



## Pace of life and behaviour: rapid development is linked with increased activity and voracity in the wolf spider *Pardosa agrestis*



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Modern life history theory hypothesizes that pace of life is a strong predictor of life history traits. Recently, the notion that life history studies should integrate animal behaviour has emerged, because between-individual differences in behaviour are often coupled with fitness differences. So far, studies have mainly focused on interspecies or interpopulation perspectives, and research on the effects of life history differences on individual behaviour remain scarce. In the present study we aimed to contribute to the understanding of how pace of life is related to consistent individual behaviour. We investigated the relationship between developmental speed and consistent behaviour of the field wolf spider, *Pardosa agrestis*. In this species, individuals originating from the same clutch can typically follow either a slow or a rapid developmental pathway, characterized by a developmental time of about 10 or 3 months, respectively. We found that spiders, regardless of their developmental speed, behaved consistently in most of the tests. Our results also show that individuals developing rapidly were significantly more active during exploration and more successful in prey-catching tests than slowly developing spiders. Although rapidly developing spiders were bolder in one of the tests, this difference did not persist over the repeated measurements. Our work seems to support the notion that pace of life and animal personality are correlated, and pace of life might predict the behavioural types of individuals.

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In recent decades, studies of animal personality have shown that individuals are consistent in their behaviour across time, and in many cases behaviour in one context or situation may predict the behaviour in another (Bell & Stamps, 2004; Brodie III & Russell, 1999; Dingemanse & de Goede, 2004; Gyuris, Feró, & Barta, 2012; Gyuris, Feró, Tartally, & Barta, 2011; Johnson & Sih, 2007; Stamps & Groothuis, 2010; Verbeek, Drent, & Wiepkema, 1994). Interindividual differences in behaviour can result in a wide range of behavioural types in a population. Wolf, Doorn, Leimar, and Weissing (2007) were among the first to propose that this variation in behaviour can be the result of trade-offs between different life history traits (e.g. longevity versus fecundity), or the timing of key life history events (such as current versus future reproduction). Although the importance of the connection between life history and consistent behaviour is becoming more recognized (Biro, Post, & Abrahams, 2005; Biro & Stamps, 2008; Nakayama, Rapp, &

Arlinghaus, 2016; Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009; Wang, Kruger, & Wilke, 2009), it is still not entirely clear how these are related. For example, Clark (1994) and Wolf et al. (2007) suggested a negative feedback between future fitness expectations and risk-taking propensity, which might maintain behavioural differences in the short term, but leads to convergence of behavioural types in the long term (McElreath, Luttbeg, Fogarty, Brodin, & Sih, 2007). An alternative scenario has also been put forward, that the long-term persistence of different personalities and behavioural types could rather be maintained by a positive feedback between boldness/aggression and gaining more assets, causing 'good-quality' individuals to be more willing to take risks, making them more capable of coping with hazardous situations (Luttbeg & Sih, 2010; McElreath et al., 2007). The intrinsic potential of individuals to cope with environmental challenges such as parasite attacks has also been proposed to be a major factor in the occurrence and persistence of personalities that are stable within, while diverse between, individuals (Kortet, Hedrick, & Vainikka, 2010). Recent theories with special emphasis on the relevance of feedback loops between behaviour and state variables suggest that interindividual variation in consistent behaviour might result from state and condition dependence, leading to the

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emergence and persistence of behavioural syndromes, although a unifying theoretical framework still seems elusive (Dingemanse & Wolf, 2010; Sih, 2011; Wolf & Weissing, 2010). However, little is known about how interindividual variation in behaviour covaries with different life history traits.

A general theoretical framework for understanding the high degree of variation in life history traits is the pace-of-life syndrome (POLS) hypothesis (Ricklefs & Wikelski, 2002). This hypothesis defines a slow–fast life history continuum, and suggests that closely related species (or populations of a species) along this continuum should differ in a specific manner regarding a suite of physiological and life history characteristics, in accordance with their environment and evolutionary history. Tropical versus temperate birds are a well-known example of this phenomenon (McNamara, Barta, Wikelski, & Houston, 2008; Wiersma, Muñoz-García, Walker, & Williams, 2007). Tropical birds live at a relatively slower pace (e.g. reach maturity later, live longer and have lower resting metabolic rate) than their close relatives in the temperate regions. While many studies have looked at the variation in life histories between species and populations (e.g. Adelman, Bentley, Wingfield, Martin, & Hau, 2010; Cardillo, 2002; Martin, Hasselquist, & Wikelski, 2006; Sandercock, Martin, & Hannon, 2005; Von Merten & Siemers, 2012; Wikelski, Spinney, Schelsky, Scheuerlein, & Gwinner, 2003), our knowledge of the consequences of within-population variation in life history traits regarding the predictions of the POLS hypothesis is still limited (Koolhaas, 2008; Koolhaas et al., 1999; Sgoifo, Coe, Parmigiani, & Koolhaas, 2005; Sih & Bell, 2008). Nevertheless, some studies suggest that life history characteristics can correlate with animal behaviour and personality. For example, individuals with a relatively fast pace of life should show increased activity (as argued in Réale et al., 2010) and propensity to take risks, compared to individuals with slow life histories (Ackerman, Eadie, & Moore, 2006; Réale et al., 2009; but see Niemelä, Dingemanse, Alioravainen, Vainikka, & Kortet, 2013).

