



# Evolution of sex-specific pace-of-life syndromes: causes and consequences

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## Abstract

Males and females commonly differ in their life history optima and, consequently, in the optimal expression of life history, behavioral and physiological traits involved in pace-of-life syndromes (POLS). Sex differences in mean trait expression typically result if males and females exhibit different fitness optima along the same pace-of-life continuum, but the syndrome structure may also differ for the sexes. Due to sex-specific selective pressures imposed by reproductive roles and breeding strategies, the sexes may come to differ in the strength of correlation among traits, or different traits may covary in males and females. Ignorance of these selective forces operating between and within the sexes may lead to flawed conclusions about POLS manifestation in the species, and stand in the way of understanding the evolution, maintenance, and variability of POLS. We outline ways in which natural and sexual selection influence sex-specific trait evolution, and describe potential ultimate mechanisms underlying sex-specific POLS. We make predictions on how reproductive roles and the underlying sexual conflict lead to sex-specific trait covariances. These predictions lead us to conclude that sexual dimorphism in POLS is expected to be highly prevalent, allow us to assess possible consequences for POLS evolution, and provide guidelines for future studies.

**Keywords** Integrated phenotype · Life history · Mating system · Personality · POLS · Sexual dimorphism

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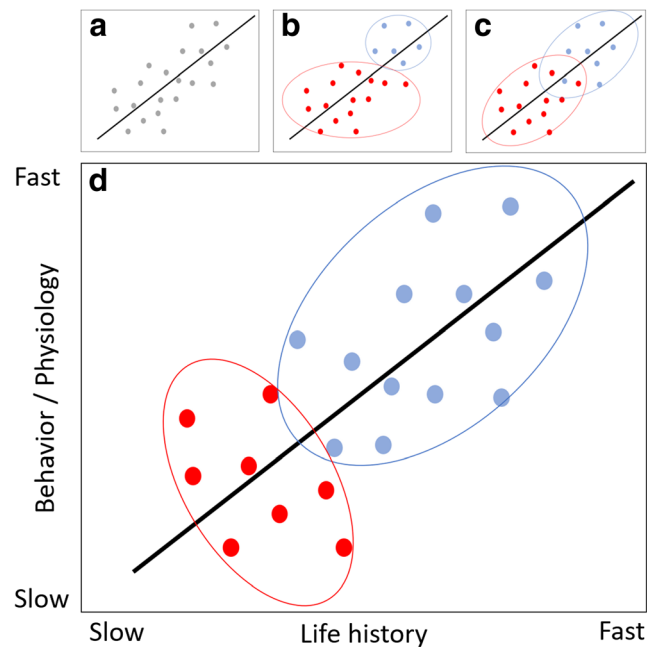
## Introduction

Trade-offs between current and future reproduction frequently lead to covariation between life-history traits (Stearns 1989), resulting in a range of life-history strategies and placing species along a pace-of-life continuum. Physiological and behavioral traits are expected to coevolve with life history to facilitate these different strategies, forming pace-of-life syndromes (POLS; Ricklefs and Wikelski 2002; Réale et al. 2010). Within species, individuals likewise vary in life history, physiology, and behavior (collectively, “POLS-traits”), providing an opportunity for the evolution of specific covariances between traits within populations, as suggested by a growing body of empirical evidence (e.g., Réale et al. 2000; Careau et al. 2010; Nicolaus et al. 2012; Schuett et al. 2015; but see Schürch and Heg 2010; Bouwhuis et al. 2014; Royauté et al. 2018, topical collection on Pace-of-life syndromes). Consistent behavioral differences among individuals (termed “animal personality” Dall et al. 2004; Wolf and Weissing 2012; Dingemans and Dochtermann 2013) are expected to form a part of the syndrome due to the role of behavioral mechanisms in facilitating pace-of-life variation within populations (Wolf et al. 2007; Biro and Stamps 2008; Réale

et al. 2010; Wolf and Weissing 2012). Covariance among behavioral, physiological, and life-history traits can arise from extrinsic selection pressures, correlational selection on physically linked or unlinked loci, or via gene pleiotropy (Badyaev 2005; Schwander and Leimar 2011; Immonen et al. 2018, topical collection on Pace-of-life syndromes). The specific composition of a syndrome and the strength of trait covariances therefore depend on selective pressures relevant to the population, and constraints of the genetic architecture.

An important source of within-species variation that has been overlooked in the POLS framework is sex: through natural and sexual selection, males and females typically have different optima along the pace-of-life continuum. For example, sex differences in potential reproductive rate (see *Anisogamy* below) and/or resource requirements can lead to sexual dimorphism in life-history traits such as lifespan and the rate of growth, reproduction, and aging (Bonduriansky et al. 2008; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014; Berger et al. 2014), as well as many relevant behavioral (e.g., Schuett et al. 2010) and physiological traits (e.g., Lee 2006; Restif and Amos 2010; Roved et al. 2016). For example, aggressiveness and boldness can facilitate rapid growth and early maturation through improved resource acquisition and defense ability, thus generating a “faster” POLS (Biro and Stamps 2008; Réale et al. 2010) in the sex that has higher resource requirements. In addition to sex differences in mean trait expression, sexes may also differ in covariance structures between traits, leading to sex-specific POLS (Fig. 1; Smith and Blumstein 2008; Cook et al. 2011; Montiglio et al. 2014; Debecker et al. 2016; Kim and Velando 2016; Ballew et al. 2017; Monceau et al. 2017; but see Krams et al. 2013a). We propose that the specific POLS structure (trait covariance matrix) depends on the reproductive roles of the sexes as well as the species’ genetic architecture.

