715–1720

Timonin ME, Carrière CJ, Dudych AD, Latimer JGW, Unruh ST, Willis CKR (2011) Individual differences in the behavioural responses of meadow voles to an unfamiliar environment are not correlated with variation in resting metabolic rate. J Zool 284:198–205

Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc R Soc Lond B 278:3355–3363

Urszán TJ, Török J, Hettyey A, Garamszegi LZ, Herczeg G (2015) Behavioural consistency and life history of *Rana dalmatina* tadpoles. Oecologia 178:129–140

Vaanholt LM, de Jong B, Garland T, Daan S, Visser GH (2007) Behavioural and physiological responses to increased foraging effort in male mice. J Exp Biol 210:2013–2024

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Vuarin P, Dammhahn M, Henry P (2013) Individual flexibility in energy saving: body size and condition constrain torpor use. Funct Ecol 27: 793–799

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Wang IJ, Bradburd GS (2014) Isolation by environment. Mol Ecol 23: 5649–5662

West-Eberhard M (2003) Developmental plasticity and evolution. Oxford University Press. In: Oxford

White SJ, Kells TJ, Wilson AJ (2016) Metabolism, personality and pace of life in the Trinidadian guppy, *Poecilia reticulata*. Behaviour 153: 1517–1543

Wiersma P, Verhulst S (2005) Effects of intake rate on energy expenditure, somatic repair and reproduction of zebra finches. J Exp Biol 208:4091–4098

Wikelski M, Ricklefs RE (2001) The physiology of life histories. Trends Ecol Evol 16:479–481

Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history tradeoffs favour the evolution of animal personalities. Nature 447:581–584

Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Stud Behav 16:229–249

Zylberberg M, Klasing KC, Hahn TP (2014) In house finches, *Haemorhous mexicanus*, risk takers invest more in innate immune function. Anim Behav 89:115–122