Behavioral Ecology and Sociobiology (2018) 72: 75
https://doi.org/10.1007/s00265-018-2477-7

ORIGINAL ARTICLE

Demographic measures of an individual's "pace of life": fecundity rate, lifespan, generation time, or a composite variable?

Yimen G. Araya-Ajoy[1] · Geir H. Bolstad[2] · Jon Brommer[3] · Vincent Careau[4] · Niels J. Dingemanse[5] · Jonathan Wright[1]

Received: 18 May 2017 / Revised: 23 February 2018 / Accepted: 5 March 2018 / Published online: 16 April 2018

Abstract

Comparative analyses have demonstrated the existence of a "pace-of-life" (POL) continuum of life-history strategies, from fast-reproducing short-lived species to slow-reproducing long-lived species. This idea has been extended to the concept of a "pace-of-life syndrome" (POLS), an axis of phenotypic covariation among individuals within species, concerning morphological, physiological, behavioral and life-history traits. Several life-history metrics can be used to place species in the fast-slow continuum; here, we asked whether individual variation in POL can also be studied using similar life-history measures. We therefore translated measures commonly used in demographic studies into individual-level estimates. We studied fecundity rate, generation time, lifespan, age at first reproduction, fecundity at first reproduction, and principal component scores integrating these different metrics. Using simulations, we show how demographic stochasticity and individual variation in resources affect the ability to predict an individual's POL using these individual-level parameters. We found that their accuracy depends on how environmental stochasticity varies with the species' position on the fast-slow continuum and with the amount of (co)variation in life-history traits caused by individual differences in resources. These results highlight the importance of studying the sources of life-history covariation to determine whether POL explains the covariation between morphological, physiological, and behavioral traits within species. Our simulations also show that quantifying not only among-individual but also among-population patterns of life-history covariation helps in interpreting demographic estimates in the study of POLSs within species.

Significance statement

It has been demonstrated that there is a continuum of life-history strategies, from fast-reproducing short-lived species to slow-reproducing long-lived species. This pattern of variation in the tempo of life-history strategies has been named the pace-of-life continuum. Recently, it has been suggested that within a population, variation in pace of life explains differences between individuals in their morphological, behavioral, and physiological traits. This paper provides guidelines on how to quantify the pace of life of individuals using demographic approaches that have been developed to study the pace of life of species.

Communicated by M. Dammhahn

This article is a contribution to the Topical Collection Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life-history – Guest Editors: Melanie Dammhahn, Niels J. Dingemanse, Petri T. Niemelä, Denis Réale.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-018-2477-7) contains supplementary material, which is available to authorized users.

✉ Yimen G. Araya-Ajoy
yimencr@gmail.com

[1] Centre for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway

[2] Norwegian Institute for Nature Research (NINA), 7485 Trondheim, Norway

[3] Department of Biology, University of Turku, University Hill, 20014 Turku, Finland

[4] Canada Research Chair in Functional Ecology, Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada

[5] Behavioural Ecology, Department of Biology, Ludwig Maximilian University of Munich (LMU), Planegg-, Martinsried, Germany

Keywords Fast-slow continuum · Individual variation · Life history trade-offs · Multi-level variation

Introduction

Understanding the causes and consequences of variation in life-history strategies in the tree of life has been a central goal of life-history theory (Stearns 1992; Roff 1993). A main axiom of life-history theory is that resource allocation trade-offs (i.e., budgetary compromises) between different aspects of an organism's life history, such as survival, growth, and reproduction, constrain the range of possible optimal life-history strategies that can evolve (Cody 1966; Stearns 1989). One such trade-off is between current and future reproduction. Individuals have a certain amount of resources and they must prioritize either their current or their future reproduction (Williams 1966; Reznick 1985). This trade-off can generate a pattern of (co)variation between life-history traits, which has been called the fast-slow continuum (Stearns 1983; Gaillard et al. 1989; Promislow and Harvey 1990; Galliard et al. 2016). At the fast end are organisms prioritizing current reproduction, which have high fecundity rates at the expense of future survival. This results in organisms that will mature early, have high reproductive rates, and short life spans. At the other (slow) end of the continuum are the organisms prioritizing survival (future reproduction) versus fecundity, which are characterized by long life spans, high survival rates, and low fecundity rates. Comparative analyses support this idea, showing that different species can be placed at different positions along this fast-slow continuum in birds (Saether 1988; Saether and Bakke 2000), mammals (Oli 2004; Bielby et al. 2007), fish (Goodwin et al. 2006; Bjorkvoll et al. 2012), reptiles (Bauwens and Diaz-Uriarte 1997), and plants (Salguero-Gómez et al. 2016). The relative allocation of resources to reproduction versus survival reflects how each species resolves the trade-off between current versus future reproduction and determines each species' position in the fast-slow pace-of-life (POL) continuum (Stearns 1992).