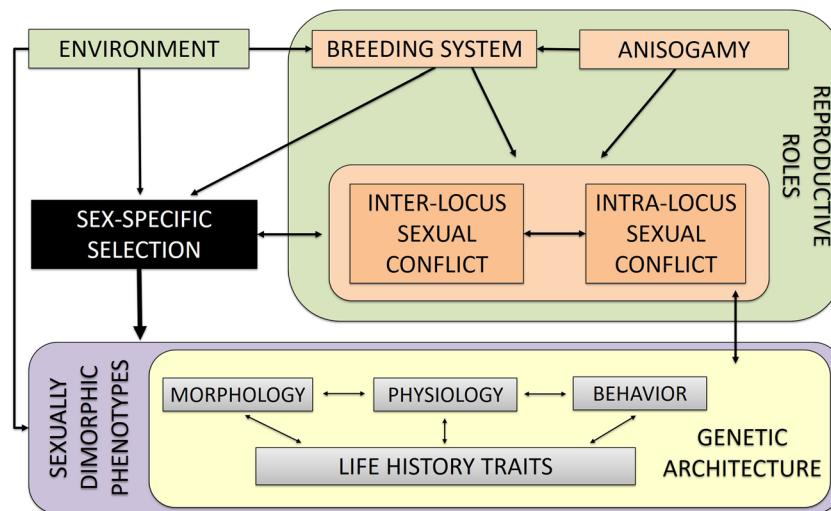
Sex-specific trait covariances might arise and be maintained through correlational selection acting on sex-specific suites of co-adapted traits (Lande 1984; Sinervo and Svensson 2002). The exact POLS outcomes will depend on the genetic associations of life history and behavioral/physiological traits, both within and between sexes. A baseline of a sexually monomorphic POLS structure may be predicted unless different trait covariances increase fitness more in one sex than the other. Sex-specific covariances could arise when the sexes gain fitness through different combinations of life history strategies, physiological adaptations, and/or behaviors, and are therefore subject to different selective pressures. Sex-specific POLS structures are generally expected when the traits only partially differ, such that genetic conflict is associated with some traits, but selection on other traits converges for the sexes (see examples in Part 2). The relative strength of trait covariances hence depends on the strength of selection within as well as among the sexes. Within-sex correlations may further depend on the relative strength of alternative life-history strategies or



**Fig. 1** Schematic of POLS trait associations among individuals within and among the sexes. This scenario indicates a positive covariance (solid black line) of life-history pace (e.g., reproductive investment) and other POLS traits observed among individuals (dots) at the population level (a). A positive relationship may be found at the population level if the sexes differ in the trait means, regardless of the within-sex trait covariance. Within-sex trait covariance may be neutral (b), completely align with the population-level covariance (c), or completely differ for the sexes (d). Ignoring the sex-specific trait covariance could hence lead to an erroneous observation of a universal POLS. In distinguishing between the levels, it is thus important to assess the sex-specific trait covariances, i.e., analysis of trait interaction with sex, or sexes evaluated separately for the same traits. Further detail shown in hypothetical example scenario (d), showing opposite within-sex trait covariance patterns for the sexes: a negative covariance among the traits in females (red) and a positive trait covariance in males (blue). For an alternative representation of these concepts see Fig. 1 in Immonen et al. (2018), topical collection on Pace-of-life syndromes

phenotypes within the sex. Immonen et al. (2018, topical collection on Pace-of-life syndromes) provides a more thorough treatment of the mechanisms generating and maintaining sex-specific POLS, especially at the genetic level.

Evidence of POLS incorporating behavior at the genetic level is rare (Niemelä et al. 2013; Han and Dingemanse 2017; Santostefano et al. 2017); no such studies of sex-specific POLS exist to date (but see Berger et al. 2014). For this reason, we will primarily focus on phenotypic evidence of trait expression and covariance. The principles largely apply to genetic covariances and trait covariances should ideally be measured at genetic level to truly understand the evolution of POLS, as the mere collection of phenotypic data might not always be suitable to test evolutionary predictions of POLS. We also recognize that environmental variables frequently shape the phenotype (Fig. 2), and that complex epigenetic, cross-generational (e.g., parental effects), environmental, and genotype-environment interactive effects plausibly also



**Fig. 2** Evolution of sex-specific POLS. Anisogamy causes the sexes to invest differently in each offspring (see Fig. S1). This is expected to result in sex-specific optima along the pace-of-life continuum. Other selective pressures may, however, change this prediction: environmental conditions, mating system, social system as well as intra- and inter-locus sexual

conflict can influence the intensity of sex-specific selection and associated sex-specific POLS evolution. Thus, sex-specific selection can result from both sexual and natural selection. Sexually dimorphic phenotypes are expected when the pace-of-life optima and/or optimal trait covariance matrices differ for the sexes

influence sex-specific POLS. Due to space restrictions, these can be only marginally considered here, but we caution that environmental conditions may alter the observed phenotypic covariances (Santostefano et al. 2017).

We propose a framework for the integration of sex-specific selection into the POLS hypothesis by predicting how selective pressures originating from reproductive roles shape sex-specific POLS (Fig. 2). We first outline ways in which sex-specific selection originating from certain reproductive roles can generate predictable sex differences in the average expression of POLS traits, leading to putative differences in among-individual trait covariances within and between the sexes (Part 1). Secondly, we formulate testable hypotheses regarding the evolution of a range of sex-specific POLS outcomes (Part 2). Our primary goal is to propose evolutionary drivers of sex-specific POLS, hypothesize on their effects on the manifestations of sex-specific POLS, and generate predictions for future studies on the role of sex in POLS evolution.

## Part 1: sources of sex-specific selection on pace of life and trait covariances

### Anisogamy

Sex differences in life-history optima are rooted in the potential rate of reproduction and relative investment into offspring, which ultimately stem from anisogamy (Fig. 2) (e.g., Bateman 1948; Lehtonen et al. 2016). The optimal way to trade off reproduction and self-maintenance differs for the sexes depending on their potential reproductive rate, leading them to maximize fitness through different reproductive strategies with

coevolving physiological and behavioral mediating traits (Supplementary Fig. S1; e.g., Bateman 1948; Trivers 1972; Maynard Smith 1982; Lehtonen et al. 2016; but see Kokko and Jennions 2008). Due to less-costly production of male gametes, male fitness is predicted to be more limited by access to mates and fertilizations, with consequent selection for behavioral traits associated with searching and competing for access to mates (Vinogradov 1998), such as high inter-male aggression, mobility, and risk taking (e.g., Magurran and Garcia 2000). Investment in reproduction at the expense of survival, for example, decreased male longevity due to low somatic maintenance relative to females (e.g., Vinogradov 1998; Bonduriansky et al. 2008; Maklakov and Lummaa 2013), should lead to associations of behaviors with life-history traits. The slower reproductive rate of females is, in turn, expected to favor a strategy of a slower pace of life with low-risk behavior and investment in self-maintenance, which both promote longevity (Fig. S1; Bonduriansky et al. 2008; Maklakov and Lummaa 2013). Anisogamy thus creates the basis for sex-specific reproductive roles that underlie sex differences in optimal pace of life: conflict over the rate of reproduction, offspring care, and survival. This basic premise and the consequences for POLS can change when other selective pressures do not align with those of anisogamy, as outlined below.

