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REVIEW

Models of pace-of-life syndromes (POLS): a systematic review

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Abstract

Variation in life history (LH) traits along the fast-slow continuum (referred to as pace of life, POL) is thought to result from a trade-off between investments in current versus future reproduction. Originally developed for understanding variation in LH strategies at the among-population level, the POL theory has more recently been applied towards understanding variation in LH traits at the within-population level, and further extended to address the covariance of LH traits with additional behavioural and/or physiological traits, referred to as pace-of-life syndromes (POLS). The article by Réale et al. (Philos T Roy Soc B 365:4051–4063, 2010), which synthesized several earlier reviews and opinions on among-individual covariation between LH, behavioural, and physiological traits, and subsequent research testing POLS in a variety of species, have collectively been cited several hundreds of times—a trend that continues. These works have interdisciplinary impact, informing research in life history biology, behavioural and developmental biology, and the social sciences. In this paper, we review the existing theoretical POLS models that provide adaptive explanations for covariances between LH traits and additional behavioural and/or physiological traits while assuming a trade-off between current and future reproduction. We find that the set of relevant models is small. Moreover, models show that covariances between life history traits and behavioural or physiological traits can arise even in the absence of a current-future reproduction trade-off, implying that observing such covariances does not provide a strong indication regarding the process generating POLS. We discuss lessons learned from existing models of POLS, highlight key gaps in the modelling literature, and provide guidelines for better integration between theory and data.

Keywords Animal personality · Consistent among-individual differences · Life history trade-offs · Physiology · Trait covariance

> Science walks forward on two feet, namely theory and experiment … Sometimes it is one foot that is put forward first, sometimes the other, but continuous progress is only made by the use of both.
> - Robert A. Millikan, Nobel Lecture 1924

Introduction

Life history (LH) traits often vary along a fast-slow continuum, with a fast pace of life (POL) characterized by fast development, early age at first reproduction, and low survival and a

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slow POL by slow development, delayed reproduction, and high survival (Saether 1988; Stearns 1992; Ricklefs 2000). These patterns of covariation may result from allocation trade-offs (Williams 1966); resources invested in current reproduction cannot be invested in growth, survival, or future reproduction. Ecological conditions can mediate the resolution of this trade-off, resulting in differences in LH traits across populations experiencing different ecological conditions (Stearns 1992). POL theory was later extended to address the coevolution of behavioural and physiological traits with the LH particularities of a species or population (Ricklefs and Wikelski 2002), referred to as pace-of-life syndromes (POLS). For example, organisms evolved towards a slow POL may invest more in traits that increase their probability of surviving long enough to realize their future reproductive potential (e.g. immunity) (Martin et al. 2006). Similarly, organisms evolved towards a fast POL may accept greater risk while foraging to build assets for immediate reproduction (Stamps 2007).

More recently, Réale et al. (2010) suggested that the POLS concept may provide a useful framework for understanding covariation between LH, behavioural, and physiological traits among individuals of the same population. Within populations, individuals exhibit differences in LH strategies (Biro and Stamps 2008), as well as consistent differences in behavioural (Bell et al. 2009) and physiological traits (Holtmann et al. 2016), and LH, behavioural, and physiological traits often covary at the among-individual level (Stamps 2007; Biro and Stamps 2008, 2010; Careau et al. 2008). In their paper, Réale et al. (2010) synthesized these previous bodies of work and developed a series of verbal arguments for how and why LH, behavioural, and physiological traits may show particular patterns of covariance at the among-individual, within-population level (see also Belsky et al. 1991; Ellis et al. 2009 for verbal models of POLS in humans; Del Giudice et al. 2015). For example, if aggressiveness facilitates the acquisition or monopolization of resources, it may have coevolved with high growth rates and early reproduction, but at the cost of increased risk of mortality. Similarly, high metabolic rates may be required to support the rapid growth required for early reproduction and high fecundity, but may simultaneously increase mortality through increased production of reactive oxygen species. Since its publication, the POLS hypothesis at the within-population level has generated a large amount of empirical research (cited over 300 times; see Dammhahn et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes).

In this paper, we provide a systematic review of the formal (i.e. mathematical) theory of POLS. We review existing models that incorporate a trade-off between current and future reproduction while addressing covariation between LH, behaviour, and physiology at the within-population level. We focus on models that incorporate the current-future reproduction trade-off, which features prominently in verbal POLS theory (e.g. Ricklefs and Wikelski 2002; Réale et al. 2010). We acknowledge, however, that other trade-offs may also produce POLS (see section "Equifinality: different processes, one outcome").