Life histories can vary among species, among populations of the same species, but also among individuals within the same population. The extended "pace-of-life syndrome" (POLS) concept takes the study of the fast-slow continuum to the among-individual level (Réale et al. 2010; Dammhahn et al. 2018, this issue). The main thesis of the POLS is that an individual's position along the fast-slow continuum explains among-individual differences not only in life-history traits but also in morphological, behavioral, and physiological traits. Testing this idea requires metrics that reflect an individual's POL and approximate its relative allocation in current versus future reproduction. While different life-history traits have proven useful in positioning species on the fast-slow axis (see: Gaillard et al. 2005; Oli et al. 2005), it remains unclear whether these metrics are useful to position individuals in the fast-slow POL axis. The existence of an integrative metric across different hierarchical levels of biological organization (individuals, populations, and species) would allow testing POL as a general explanation for phenotypic (co)variation in life-history, physiological, morphological, and behavioral traits. The objective of this paper is therefore to explore whether life-history measures used to study the fast-slow continuum at the species level can be used to characterize individual POL at the within-population level.

Life-history measures that have been used to study the fast-slow continuum at the species level can be divided into two broad categories: single indicator variables (e.g., age at first reproduction, lifespan, fecundity rate, fecundity at first reproduction) versus composite measures summarizing different life-history traits. Composite measures can be estimated from multivariate techniques like principal components analysis (PCA: Stearns 1983) or factor analysis (Bielby et al. 2007). They can also be estimated as derived quantities, for instance the ratio of fecundity versus age at maturity (Oli and Dobson 2003) or generation time (the mean age of mothers at childbirth; Charlesworth 1994, Gaillard et al. 2005). Such derived quantities can be data hungry and a lack of data on only one of the constituent variables may limit their practical use. Absolute comparisons of a composite measure like PCA scores can also be problematic across studies, because axes derived from a PCA analysis are specific to the dataset used to calculate them. In addition, some composite measures compound the sampling or measurement errors from all their separate components. The resulting magnification of error may lead to an erroneous interpretation of the position of an organism on the fast-slow continuum. In comparison, single-indicator variables are often easier to estimate and are more broadly available for many study systems, but there is concern that a single measure may not adequately quantify the fast-slow POL continuum within and across populations or species (Oli and Dobson 2003; Dammhahn et al. 2018, this issue).

Two key life-history metrics that have been related to a species life-history strategy are fecundity rate and lifespan. An individual's fecundity rate can be defined as the mean number of offspring produced by an individual that become independent per breeding attempt (e.g., annual fecundity). Thus, the fecundity rate of a population or species is the average fecundity rate of all the individuals belonging to that population or species (Saether and Bakke 2000). If there is among-individual variation in fecundity rate, this metric will capture variation among individuals in their allocation in current reproduction via activities like mate searching and parental care. In birds, for instance, this metric could be the mean number of fledglings that an individual produced over a year (i.e., annual fecundity). According to the hypothesized trade-off between current and future reproduction, the resources invested in fecundity cannot be invested in survival, making fecundity rate a potentially good measure of an individual's POL. Consequently, the life span of an individual is also an intuitively good measure of an individual's POL, because individuals that prioritized current reproduction over survival are expected to have a shorter life span, whereas individuals that prioritize future reproduction over fecundity should have a longer lifespan. This is captured nicely in the phrase "live fast and die young" that is commonly used to describe the fast-slow POL continuum at the species level (Promislow and Harvey 1990).

Generation time has also been suggested to be a good measure of a species position along the fast-slow POL continuum (Gaillard et al. 2005), because it is a function of all the vital rates describing the life cycle of a population. Species generation time has also been shown to predict the onset of senescence (Jones et al. 2008), supporting the idea that generation time captures important variation in the tempo of life-history strategies. Generation time is a population level concept and is often defined as the average age of mothers of newborns in the population (Charlesworth 1994). The changes in population growth rate can be written as a function of generation time, and Lande (1982) showed that the evolutionary response to selection of a trait per unit time is directly proportional to the inverse of generation time. Therefore, generation time is an appealing measure of POL, because it directly connects measures of life history with evolutionary theory (Saether et al. 2005). We investigated the utility of generation time measured at the individual level as a weighted mean age of reproduction for each individual; the weighted average of individual generation time across all individuals consequently equals the generation time of the population (see the "Methods" section for details).

The fast-slow POL continuum at the species level has been inferred from patterns of covariation among species in their life-history traits (Stearns 1983; Gaillard et al. 1989; Promislow and Harvey 1990). Therefore, metrics that summarize among-individual covariation between several life-history traits within a population are also an appealing measure of an individual's relative allocation in current versus future reproduction. The scores from PCAs applied to several life-history measures have been used to determine the position of a species in the fast-slow POL continuum (Stearns 1983). Similarly, within populations, these composite scores maybe a good proxy for an individual's proportional allocation in current versus future reproduction.

The study of the POL at the individual level presents some additional complications when compared to its study at the species and population levels. Among-individual variation in resources can mask life-history trade-offs (van Noordwijk and de Jong 1986; Houle 1991; Fry 1993; Reznick et al. 2000). Individuals with more resources can have both a higher fecundity and a longer lifespan than individuals with fewer resources. This may cause a positive covariation between fecundity and longevity, instead of the negative correlation expected by a trade-off between current and future reproduction (van Noordwijk and de Jong 1986; Stearns 1989). Moreover, stochastic variation in individual measures of life-history traits could arguably obscure the relationship between assessed life-history traits and the POL of individuals. Therefore, in this paper, we assess whether the different life-history measures that have been used to study the position of species in the fast-slow POL continuum can be also used to quantify the POL of individuals within populations. We describe how the performance of individual-level POL metrics is affected by variation in resources and demographic stochasticity for species in different position of the fast-slow continuum. Finally, we discuss how partitioning the sources of life-history (co)variation can be used to study whether individual variation in POL can explain the POLS involving covariation among behavioral, morphological, and physiological traits within a population.