### Sexual conflict

Different evolutionary interests, originating from anisogamy, frequently cause sexual conflicts over reproductive rates and parental effort, leading to an evolutionary tug-of-war between the sexes (“inter-locus” sexual conflict, Fig. 2; Arnqvist and Rowe 2005; Parker 2006; Bonduriansky et al. 2008; Immonen

et al. 2018, topical collection on Pace-of-life syndromes). This antagonistic co-evolution involving separate traits in the sexes is now recognized as a key process shaping life histories. For example, male behavior or physiology can affect female pace of life via physical damage or manipulation of female reproductive schedules (Bonduriansky et al. 2008; Immonen et al. 2018, topical collection on Pace-of-life syndromes). Females, in consequence, can show counter-adaptations to such interference through increased aggressiveness towards potential mates, which also affects their energy expenditure and predation risk, and eventually mortality rates (Bonduriansky et al. 2008). These adaptations are likely candidates for generating sex-specific covariances between POLS traits, leading to sex-specific POLS. In this example, the pace of female life history would increase when male manipulation is successful. If female counter-adaptations are successful, however, rate of reproduction should decrease, but rates of aggression increase. Higher aggression and slow life history could thus be under correlative selection in females, whereas a fast life history may still be paired with a fast life history in males.

Sexually antagonistic selection on POLS traits can also result in an “intra-locus” conflict over optimal trait expression in the sexes due to the largely shared genome, if strong intersexual genetic correlations prevent the sexes from achieving their differing pace-of-life optima. This can have dual consequences on the evolution of POLS. First, if unresolved, it will hinder the evolution of sexual dimorphism. At least a partial resolution to intra-locus sexual conflict is required for the independent trait expression in each sex, allowing different patterns of POLS to evolve in the sexes. We discuss the genetic and hormonal underpinnings for this in Immonen et al. (2018), topical collection on Pace-of-life syndromes. Second, sexually antagonistic selection plays a central role in maintaining variation within and among the sexes (Connallon and Clark 2012, 2014) and can therefore have important implications for the maintenance of variation within each sex in POLS traits. In principle, when male and female life-history strategies are selected in opposite directions along the pace-of-life continuum, males with a selectively favored (e.g., “fast”) phenotype may father less-fit (“fast”) daughters, while sons of successful “slow” mothers express traits more beneficial for females. The same principle applies for behavioral phenotypes such as sex-biased aggressiveness (Mills et al. 2012). Genotypes disfavored in one sex can thus persist in the population. Sexually antagonistic selection has been found to act on several POLS traits across taxa (Brommer et al. 2007; Long and Rice 2007; Arnqvist and Tuda 2010; Lewis et al. 2011; Mills et al. 2012), as well as on the integrated POLS phenotype (Berger et al. 2014), suggesting it plays a pervasive role in POLS evolution.

The mating system and reproductive roles can affect the strength of sex-specific and sexually antagonistic selection. We will next outline how different reproductive roles are

expected to affect sex differences in traits closely associated with sex-specific fitness.

### Variation in reproductive roles between the sexes

The differential costs of male and female gametes lead to reproductive roles in which males typically show a faster pace of life than females, with associated higher aggression and risk taking, and increased mortality risk. Such predictions can be overturned by other selective forces (see below), but tend to hold in polygynous mammals, where males are shorter-lived and age faster compared to females, presumably due to higher costs of sexual competition and potentially lower investment into somatic maintenance (Clutton-Brock and Isvaran 2007). Generally, females tend to live longer in species with high male-male competition (birds: Liker and Székely 2005; mammals: Promislow 1992). While strict polygyny would likely increase selection on male activity or aggression, in promiscuous systems where females mate multiply (e.g., Wolff and Macdonald 2004), males may invest more into post-copulatory sperm competition, at the expense of pre-copulatory traits (Mank et al. 2013; Lüpold et al. 2017). This could influence the specific traits that confer fitness to males, and shape the associated trait covariances within and between the sexes.

If female reproductive rate exceeds that of males (Clutton-Brock and Vincent 1991), females may compete for mates or resources more than males. Such reproductive role reversal (sensu Trivers 1972; Williams 1975) can lead to females with a fast, and males with a slow pace of life. This may be accompanied by a reversal also in the expression of some behavioral, physiological, and morphological traits (Jenni 1974; Emlen and Oring 1977; Ketterson and Nolan 1999; Eens and Pinxten 2000; Andersson 2005) but not necessarily hormone function (see Eens and Pinxten 2000). Consequently, POLS-trait covariances may also change, for example, so that hormone levels covary with behavioral and life-history traits in one sex, but the traits are unassociated in the other sex. Species with male-biased offspring care are therefore particularly interesting for testing how reproductive roles affect the evolution of POLS-trait covariance within and among the sexes.

Monogamy, biparental care, and cooperative breeding tend to reduce the level of sexual selection and conflict, and therefore unify the life-history optima of the sexes (Klug et al. 2013). For example, evolution under monogamy can result in reduced dimorphism in lifespan or development time because of the convergence in the reproductive costs in the sexes (Promislow 1992; Liker and Székely 2005). Similarly, cooperative breeding can converge the reproductive roles and life history profiles of the sexes (Arnold and Owens 1998; Promislow 2003; Rubenstein and Lovette 2009). In the absence of antagonistic selection, the sexes may therefore be expected to exhibit a similar POLS covariance structure, and



similar optima along the pace-of-life continuum when the overall reproductive costs are similar for the sexes.

### Parental care and reproductive behavior

Reproductive behaviors, including parental care, often covary with other behavioral traits, such as exploration (Hollander et al. 2008), as well as physiological traits (hormones, e.g., Hau and Goymann 2015; Lynn 2016; Bendesky et al. 2017), and adult mortality (e.g., Owens and Bennett 1994; for potential mechanisms see Immonen et al. 2018, topical collection on Pace-of-life syndromes). Parental care is often sex-biased and therefore represents a source of sexual conflict even in species with biparental care (e.g., Clutton-Brock 1991). It can play an integral role in sex-specific POLS by mediating links between life history, physiology, and behavior in a sex-specific way (Mutzel et al. 2013; Krams et al. 2014). Parental care can vary substantially within mating systems (e.g., Bendesky et al. 2017), but is consistent within individuals across contexts (Wetzel and Westneat 2014; Stein and Bell 2015) and time (Fresneau et al. 2014). Males are often more consistent in parental care behavior than females (Schuett et al. 2010; but see Burtka and Grindstaff 2013). This carries evolutionary significance because females of biparental species may benefit from choosing partners with predictable behavior (Holveck and Riebel 2010; Schuett et al. 2010). Since mate choice mostly occurs in the absence of parental care behaviors, choice may target other traits that act as reliable indicators of parental skill or consistency (e.g., Kokko 1998). Neural pathways involved in parental behaviors also affect many other traits including aggressiveness, anxiety, sociality, and responsiveness to stress (Immonen et al. 2018, topical collection on Pace-of-life syndromes). It is an interesting prospect that correlational selection arising from mate choice for parental care could have contributed to the evolution of pleiotropic genetic architecture between consistent parental behavior and other behavioral traits.

