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REVIEW

Temperature and the pace of life

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Abstract

The pace-of-life syndrome (POLS) is a framework that attempts to explain empirically observed covariation between physiological, behavioral, and life history traits, whereby individuals fall along slow-fast and shy-bold continuums. The fundamental driver of the position of individuals along these trait axes is thought to be their metabolic rates, with high metabolism leading to faster growth, greater reproductive output, and bolder behavior. However, numerous exceptions to these patterns have been observed in nature, suggesting that crucial components are missing from the classical POLS framework. As many metabolic, physiological, and life history traits are temperature dependent, a growing number of studies have begun to test the role played by the thermal physiology of individuals and the thermal environments in which they live in mediating the trait relationships within POLS. These studies have led to an expansion of classical POLS into what has been called "extended POLS." Here, we review the recent literature on extended POLS and identify the major themes and patterns that are emerging in this nascent field. We further identify gaps and key outstanding questions in how temperature may drive or modify classical POLS. Finally, we address issues with how temperature and POLS are integrated in empirical studies and suggest pathways by which progress can be made towards a cohesive understanding of the physiology-behavior-life history nexus.

Significance statement

The pace of life syndrome (POLS) is an integrative framework that links life-history, behavioral, and physiological traits into covarying axes that are structured by metabolism. Recent studies have provided only mixed support for the original POLS hypothesis and instead have highlighted the potential importance of thermal physiology in explaining patterns of trait covariation. We review this nascent literature and argue that environmental temperature, the thermal sensitivity of traits, and acclimation to thermal environments can influence the presence and/or direction of trait covariations within individuals or populations. Though some patterns have emerged in the recent POLS literature, important remaining gaps are slowing progress in this field. We suggest avenues by which future investigations can test the proximate and ultimate mechanisms underlying trait covariation in wild animal populations.

Keywords Behavior · Life history · Metabolism · Thermal physiology · Trait covariation

Introduction

Organisms are assemblages of many traits, each of which may be adapted to different aspects of the local environment. Many of these traits do not evolve independently and instead are co-adapted into "complex phenotypes." For example, historical understanding of life history evolution revolved around the concept of r-K selection, in which life history traits, such as growth rate, age at maturity, and reproductive output, covary along a "slow-fast" axis (Pianka 1970). In other words, individuals that grow quickly and mature at an early age should also produce more offspring per unit time. Although researchers no longer strictly adhere to the r-K

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selection framework, covariation among life history traits is nevertheless a ubiquitous feature of the natural world (e.g., the well-established trade-off between offspring quantity and quality, Smith et al. 1989; but see Beldade et al. 2012). Other types of traits, such as behavioral and morphological traits, can also occur in co-adapted complexes. Male side-blotched lizards (*Uta stansburiana*) come in three genetically determined throat color morphs, each of which is associated with distinct behaviors for sexual display and territory guarding (Sinervo et al. 2001). *Anolis* ecomorphs in the Greater Antilles are distinguished by sets of behavioral and morphological traits which are characteristic of the particular habitats they occupy (Irschick and Losos 1996; Losos 2011). We have a deep understanding of the agents of selection that favor covariation among some well-known life history traits, and between sets of morphological and behavioral traits in specific taxa. However, broader suites of traits (e.g., physiology, behavior, and life history) often covary within populations, and both the proximate and ultimate mechanisms underlying these patterns remain unresolved.

A far-reaching framework has been proposed that links trait covariation across physiology, life history, and behavior (Montiglio et al. 2018). This framework, referred to as the "pace-of-life syndrome" (or POLS), has the potential to be a unifying theory in the field of trait coadaptation and the evolution of complex phenotypes. Interest in POLS has burgeoned in the last several years as a growing number of species have been identified which show patterns consistent with POLS. Regardless, several studies have identified notable exceptions to POLS (see Royauté et al. 2018), and both the proximate and ultimate causes of POLS remain unresolved. In this review, we highlight a recent extension of the classical POLS hypothesis, called "extended POLS," which expands the model's framework to include the thermal dependence of life history, behavioral, and physiological traits. Furthermore, we identify emerging patterns and outstanding questions in this literature and suggest avenues of future research that might improve the generality of the POLS framework.

The POLS framework

The POLS framework describes axes of trait covariation among individuals, populations, or species. POLS was first developed as a way to conceptualize correlations between life history and physiology, such that individuals (or populations) were categorized as occurring along a slow-fast axis, whereby "slow" individuals have lower metabolic and growth rates, and reduced reproductive output, relative to "fast" individuals (Ricklefs and Wikelski 2002). On its own, the slow-fast axis is similar to the concept of r-K selection. Subsequently, POLS expanded to include a behavioral "shy-bold" axis (Stamps 2007; Biro and Stamps 2008; Careau et al. 2008; Réale et al. 2010). "Shy" individuals are those that are less aggressive and exploratory, and more social, compared to "bold" individuals. Within POLS, not only do traits vary along these axes but also the slow-fast and shy-bold axes are predicted to covary with each other such that there is an overarching slow/shy to fast/bold continuum (Fig. 1). As with many theories that attempt to explain complex biological phenomena, POLS has been developed piecemeal, with traits added over time and interpretations of the framework varying from study to study. This has led to uncertainty in the literature over exactly which traits should be considered part of the framework or even on how to define POLS. Nevertheless, a common theme among researchers who study POLS-related phenomena is that metabolism is the fundamental lynchpin that links life history with behavior (Careau and Garland 2012). Therefore, we define POLS as *a conceptual framework predicated on the idea that physiological, behavioral, and life history traits covary,* via *their relationships with metabolism, along slow-fast and shy-bold axes.*