Our results show that *there is in fact little formal theory about POLS*, particularly at the among-individual, within-population level, and *many empirical tests of POLS have no formal bases for their predictions*. We discuss the key assumptions and predictions of existing models, highlighting the mismatch between current empirical tests and model assumptions. Further, we discuss models that predict patterns of covariance between LH, behavioural, and physiological traits via different processes than a current-future reproduction trade-off. Such models are relevant for the evolution of POLS but are rarely cited in the POLS literature. The mismatch between formal theory and empirical work does not, of course, undermine either; rather, it highlights the need and potential for the development of novel theory addressing the evolution of POLS. Our aim is thus to facilitate better integration of theory and empirical work by highlighting gaps in the current set of models to stimulate the development of further theory and offer guidelines that help in devising tests of extant theory.

Models of POLS at the within-population level

In reviewing the literature, we followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol (Moher et al. 2009). We searched the Web of Science database (search date 1 August 2016) for articles that included the key words "Pace of life" and "Model" or articles that cited Réale et al. (2010). This produced 166 unique references. We read the title and/or abstract for each of these references to assess whether the paper developed a formal model including a life history trait (e.g. age at first reproduction, survival, etc.) and any additional behavioural and/or physiological trait. We considered models that addressed the co-evolution of LH and behavioural and/or physiological traits, as well as the development of POLS over ecological time (e.g. models of phenotypic plasticity). These models tended to address among- and within-individual covariation respectively. We selected papers that met these criteria ($N = 7$) for reading the full text. We identified an additional 11 articles from the reference lists of these seven articles and a further 12 articles which were known to the authors or to attendees of the workshop "Towards a general theory of pace-of-life syndrome" (see ESM Fig. S1 for PRISMA flow diagram).

We thus selected a total of 30 papers for reading full text based on our search criteria. KJM and WEF independently read each of these 30 papers to evaluate whether they should be included in the systematic review. We established that models should meet all three of the following criteria in order

Table 1 Overview of papers that were evaluated in the context of POLS

Reference	POLS criteria			Model attributes summarized in Tables 2 and 3[d]
	POL[a]	Additional trait(s)[b]	Covariances evaluated[c]	
Baldauf et al. (2014)	N (D)	Y (1)	NA	N
Baldini (2015)	Y (A)	N	NA	N
Chan and Kim (2014)	Y (A)	Y (1)	I	N
Charlesworth (1990)	Y (A)	N	NA	N
Clark (1994)	Y (RRV)	Y (1)	Y	Y
de Jong and van Noordwijk (1992)	Y (A)	Y (1)	Y[e]	Y
de Jong (1993)	Y (A)	Y (1)	Y	Y
Delaguerie et al. (1991)	Y (A)	N	N	N
Engqvist et al. (2015)				
I. All else being equal model	N[h]	Y (1)		N
II. higher baseline mortality for attractive males	Y	Y (1)	Y	Y
Frankenhuis et al. (2013)	Y (A)	N	NA	N
Houle (1991)	N (D)	Y (1)	NA	N
Houston and McNamara (1989)	Y (RRV)	Y (2)	Y	Y
Jonsson et al. (1998)	Y (A)	N	NA	N
Luttbeg and Sih (2010)	N (D)	Y (1)	NA	N
Mangel and Stamps (2001)	N (E)	Y[g] (1)	Y	N
Mallpress et al. (2015)	Y (A)	Y (1)	N[f]	N
McElreath and Strimling (2006)	N (D)	Y (1)	NA	N
McNamara and Houston (1996)	Y (RRV)	N	NA	N
Mullon et al. (2016)	N (E)	Y (1)	Y	N
Riska (1986)	Y (A)	N	NA	N
Sibly and Calow (1984)	Y (A)	N	NA	N
Stamps et al. (1998)	N (E)	Y[g] (1)	Y	N
Teriokhin (1998)	Y (A)	Y (1)	N	N
van Doorn et al. (2009)	Y	Y (1)	Y	N
van Noordwijk and de Jong (1986)	Y (A)	Y (1)	Y	Y
Wolf and McNamara (2012)	N (D)	Y (2)	NA	N
Wolf et al. (2008)	N (D)	Y (1)	NA	N
Wolf et al. (2011)	N (D)	Y (2)	NA	N
Wolf et al. (2007b)	Y (ST)	Y (2)	Y	Y
Worley et al. (2003)	Y (A)	N	NA	N

[a] Is the trade-off between current and future reproduction implicit in the model assumptions? Yes (Y) or No (N). The implicit trade-off can be modelled either as a single trait that captures the trade-off (ST) (e.g. trait values are either early reproduction/low survivals or late reproduction/high survival) or residual reproductive value (RRV), or as an allocation decision (A). The allocation decision can be directly between current and future reproduction, or between current reproduction and survival as these are nested within current/future reproduction trade-offs (i.e. if you die, you necessarily cannot reproduce). Note, however, that current/future reproduction trade-offs do not necessarily imply differences in survival. Models did not meet the LH trade-off criteria if they did not allow for variation in investment to current versus future reproduction because models were structured with discrete non-overlapping generations (D), or because there was no implicit trade-off between current and future reproduction. However, even in the absence of an implicit trade-off, variation timing of reproductive events can arise as an emergent property of a model (E)