A potential complication of studying parental care behaviors in the POLS context arises from the inherent association of parental care with investment in current reproduction. The premise of life-history pace is based on trade-offs between investment in current and future reproduction, or current reproduction and survival. The concept is thus of primary importance in linking pace of life to behavior. While parental behaviors are of key interest in terms of sex-specific POLS evolution, it is important to recognize that they are often indistinguishable from classic life-history trade-offs. Simply describing a correlation between (sex-specific) pace-of-life or life-history strategy and the degree of parental care is generally not sufficient proof of POLS, but including parenting behaviors along with other life-history and behavioral traits in a broader study of POLS could be informative.

### Breeding schedule

Sex-biased frequency of breeding or the lifetime number of breeding opportunities can have vast consequences for sex-specific pace-of-life optima and consequent POLS outcomes in each sex. When the temporal window for breeding is limited, or juvenile survival is highly predictable and adult survival low (Stearns 1992; Lessells 2005), extreme investment in current reproduction may be selected at the expense of all future reproduction. As a result, semelparity can occur in one (e.g., Bradley et al. 1980; Huse 1998; Fromhage et al. 2005; Suzuki et al. 2005; Bonnet 2011; Fisher and Blomberg 2011) or both sexes (Hendry et al. 1999). In systems with sex-specific semelparity, the semelparous sex is expected to invest minimally in survival beyond maturity (e.g., Bonnet 2011; Fisher et al. 2013) and thus to exhibit a “faster” pace of life. Semelparous breeding is an exceptionally strong selective force that shapes not only life history but also physiology (Bradley et al. 1980). Consequently, behavioral traits are also likely affected in the semelparous sex, potentially leading to sex differences in POLS when the breeding schedules of the sexes differ.

### Resource availability and condition-dependent selection

Phenotypic plasticity in response to environmental conditions, such as early-life resource availability, weather, cues of predation risk, or intraspecific competition (e.g., Lindström 1999) can determine individual pace of life and personality (e.g., Liedtke et al. 2015; Krause et al. 2017). Environment, in interaction with the individual genotype and parental effects, thus produces the range of life-history strategies of individuals. For example, growth and development, reproductive investment, and survival can all be constrained by energy availability. Such constraints have the potential to influence the sexes differently due to their differing resource requirements and environmental sensitivities (e.g., body growth in sexually dimorphic species; Hamel et al. 2016). The sex-specific effects of environment on life history and other POLS traits is an extremely complex topic and we cannot tackle it here in detail; we merely point out that resource availability and associated selective mortality or reproductive success can drive sex-specific, condition-dependent selection, which in turn influences POLS outcomes. The basic prediction is that the sex with higher resource requirements suffers more from resource limitations and is more susceptible to condition selection as fewer individuals breed successfully. Environmentally-determined, alternative life-history strategies may also be observed, increasing the variance for one of the sexes.

Condition dependence is expected to lead to stronger net selection (e.g., Lorch et al. 2003; Bonduriansky 2006) in the more variable sex, which could result in a stronger selection for a syndrome if certain physiological and

behavioral traits in combination with a specific life-history strategy increase fitness. Condition dependence should be especially relevant in mating systems where the reproductive success or survival of one sex is more strongly linked to their (genetic) condition or quality. Typically, when male potential reproductive rate exceeds female rate, males tend to be more susceptible to condition-dependent selection due to the higher extrinsic costs incurred by males through searching or competing for mates. Under condition selection, correlations among life-history traits can diminish or become reversed, if individuals of higher “quality” can afford to invest in both reproduction and survival (Stearns 1992; Cam et al. 2002) with potential effects on covariances with other POLS traits. For example, selection on condition can increase life span and somatic maintenance in males despite their faster potential reproductive rate relative to females (Williams and Day 2003; Bonduriansky et al. 2008; Chen and Maklakov 2014; Hämäläinen et al. 2014).

## Part 2: predictive framework for the evolution of sex-specific POLS

The patterns of sexual dimorphism in POLS are thus expected to result from interactions of a range of intrinsic and extrinsic conditions and their relative effects on each sex (Fig. 2). As a result, the sexes may express identical or completely different pace-of-life optima and POLS covariance structures. We propose a general framework to encompass the effects of multiple selective forces on sex-specific POLS. As evidence for these outcomes is presently scarce, this framework is conceptual rather than a review of the evidence, with some predictions more deeply rooted in existing literature than others.

To meaningfully assess POLS evolution, it is useful to select traits that are relevant for the life-history strategy (e.g., rate of reproduction), and physiological/behavioral traits that are relatively consistent over the lifetime (e.g., personality; physiological coping style). If POLS is adaptive, traits most likely to covary are those relevant to fitness in each sex. Thus, sex differences in POLS are especially expected where the fitness of the sexes is optimized via different traits or strategies. Life-history traits associated with pace of life reflect trade-offs between current and future reproduction, and behavioral traits most likely to covary genetically with life history may be related to risk taking and lie on the proactivity-reactivity axis (Stamps 2007; Smith and Blumstein 2008; Schuett et al. 2015; Santostefano et al. 2017). Notably, sex-specific selection can act on average trait expression as well as (co)variances of specific traits (Killen et al. 2013), and a trait may be under stronger selection in one sex if it confers an advantage also in a breeding context (Biro and Stamps 2008, e.g., aggressiveness, Seebacher and Wilson 2006). As a result,

we would expect sexual dimorphism in the strength of the association between such traits and life history. The exact traits and their measurement are necessarily specific to the species (see also similar discussion in Stamps 2007), and ecological and genetic knowledge of the study species is required to predict which traits are likely to coevolve. For a meaningful comparison of the sexes, the selected traits must be homologous for males and females.

As a note on terminology, we generally refer to associations between traits as *covariances*, which is the relevant measure of association for many analytic approaches. Although covariance is often used interchangeably with *correlation* (standardized covariance) in the literature, it is worth noting that covariances are sensitive to the scale and variance in trait values, whereas correlations are not. This distinction may be relevant when sex differences in trait *variance* contribute to the predicted POLS structure, because sex-specific covariances among traits then differ even if the correlations are similar for the sexes.