The ultimate (evolutionary) mechanism presumably driving POLS is correlational selection favoring phenotypic integration (Réale et al. 2010; Royauté et al. 2018). Correlational selection occurs when particular combinations of trait values are favored in the local environment (Sinervo and Svensson 2002). Thus, an individual's fitness cannot be predicted based on the value of a single trait, but instead depends on the values of one or more additional traits. In the case of POLS, it is thought that individuals with high metabolic rates and bold behavior (or slow metabolism and shy behavior) are favored over individuals with high metabolic rates and shy behavior (or slow metabolism and bold behavior). One example of this is the olive flounder fish (*Paralichthys olivaceus*), where bold individuals have higher aerobic scope, maximum metabolic rate, and standard metabolic rate, which permit fighting against or quickly escaping from a threat (which they are more likely to encounter because they are bold; Rupia et al. 2016). By contrast, shy flounders have increased survival if they have lower metabolic rates because they remain still and undetectable until the threat passes and do not waste energy on maintaining a high metabolism. Similar patterns have been observed in other systems (McKenzie et al. 2015; Myles-Gonzalez et al. 2015; Binder et al. 2016). Over time, correlational selection on these trait combinations might lead to genetic covariance via proximate mechanisms like linkage disequilibrium (physical proximity on a chromosome) and pleiotropy (one gene affecting multiple traits), which could in turn constrain the potential for these populations to evolve away from POLS.

A wide range of studies in diverse taxa have found trait associations that follow at least some predictions of POLS

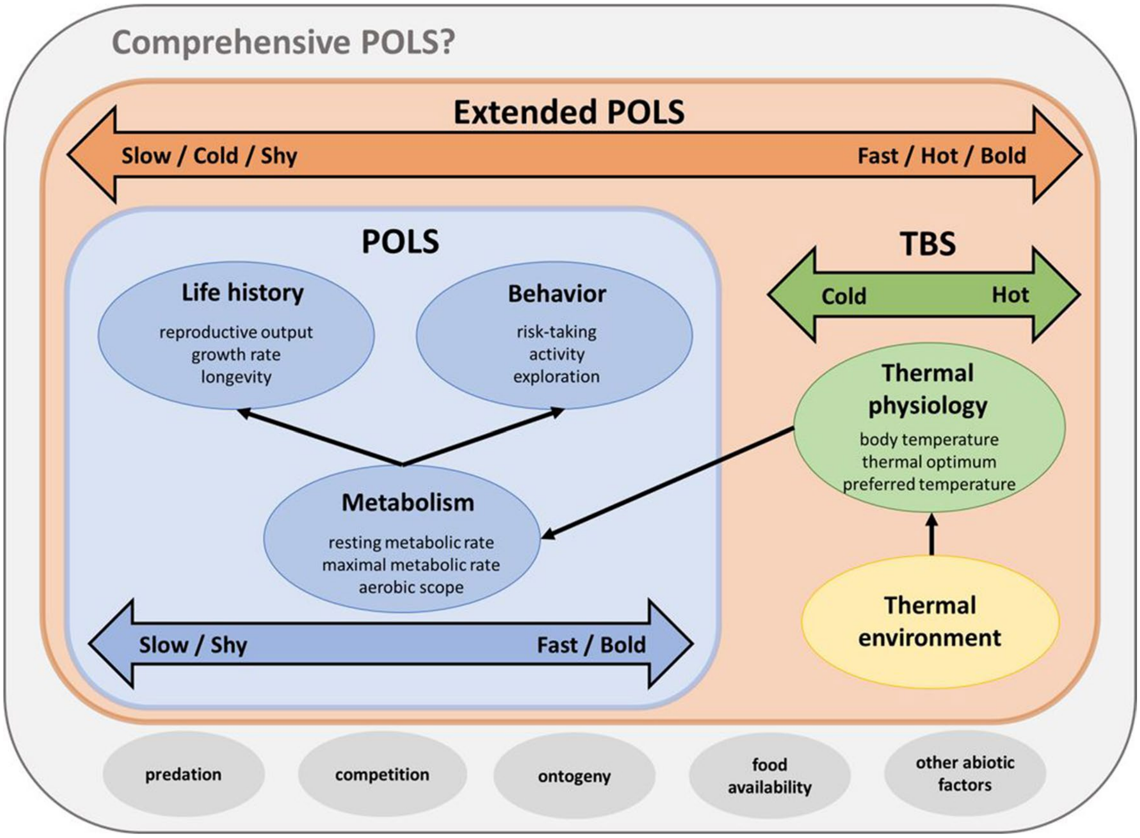


Fig. 1 Conceptual links within the extended POLS framework. The classical POLS hypothesis (blue box) links metabolic physiology with life history and behavior, whereas the extended POLS hypothesis (orange box) includes the role of the thermal environment and thermal physiology in modulating animal behavior via the thermal behavioral syndrome (TBS). The arrows represent directions of mechanistic links between trait categories. Finally, a truly comprehensive POLS hypothesis (light gray box) might integrate the roles of a myriad factors (or explain under which ecological contexts data are likely to violate POLS)

