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## Pace-of-Life Syndrome (POLS)

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### Synonyms

Behavioral traits; Ecology; Life istory traits; Physiology; Sex differences

### Definition

POLS predicts that life history traits, physiological, and behavioral characteristics covariate and form a syndrome that distinguishes species, populations, and individuals on the "fast-slow" continuum.

### The Basic Tenets of Pace-of-Life Syndrome (POLS)

Evolutionary social scientists are relatively well acquainted with the core assumptions of life history theory: due to evolutionary trade-offs (i.e., growth-fertility, quantity-quality, fertility-mortality, mating-parenting, early or delayed reproduction), species and individuals cannot straightforwardly maximize fitness (Pianka, 1970). The allocation of resources to specific fitness components is performed at the expense of other fitness components. Hence, life history trajectories emerge: investment in earlier pubertal timing and reproduction, followed by higher offspring quantity, is associated with diminished parental investment and longevity – this is labeled as "fast" life history dynamics. The opposite pattern (delayed reproduction, lower number of offspring, with higher parental care and longevity) is considered "slow" life history. The pace-of-life hypothesis (POL) is deeply rooted in life history but extends this framework in two important ways: it includes physiology and behavioral traits into evolutionary-ecological dynamics (Ricklefs & Wikelski, 2002). Simply put, physiological and behavioral processes mediate evolutionary trade-offs: this nexus generates associations between life history outcomes, physiology, and behavior and leads to pace-of-life syndrome (POLS). Similarly to the life history framework, POLS aimed to explain interspecies and interpopulation differences at first, but the most recent advances include interindividual differences in the POLS framework (Réale et al., 2010). It is also important to mention that the POLS perspective involves an additional level of biological organization: intraindividual variation. Evolutionary ecologists frequently emphasize that the majority of POLS traits should be measured repeatedly in time because behavioral and physiological traits show considerable intraindividual variation. This stands even for life history traits in animals (but perhaps not so much in humans); for


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example, reproduction is a seasonal outcome for many animal species. Therefore, it is important to measure the clutch size per reproductive event and calculate variation in fecundity besides the main or total number of offspring. Hence, POLS is so far the broadest evolutionary ecological framework that links life history, physiology, and behavior into a single framework, aiming to examine its dynamics and explain variation and covariation in these three sets of traits that are commonly observed in humans and other animals.

How may POLS may look like? In accordance with the parsimony principle, POLS is also based on the fast-slow continuum, similarly as in the life history framework. A faster pace of life may include (Réale et al., 2010) lower longevity and higher reproductive success (life history), higher aggressiveness, boldness, activity, exploration, impulsiveness (behavioral traits), higher metabolism, and lower immune response and HPA axis reactivity (physiology). Components of POLS are still explored and additional traits may be included in the syndrome. For example, it has been suggested that thermal physiology may be intertwined in POLS: animals with high thermal traits should exhibit a faster pace of life (Goulet et al., 2018). Considering the behavioral level, the basic POLS assumptions included animal personality traits; however, other traits can participate in POLS as well. For example, cognitive abilities are presumed to be involved in POLS due to speed–accuracy trade-off (Sih & Del Giudice, 2012). A faster pace of life is thought to be characteristic of animals that sample information faster but, at the same time, make more errors. Social behavior is involved as well: the longest-living animals may have higher fitness benefits in forming stable and differentiated social relationships and consequently generating a more complex social hierarchy (Silk & Hodgson, 2021).

## Empirical Support and Further Conceptual Extensions

Empirical support for POLS is equivocal. There are studies that have found the associations predicted by the syndrome, but there are also findings describing null associations or even the links with the opposite sign than was predicted (Montiglio et al., 2018). Meta-analytic results showed little empirical evidence in line with POLS but with many moderators that affected the size and sign of correlations (Royauté et al., 2018). Some of the major findings include: (1) stronger evidence in concordance with POLS in invertebrates compared to vertebrates; (2) phenotypic correlations are more in line with POLS, but genetic correlations even have opposite signs than the ones predicted by POLS; (3) correlations with different magnitude and sign in males and females; and (4) different associations between the three major POLS constituents – life history, physiology, and behavior (stronger associations between life history and behavior than between behavior and physiology).

If there is little unequivocal evidence for POLS, does that mean that there is something fundamentally wrong with the POLS hypothesis? Many scholars (e.g., Montiglio et al., 2018) believe that it is premature to conclude this; the core POLS assumption (fast-slow continuum) is probably too simplistic and it needs to be broadened to include more conditions that can moderate the emergence of POLS, the sign and strength of its associations. The specific organism under study is probably a large source of variation for the POLS nexus: different species differently develop their life history trajectories as a response to ecological conditions and have distinct associations between physiology and behavior. For example, endotherm vertebrates (compared to ectotherm) may differently respond to ambient temperature in their life history outcomes; furthermore, the lack of internal thermoregulation can have a higher effect on the magnitude of the physiology-behavior association in these organisms (Hämäläinen et al., 2021). POLS theory and research usually highlights the role of resource allocation in mediating the trade-off of first reproduction. Therefore, the role of resource acquisition may be neglected: organisms in good condition (or state, e.g., energy reserves) may have higher success in resource acquisition but without elevated mortality rates (Laskowski et al., 2021). In these organisms, some expected