Methods

We used data simulations to study how different life-history measures can recover an allocation trade-off between current and future reproduction (i.e., the POL) across a range of scenarios. We explored the performance of the following life-history measures: fecundity rate, fecundity in the first reproductive event, age at first reproduction, lifespan, individual generation time, and PCA scores summarizing the correlation between the different life-history measures. PCA scores were extracted from the first principal component of a principal component analyses on the correlation matrix between fecundity rate, fecundity at first reproduction, age at first reproduction, lifespan, and generation time.

Individual fecundity rates

An individual's fecundity rate (r_i) is the mean fecundity per breeding season (e.g., year) of an individual and can be calculated as

$$r_i = \sum \frac{o_{hi}}{b_i} \tag{1}$$

where r_i is the fecundity rate of individual i, o_{hi} is the number of offspring from individual i that are independent at the end of a breeding season h, and b_i is the number of breeding seasons experienced by individual i. The fecundity rate of the population is therefore the mean of all the individual fecundity rates of the population.

Individual generation time

The generation time of a population can be estimated as the average age of an offspring's mother when it was born. If a_g is the age of the mother of offspring g, and n is the total number of offspring produced in a population, the population's generation time $\overline{T}$ is given by

$$\overline{T} = \sum \frac{a_g}{n} \tag{2}$$

An intuitive measure of individual generation time is the weighted mean age of an individual when it reproduced

$$T_i = \sum \frac{a_{gi}}{n_i} \tag{3}$$

where T_i is the generation time of individual i, a_{gi} is the age of individual i when it produced offspring g, and n_i is the total number of offspring produced by individual i. However, the mean of t_i over all mothers is not the generation time of the population; this is given by the individual contribution to the generation time of the population, which is the individual generation time multiplied with the relative number of offspring:

$$t_i = T_i \frac{n_i}{\overline{n}} \tag{4}$$

where $\overline{n}$ is the average number of offspring of the parents in the population. Generation time at the population level usually only considers mothers, but it can also be defined as the mean age of all parents when they reproduce. Individual contributions to generation time considering both sexes are thus given by

$$t_i = T_i \frac{n_i}{2\overline{n}} \tag{5}$$

The mean of the individual contributions to the generation time of the population (t_i) will thus be equal to the generation of the population (T). This definition of individual generation time allows the study of generation time as a measure of an individual's pace of life while keeping its connection to population dynamics and quantitative genetics theory.

Simulating the trade-off and variation in POL

We simulated a hypothetical community of mythical creatures that behave pretty much like birds, to show how demographic stochasticity and among-individual variation in resources affect POL metrics at the individual level. The trade-off between current and future reproduction is most easily represented when organisms can either allocate their resources to reproduction or survival. We assumed that each individual had a fixed value in its life for the proportion of resources allocated in current reproduction (p). Individual allocation in reproduction will then fully define its allocation in survival (s), and therefore individual allocation in survival was calculated as one minus the proportion of resources allocated to fecundity ($1-p$). This causes a budgetary trade-off between allocating resources to fecundity versus survival. Based on this simple budgetary compromise (i.e., allocation trade-off), we aimed to create a continuum of species ranging from those with high allocation in reproduction and a short lifespan to those with long lifespan and low allocation in reproduction. Similarly, within species, we created populations and individuals with relatively long life spans and relatively low fecundity and vice versa. We then used simulations based on this allocation trade-off to study how the different life-history measures are able to quantify an individual's proportional allocation to current reproduction in species with different life-history strategies.

We use a beta distribution to simulate the proportional allocation in fecundity versus survival of individuals belonging to different species (Descamps et al. 2016). The beta distribution is defined by two parameters (alpha and beta) that can be used to generate a distribution of proportional values with defined mean and variance (Ferrari and Cribari-Neto 2004). We specified each species' mean and variance in the proportional allocation in current reproduction (Fig. 1a). We simulated seven hypothetical species with different mean levels of allocation in current reproduction (0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8). Species with low allocation in current reproduction are the "slow" species that allocate more resources to survival, whereas species with high values are the "fast" species that allocate more resources into reproduction. Within these species, we simulated populations that varied in their allocation in current versus future reproduction, and within each population, we also simulated individuals that varied in their proportional allocation in current versus future reproduction. The proportional allocation in current reproduction (p_j) of population j from species k is drawn from a beta distribution with a species-specific mean allocation (p_k) and among-population variance in allocation (V_{alloc_pop}), whereas the proportional allocation to reproduction of individual i is drawn from a beta distribution with population mean allocation in current reproduction p_j and among-individual variance in allocation (V_{alloc_ind}):

$$\begin{aligned} p_j &\sim beta\left(p_k,\ V_{alloc\_pop}\right) \\ p_i &\sim beta\left(p_j,\ V_{alloc\_ind}\right) \end{aligned} \tag{6}$$