(Biro and Stamps 2008; Careau et al. 2008; Ariyomo and Watt 2011; Pettersen et al. 2016; Auer et al. 2018). For example, recent work on marine gastropods (*Littoraria irrorata*) showed that metabolic and somatic growth rates were higher in bolder individuals (Cornwell et al. 2020). However, a number of studies have shown only partial support while others have directly contradicted the predictions of POLS. Indeed, a meta-analysis of POLS studies showed only mixed support for the hypothesis (Royauté et al. 2018). Research has found that correlations between traits can differ between the sexes, and evidence for POLS is found more frequently in invertebrate systems compared to vertebrate systems (Royauté et al. 2018). Additionally, some studies have found only weak associations between metabolic, behavioral, and life history traits (Le Galliard et al. 2013) or no associations at all (Royauté et al. 2015). Other investigations have shown that boldness and growth rates covary in the opposite direction from that predicted by POLS (Adriaenssens and Johnsson 2011) or that the direction of trait correlations depend on context (Niemelä et al. 2012; Krams et al. 2014; Mathot et al. 2015). This breadth of prior work on POLS across many species strongly indicates that the hypothesis's current formulation does not capture the full panoply of trait covariation in nature, indicating that the conceptual framework is incomplete.

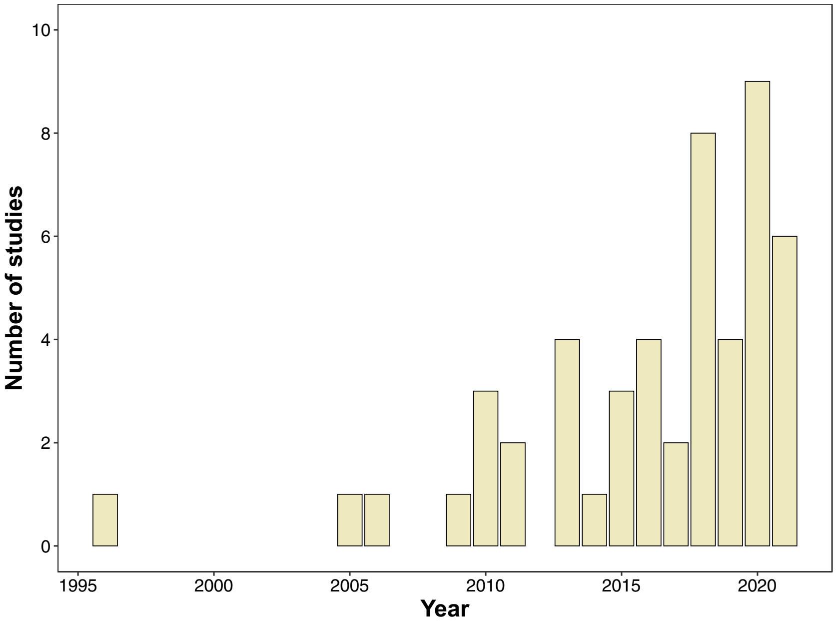
Metabolism, temperature, and the thermal behavioral syndrome

POLS posits a crucial role for metabolism as the lynchpin that links physiology with both life history and behavior. However, there are different ways that metabolism can be considered in POLS investigations, and the choice of metabolic trait may affect whether and how trait covariation is detected. POLS studies have tested the role of metabolism by measuring basal metabolic rate, resting metabolic rate, and maximal metabolic rate, or even by integrating resting and maximal metabolic rate to estimate aerobic scope, although rarely are more than one measure of metabolism included in the same study. As such, there is ongoing debate around which measures of metabolism are valid proxies for energetic constraints when linking behavior to energetics (Careau and Garland 2015; Mathot and Dingemanse 2015a, b). Here, we use the terms "metabolism" and "metabolic rate" as umbrella terms that encompass any estimate of metabolism reported in a given study, although in many cases, we specify which form of metabolism was measured.

Irrespective of the form of metabolism being considered, it is highly thermally sensitive because the enzymatic reactions involved in metabolic pathways have lower activation energy at higher temperatures (Hochachka and Somero 2002). This observation has led to the suggestion that temperature (and variation in thermal physiology among individuals) may be a key missing component to POLS. For example, individuals maintaining higher body temperatures should also have higher metabolic rates which should translate to greater scope for activity or exploration because the latter traits require energetic expenditure (Clarke and Fraser 2004). This is particularly pertinent for ectotherms, as their metabolic rates increase exponentially with body temperature (unlike endotherms that have a thermal neutral zone). It should also be noted that while temperature, through metabolism, might have indirect effects on both life history and behavioral traits (Rocha and Bergallo 1990; Ciota et al. 2014; Forsatkar et al. 2016), temperature can also affect life history and behavior directly, via its effects on processes such as muscle fiber contraction and protein synthesis (Pörtner 2002).

Regardless, the fact that animal physiology, life history, and behavior are all thermally sensitive suggests that an explicit consideration of the relationships between POLS traits and temperature might be needed to explain the plethora of results that are inconsistent with the classical hypothesis. The growing acknowledgement that temperature may play a crucial role in modulating trait relationships within POLS has led to the development of a new concept known as the thermal-behavioral syndrome (TBS). Goulet et al. (2017a) posited that physiological traits covary along a "cold-hot" axis, much as classical POLS suggests that individuals can be classified as slow/fast or shy/bold with respect their life history and behavioral traits, respectively. In TBS, a "cold" individual is one that selects and performs best at lower body temperatures, whereas "hot" individuals select and perform best at higher body temperatures (Fig. 1). Goulet et al. (2017a) suggested that thermal type might remain fixed across internal (e.g., digestion) or external (e.g., phenology) conditions and supported this hypothesis with a laboratory-based experiment on delicate skinks (*Lampropholis delicata*). They found that the thermal types of individuals stayed consistent after 9 weeks of laboratory acclimation. Cold skinks consistently selected lower body temperatures and had lower thermal optima for performance, while hot skinks selected high body temperatures and had high thermal optima. In a follow-up experiment using the same system, Michelangeli et al. (2017) found that thermal type influenced habitat use such that hot and cold skinks occupied hotter and colder microhabitats, respectively. A third study by this group (Goulet et al. 2017b) demonstrated that the shy-bold axis covaried with the cold-hot axis, such that hot individuals had higher sprint speeds, greater activity levels, and increased exploratory behaviors. Goulet and colleagues termed this expansion of POLS to include thermal considerations "extended POLS," and a growing number of studies have subsequently explored the