[b] Additional trait(s): were additional traits considered in the models that can be interpreted as behavioural and/or physiological traits? Yes (Y) or No (N). The number of additional traits is provided in parentheses

[c] Was the covariance between the LH traits and the additional trait(s) evaluated? Not applicable (NA) if either LH trait or additional trait is absent, yes (Y) if the model directly evaluates the covariance structure between LH and the additional trait or the covariance structure can be directly extrapolated based on information provided in the text, no (N) if the model does not directly evaluate covariance structure nor is information directly available in current results, or imposed (I) if the covariance between traits is imposed by the model assumptions in such a way that only a single covariance is possible (e.g. trait A ~ trait B + constant)

[d] Model attributes summarized in Table 2, predictions outlined in Table 3: yes (Y) or no (N). Models were selected for more detailed summaries if they met all four criteria for POLS at the within-population level. We additionally included models that met all criteria except for evaluating the consistency in trait expression over the lifetime of individuals as these may be relevant for understanding POLS at different levels of variation (e.g. among populations or within individuals) (see Table 2)

[e] Analyses predict the fixation of trait R (allele for resource acquisition); therefore, there is no possibility for genetic covariance between resource acquisition and allocation (C) and between reproduction and survival. Phenotypic variance in R is all due to stochastic processes

[f] Consistency and/or covariances not evaluated for the traits relevant for POLS (e.g. consistency of POL or additional trait, or covariance between POL and additional trait)

[g] Additional trait is body size (i.e., morphological, not behavioural or physiological)

[h] In the model version where only attractiveness (i.e. reproductive value, RV) differs among males, variation in survival comes about because less attractive males are expected to be more risk-taking. This is not a POLS trait, however, because there is no implicit trade-off between current and future reproduction, and the covariance between RV and survival that emerges from the model is opposite to the covariance that would be expected given the trade-off

to address the evolution or development of POLS within populations:

1. *The study presents a formal model that includes a POL trait.* POL refers to covariances between LH traits resulting from a current-future reproduction trade-off. We considered two ways of capturing this trade-off: (a) as a single trait that allows only for certain combinations of trait values (e.g. the couples of early reproduction/low survival and late reproduction/high survival) and not for others (e.g. early reproduction/high survival and late reproduction/low survival) and (b) as two separable life history traits (i.e. survival and reproduction), such that all combinations of reproduction and survival were in principle possible. However, a current-future reproduction trade-off was implicit such that within individuals, a higher investment in current reproduction implied a lower investment in future reproduction. We excluded models with discrete, non-overlapping generations (i.e. a single reproductive event per lifetime), because these do not allow for a current-future reproduction trade-off.
2. *There was at least one additional trait in the model that could represent a behavioural and/or physiological trait.* This criterion was met either when a paper explicitly described a trait as behavioural and/or physiological or when the assumptions and descriptions of a model parameter were sufficiently general that even when not described as a behavioural or physiological trait, the parameter could be viewed as representing such a trait. For example, a parameter that describes resource level in the environment and whose level can vary could also be taken to represent among-individual variation in the ability to monopolize resources (e.g. due to variation in dominance).
3. *The model evaluated the covariance between the POL trait and the behavioural and/or physiological trait.* This criterion was met either if the covariance structure between LH traits and the additional trait was explicitly quantified or if the covariance structure could be extrapolated based on information provided in the text. For some models, covariances between the LH trait and the behavioural and/or physiological trait were imposed by the model assumptions (i.e. the relationship between the two traits is fixed), rather than evolutionary outcomes. We did not consider that such models address the evolution or development of POLS.

KJM and WEF resolved any discrepancies in the evaluation of whether or not a given study met each of these criteria by discussion. Table 1 summarizes each of the 30 full texts evaluated for the three above-mentioned criteria.

Within-population models of POLS: within individuals versus among individuals

Our systematic review yielded only eight papers (one of which included two relevant models) of formal models of POLS, i.e. which address the evolution of covariances between LH traits and additional behavioural and/or physiological traits while assuming a trade-off between current versus future reproduction. We summarize each of these models in Tables 2 and 3, highlighting aspects of the model assumptions and predictions that are crucial to developing empirical tests of the models. These models address the evolution of covariance between LH and behavioural and/or physiological traits at two different levels of biological organization: (1) within individuals (Houston and McNamara 1989; Clark 1994) and (2) among individuals within the same population (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; Wolf et al. 2007b; van Doorn et al. 2009; Engqvist et al. 2015).