Following the assumption that the allocation trade-off causes that the resources allocated to reproduction cannot be

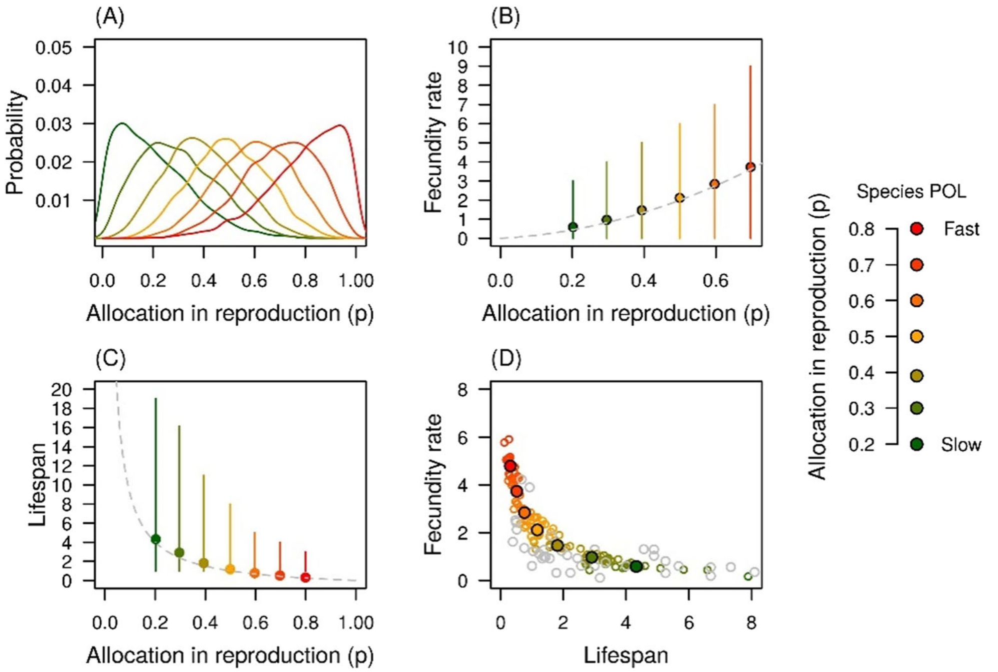


Fig. 1 Simulated variation in the allocation in current reproduction, fecundity, and longevity for 7 species, each with a different pace-of-life (POL). Red colors are associated with a fast POL and green colors with a slow POL. Gray dotted lines represent the expected relationships. **a** Distributions of individual allocation in current reproduction for the different species. **b** Mean (circles) and 95% confidence interval (lines) for the fecundity rate for each species as a function of their mean allocation in current reproduction. **c** Mean (circles) and 95% confidence interval (lines) for fecundity as a function of lifespan for each species. **d** The resulting relationship between fecundity rate and lifespan at the among-population and among-species level. Filled colored circles represent species means, unfilled colored circles represent populations means, and gray circles represent the values for bird species extracted from Sæther and Bakke (2000)

allocated to survival, the survival probabilities s for individual i is calculated as one minus its allocation in reproduction.

$$s_i = 1 - p_i \tag{7}$$

Individual i thus survives to the next reproductive event as function of survival probability s_i. This results in a linear relationship between proportional allocation in reproduction and survival probability. Equation 8 describes the relationship between survival probability (s) and the expected lifespan (l) of an individual if survival probability is constant from the age at first reproduction to the oldest age:

$$l_i = \frac{s_i}{1 - s_i} \tag{8}$$

Individuals that survive to the next breeding season reproduce according to their fecundity rate (r_i). The interval between breeding attempts is the same for all individuals; individuals may not reproduce 1 year depending on their fecundity rate, but they will reproduce until they die. The proportional allocation in current reproduction (p_i) of individual i is translated into a fecundity rate (r_i), which is defined as the mean number of offspring (assuming an equal sex ratio) that fledged at the end of a breeding season. Logically, allocation in current reproduction should positively affect fecundity rate (Fig. 1b). We set the relationship between fecundity rate and proportional allocation in current reproduction to match the among-species relationship between fecundity rate and survival estimated from a comparative study of avian demographic strategies by Sæther and Bakke (2000):

$$r_i = p_i + 6p_i^2 \tag{9}$$

The number of offspring (o_{hi}) that individual i produces in breeding attempt h is sampled from a Poisson distribution that has a mean equal to its fecundity rate (r_i):

$$o_{hi} \sim pois(r_i) \tag{10}$$

Among-individual variation in resources

We introduce among-individual variation in resources to determine how this will affect the relationships between the different individual-level POL metrics and the simulated proportional allocation in current reproduction. When there is no variation in resources, the amount of resources available to all individuals is equal to one. When the assumption of homogeneity of resources among individuals is relaxed, the available resources for an individual (R_i) is simulated from a normal distribution with a mean of one and variance of 0.5 (Eq. 11):

$$R_i \sim N(1, \quad 0.5) \tag{11}$$

Individuals with more resources increase their allocation in reproduction (p_i) and survival probability (s_i) proportionally to their resources (R_i) following Eqs. 12 and 13, respectively:

$$\overline{p}_i = p_i R_i \quad (12)$$

$$\overline{s}_i = 1 - \frac{p_i}{R_i} \quad (13)$$

Thus, our simulations were based on the premise that the POL of an individual is defined by its relative allocation to reproduction versus survival. We simulated this "latent trait" as a proportional value that determines how each individual allocates its resources to reproduction versus survival. We simulated a population/cohort of individuals with different POL and follow its reproductive output until they die. Individuals survive to the next year based on the probability of surviving and produce offspring proportionally to their fecundity rate. Each individual's life history is then used to estimate the different life-history measures.