Fig. 2 There has been a recent boom in the number of published studies that test aspects of the extended POLS hypothesis



role of temperature and thermal physiology in trait covariation across a range of species (Fig. 2).

Emerging patterns in the extended POLS literature

It is widely accepted that metabolic, life history, and behavioral traits are thermally sensitive (Clarke and Fraser 2004; Shine 2005; Abram et al. 2017), but it is less known if and how temperature mediates trait covariation. We conducted a review using Web of Science (years 1965–2022) with the following search term combinations: "pace of life AND temperature," "temperature AND personality," "temperature AND life history," and "temperature AND metabolism AND pace of life." We then ran a separate set of searches but replaced the term "temperature" with "thermal." All results were ordered by relevance, and we examined the first 100 results of each search. We included papers if they tested at least one POLS trait in association with either a temperature treatment or a thermophysiological trait, and we only included papers on ectothermic organisms. These searches resulted in a total of 51 papers that we compiled for this review (Table 1; Fig. S1). Below, we outline the major patterns that are emerging from these studies.

Support for covariation between slow-fast, shy-bold, and cold-hot axes is limited, at best Only 25.5% of the papers considered for this review explicitly examined covariation between POLS traits and thermal traits (e.g., body temperature, thermal tolerance, thermal preference, or a thermal performance curve), and less than half of those studies (6 of 13; Stapley 2006; Rey et al. 2015; Cerqueira et al. 2016; Goulet et al. 2017b; Kashon and Carlson 2017; Michelangeli et al. 2017) found clear support for extended POLS. While these studies showed that individuals who prefer or maintain higher body temperatures are also bolder, the opposite result was found in two additional studies (Goulet et al. 2018; Enders et al. 2019), where bolder individuals selected lower body temperatures. Finally, Horváth et al. (2020) found a weak link between preferred body temperatures and risk-taking, but a strong correlation between preferred body temperatures and activity in Carpetane rock lizards (*Iberolacerta cyreni*). Within the delicate skink system in which so much of this work has been done, there is limited support for the alignment of the behavioral and thermal trait axes, although Goulet et al. (2018) indicated that a difference in sample sizes may have been the reason why bolder individuals preferred higher temperatures in one study (Goulet et al. 2017b) but not the other (Goulet et al. 2018). Importantly, all the studies referenced in this section tested for covariation between the cold-hot and shy-bold axes but did not consider life history traits or account for the effects of metabolism. In fact, the role of metabolism was only investigated in 2 of 13 studies. These studies contradicted the predictions of extended POLS, finding that (1) there was no relationship between resting metabolism and thermal preference in common lizards (*Zootoca vivipara*; Artacho et al. 2013) and (2) fast individuals had lower thermal optima for metabolic performance in damselfly larvae (*Ischnura elegans*; Tüzün and Stoks 2022). Life history traits were only considered in three studies on insects, and these again showed only mixed support for extended POLS depending on the combination of thermal and life history trait examined (Boher et al. 2010; Struelens et al. 2018; Tüzün and Stoks 2022). Most studies testing extended POLS focused on fish (35.3%), followed by insects (23.5%) and reptiles (21.6%). Of the 13 studies that explicitly tested thermal traits, the most commonly assessed trait was thermal preference (69%), with critical thermal limits, voluntary thermal limits, and thermal optima tested in only one study each.

Acclimation to different thermal regimes affects POLS traits, but often in inconsistent ways Of the studies included in our review, 38 tested whether one or more POLS traits differed across temperature treatments. Of the 20 studies that involved long-term acclimation treatments on adult individuals (e.g., acute, rather than developmental, plasticity), there were seven that supported, ten that partially supported, and three that did not support extended POLS. Several experiments showed that individuals acclimated to higher environmental temperatures had faster life-histories (e.g., higher fecundity, shorter lifetimes, and higher growth rates; Karlsson and Wiklund 2005; Ciota et al. 2014; Wenjie et al. 2019; Günter et al. 2020) or were bolder (e.g. increased activity and exploration; Forsatkar et al. 2016; Magellan et al. 2019; Culumber 2020). Other analyses provided partial support for the role of thermal acclimation, reporting evidence of trait covariation along POLS axes but with some behaviors (Segev et al. 2017; White et al. 2020; Le Roy et al. 2021), life history traits (Junge-Berberović 1996; Frost et al. 2013; Rutschmann et al. 2016), and metabolism (Moffett et al. 2022) deviating from the predictions of extended POLS. For example, ants (*Temnothorax longispinosus*) acclimated to warm temperatures were not only more exploratory but also less aggressive than those that were acclimated to cool conditions (Segev et al. 2017). Three studies that detected partial support highlighted factors that may have influenced why trait covariations deviated from POLS predictions including how effects of colony composition may influence behavioral types (Goulet et al. 2016) and how behavioral types may fluctuate in repeatability or converge at an intermediate type with increasing temperatures (Maskrey et al. 2020, 2021). A few studies on fish either