The three models addressing POLS (derived from two papers: Houston and McNamara 1989; Clark 1994) at the within-individual level have common features. Both use stochastic dynamic programming (Mangel and Clark 1988; Houston and McNamara 1999) to model risk-taking (specifically, a trait that increases resource acquisition at the expense of increased probability of mortality) as a function of residual reproductive value (RRV), where RRV represents the ratio of expected future reproduction to expected current reproduction. Both models involve asset protection, whereby

Table 2 Subset of papers summarized in Table 1 that met the three minimum criteria laid out for a model to address POLS. Additional details on model structure are provided to facilitate interpretation of model applicability

Ref	Source of initial variation[a]	Model attributes								
		Model type[b]	Environment structure[c]	Social environment[d]	Feedbacks[e]	Lagged effects[f]	Additional factors	Inheritance system[g]	Consistency evaluated	Applicable levels[h]
Clark (1994)[j]										
Continuous reproduction	NA	Stochastic dynamic	No	No	Yes (−)	No	No	NA	No	WI
Growth and episodic reproduction	NS	Stochastic dynamic	No	No	Yes (−)	Yes	No	NA	No	WI
de Jong (1993)	NS	Deterministic	No	No	No	No	No	NA	NA[k]	AI[m]
de Jong and van Noordwijk (1992)	NS (genetic) S (phenotypic)	Genetic	No	No	No	No	No	Diploid, single locus	NA[l]	AI[m]
Engqvist et al. (2015)	NS	Stochastic dynamic	No	FD, DD	No	No	No	NA	Y (can be inferred from information given in text)	AI
Houston and McNamara (1989)	NS	Stochastic dynamic	No	No	Yes (−)	No	Yes (metabolic rate)	NA	No	WI
van Doorn et al. (2009)	M	Individual-based simulation	Yes (discrete habitat patches)	FD	Yes (explore both + and −)	Yes	No	Diploid, multilocus	NA	AI
van Noordwijk and de Jong (1986)	NS	Deterministic	No	No	No	No	No	NA	NA[l]	AI[m]
Wolf et al. (2007b)	M (POL trait) NS (behavioural traits) Later variation in behavioural traits also arises via mutation	Individual-based simulation	No	FD, DD	Yes (−), but effect is constrained to be small relative to differences arising from LH variation	Yes[i]	No	H-ML, D-ML	Yes, but under restrictive conditions (traits expressed only twice in lifetime)	AI

[a] Source of initial variation: assumed, but origin not specified (NS), mutation (M), stochasticity (S), not applicable because no among-individual differences taken to exist (NA)

[b] Model type: genetic (G), deterministic state dependent, stochastic dynamic state dependent, (co-)evolutionary

[c] Environmental structure refers to attributes of the environment that affect all individuals simultaneously (e.g. high versus low resource availability, different patches, stochastic environmental fluctuations) but not to attributes that affect individuals singly (e.g. stochastic variation in prey encounter rates). Variation in these attributes must exist either within the lifetime of an individual (within generation, WG) or of the lineage (among generation, AG)

[d] Social environment: Is there social environment structure? Yes, frequency-dependent payoffs (FD) or density-dependent payoffs (DD) or no

[e] Feedbacks: yes, the output of trait A affects the input of trait B and vice versa. When the effects of A on B and of B on A are in the same direction (e.g. higher value of A increases B, higher value of B increases A), the feedback is positive (+); when they are in opposite directions, the feedback is negative (−)

[f] Lagged effects: yes, the consequences of behaviour for reproduction are delayed; no, the consequences are immediate. Y/N indicates that both lagged and non-lagged effects were explored

[g] Inheritance system: not applicable (NA, non-genetic model), haploid (H), diploid (D), single locus (SL), multi-locus (ML)

[h] Applicable levels: What level of variation was the model constructed to explain? Among populations (AP), among individuals within the same population (AI), within individuals (WI)

[i] The model involves many iterations in each of the 2 years of an individual's life, but the consequences of POL (exploration) in year 1 for resource level only emerge in year 2. The survival effect, however, is immediate

[j] Note that Clark (1994) involves multiple models (1) continuous reproduction (included because it addresses WI covariation) and (2) growth and episodic reproduction (included because it explores lagged effects)

[k] R (resource acquisition) is expressed only once in an individual's life, no within-individual variation possible. However, consistency of allocation decisions was evaluated

[l] R (resource acquisition) and c (allocation decision) each expressed only once in an individual's lifetime

[m] Although predicted covariances between LH and additional behavioural and/or physiological trait are applicable at the among-individual level, the additional trait is not expressed repeatedly in an individual's lifetime, and therefore, the model does not address the stability of repeatedly expressed traits (i.e. animal personality)

individuals with high assets (i.e. high RRV) are risk averse (i.e. avoid variability in outcomes) to protect their assets. Although neither of these models evaluates the long-term consistency of risk-taking, among-individual variation in RRV and risk-taking would be expected to erode over time given that asset protection is a negative-feedback mechanism (McElreath et al. 2007; Luttbeg and Sih 2010) (but see Wolf et al. 2007a for a discussion of why negative feedbacks may not always erode among-individual differences). Thus, the patterns of covariance predicted at the within-individual level by these models cannot be extrapolated to predict patterns of covariance at the among-individual level.