Comparing POL metrics

We simulated 300 individuals from 100 populations for each of the 7 species to assess how well the different metrics map onto the allocation in current versus future reproduction simulated in the different scenarios. We calculated the different POL metrics from the simulated life histories for each individual. Then, we estimated the correlation between each of the metrics and the simulated proportional allocation to fecundity versus survival. We proceeded to estimate the accuracy of each life-history trait as an individual measure of the relative allocation to current reproduction using R-squared values. R-squared values were calculated from a linear model where the life-history traits were used to predict the simulated allocation in current reproduction. We fitted linear and quadratic relations between the life-history variables and the proportional allocation in current reproduction to account for any nonlinear relationships. Finally, we studied whether the overall correlation between fecundity rate and lifespan reflected the simulated trade-off between reproduction and survival. All simulations, graphs, and analysis were performed in R v.3.3.2 (R Core Team 2017). All the code to generate the data and perform the analyses and graphs is in the Supplementary material as an R markdown file. The code provides functions that can create specific sets of the parameters not considered in the main body of the paper.

Results

Among-species and among-population variation in life-history traits

Our simulation, which incorporates the budgetary trade-off between allocating resources to reproduction versus survival, produced a range of slow (species 1) to fast species (species 7). Fast species had higher values for fecundity rate and fecundity at first reproduction, and lower values for age at first reproduction, generation time, and life span (Fig. 1). Slow species, on the other hand, had lower values for fecundity rate and fecundity at first reproduction and higher values for age at first reproduction, generation time, and life span (Table 1). Therefore, as expected, allocation in current reproduction was positively related to the species fecundity rate (Fig. 1b) and negatively related to its longevity (Fig. 1c). Altogether, this generates a negative correlation between fecundity rate and longevity among species, as predicted by the resource allocation trade-off. Importantly, this relationship mimics the covariance pattern of actual avian life histories (Fig. 1d, gray circles) presented in Saether and Bakke (2000). We find the same pattern among populations within species; populations that had a relatively higher allocation in current reproduction had relatively higher mean fecundity rates and relatively lower average life spans (Fig. 1d).

Individual-level correlations between POL and life-history measures

Within all the simulated populations, individual fecundity-related measures (namely, fecundity at first reproduction and fecundity rate) were positively correlated with an individual's proportional allocation in current reproduction, whereas age-related measures (namely, age at first reproduction and lifespan) were negatively correlated with an individual's proportional allocation in current reproduction (Table 2). The correlation with fecundity rate was strongest for the long-lived species and weakest for the short-lived species (Table 2), while the correlation with fecundity at first reproduction did not vary across species. The lifespan of an individual and its age at first reproduction were more strongly correlated to an individual's POL in the slow long-lived species. We find a similar pattern for generation time, where an individual's generation time was negatively correlated with its proportional allocation in current reproduction and that this relationship was strongest for long-lived species. The average correlation between individual PCA scores and the simulated allocation trade-off was stronger for the slow species (Fig. 2; also see Table S1 for details on the variance explained by PC1). However, correlations changed from negative to positive, for all the species (Table 2). This shows that the direction of the major axis

Table 1 Mean and variance (in parenthesis) for the allocation in reproduction and the life-history traits of the different species. The estimates are based on 100 populations consisting of 300 individuals for each of the 7 species

Species	POL	Fecundity 1st rep	Fecundity rate	Age 1st rep	Lifespan	Generation Time
1	0.2	0.96	0.56	2.85	5.33	4.09
	(0.02)	(0.95)	(0.73)	(10.89)	(24.6)	(14.27)
2	0.3	1.33	0.98	1.82	3.82	2.82
	(0.02)	(1.33)	(1.16)	(3.81)	(14.91)	(6.93)
3	0.41	1.78	1.52	1.34	2.76	2.05
	(0.02)	(2.04)	(1.87)	(1.01)	(7.54)	(2.87)
4	0.51	2.28	2.11	1.15	2.2	1.68
	(0.02)	(2.88)	(2.69)	(0.32)	(4.1)	(1.38)
5	0.6	3	2.9	1.06	1.76	1.41
	(0.02)	(4)	(3.72)	(0.1)	(1.85)	(0.58)
6	0.7	3.85	3.8	1.03	1.49	1.26
	(0.02)	(5.46)	(5.19)	(0.04)	(1.08)	(0.33)
7	0.8	4.73	4.7	1.01	1.31	1.16
	(0.02)	(6.75)	(6.52)	(0.02)	(0.65)	(0.19)

of covariation can sometimes change in relation to the allocation in current reproduction; that is, for some populations, higher PC score values reflected a faster pace of life and for others a slower pace of life.