links between behavior and life history may be absent; this example suggests that resource acquisition should be more thoroughly integrated in POLS both on a conceptual and empirical level. Many POLS studies do not explicitly include environmental characteristics into the examination of the syndrome. However, local ecology may be crucial in the POLS nexus: for example, if the environment is not abundant with predators, bold, aggressive, and explorative individuals will not experience higher mortality since the risk of predation is low (Hämäläinen et al., 2021). Therefore, the findings showing that POLS may be completely environmentally generated are not surprising (Niemelä et al., 2013). As suggested by meta-analysis, sex may highly influence the syndrome. Sexual selection pressures affect some of the major trade-off components like mating behavior, age of first reproduction, and maternal care differently (Hämäläinen et al., 2018). This may generate different associations between POLS components in males and females and the failure to explicitly analyze sex as the condition for POLS may generate invalid results for the study population. Finally, it is also noted that the formal models of POLS are largely missing – constructing and running formal models would provide an invaluable research guide for empiricists and provide new venues for POLS especially by pointing out the differences in the nexus associations on the different levels of biological organization (Mathot & Frankenhuis, 2018).

## POLS in Humans

Research in humans that explicitly uses the POLS framework is very rare (nevertheless, note that a lot of research using broad life history assumptions is conducted in evolutionary social sciences). One example may be the research between personality and physiology in humans that found negative associations between resting metabolic rate and trait Extraversion (Bergeron et al., 2021). However, life history is not measured in this study: due to its clear evolutionary origins, we are not sure if research that does not include life history can be considered as validly assessing POLS. The only study we found that covers all aspects of POLS was conducted on German adolescents (Lehmann et al., 2018). The findings showed that individuals with early maturation (measured by menarche in girls and voice break in boys) had elevated some forms of risky behavior and higher blood pressure. In fact, some associations were sex-specific: for example, the associations between physiology and life history had a lower magnitude in girls, while the links between behavior and life history were weaker in boys. In sum, this study clearly shows the applicability and benefits of examining POLS in humans and provides strong incentive for future research.

## Implications of POLS for Human Research

There are several very important implications of the POLS framework for human evolutionary sciences. First, there is the question of terminology. Evolutionary psychologists sometimes label behavioral traits as life history traits (e.g., Figueredo et al., 2004). However, life history traits are precisely defined in evolutionary biology: growth rates, pubertal timing, age of first reproduction, number of offspring, longevity, and others. Therefore, behavioral traits cannot be considered life history but POLS traits: behavioral patterns associated with life history. These distinctions are not trivial because terminological confusion can facilitate conceptual ant theoretical fallacies, which can impede knowledge. Another example comes from the problem of translation of animal behavior into human behavior: risk-taking behavior was measured by unhealthy behavior in the previously described study on POLS in humans; however, this behavior is largely different than the risk-taking behavior measured in animals. This example warns us that the measures assessed in animals should be translated for human research in order to formulate a hypotheses based on the POLS framework in animals (Međedović, 2018). Only this way can we nurture a comparative approach, which represents one of the strongest features of POLS in understanding

evolutionary roots in variation and covariation between POLS components in humans.

Second, there are methodological issues. Psychometrical measures of life history are frequently used to map individuals on the fast-slow continuum in human research (Figueredo et al., 2014). However, these measures have only sporadic, low in magnitude, and sometimes associations with opposite signs with demographic life history indicators (Međedović, 2020). The POLS framework highlights that the trade-off related to first reproduction is crucial for assessing whether individuals, populations, or species have a faster or slower pace of life. Beside this indicator, the research found that reproductive success is probably the best measure that could be used for mapping the fast-slow dimension (Araya-Ajoy et al., 2018). Therefore, research in humans should measure life history directly, using the established biological events, preferably number of offspring and age of first reproduction.

Third, POLS can open new avenues of research for human studies. For example, evolutionary social scientists frequently explore the associations between harsh and sometimes unpredictable environments and life history indicators. However, some researchers suggest that we should not only measure the associations between ecological characteristics and POLS but also examine whether the strength and the sign of associations are different in different environments (Hämäläinen et al., 2021). For example, POLS may emerge only in certain environments (e.g., harsh environmental conditions) but not in others. Similarly, POLS can be qualitatively different in males and females (Hämäläinen et al., 2018). Hence, environment and sex may be moderators of POLS: the syndrome can be examined separately in different environments and sexes.

Finally, having in mind the importance of studied biological systems in POLS, it is quite probable that the syndrome would need additional conceptual clarifications in humans. For example, according to POLS assumptions, sociability belongs to a slow pace of life while activity is characteristic of a fast pace of life (Réale et al., 2010). However, these two personality characteristics belong to the same higher order personality trait – Extraversion. Hence, this specific assumption does not hold up in humans. We may look into another more theoretically implicative example: some of the basic life history trade-offs like fertility–longevity or quantity–quality may be very weak or even nonexistent, at least in certain human populations. This is partly a consequence of the peculiar environment contemporary humans live in: ecologies where medical care has significantly elevated longevity and where contraception and other reproductive technologies have partly led to low and even beyond-replacement fertility rates. Therefore, we must start from the very beginning and ask ourselves what POLS in humans is in the first place? In answering this exciting question, we should pay close attention to the direct measurement of demographic life history outcomes and specific ecological (physical, social, and cultural) conditions of the population we study.

## Cross-References


- ▶ Immune Function
- ▶ Life History Strategy
- ▶ Personality/individual Differences


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