Table 1 Summary of all studies reviewed here. The POLS trait categories considered by a particular study are indicated with a "+" or "-" in the "LH" (life history), "B" (behavior), and "M" (metabolism) columns. "Thermal category" indicates whether the study measured at least one thermal trait, used a thermal acclimation treatment, or included both (A = long-term acclimation of adults, B = short-term acclimation of adults, C = manipulation of rearing temperature). We scored support for extended POLS as either "yes," "no," or "partial." We used "partial" when some, but not all, of the results of the particular study supported the hypothesis. Only studies on ectotherms were considered for this review

Author, year	Taxon	Study design	LH	B	M	Thermal category	Support for ext. POLS?
Arthropods							
Betini et al. 2020	*Daphnia magna*	lab	+	-	-	Acclimation (C)	Yes
Biro et al. 2013	*Ozius truncatus*	lab	-	+	-	Acclimation (B)	Yes
Boher et al. 2010	*Drosophila* sp.	lab	+	-	-	Thermal trait	No
Brans and De Meester 2018	*Daphnia magna*	lab	+	-	-	Acclimation (C)	Yes
Briffa et al. 2013	*Pagurus bernhardus*	lab	-	+	-	Acclimation (B)	Partial
Carbonell and Stoks 2020	*Ischnura elegans*	lab	+	-	-	Acclimation (C)	Partial
Carbonell et al. 2021	*Ischnura elegans*	lab	+	-	+	Acclimation (C)	Partial
Ciota et al. 2014	*Culex* sp.	lab	+	-	-	Acclimation (A)	Yes
Debecker and Stoks 2019	*Ischnura elegans*	lab	+	+	+	Acclimation (C)	Partial
Goulet et al. 2016	*Anelosimus studiosus*	lab	+	+	-	Acclimation (A)	Partial
Günter et al. 2020	*Pieris napi*	lab	+	-	-	Acclimation (A)	Yes
Junge-Berberović 1996	*Drosophila* sp.	lab	+	-	-	Acclimation (A)	Partial
Karlsson and Wiklund 2005	*Hipparchia semele* *Coenonympha pamphilus* *Aphantopus hyperantus* *Pararge aegeria*	lab	+	-	-	Acclimation (A)	Yes
Niemelä et al. 2019	*Gryllus bimaculatus*	lab	-	+	-	Acclimation (C)	Yes
Segev et al. 2017	*Temnothorax longispinosus*	lab	-	+	-	Acclimation (A)	Partial
Struelens et al. 2018	*Copitarsia incommoda*	mathematical model	+	-	-	Thermal trait and acclimation (C)	Yes
Tüzün and Stoks 2022	*Ischnura elegans*	lab	+	+	+	Thermal trait and acclimation (C)	Partial
Zhao and Feng 2015	*Procambarus clarkii*	lab	-	+	-	Acclimation (B)	Partial
Fish							
Biro et al. 2009	*Pomacentrus* sp.	lab	-	+	-	Acclimation (B)	Yes
Cerqueira et al. 2016	*Oreochromis niloticus*	lab	-	+	-	Thermal trait	Yes
Chung et al. 2018	*Fundulus heteroclitus*	lab	+	+	+	Acclimation (A)	No
Culumber 2020	*Pseudoxiphophorus jonesii*	lab	-	+	-	Acclimation (A)	Yes
Enders et al. 2019	*Notropis percobromus*	lab	-	+	-	Thermal trait	No
Forsatkar et al. 2016	*Betta splendens*	lab	-	+	-	Acclimation (A)	Yes
Frost et al. 2013	*Oncorhynchus mykiss*	lab	+	+	-	Acclimation (A)	Partial
Hébert and Dunlop 2020	*Salvelinus namaycush*	lab	+	-	+	Acclimation (B)	No
Le Roy et al. 2021	*Danio rerio*	lab	-	+	+	Acclimation (A)	Partial
Li et al. 2021	*Gambusia affinis*	lab	-	+	-	Acclimation (C)	Partial
Lukas et al. 2021	*Poecilia reticulata*	lab	-	+	-	Acclimation (A)	No
Magellan et al. 2019	*Gambusia affinis*	lab	-	+	-	Acclimation (A)	Yes
Moffett et al. 2022	*Gambusia affinis*	lab	-	+	+	Acclimation (A)	Partial
Pilakouta et al. 2023	*Gasterosteus aculeatus*	lab	-	+	-	Acclimation (C)	Yes
Rey et al. 2015	*Danio rerio*	lab	-	+	-	Thermal trait	Yes
Tang and Fu 2021	*Zacco platypus*	lab	-	+	-	Acclimation (A)	No
White et al. 2020	*Micropterus salmoides*	lab	-	+	-	Acclimation (A)	Partial
Závorka et al. 2020	*Phoxinus phoxinus*	lab	-	+	+	Acclimation (C)	Partial

Table 1 (continued)