The following broad scenarios (Fig. 3; Table 1) may evolve, generated by combinations of parallel or opposing trait covariance patterns between and within the sexes:

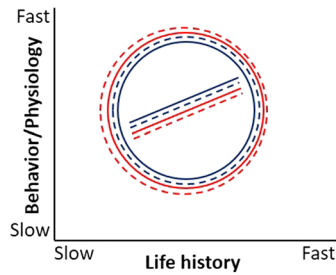
- (I) Males and females exhibit similar POLS trait covariances among individuals, i.e., a *uniform POLS* exists within a species or population (Fig. 3a, b). The within-sex, among-individual covariances are similar in both sexes, but the sexes may differ in their position along the pace-of-life continuum, showing sex-specific mean phenotypes (Fig. 3b).
- (II) POLS trait covariances are similar for the sexes (i.e., uniform POLS), but they differ in the *strength of covariation* among traits. Covariances may be weaker or absent in one sex, or positive associations among certain traits in one sex may be reversed in the other sex (Fig. 3c). If trait variances are sex-biased, correlation structures may or may not be sex-specific despite different covariances.
- (III) *Sex-specific POLS composition* exists, i.e., the specific traits that form a POLS differ between the sexes (Fig. 3d).
- (IV) Alternatively, no within-sex POLS may be present, i.e., expected covariation among traits is not found among individuals of either sex, although at population level, the sex differences in mean trait expression may produce an apparent POLS (Fig. 3e, f).

Below, we make predictions about the conditions where each of these broad scenarios may evolve, with examples from empirical data where available. The scenarios and the selective forces we predict to contribute to each POLS outcome are summarized in Table 1.

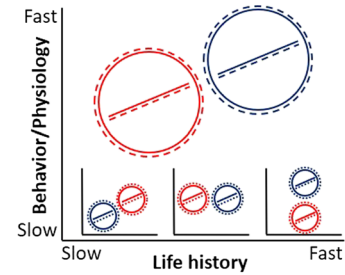
**Fig. 3 a–f** Alternative predictions for sex-specific patterns of covariance between the pace of life history (e.g., onset of reproduction, rate of reproduction, senescence, and lifespan) and physiological and behavioral traits (predicted continuum from “slow” to “fast” trait values; see Réale et al. (2010) for a partial list of traits). Red, sex A (typically females); blue, sex B (typically males); dashed line, physiological traits; solid line, behavioral traits. Circles represent trait means and hence illustrate differences in trait means between sexes. Lines indicate trait correlations among individuals within each sex. For simplicity, we show parallel lines for physiological and behavioral traits within sexes (except in inset 2, panel c). Note that the strength of these covariances may differ even when the sign of the association is the same, and a covariance of behavior and physiology cannot necessarily be inferred from their independent relationships with life history

#### I. Uniform POLS structure

**a** Uniform POLS structure with no sex-specific selection

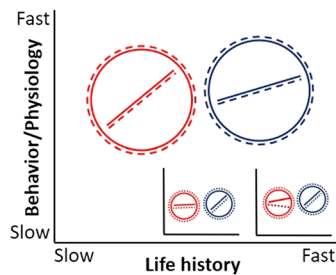


**b** Uniform POLS structure, sex-specific pace-of-life optima



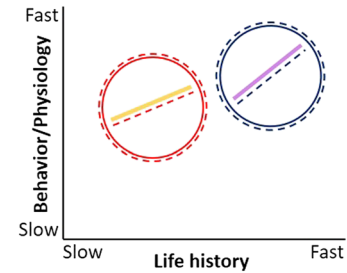
#### II. Sex-specific POLS structure with different strength trait correlations

**c** Sex-specific strength of correlations among the same POLS traits



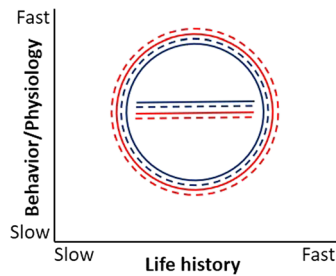
#### III. Distinct POLS structure in each sex

**d** Sex-specific combination of trait covariances forming POLS

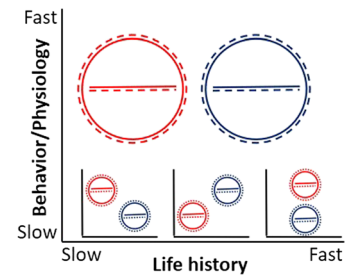


#### IV. No POLS

**e** No trait covariance, no sex differences in POLS-traits



**f** No trait covariance, sex differences in POLS-trait optima



### Uniform POLS covariance structure

#### Similar pace-of-life optima (Fig. 3a)

In this first scenario, pace of life and within-sex trait covariances among individuals are similar for males and females. This outcome would be expected when sexual conflict is either (1) completely unresolved, so that high genetic correlations between the sexes prevents the evolution of dimorphism (see also Immonen et al. 2018, topical collection on Pace-of-life syndromes) or (2) absent, because the life-history strategies of the sexes converge. In the latter case, this outcome would be expected when both sexes have a similar reproductive span,

potential rate of reproduction, and/or energetic demands of breeding. Such conditions may be fulfilled for example in mutually semelparous species, in systems without any parental care, under strict monogamy with biparental care, or in socially monogamous species with a high degree of extra-pair mating and thus a reduced skew in male reproductive success (Schlicht and Kempenaers 2013). A uniform POLS with no sex difference in pace of life has been found in mealworm beetles, *Tenebrio molitor*, in which individuals with a high metabolic rate and reduced antipredator behavior suffer high predation mortality, with no sex difference in metabolic rate, behavior, or predation risk, or in the correlations among these traits (Krams et al. 2013a, b; but see *Sex-specific POLS structure with*

**Table 1** Hypothetical conditions under which different selective pressures are predicted to lead to given sex-specific POLS outcomes. Note that multiple plausible alternative predictions are provided, as similar sex-specific POLS outcomes may result from combinations of different selective forces; not all characteristics of breeding system, sexual conflict, and anisogamy listed for a given POLS outcome are necessarily expected to be met in any given system. "Schedule" refers to reproductive lifespan or breeding schedule, ranging from semelparity to prolonged iteroparity