We identified six models that address covariances between LH and behavioural and/or physiological traits at the among-individual, within-population level. Four of these models did not address POLS for repeatedly expressed behavioural and/or physiological traits. In the models by van Noordwijk and de Jong (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993), the additional trait (resource acquisition) is expressed only once per lifetime. Similarly, in the model by van Doorn et al. (2009), consistency of the trait expression (foraging) is an assumption, rather than an outcome, of the model. Therefore, these models cannot illuminate when individuals would be expected to exhibit consistent among-individual differences in a repeatedly expressed trait and when the average expression of such traits is expected to co-vary with LH traits. However, most empirical tests of POLS (see reviews by Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes) consider covariances between LH and behavioural and/or physiological traits that are expressed repeatedly throughout an individual's lifetime (e.g. activity, foraging boldness, parental care, aggression, metabolic rate, etc.).

We found only two models that address the evolution of POLS for repeatedly expressed behavioural and/or physiological traits (Wolf et al. 2007b; Engqvist et al. 2015). The model by Engqvist et al. (2015) analyzes the conditions under which males of varying degrees of attractiveness (i.e. reproductive value) should signal for mates (a "risky" behaviour in that it increases access to potential mates at the cost of increased probability of mortality due to predation). The model by Wolf et al. (2007b) analyzes the co-evolution of pace of life (early versus late reproduction) and two "risky" behaviours: foraging boldness and conspecific aggression. These models share several key features. Both assume frequency- and density-dependent payoffs to alternative behavioural tactics, and both models limit the scope for negative feedbacks to erode among-individual differences in reproductive value. In the model by Wolf et al. (2007b), behavioural actions in the first hawk-dove game (i.e. foraging boldness) influence their reproductive value, which in turn affect their optimal level of aggression in the second hawk-dove game. However, the magnitude of these effects is assumed to be small, such that

Table 3 Subset of papers summarized in Table 1 with details on model predictions

Reference	POL i.e. *how POL is modelled*	Additional trait(s) i.e. *how the paper describes the additional trait*	Predicted covariance *Between POL and additional trait*	Conditions i.e. *parameter space explored*
Clark (1994)				
Continuous reproduction	RRV[a]	Risk-taking while foraging (implicit trade-off between gaining resource and survival)	Risk-taking increases with decreasing RRV. Animals become more risk-taking as they age. Stability not directly analyzed, but not expected based on negative feedback	Changing T (maximum number of time steps)
Growth and episodic reproduction)	RRV[a]	Risk-taking (foraging tactics: implicit trade-off between gaining resources and survival)	Stability of syndromes not analyzed Generally, higher RRV favours lower risk-taking	Explore consequences of different levels of starting body mass
de Jong (1993)	Allocations (successive)	R (resource availability) Can be thought of as a behavioural or physiological trait that influences access to resources	Predicted covariance between fecundity and survival at different points in time depends on mean acquisition, variance in acquisition, and initial allocation decision (see Figs. 3 and 4 from de Jong (1993)	Explore consequences of varying R and varying allocation decisions at different times in life
de Jong and van Noordwijk (1992)	Allocation	R (resource availability) Can be thought of as a behavioural or physiological trait that influences access to resources	When there is large among-individual variance in R, among-individual covariation between reproduction and survival is positive, and both co-vary positively with R When there is little among-individual variation in R, reproduction and survival are negatively correlated. There is no covariance with R (because R does not vary, or varies little, among individuals)	Explore consequences of varying R among individuals
Engqvist et al. (2015)	Parameter values for two traits set to encompass trade-off (baseline mortality greater for males with high reproductive value)	Risky signalling (signalling behaviour to attract mates, increases mating success but increases predation rate)	When signalling costs are relatively low, fast POL covaries positively with risky signalling (boldness) When differences in baseline mortality are low, slow POL individuals are more risk-taking	Explore consequences of varying differences in baseline mortality, explore consequences of varying predation costs of signalling
Houston and McNamara 1989[3]	RRV[a] (note that the term used in the paper is expected future reproductive success)	g (gross rate of gain while foraging, could reflect food availability or variation in energy assimilation rates) u (proportion of time allocated to foraging, considered "risky" in the sense that it increases risk of predation relative to non-foraging)	Stability of syndromes not analyzed Generally, higher RRV favours lower risk-taking	Explore consequences of variation in gross energy gain and energy reserves for the relationship between risk-taking and RRV
van Doorn et al. (2009)	Choice between current versus future reproduction (decision to breed immediately or queue for a territory)	Foraging. Individuals can choose between foraging under predation risk (risk declines with age) or under low risk (risk does not vary with age) Decision taken only once in an individual's lifetime; switching is not possible	Variation in POL and behaviour evolve first via frequency dependence. Then, correlation evolves such that individuals with a slow POL (those that queue for reproduction) are expected to forage under predation. When negative feedbacks between assets and risk-taking are allowed, the among-individual differences erode	Explore consequences of + versus − feedbacks between assets and risk-taking
van Noordwijk and de Jong (1986)	Allocation	R (resource availability)	When there is large among-individual variance in resource acquisition (R), [a] higher R is	Explore consequences of varying R among individuals