Author, year	Taxon	Study design	LH	B	M	Thermal category	Support for ext. POLS?
Reptiles							
Artacho et al. 2013	*Zootoca vivipara*	lab	-	-	+	Thermal trait	No
Gangloff et al. 2015	*Thamnophis elegans*	lab	+	-	+	Acclimation (C)	Partial
Goulet et al. 2017b	*Lampropholis delicata*	lab	-	+	-	Thermal trait	Yes
Goulet et al. 2018	*Lampropholis delicata*	lab	-	+	-	Thermal trait	No
Horváth et al. 2020	*Iberolacerta cyreni*	lab	-	+	-	Thermal trait	Partial
Kashon and Carlson 2017	*Terrapene carolina*	field	-	+	-	Thermal trait	Yes
Michelangeli et al. 2017	*Lampropholis delicata*	lab	-	+	-	Thermal trait	Yes
Rutschmann et al. 2016	*Zootoca vivipara*	lab	+	-	-	Acclimation (A)	Partial
Stapley 2006	*Pseudemoia entrecasteauxii*	lab	-	+	-	Thermal trait	Yes
Trnik et al. 2011	*Coleonyx elegans*	lab	-	+	-	Acclimation (C)	No
Warner et al. 2010	*Amphibolurus muricatus*	lab and mesocosm	+	+	-	Acclimation (C)	Partial
Other							
Dalesman and Rundle 2010	*Lymnaea stagnalis*	lab	-	+	-	Acclimation (C)	Partial
Maskrey et al. 2020	*Actinia equina*	lab	-	+	-	Acclimation (A)	Partial
Maskrey et al. 2021	*Actinia equina*	lab	-	+	-	Acclimation (A)	Partial
Wenjie et al. 2019	*Euchlanis dilatata*	lab	+	-	-	Acclimation (A)	Yes

showed no support for an association between acclimation temperature and behavior (*Poecilia reticulata*, Lukas et al. 2021; *Zacco platypus*, Tang and Fu 2021) or they found that populations acclimated to cold environments had faster life histories, higher metabolism, and higher activity (*Fundulus heteroclitus*, Chung et al. 2018).

In addition to studies of acclimation in adult animals, some researchers have examined developmental plasticity, focusing on the effect of temperature during incubation and rearing. Growth rate was frequently lower when individuals were incubated or reared in cold environments (Gangloff et al. 2015; Brans and De Meester 2018; Debecker and Stoks 2019; Betini et al. 2020; Carbonell and Stoks 2020; Carbonell et al. 2021). However, higher rearing temperatures were associated with higher metabolic rates but slower growth in lake trout (*Salvelinus namaycush*, Hébert and Dunlop 2020). Another study found that the highest growth rates of jacky dragons (*Amphibolurus muricatus*) were at an intermediate temperature and that extreme temperatures resulted in slower growth (Warner et al. 2010). The studies that looked at the effects of rearing temperature on behavior had mixed results, with some showing higher exploration and sociability at higher temperatures (Niemelä et al. 2019; Pilakouta et al. 2023), while others showed higher exploration but similar latencies to emerge amongst treatment groups (Li et al. 2021), higher activity or exploration at lower temperatures (Trnik et al. 2011; Závorka et al. 2020), or rearing temperature of juveniles having little effect on the behavior of adults (Dalesman and Rundle 2010).

The thermal sensitivity of POLS traits frequently varies among individuals in a population, and the position of an individual along a given POLS axis is often repeatable Within a population of damselfish (*Pomacentrus bankanensis*), activity rates of some individuals dramatically increased with temperature, while activity rates were not plastic in others. Moreover, fish that were more active at a given temperature were also quicker to emerge after a simulated predation attempt (Biro et al. 2009). Similarly, inter-individual differences in behavioral responses to temperature were observed in a marine crab (*Ozius truncates,* Biro et al. 2013) and a hermit crab (*Pagurus bernhardus,* Briffa et al. 2013). Activity, aggression, and latency to respond to a simulated threat were correlated across temperatures (albeit not always in the direction predicted by POLS) in red swamp crawfish (*Procambarus clarkii*; Zhao and Feng 2015). The authors in many of these studies speculate that metabolism is the proximate mechanism that explains individual differences in thermal sensitivity of behavior.

Metabolism is regularly proposed as a crucial driver of trait covariation, but this has rarely been tested The majority of studies highlight metabolism as the likely mechanism behind the thermal sensitivity of behavior and life history traits and thus the position of individuals along the different trait covariation axes. Nevertheless, very few studies have explicitly tested this hypothesis. Only 10 of the studies reviewed here included a measure of metabolism in their study design. Of these, four found that higher mean metabolic rates were associated with acclimation to lower temperatures (a process known as “metabolic compensation”; Gangloff et al. 2015; Chung et al. 2018; Carbonell et al. 2021; Moffett et al. 2022) and one found no association between metabolism and thermal traits (Artacho et al. 2013). While five studies found that metabolism covaried with the cold-hot axis (Debecker and Stoks 2019; Hébert and Dunlop 2020; Závorka et al. 2020; Le Roy et al. 2021; Tüzün and Stoks 2022), none of these represented strong support for extended POLS as the correlations between metabolic rates, life history, and behavioral traits were weak or in the opposite direction to that predicted by the hypothesis. For example, hot damselfly larvae had higher thermal optima for metabolic rate and displayed bolder behavior compared to cold larvae (Tüzün and Stoks 2022), suggesting that the thermal sensitivity of metabolic rate might be the primary driver of the position of larvae on the shy-bold axis. However, in the same study, the cold-hot and slow-fast axes were negatively correlated. Faster growing larvae had lower thermal optima for swimming speed, which the authors suggest may have resulted from a trade-off between growth and thermal performance (Tüzün and Stoks 2022). This implies that metabolism may be the underlying mechanism of some trait correlations, but not others, or that extended POLS may not apply when trade-offs are present between life history or behavioral traits and thermal performance.