Selective pressures predicted to contribute to POLS outcomes		POLS outcome	
Breeding system characteristics	Sexual conflict	Anisogamy	
<b>I) Uniform POLS structure in both sexes</b>			
<ul style="list-style-type: none"> <li>• Breeding system: monogamy/cooperative breeding (polygamous/promiscuous)</li> <li>• Parental care: equal biparental care/no parental care by either sex</li> <li>• Schedule: similar reproductive span, or semelparity in both sexes;</li> <li>• Fitness optimizing: similar traits and trait optima determine fitness for both sexes (e.g., mutual or "random" mate choice; low within-sex competition due to low reproductive skew)</li> <li>• Breeding system: polygamous/polygynous/promiscuous ("classic" reproductive roles)</li> <li>• Parental care: female-biased</li> <li>• Schedule: iteroparity in both sexes, or male-biased semelparity</li> </ul>	<ul style="list-style-type: none"> <li>• Similar potential reproductive rates, negligible conflict over rate of reproduction</li> <li>• Possible unresolved conflict</li> <li>• When genetic correlations between sexes are strong, strong correlational response in the sex under indirect selection</li> <li>• Natural selection stronger than sexual selection</li> <li>• Higher potential reproductive rate in males; high conflict over rate of reproduction and parental care</li> <li>• Possible unresolved sexual conflict</li> <li>• Sexual selection (primarily in males) equals or exceeds natural selection</li> <li>• Higher reproductive rate in females</li> <li>• Sexual conflict over parental investment</li> <li>• Sexual selection (primarily in females) equals or exceeds natural selection</li> </ul>	<ul style="list-style-type: none"> <li>• Predictions based on anisogamy (Fig. 2) may not apply (overridden by other selective pressures)</li> <li>• Fig. 3a</li> <li>• Uniform syndrome</li> <li>• No sex-specific selection</li> <li>• Similar pace-of-life and POLS trait optima</li> </ul>	
<ul style="list-style-type: none"> <li>• Breeding system: polyandry ("reversed" reproductive roles). Possible male mate choice due to female-biased operational sex ratio</li> <li>• Parental care: male-biased</li> <li>• Schedule: iteroparity in both sexes, or female-biased semelparity</li> </ul>		<ul style="list-style-type: none"> <li>• Reversal of anisogamy predictions due to other, strong selective pressures</li> <li>• Fig. 3b (inset 1)</li> <li>• Uniform syndrome</li> <li>• Sex-specific POL optima ("fast-paced" females)</li> </ul>	
<b>II) Sex-specific POLS structure with different strength of trait covariances</b>			
<ul style="list-style-type: none"> <li>• Breeding system: polygamous/promiscuous; alternative breeding strategies with associated distinct phenotypes in one sex and fixed strategy in other sex; different traits confer fitness in each sex</li> <li>• Parental care: uniparental, or different roles of parents in offspring care</li> <li>• Schedule: sex-biased reproductive span or semelparity</li> <li>• Breeding system: polygamous/promiscuous;</li> <li>• Condition- or age-dependent success in either sex alters/reverses predicted covariance of life history with behavioral or physiological traits in the sex under condition selection</li> <li>• Schedule: variable, excluding semelparity in condition-selected sex</li> </ul>	<ul style="list-style-type: none"> <li>• Strong conflict/conflict resolved via stable sexual dimorphism</li> <li>• Strong selection in one sex leads to indirect evolutionary response in the other sex (dependent on strength of genetic correlations)</li> <li>• Sexual selection stronger than natural selection</li> <li>• As above, or</li> <li>• convergent selection in both sexes on some traits, opposing selection on other traits due to sex-specific genetic architecture or condition selection</li> </ul>	<ul style="list-style-type: none"> <li>• Predictions typically align with those of anisogamy</li> <li>• Fig. 3c</li> <li>• Sex-specific POLS with different correlation strength</li> <li>• Sex-specific POL optima</li> </ul>	<ul style="list-style-type: none"> <li>• Fig. 3c (inset 2)</li> <li>• Sex-specific POLS with opposite sign correlations in the sexes</li> <li>• Similar or sex-specific POL optima</li> </ul>



**Table 1** (continued)

Selective pressures predicted to contribute to POLS outcomes		POLS outcome	
Breeding system characteristics	Sexual conflict	Anisogamy	
III) Sex-specific POLS composition (different trait associations) <ul style="list-style-type: none"> <li>• Breeding system: any system with highly divergent strategies between the sexes (polygamous / promiscuous)</li> <li>• Two or more alternative strategies in one sex, single strategy in other</li> <li>• Parental care: uniparental, or different roles of parents in offspring care</li> <li>• Sex-biased reproductive span or semelparity</li> </ul>	<ul style="list-style-type: none"> <li>• Unresolved sexual conflict over reproductive rate; different ways for sexes to optimize fitness</li> <li>• Strong conflict over reproductive rate and/or sex-biased traits associated with breeding</li> <li>• Strength of genetic correlations affects how much sexes can diverge</li> </ul>	Predictions typically align with those of anisogamy	<ul style="list-style-type: none"> <li>• Fig. 3d</li> <li>• Sex-specific POLS with different trait constellations forming syndromes in each sex</li> <li>• Similar or sex-specific POL optima</li> </ul>
IV) No within-sex POLS <ul style="list-style-type: none"> <li>• Highly flexible; no single superior strategy in either sex</li> </ul>	<ul style="list-style-type: none"> <li>• Strong unresolved conflict over reproductive rate and optimal syndrome structures</li> <li>• Sex-specific pleiotropy</li> </ul>	Predictions typically align with those of anisogamy	<ul style="list-style-type: none"> <li>• Fig. 3e, f</li> <li>• No syndrome</li> <li>• Similar or sex-specific POL optima</li> </ul>

different strength of trait covariances below for contrasting findings in the same species). The species has a promiscuous mating system with potential for high sexual conflict, but conflict may be attenuated by semelparity with a similar reproductive window in both sexes and the absence of offspring care.

### Sex-specific pace-of-life optima (Fig. 3b)

It may be more common that the sexes differ in their optimal pace of life (i.e., a “population-level” or between-sex POLS, Fig. 1b–d) but exhibit a similar within-sex covariance between life history and personality/physiology traits (Fig. 1b, c; Fig. 3b). Whether POLS is uniform across the sexes depends on the traits required for acquiring fitness, such as a sex-specific threshold size for breeding (Bonnet 2011) or uniparental care. Sex-specific selection through promiscuous mating and offspring care provided solely by females likely contribute to this outcome in yabbies, *Cherax destructor*, in which a positive correlation between growth rate and boldness in both sexes suggests a uniform POLS, with “fast” males expressing both faster growth and higher boldness than females (Biro et al. 2014). Sex differences in potential reproductive rate or mating skew within a single short breeding season may also lead to sex-specific syndromes (Cook et al. 2011).