Table 3 (continued)

Reference	POL i.e. *how POL is modelled*	Additional trait(s) i.e. *how the paper describes the additional trait*	Predicted covariance *Between POL and additional trait*	Conditions i.e. *parameter space explored*
		Can be thought of as a behavioural or physiological trait that influences access to resources	associated with higher fecundity and higher survival When there is low among-individual variance in resource acquisition, higher fecundity is associated with lower survival, but there is no covariance with *R* (because *R* shows little variance)	
Wolf et al. (2007b)	Single trait encompassing trade-off[b]	Two separate risk-taking behaviours: Boldness/shyness Aggressiveness (hawk/dove)	Covariation between POL and risk-taking behaviours arises due to state (POL)-dependent payoffs. Mix of types maintained in populations via frequency and density dependence	Explore different payoff combinations in anti-predator and hawk-dove games

RRV residual reproductive value, the ratio of expected future reproduction to expected current reproduction

[a] Individuals have a total finite resource amount available, which they can allocate to current reproduction (fecundity) or future reproduction (survival)

[b] POL capture by life history trait encompassing trade-off between current and future reproduction. Trait is called "exploration." Higher exploration = lower current reproduction but higher future reproduction; lower exploration = higher current reproduction but lower future reproduction. Other combinations of current/future reproduction (e.g. high-high, low-low) are not possible

negative feedbacks between state and behaviour can never negate differences in reproductive value caused by differences in life history strategy. The Engqvist et al. (2015) model does not allow for any negative feedbacks between state and behaviour; risky signalling for mates does not produce any lasting effect on male attractiveness independent of the signalling itself. The models both predict that individuals with a fast POL will have consistently higher levels of risk-taking behaviours compared to individuals with a slow POL.

These two models also differ in several ways. Wolf et al. (2007b) address covariances between POL and two additional traits, while Engqvist et al. (2015) address covariances between POL and one additional trait. The Engqvist et al. (2015) model emphasizes which changes in parameter values are required to alter the predicted covariance structure. It shows that the predicted covariance between POL and risk-taking reverses when differences in baseline mortality between attractive and unattractive males are small (i.e. when the trade-off between reproduction and survival is weak). Additionally, in the Engqvist et al. (2015) model, lifespan varies probabilistically among individuals as a function of their attractiveness, their level of risk-taking, and the frequency of their types in a population. In the Wolf et al. (2007b) model, maximum lifespan is fixed at two reproductive periods (for A discussion of developmental modelling of many time periods, including incremental learning about the environmental state, see Stamps and Frankenhuis 2016).

What the current models do not teach us

Given the number of empirical studies aimed at testing POLS at the among-individual, within-population level (reviewed in Royauté et al. 2018, topical issue on Pace-of-life syndromes), the scarcity of formal theory is surprising. Here, we highlight two major gaps in the existing modelling literature.

What types of behavioural and/or physiological traits co-evolve with POL?

The POLS hypothesis predicts covariation between LH traits and multiple, diverse, behavioural, and physiological traits. However, we find that existing models of POLS address co-variation of LH traits with a small number of additional traits (one or two), and moreover, these (non-LH) traits share a key characteristic: they directly affect resource acquisition. In some cases, an increase in resource acquisition is traded off against survival (Houston and McNamara 1989; Clark 1994; Wolf et al. 2007b; Engqvist et al. 2015), and in others, there was no direct consequence for survival (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; van Doorn et al. 2009).

In their paper, Réale et al. (2010) list 13 potential traits for integration within the POLS framework (seven behavioural, six physiological). We suggest that the payoff structures (how the trait value affects fitness-relevant parameters, such as survival probability and resource levels) used in current models of POLS apply to a limited number of these traits. For example, greater foraging boldness may increase resource acquisition at the expense of increased probability of mortality due to predation and increased metabolic rate may increase access to resources (but see Careau and Garland 2012; Mathot and Dingemanse 2015) at the cost of increased mortality due to higher rates of oxidative damage. However, other traits are likely to have different payoff structures. For example, increased immune function may cost resources but increase the probability of survival. For traits such as sociability or HPA axis reactivity, the probable effects on resource acquisition (or net resource costs) and survival are not obvious. Whether traits with these types of alternative payoff structures will also coevolve with POL is presently unclear.

What processes and conditions favour (or hinder) the development of POLS?

The current models of POLS do not allow for general conclusions about the processes that favour or hinder the development of POLS, in part because this set is small (eight models). Further, only two of these studies addressed POLS at the among-individual, within-population level for repeatedly expressed behavioural traits (Wolf et al. 2007b; Engqvist et al. 2015). In these two models, there is either no (Engqvist et al. 2015) or only limited (Wolf et al. 2007b) possibility for feedbacks between state (reproductive value or assets) and behaviour. They are also the only two studies to assume both frequency- and density-dependent payoffs (Table 2). Whether such assumptions are necessary to evolve POLS at the among-individual level for repeatedly expressed traits is currently unclear and would require modification of these assumptions.