Outstanding questions and future directions

While the extended POLS literature has matured in recent years, there are several outstanding questions, the pursuit of which may represent a fruitful path for improving our knowledge of the proximate and ultimate mechanisms that generate trait covariation in nature.

How does extended POLS arise in nature? The fact that traits often covary across disparate categories (life history, behavior, etc.) begs the question of what forces generated these covariances in the first place. These patterns are usually assumed to be adaptive, but this is a hypothesis that must be tested (Gould and Lewontin 1979). When traits covary along axes, a reasonable hypothesis is that correlational selection favoring particular combinations of trait values has occurred (or continues to occur). Despite the existence of well-established methods to estimate correlational selection in the wild (Lande and Arnold 1983), to our knowledge, no one has yet attempted to measure selection gradients of any kind in the context of extended POLS. Indeed, of the 51 studies reviewed here that tested aspects of extended POLS, only one was field-based. Future work should examine the relative survival probabilities and reproductive success of wild individuals as a function of variation in POLS traits. In principle, these sorts of studies are straightforward. For example, one could measure variation across individuals in the thermal sensitivities of both behavior (e.g., boldness) and metabolic rate in the lab, mark these individuals, and then release them into the wild. Mark-recapture can then be used over the breeding season to evaluate relative survival probabilities (to estimate viability selection) or over multiple generations in combination with a pedigree to estimate fitness via lifetime reproductive success. Standard regression and spline techniques (Schluter 1988) could then be used to quantify and visualize fitness landscapes, with an emphasis on calculating correlational selection surfaces for the pairs of traits that are predicted by extended POLS to covary. A similar but even more powerful approach would be to manipulate aspects of the environment to change local fitness optima. Predators could be added or removed, or the strength of competition could be manipulated (with respect to a control), and then the same set of mark-recapture and analytical techniques could be used with the prediction that fitness surfaces should differ between the manipulated environment and the control. Of course, these sorts of studies are challenging in practice because they require large sample sizes, measuring behavioral and physiological traits on large numbers of individuals can be prohibitive, and manipulating predation and competition in natural environments can be logistically insurmountable. Regardless, we think this approach may be feasible in some systems and would garner much insight into the evolutionary forces that lead to trait covariation within POLS.

Even if selection studies determine that POLS traits are rarely under selection in contemporary environments, this does not mean that past selection has not shaped trait covariation. In fact, we know virtually nothing about the proximate basis of extended POLS. If correlational selection has been an important force generating trait covariation along slow-fast, shy-bold, and cold-hot axes, then we might predict that the associated traits would be correlated at the genetic level via mechanisms like linkage disequilibrium or pleiotropy. This is because persistent correlational selection should build genetic correlations over time (Sinervo and Svensson 2002; Immonen et al. 2018). Controlled breeding studies can elucidate the quantitative genetic basis of POLS traits, including the degree to which they are genetically correlated and thus constrained from evolving away from POLS. In combination with selection gradients estimated from mark-recapture studies, this information can be used to model future evolutionary trajectories in changing environments.

What is the role, if any, of metabolism in extended POLS? Metabolism is assumed to be the underlying mechanism that links all traits within the classical POLS framework, and since it is itself a thermally sensitive trait, it should be integral to extended POLS as well. However, as with the assumption that trait covariation is adaptive, the assertion that metabolism underlies covariation among trait categories is a hypothesis that should be explicitly tested. Indeed, contrasting models for how metabolic processes should influence higher order traits have been proposed. The "independent model" states that there should be no mechanistic link between resting metabolic rate and higher level organismal performance (e.g., life history, behavior) and the "allocation model" assumes a negative association between resting metabolic rate and performance caused by a trade-off in allocating available energy to competing functions (Careau and Garland 2012; Careau 2017). Each of these models has received empirical support in the literature, providing evidence for positive, negative, or lack of correlations between basal or resting metabolic rates and different energy-demanding performance and behavioral traits (Burton et al. 2011; Careau and Garland 2012). Unfortunately, in the context of extended POLS, very few studies have included measurements of metabolic rates under any condition, let alone across a thermal gradient (Table 1). Progress in understanding the generality of extended POLS and evidence supporting the hypothesized role of metabolism will require the measurement of the thermal sensitivity of metabolic rate (and its plasticity) in many taxa and across a broad range of ecologically relevant temperatures. Furthermore, deep consideration should be given to the specific measure of metabolism (e.g., resting, maximal, aerobic scope) that researchers choose to quantify given their study system and the types of trait covariations being investigated.

What is the role of plasticity in extended POLS? It is unlikely that the majority of traits normally considered within the extended POLS framework are genetically canalized. Instead, many of these traits respond to changes in the environment within the lifespan of individual organisms, that is, they are plastic. It is well documented that behavioral, life history, and physiological traits, as well as their thermal sensitivities, can all shift via short-term, reversible plasticity or fixed, developmental plasticity (Snell-Rood 2013; Baker et al. 2015; Gunderson et al. 2017; Montiglio et al. 2018; Cloyed et al. 2019). Indeed, the assumed driver of trait covariation within extended POLS, the thermal sensitivity of metabolic rate, has been shown to be plastic when individuals are exposed to different thermal regimes (Artacho et al. 2013; Cloyed et al. 2019; Réveillon et al. 2019). Nevertheless, to our knowledge, the role of plasticity in generating, maintaining, or eroding extended POLS has not been studied. Studies where POLS trait associations are measured in individuals that are recaptured across seasons might reveal a role for plasticity in generating or eroding extended POLS over time. Similarly, individuals can be exposed to varying environmental conditions in the laboratory and both the magnitude of plasticity and extended POLS trait associations can be remeasured after exposure. Additionally, the potential role of intergenerational plasticity (e.g., maternal effects) has not been considered and might play a role in modulating trait correlations. Studies like these might begin to reveal a role for plasticity in generating the exceptions to both classical and extended POLS that are so common in the literature.