Predictive power of individual life-history measures

In general, demographic stochasticity and among-individual variation in resources increased variation in life-history trait values, which as expected, decreased the accuracy of all life-history traits as measures of an individual's POL (Fig. 2). Fecundity rate and PC1 scores were the measures that best reflected the simulated allocation trade-off. When there was no among-individual variation in resources, fecundity rate and PC1 scores explained around 60% of the among-individual variation in allocation to reproduction versus survival in the long-lived (slow) species and around 30% in the short-lived (fast species). This contrasts with the correlation between the PCA scores and the simulated allocation trade-off (Table 2), because the R^2 values do not incorporate the directionality of the relationship. Age-related measures performed better in species with a slow POL than in species with a fast POL. As expected, introducing among-individual variation in acquired resources also decreased the predictive power of all the life-history measures.

Table 2 The correlation between the different derived life-history traits and the simulated proportional allocation to fecundity versus survival for seven species with different POL. Species 1 is the species with the slowest POL and species 7 is the species with the fastest POL. The estimates are based on 100 populations consisting of 300 individuals for each of the 7 species. We present the mean and the 95% confidence intervals in parenthesis

Species	Fecundity 1st rep.	Fecundity rate	Age 1st rep	Lifespan	Generation time	PC scores
1	0.53	0.77	− 0.49	− 0.48	− 0.53	− 0.4
	(0.4, 0.64)	(0.72, 0.81)	(− 0.55, − 0.44)	(− 0.55, − 0.41)	(− 0.59, − 0.48)	(− 0.74, 0.71)
2	0.51	0.71	− 0.44	− 0.44	− 0.49	− 0.27
	(0.42, 0.6)	(0.64, 0.77)	(− 0.5, − 0.37)	(− 0.52, − 0.35)	(− 0.55, − 0.4)	(− 0.71, 0.66)
3	0.5	0.67	− 0.39	− 0.4	− 0.44	0
	(0.42, 0.58)	(0.6, 0.73)	(− 0.44, − 0.31)	(− 0.49, − 0.32)	(− 0.51, − 0.35)	(− 0.66, 0.64)
4	0.51	0.62	− 0.33	− 0.36	− 0.39	0
	(0.44, 0.58)	(0.56, 0.68)	(− 0.42–0.24)	(− 0.45, − 0.25)	(− 0.48, − 0.29)	(− 0.65, 0.62)
5	0.51	0.59	− 0.27	− 0.35	− 0.37	− 0.1
	(0.44, 0.57)	(0.51, 0.64)	(− 0.38, − 0.17)	(− 0.45, − 0.25)	(− 0.46, − 0.28)	(− 0.64, 0.61)
6	0.53	0.57	− 0.24	− 0.36	− 0.37	− 0.08
	(0.45, 0.58)	(0.51, 0.63)	(− 0.35, − 0.1)	(− 0.46, − 0.25)	(− 0.48, − 0.26)	(− 0.65, 0.63)
7	0.52	0.55	− 0.2	− 0.39	− 0.39	− 0.21
	(0.45, 0.59)	(0.49, 0.62)	(− 0.33,-0.02)	(− 0.51, − 0.26)	(− 0.53, − 0.24)	(− 0.65, 0.64)