This relates to a general limitation of the current models of POLS: they explore a narrow parameter space. Although each model summarized in Tables 2 and 3 included at least some exploration of changes in parameter values on model outcomes (Table 3), these were limited to modifying values for one or two parameters. A notable exception to this was the model developed by Engqvist et al. (2015), where there was extensive exploration of parameter space for multiple combinations of parameter values. If the goal of studying trait covariances within the POLS framework is to understand the processes that generate particular patterns of covariance, then exploration of parameter space is essential to illuminate when different processes can lead to the same outcome (equifinality; see below) and when the same process can lead to different outcomes (multifinality; see below). Explicit consideration of the effects of parameter values on model outcomes will provide more detailed predictions that may enable empiricists to discriminate between alternative processes, and will simultaneously emphasize the importance of matching empirical tests to model assumptions.

Equifinality: different processes, one outcome

Our review shows that POLS can emerge via at least two distinct processes: (1) a direct trade-off between current and future reproduction (Houston and McNamara 1989; Clark 1994; Wolf et al. 2007b; van Doorn et al. 2009) or (2) a direct trade-off between current reproduction and survival (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; Engqvist et al. 2015). In the former case, the covariance between LH parameters (e.g. age at first reproduction and survival) results from interacting model assumptions. In the latter models, covariance between LH traits is assumed (i.e. fixed combinations of trait values).

We also identified three models that involved neither of the aforementioned trade-offs, but which nonetheless predict trait covariances that match predictions from POLS (Stamps et al. 1998; Mangel and Stamps 2001; Mullon et al. 2016). For example, in the models by Stamps et al. (1998) and Mangel and Stamps (2001), organisms face a trade-off between growth and survival, which results in covariances between age at first reproduction, survival, and morphological characteristic (see Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes for discussion of integrating morphology into the POLS framework). The model by Mullon et al. (2016), in which one trait has positive indirect fitness benefits and the second trait increases pairwise relatedness (i.e. when two individuals that show an increase in the value of a trait have a greater probability of being related than two randomly selected individuals), predicts positive covariances that match POLS predictions (i.e. higher survival associated with lower dispersal and greater helping behaviour). This prediction highlights that observations of particular patterns of covariance between LH and additional traits do not allow for strong inferences about the *processes* generating these patterns. If the same patterns of covariance can arise via multiple processes, how can we increase our understanding of the processes generating patterns of trait covariance observed in biological systems? We suggest that changing the focus of current models from “can POLS evolve?” (i.e. proofs of principle) to “when do POLS evolve?” (i.e. what processes give rise to POLS depending on environmental context and the organism’s state and in what conditions are these processes likely to eclipse other processes that erode POLS) will help in achieving this aim (see also Montiglio et al. 2018, topical collection on Pace-of-life syndromes). Ideally, modellers would also stipulate how model assumptions might be tested, and explicitly list suitable empirical systems, which satisfy their models’ assumptions.

Multifinality: one process, different outcomes

Of the models summarized in Tables 2 and 3, those that involved the most detailed exploration of parameter space (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; Engqvist et al. 2015) also highlight that the same process can lead to different outcomes. For example, the models by de Jong and van Noordwijk (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993) illustrate how changing the degree of among-individual variation in resource acquisition can change the covariance between two life history traits linked via a trade-off. When among-individual differences in resource acquisition are small relative to the among-individual variance in allocation, the correlation between LH traits among individuals reflects the within-individual trade-off (i.e. there is a negative correlation between survival and reproduction). However, when the among-individual differences in resource acquisition are relatively large, the inherent trade-off becomes masked and there is a positive correlation between reproduction and survival at the among-individual level. This insight has been tremendously influential (Metcalfe 2016).

Engqvist et al. (2015) similarly show that the specific combinations of parameter values can have large effects on predicted trait covariances. When the POL-related differences in baseline mortality are large, the predicted covariance between POL and risk-taking is consistent with the prediction of Réale et al. (2010) that a fast POL will be associated with greater risk-taking. However, when the POL-related differences in baseline mortality are small, individuals with a slow POL are predicted to be more risk-taking. This result arises because when differences in baseline mortality are large, the cost to individuals with high reproductive value (attractive males) of signalling in the presence of predators is relatively small, and therefore, attractive males signal. In contrast, when the differences in baseline mortality are low, the cost of signalling for mates in the presence of predators is large (relative to baseline mortality). As attractive males have more reproductive assets to protect, there is selection against signalling by attractive males in the presence of predators. This trade-off results in a relaxed competitive environment for unattractive males which favours greater signalling for mates by unattractive males under predation risk. By highlighting that model assumptions and parameter values influence predicted trait covariances, these papers provide more detailed predictions for empiricists (e.g. positive covariance expected under condition *x*, but negative covariance under condition *y*). They also provide a reminder of the critical importance of matching empirical tests to model assumptions.