How should we define the ends of the shy-bold continuum? In the POLS literature, bold individuals are usually characterized by having higher aggression, shorter response latency, less risk aversion, and lower sociality. But the interpretation of a particular behavior as shy or bold often varies by system. This seems due to fundamental differences in the way that behaviors are perceived by researchers who study different taxa. For example, sociality and exploration are traits often used to assess behavior with the baseline assumption that bolder individuals are less social and more exploratory, yet these traits may not be accurate proxies for the position of individuals on the shy-bold axis. Some experiments have found that bold individuals are more social or that shy individuals are more exploratory (Rey et al. 2015). A study on leopard lizards (*Gambelia wislizenii*, Crowley and Pietruszka 1983) scored individuals that fled from predators as bold and those that stood their ground were scored as shy. These differences in interpretation of behavior across taxa are crucial because they result in individuals being placed at different positions along the shy-bold axis and therefore change the way that associations between the axes of extended POLS are interpreted. Beckmann and Biro (2013) make the case that a single behavioral assay may not be sufficient to describe the boldness or shyness of an individual. If possible, researchers should incorporate multiple behavioral assays and justify why particular traits are chosen as proxies for boldness based on the biology of their particular study organism. While we recognize that the diverse sets of behaviors displayed by organisms across the tree of life will always lead to some inconsistencies in this literature, we urge researchers to critically assess which traits are used to define positions along the shy-bold axis in their systems, as a lack of clarity here is likely to cause confusion over whether the study supports the extended POLS hypothesis.

How much do trends and inconsistencies in study design and methodology prevent us from judging the generality of extended POLS? Given that the classical POLS framework was created piecemeal over many years, and that extended POLS was proposed recently, there is understandably a wide range of methods and approaches that biologists have taken to test aspects of these ideas. Nevertheless, inconsistencies and tendencies in approach, analysis, and interpretation have made it challenging to understand the contexts in which extended POLS applies and those in which it does not, in wild populations. Few studies have incorporated multiple trait categories into their design, making it difficult to understand the larger patterns of covariation between life history, behavior, metabolism, and thermal traits either within or across systems. Evaluating the role of temperature in mediating trait covariation is admittedly a complex and challenging task, but growth in this field will require experimental designs that test the role of temperature in detailed and multi-faceted ways. We suggest that careful thought be put into experimental design, including which types of temperature (e.g., internal body temperature, body surface temperature, environmental temperature, operative temperature) will be measured, how these variables will be measured and manipulated (e.g., static or fluctuating), and at what life stages the organism will be exposed to experimental treatments. Most studies incorporate a thermal element by using static environmental temperature treatments or providing a thermal preference gradient for adult-stage individuals, and they usually only consider the effect of temperature on one or a few traits (e.g., Brodie and Russell 1999; Stapley 2006; Goulet et al. 2017b). By its nature, extended POLS involves the thermal dependence of many different types of traits, and thus, future work should consider the thermal dependence of multiple traits (physiological, life history, and behavior) across ecologically realistic temperature regimes.

In addition to the varied ways in which researchers have integrated thermal biology into the study of POLS, the taxonomic scope of these investigations has been relatively limited (Table 1; Fig. S1). Outside of several studies on insects, much work to date has focused on vertebrates (primarily fish and squamate reptiles). Tests of trait associations and their drivers across a wider range of taxa would deepen our understanding of extended POLS.

Towards a comprehensive POLS framework

In the deep pantheon of theories in ecology and evolutionary biology, extended POLS has only recently emerged. Nevertheless, the incorporation of thermal physiology into the classical POLS hypothesis has revived hope that a general explanation for trait covariation, and why it may be adaptive, exists. The realization that temperature plays an outsized role in mediating physiology, life history, and behavior has led to a surge of studies aimed at exploring links between the slow-fast and shy-bold axes, and the newly discovered cold-hot axis, of trait covariation. However, progress has been slow due to inconsistencies in experimental design, analysis and interpretation, assumptions that metabolism plays a central role and that trait correlations are adaptive, and a complete lack of field studies. We thus have a growing literature with some common patterns emerging but many notable deviations from these patterns. If we are to develop a comprehensive and generalizable POLS framework, it will likely require re-thinking how we categorize behavioral traits across taxa, a concerted effort to test the role of metabolism (and other potential traits) as the fundamental mechanism linking POLS trait categories, an exploration of the role of phenotypic plasticity in generating or eroding trait correlations, and an understanding of how selection and genetic variation give rise to, and maintain, trait covariation in nature. If this effort ultimately fails, we should attempt to understand why by studying the ecological conditions (e.g., predation, competition, food availability, habitat structure) over which it failed. Ultimately, this endeavor will move us closer to understanding how and why animals behave, grow, and function as they do.

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Declarations

Competing interests The authors declare no competing interests.

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