To investigate whether individual differences in pace of life are coupled with behavioural differences, we studied the field wolf spider, *Pardosa agrestis*. This semelparous spider species exhibits a unique phenology: while its close relatives (e.g. *Pardosa saxatilis* and *Pardosa minutus*, see Dondale, 1976; *Pardosa hortensis*, discussed in Kiss & Samu, 2002) have only one sexually mature cohort in each reproductive season, in *P. agrestis* populations, a facultative second generation might arise because of differences in the developmental speed of spiderlings hatching in early summer (Kiss & Samu, 2002, 2005; Samu et al., 1998). Some spiderlings become mature in the next spring or summer (i.e. after overwintering), while others (often from the same brood) reach adulthood and reproduce in about 3 months, in the same season they hatched. Hence, these latter, rapidly developing individuals represent a cohort with a considerably faster pace of life in the population. This case of cohort splitting is unique, because generally cohort splitting occurs when the offspring from early and late clutches follow different developmental pathways, which are strongly determined by environmental factors (e.g. seasonal or maternal effects). In *P. agrestis*, however, cohort splitting also occurs within and not only between clutches (Kiss & Samu, 2005).

Because of within-clutch cohort splitting, *P. agrestis* seems to be an ideal model organism to study the behavioural correlates of alternative life histories along the pace-of-life continuum within the same population. In our study, we assessed the consistency of individual behaviour of *P. agrestis* individuals and, following Réale et al. (2010), we tested the predictions of the POLS hypothesis regarding behaviour, namely that rapidly developing individuals should (1) be more active in a novel environment, (2) catch a potential prey more readily and (3) be bolder than those developing more slowly.

## METHODS

### Test Specimens

Two groups of specimens were reared under controlled laboratory conditions and tested in two separate test sessions. Specimens of both groups originated from cocoon-carrying female spiders collected in early summer of 2014 (first group) and 2015 (second group), at an uncultivated plot next to a maize field between Hajdúszoboszló and Nádudvar, Hungary (47°26'57.49"N; 21°18'01.96"E). After hatching from the cocoons, each spiderling was kept separately in a plastic cup with a floor area of 25.5 cm<sup>2</sup>. These cups contained ad libitum water (wet cotton wool) and food (tropical Collembolae specimens for young spiderlings from commercially available cultures, and *Drosophila* sp. specimens reared in our own laboratory, for aged spiders after several moults). With artificial lighting, we applied increasing day length until mid-July, followed by decreasing day length until the end of the tests, mimicking natural day:night lengths at the collection site. Spiders reaching maturity (i.e. possessing fully developed genitals) by 1 September were considered as rapidly developing.

The first group of spiders ( $N = 24$ , of which 12 showed rapid development) hatched in June 2014. They originated from two females: 11 from one female, of which five (46%) developed rapidly, and 13 from the other, of which seven (54%) developed rapidly. The second group of spiders ( $N = 74$ , of which 59 developed rapidly) originated from eight females and hatched in May 2015. In this latter group, the number of spiders from the different females varied from two to 20 ( $9.25 \pm 6.5$ , mean  $\pm$  SD), with 50–100% ( $75.3 \pm 22.5$ , mean  $\pm$  SD) of spiders within clutches developing rapidly.

Identification of sex was only possible for adult individuals, and during (and following) the tests not all the spiders matured; therefore, we could record sex only for some specimens. Because of this and of the main aim of our study (comparing individuals with slow and rapid development), we decided not to include sex in the later analyses.

### Behavioural Tests

We performed two behavioural test sessions (Table 1). Within each session, multiple repetitions of several behavioural tests were carried out, at random times of day, and all spiders were tested in a random order within test rounds.

The first test session was carried out on the first group of spiders, in July and August 2014. In this session, we used two types of tests in four rounds for each individual to assess willingness to catch a potential prey and activity in a novel area. On average, there was 1 week between consecutive test rounds and about 1 month between the first and last test rounds. To control for the hunger level of the spiders (which might affect their behaviour), each spider received three fruit flies, 2 days before the tests, and then

**Table 1**  
Set-up of the two test sessions

Session	Test
First ( $N=24$ )	Willingness to attack artificial prey (small)
	Willingness to attack artificial prey (large)
Second ( $N=74$ )	Activity in a novel area
	Emergence from shelter
	Activity in a novel area
	Willingness to catch living prey

The order of test methods represents their order of application in the tests. The first test session comprised four test rounds and the second two test rounds.

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