Guide for empiricists

Scientific progress depends on a good fit between theory and data. In Table 2, we highlighted several aspects of model assumptions that are relevant in devising sound empirical tests of theory, such as the type of trait represented, whether payoffs are frequency or density dependent, and the level of biological variation. Here, we discuss some assumptions of existing models in order to provide guidelines that can aid in the development of empirical tests that are well matched to theory. Predictions arising from the existing set of POLS models are summarized in Table 3.

The POLS concept develops verbal predictions for covariances between POL and a range of behavioural and physiological traits. However, the formal models of POLS are relevant for only a subset of the traits outlined in Réale et al. (2010). Empiricists should be careful to ensure that the traits they study are likely to show the type(s) of relationships and payoff structure(s) assumed by the models. In other words, before testing model predictions, empiricists should first examine, and ideally test, model assumptions in their system. For all existing models, the additional non-LH trait increases access to resources and either decreases survival or has no effect on survival. Thus, for many behavioural and physiological traits (e.g. immune function, HPA axis reactivity, sociability, etc.), there are in fact no formal predictions regarding their expected covariance with LH traits, and therefore, quantification of their covariance with LH traits does not constitute a test of extant formal POLS theory.

Focusing on the payoff structures incorporated into models when selecting traits will help empiricist avoid so-called jingle-jangle fallacies, when a single trait label describes two functionally different traits or when two different labels actually describe the same trait (Carter et al. 2013). For example, in the model by Wolf et al. (2007b), the POL trait is called “exploration,” and the model predicts covariance between “exploration” and risk-taking behaviours. However, in the animal personality literature, exploration is typically a measure of how an organism moves through a novel environment (Réale et al. 2007), not a measure of their life history strategy. In fact, a recent meta-analysis reveals that exploration does not reliably co-vary with measures of reproductive performance or survival (Smith and Blumstein 2008). Thus, the validity of using exploration as a proxy for POL requires testing on a system-by-system basis. Testing for covariation between exploration (of a novel environment) and risk-taking does not constitute a test of the Wolf et al. (2007b) model, nor does a positive covariation constitute support for it, unless the assumption that exploration reflects POL has been tested.

In addition to choosing traits whose payoff structures are properly captured by existing models, assumptions related to the timing of their effects on resource (acquisition or allocation) and survival should be matched to the biology of the empirical system. For example, in the Engqvist et al. (2015) model, resources gained by risky mate signalling behaviour are converted instantly to reproductive output; reproductive assets do not accrue. In the Wolf et al. (2007b) model, resources gained by risk-taking behaviour can accrue between year 1 and year 2, but the potential increase in asset is small compared with differences caused by differences in life history strategy. These may be valid assumptions when considering the risk-taking behaviour of income breeders during the reproductive period, where the entire energy requirements for current reproduction are met by current energy intake. It may similarly apply to risky signalling for mates, as described in the Engqvist et al. (2015) model: signalling for mates now increases access to mates now, but has no carry-over effect on access to mates in future reproductive bouts. In contrast, behaviour outside of the reproductive period by definition is not converted immediately to reproductive output and, therefore, should be expected to affect reproductive assets in ways that feedback to influence risk-taking (McElreath et al. 2007).

Similarly, the assumption that the accrued assets will be small relative to differences in assets associated with life history decisions (Wolf et al. 2007b) may be unrealistic for behaviours that are expressed repeatedly between reproductive bouts (e.g. foraging boldness). For example, the assets that might be gained from a single expression of foraging boldness may reasonably be expected to have small effects on assets relative to differences in assets associated with life history strategy. However, the cumulative effect of hundreds of instances of risk-taking decisions between two reproductive bouts may be more reasonably expected to have potentially large effects on assets. In fact, many empirical "tests" of POLS involve traits where the assumption of no (or limited) feedback between behaviour and assets is unlikely to be upheld (e.g. foraging boldness during the non-breeding season).

Conclusions

We conclude that there is, at present, little formal theory about POLS. Further, the only two models of POLS at the within-individual, among-population level for repeatedly expressed traits (Wolf et al. 2007b; Engqvist et al. 2015), although pioneering and insightful, shared numerous characteristics that limit the range of empirical applications. Both models address covariance between POL and a trait that increases access to resource at the cost of increased probability of mortality (e.g. due to predation) (or two additional traits in the case of Wolf et al. 2007b). At the same time, they explicitly do not allow (Engqvist et al. 2015) or limit (Wolf et al. 2007b) feedbacks between behaviour and reproductive value. We discuss scenarios where these assumptions are likely to be met and which, therefore, would constitute the best possible tests of the existing theory. However, we also point out that many studies that aim to test POLS do not satisfy these model assumptions; hence it is unclear how much support exists for current theory. Future modelling work can contribute to our understanding of POLS by shifting focus from demonstrating that POLS *can* evolve to demonstrating *when* POLS evolve (providing a flashlight for empiricists), and by modelling a wider range of traits (e.g. immunity, sociability, etc.).

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