### Sex-specific POLS structure with different strength of trait covariances (Fig. 3c)

In the most complex of the potential sex-specific POLS outcomes, sexually dimorphic trait covariance patterns are expected to result from a range of different selective forces in interaction with the species’ ecology. Divergence in POLS between the sexes depends on the strength and direction of selection as well as the genetic architecture of correlated traits between the sexes (Immonen et al. 2018, topical collection on Pace-of-life syndromes). If strong trait associations are selectively favored only in one sex, weaker associations in the same direction in the other may arise due to genetic correlation between the sexes when the focal trait association is selectively neutral or even selected against in the other sex (e.g., Berger et al. 2014; De Lisle and Rowe 2015). One sex may also experience a stronger net (correlational) selection if, in addition to natural selection on the trait in both sexes, there is additional sexual selection acting on these traits in one sex (Biro and Stamps 2008). Trait covariance might then only be observed in a single sex, with a weak, absent, or reversed POLS in the other sex.

Such sex-specific POLS structures might be particularly expected if secondary sexual traits are expressed in an age-dependent manner in one sex or if one sex experiences stronger condition-dependent selection (see section “Resource availability and condition-dependent selection”). De Lisle and Rowe (2015) suggest that condition-dependent selection

in male salamanders may shift trait evolution in females in the same direction, potentially reducing the degree of sexual dimorphism. They describe a sex-biased trait covariance strength in *Notophthalmus viridescens* salamanders, with a strong negative relationship between a sexually selected trait and parasite load in males, and a substantially weaker association in females. This finding of different strength covariances may also be suggestive of sex-specific combined effects of sexual and natural selection. A greater *variance* in pace-of-life might also result in the sex whose fitness is more dependent on condition, as low-condition individuals are expected to invest more in early and/or terminal reproduction through higher risk taking, whereas a better condition may facilitate a slower pace-of-life (Wolf et al. 2007). Similarly, we might expect stronger trait covariances (although not necessarily correlations) in the sex that exhibits alternative reproductive strategies. In line with this prediction, males but not females seem to exhibit POLS in largemouth bass, *Micropterus salmoides*, with alternative male breeding strategies (Ballew et al. 2017; but see pink salmon, *Oncorhynchus gorbuscha* Cook et al. 2011).

Offspring care is a prime candidate for generating sex-specific syndromes because of the complex and frequently sex-specific behavior, physiology, and energy investment involved (see section “[Parental care and reproductive behavior](#)”). Correlated expressions of parental behaviors and other POLS traits (e.g., personality, Royle et al. 2010) would be expected particularly in the sex that is less “choosy” in terms of mate choice. This bias may only apply when parental care is provided by both sexes, or in the rare event that care is solely provided by the less-choosy sex. In fact, in several fish species with sex-biased parental care, POLS seemed to be only expressed in the caring sex: in species with male-biased offspring care, only males appear to exhibit POLS (Kim and Velando 2016; Ballew et al. 2017), whereas in the pink salmon, *O. gorbuscha*, with offspring care provided exclusively by females, POLS was found only in females (Cook et al. 2011).

In a special case of sex-specific POLS structure with different strength of trait covariances, the sign of the trait covariances may differ between the sexes when the genetic architecture permits complete divergence in the sexes. This situation may arise when strong sexually-antagonistic selection operates directly on a given trait, while other selective pressures converge for the sexes. Perhaps reflecting such a scenario, different covariances have been suggested to result from limited breeding opportunities in both sexes (short breeding window) in combination with different immune strategies of the sexes in mealworm beetles, *T. molitor* (Monceau et al. 2017). In contrast to studies on the species described above (*uniform POLS structure, similar pace-of-life optima*) on a different set of traits, Monceau et al. (2017) observed POLS in both sexes, but the direction and strength of these correlations were sex-specific. Immune status, proactive personality,

and reproductive output were positively correlated in females, the shorter-lived sex. In contrast, immune status correlated negatively with proactivity in males, with no correlation with reproductive output.

Finally, sex-biased strength of POLS trait covariance might arise where a life history tactic causes strong selection in one sex, while there is no selective advantage in the other sex, in which the covariance is a result of correlational evolutionary response to selection in the other sex. This type of selection bias may occur under sex-specific semelparity associated with self-sacrifice. The semelparous sex is expected to experience stronger selective pressures on traits such as growth rate, hormonal state, and behaviors such as foraging and mate-searching activity, as well as their covariance where genetic integration or hormonal pleiotropy facilitate this. To our knowledge, no species with such life histories have been studied in the POLS context; thus, this possibility remains to be tested.

### Sex-specific POLS composition (Fig. 3d)

In the most extreme case, the sexes may express completely distinct POLS, with a different set of traits covarying and thus forming the syndrome in each sex. The within-sex covariances of a set of traits would thus differ, while the trait means for the sexes may be similar or differ for the sexes. Note that the scenario where POLS is found in only one sex (detailed in section “[Sex-specific POLS structure with different strength of trait covariances](#)” above) can be analogous to the present scenario when the traits selected for study are irrelevant for one of the sexes. An absence of covariation among a set of traits relevant for male fitness does not necessarily mean that no syndrome is present in females, rather, the set of traits that covary in females may differ substantially from those found to covary in males if different traits or covariance structures determine female fitness. For both cases, the genetic architecture of the relevant traits must allow the sexes to independently respond to selection.

This scenario is most likely to occur in species with very different reproductive roles of the sexes, for instance, in species with polygamous breeding, uniparental care, sex-specific roles during offspring care, and/or sex-biased reproductive lifespan. Although there is currently little empirical evidence for this scenario, studies conducted in other contexts suggest potential for its prevalence (e.g., morphological traits: Jensen et al. 2008). Sex-specific POLS structures could emerge if the traits that advance fitness differ dramatically for the sexes. Hypothetically, for example, reproductive rate, aggression and metabolic rate might form a syndrome in one sex, but reproductive rate, sociability and stress responsiveness in the other sex. Where the sexes achieve reproductive success through different behaviors, a given syndrome

composition would only be found in a single sex. Future work should strive to differentiate between POLS trait covariances in a single sex (see “[Sex-specific POLS structure with different strength of trait covariances](#)”) with POLS composed of different traits in each sex.

In addition to condition-dependent selection operating on reproductive performance, sex-biased condition-dependent mortality is also expected to lead to sexually dimorphic POLS, and different traits may form the syndrome in each sex. Hypothetically, a “slow” life history may be paired with behaviors and physiology more typically associated with a faster pace-of-life in the sex under strong selection, although the realized outcomes will depend on the genetic organization of trait covariances. Different traits can also covary in each sex when the expression of a given mutually beneficial behavior is under different hormonal control in the sexes, or the same hormone affects behavior in a sex-specific way (see Immonen et al. (2018, topical collection on Pace-of-life syndromes) for mechanisms). For example, in some polygynous birds, aggressiveness covaries with a physiological and a life-history component in each sex, but the exact physiological elements involved differ for the sexes (Veiga et al. 2001; Wingfield et al. 2001; Pärn et al. 2008), generating sexually dimorphic syndromes.