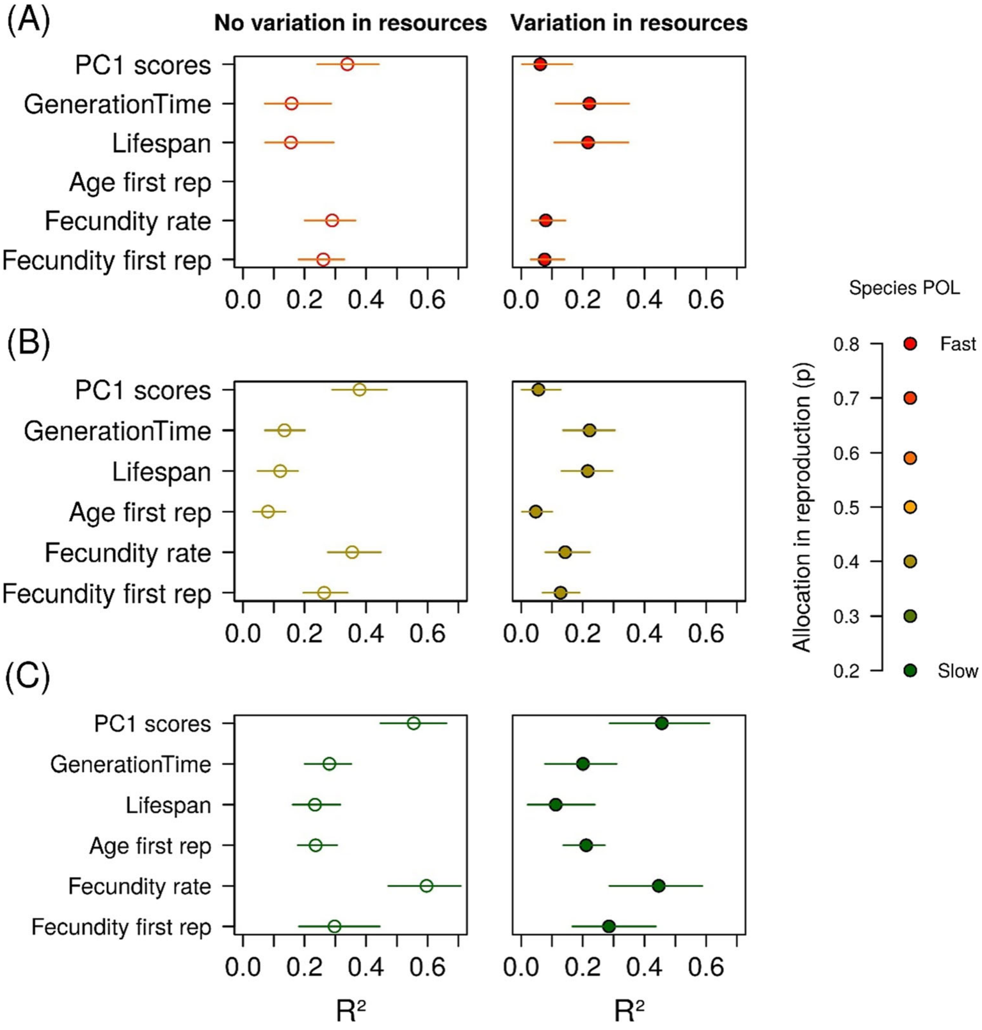


Fig. 2 The proportion of the variation (R^2) in the individual-level proportional allocation in current versus future reproduction (POL) that is explained by different metrics in species positioned at the **a** fast, **b** intermediate, and **c** slow ends of the pace-of-life continuum. Open circles in the left-hand plots represent a scenario where there was no among-individual variation in resources, and solid circles in the right-hand plots represent a scenario where there is variation in resources. Note that R^2 values for age at first reproduction in the fastest species are missing because there was no variation in this trait for this species

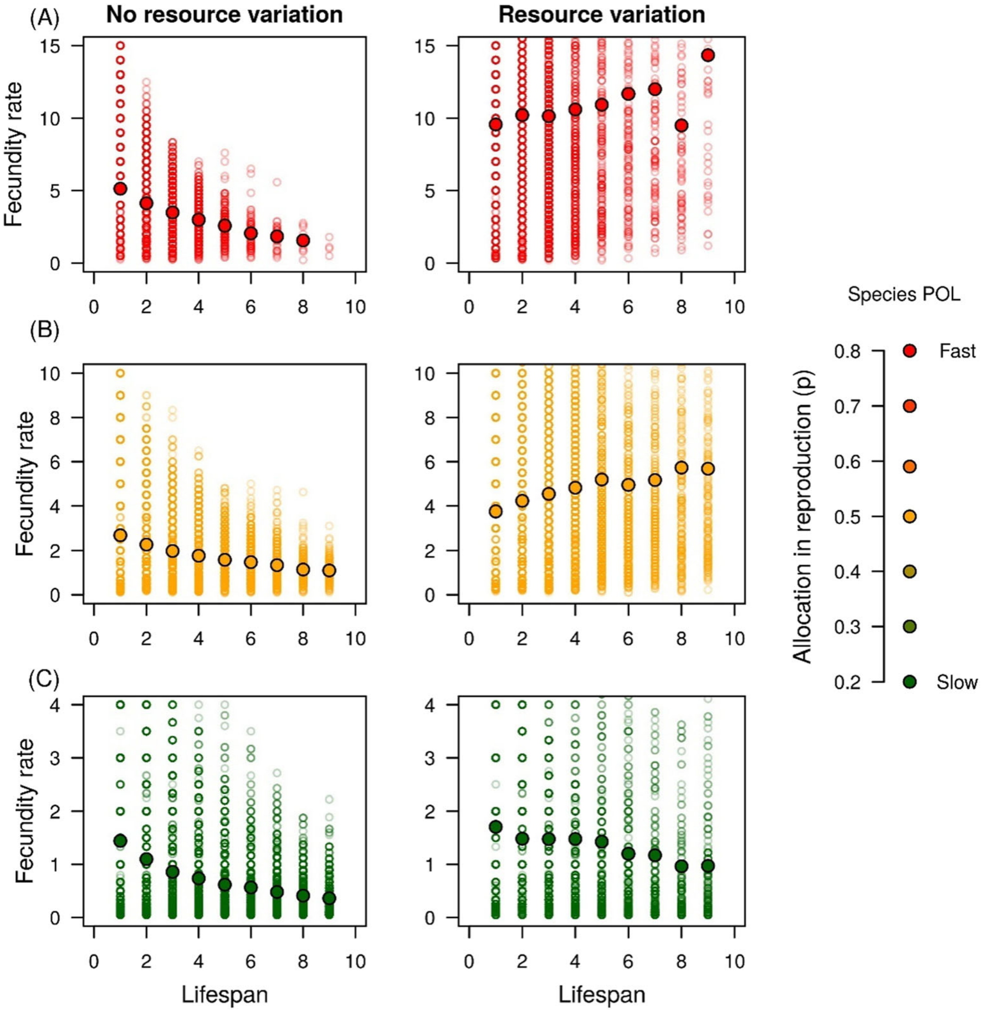
The reproduction and survival trade-off among species, populations, and individuals