### No within-sex POLS (Fig. 3e, f)

To complete the predictive framework, it is necessary to consider a scenario where no trait covariances would be observed in either sex. Where specific trait covariances yield no fitness benefit in either sex, no consistent within-sex covariances of life history with behavior and physiology should be predicted. However, an absence of a trait covariance may also result from a genetic constraint or a stochastic environment. A strong intra-locus sexual conflict could, at least hypothetically, constrain a within-sex POLS in both sexes, if antagonistic selection operates on the sign of trait associations. If the net strength of selection on the sexes is equal, trait covariation may not be found in either sex despite selection favoring POLS in both. Alternatively, POLS may be absent under stochastically varying social or physical environment that favors a range of different breeding styles and reproductive roles in both sexes. The benefits of a certain phenotype may diminish as a result, possibly decoupling behavioral style from life history. Deterioration of POLS or an alternative POLS trait composition (see above) would then be expected. In an example suggesting this outcome, no evidence of covariance between behavior and life history was found in either sex of two damselfly species studied by Debecker et al. (2016), although the males exhibited a faster life history. However, the evidence is insufficient to propose mechanisms for this result.

## Part 3: the promise and challenges of studying sex-specific POLS

The POLS hypothesis presents a useful framework for an in-depth understanding of the evolution of trait covariances and alternative life histories by promoting the integration of many biological disciplines. We have highlighted a key role for sex-specific selective pressures in predicting and interpreting POLS patterns, and concluded that sex differences are expected under a broad range of conditions. The predictive framework we have proposed generates opportunities for testing broad hypotheses of sex-specific POLS, which should focus on determining the life-history strategies and covarying behaviors that provide the highest fitness in each sex across study systems. However, there are a number of important considerations for study design, choice of study system, and POLS traits measured, to reach relevant and unambiguous conclusions about the evolution of POLS.

1. Ignoring sex differences in trait optima and sex-specific trait covariances will impede the study of POLS. If potential sex differences are not considered, it is possible that either POLS is not detected at population level due to sex-specific POLS or an apparent POLS is observed across sexes at the population level because of sex-specific trait optima, even in the absence of among-individual trait covariances (Fig. 1).

To avoid this fallacy, one should (a) study both sexes in parallel whenever possible; (b) carefully measure homologous traits relevant to fitness in each sex; (c) make predictions about the likeliest sex-specific POLS outcomes (Table 1) based on the most relevant selective forces operating on both sexes in the species, and genetic architecture when such information is available; and (d) assess syndrome structure as well as trait means in each sex. Investigations of POLS in a single sex should consider the possibility that any observed POLS in one sex may be affected by an evolutionary tug-of-war between the sexes, and trait covariances may be a product of neutral correlational selection and a shared genetic architecture. Needless to say, conclusions on POLS in one sex cannot be assumed to apply to the other. An examination of cross-sex genetic correlations can be used to reveal sex-specific genetic architecture of POLS traits. A cross-sex genetic correlation  $< 1$  suggests sex-specific genetic covariances (e.g., Han and Dingemanse 2017).

2. Addressing the underlying genetic mechanisms of POLS, by using both molecular and quantitative genetic tools is needed, as phenotypic trait covariances may not accurately reflect the genetic covariances (Hadfield et al. 2007; Santostefano et al. 2017; Immonen et al. 2018, topical collection on Pace-of-life syndromes). This may help reconcile contrasting findings on POLS trait covariances

within species and sexes. These may be largely due to the use of phenotypic traits (often under uncontrolled environmental conditions) without knowledge of the underlying genetic correlations. Other explanations include potentially different syndromes that evolve within each sex, in combination with constraints to the covariances due to sexually antagonistic trait selection, and the choice of traits tested. In the best example to date, two studies on the mealworm beetle revealed either seemingly identical POLS for the sexes (Krams et al. 2013a, b) or a distinct POLS in each sex (Monceau et al. 2017) by examining different traits, epitomizing the potential complexity of sex-specific POLS at the phenotypic level within a single species.

3. Experimental studies are needed to complement observational studies. Insights into the prevalence of different strategies could be gained through the creation and testing of artificial selection lines for POLS, personality, and/or breeding system, or by utilizing experimental evolution to test how life-history strategies may coevolve with personality. The aim should be to understand how correlated traits respond to indirect selection and how sex-specific correlational selection operates on POLS. Testing the fitness effects of different strategies in the sexes in such studies will allow assessment of the evolutionary mechanisms, including an understanding of which traits or covariances selection preferentially operates on.
4. Meta-analyses of trait (co)variances across environmental gradients or mating systems (see Tarka et al. 2018, topical collection on Pace-of-life syndromes; Smith and Blumstein 2008) or simulation approaches may provide clues to the evolutionary origins of certain trait associations. An alternative approach to testing broader predictions on reproductive roles is to compare POLS traits and covariance structures among different populations of the same species, or related species with different breeding systems. The first comparative study on four related *Ischnura* damselflies discovered species-specific variation in sex-specific POLS structures, ranging from no trait covariation in either sex to negative relationships in both sexes on a subset of life-history and behavioral traits, and sex-specific trait associations with a positive covariance in females and no covariance in males in yet another species (Debecker et al. 2016).
5. It is important to consider the possibility that strong selection operating on a third, unmeasured trait that is associated with the traits that are being measured, will generate apparent covariation. For example, POLS traits often correlate with morphological traits such as body size, which is frequently sexually dimorphic, and has previously been considered a component in the fast-slow life-history continuum and should be controlled for when testing sex-specific POLS (Reynolds 2003; Immonen et al. 2018, topical collection on Pace-of-life syndromes).

A focus on sex-specific POLS patterns can clarify (1) the potential for sex-specific selection to accelerate or prevent the formation of POLS at the species/population level and (2) the significance of different selective pressures in producing differences in mean trait values and correlation structures between the sexes. Examining whether within-sex covariances are in the same or opposite direction as the population- and species-level covariances can illuminate the influence of sexual conflict on POLS evolution. A population- or species-level POLS might be strengthened, or more likely to evolve, if the within-sex covariance patterns of both sexes align with among-sex covariances in the same traits. The outcomes are vital for understanding the consequences of syndromes for the evolution of sex-specific life histories and constraints in the expression of individual traits.

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## Compliance with ethical standards

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

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