At the species level, lifespan was strongly and negatively correlated with fecundity rate (mean = − 0.79, 95% confidence interval (CI) = − 0.82, − 0.76, Fig. 1d). At the among-population within-species level, the correlations were also negative and strong (Table S2). At the within-population among-individual level, lifespan and fecundity were also negatively correlated (Fig. 3a–c, left panels). However, these within-population negative correlations were much weaker than the among-species and among-population correlations, despite correlations at different levels being generated by the allocation trade-off between fecundity and survival. This pattern occurred because the individual-level correlations were obscured by demographic stochasticity. As expected, introducing among-individual variation in acquired resources further obscured the allocation trade-off between fecundity and survival at the individual level and, in some instances, this even resulted in a positive correlation between lifespan and fecundity rate (Fig. 3a, right panel). This scenario is one where most of the variation in life-history traits is caused by differences between individuals in their ability to acquire resources; thus, animals with a high fecundity are also the ones that live longer.

Discussion

We investigated demographic estimates that can be used to study individual variation in POL. Using a budgetary trade-off between current and future reproduction, measured as allocation in reproduction versus survival, we simulated an among-species pattern of life-history (co)variation consistent with the observed life-history strategies of bird species (Saether and Bakke 2000). Following the hypothesis that variation in the relative allocation in current (fecundity) versus future reproduction (survival) generates variation along the fast-slow POL continuum across different levels of biological organization, we used this same allocation trade-off to create

Fig. 3 Fecundity rate (average offspring per year) as function of lifespan (years) in species with a **a** fast, **b** medium, and **c** slow pace of life (POL). Results for each type of species are shown with (right panels) and without (left panels) variation in individual resources to illustrate its effects on this life-history trade-off (see text for details). Filled larger circles represent the mean for each lifespan, while empty circles show individual values. Mean values were calculated only when there were more than 10 individuals alive at that lifespan



life-history variation among individuals, populations, and species. Our simulations show that individual life-history measures are affected differently by demographic stochasticity and that their accuracy as POL measures depends upon the species position along the POL continuum. Our simulations also corroborate the results by van Noordwijk and de Jong (1986), showing that among-individual variation in resource acquisition can obscure the relationship between life-history metrics and an individual's proportional allocation to current reproduction. The results of these simulations may also explain the variable and contrasting outcomes of studies intended to relate morphological, behavioral, and physiological traits to slow and fast life-history strategies (Montiglio et al. 2018; Tarka et al. 2018; both in topical collection on Pace-of-life syndrome).

In our simulations, fecundity rate is always among the best individual POL measures across the different types of species. As we detail below, this is because fecundity rate is a measure based upon repeated observations across an individual's life time and therefore suffers less from the biasing effects of demographic stochasticity. In the "slow" species, fecundity rate performs substantially better than the other metrics, and for the "faster" species, it is as good a metric as any other (Fig. 3). This is partly because in our simulation, demographic stochasticity varies systematically across the POL axis. Any stochastic variation in fecundity rate is caused by the Poisson process that translates the fecundity rate of each individual into the number of offspring produced in each breeding attempt. In species with a higher fecundity rate, there will be more stochastic variation in offspring production, because species with a higher mean fecundity rate will also have more (stochastic) variance in offspring production, as compared to species with a low fecundity rate where stochastic variation is smaller. The assumption that annual reproductive success follows a Poisson distribution is perhaps rather simplistic, since it has been shown that annual reproductive success might be better described as a generalized Poisson distribution (Kendall et al. 2010). Despite this simplifying assumption, a general pattern emerges. When the stochastic variance in a life-history trait is a function of the POL of a species, the accuracy of the life-history trait as a measure of an individual POL will depend upon the species' position in the fast-slow continuum (see Hamel et al. 2010).

On average, age-related measures prove to be better proxies for the POL of individuals in slow species, as compared to fast species. In short-lived species, lifespan or age at first reproduction are not good predictors of an individual's POL, because there is little scope for variation. For instance, the fastest species in our simulation had an adult survival probability of 0.2, where only 20% of the individuals reproduced twice, and less than 5% reproduced three times. Given that short-lived (fast) species have such low survival probabilities, there is a high chance that an individual investing relatively more in survival will nevertheless still die (see Saether et al. 2004). In a similar fashion as with fecundity rate, the within-species variance in lifespan is a function of a species' position along the fast-slow continuum, but in this case, it is the variance associated with individual differences in allocation. Species with high survival probabilities will therefore have a higher variance in lifespan and will therefore be easier to approximate individual variation in POL with age-related measures. This agrees with results found in a comparative analysis of mammals, where the chance of detecting a cost of reproduction (allocation trade-off) was lower when the life-history trait studied had a low variance (Hamel et al. 2010). But note that in this paper, we explicitly refer to the amount of variation caused by individual differences in allocation in relation to other sources of variation (see below). Even in slow, long-lived species, the accuracy of lifespan as an individual POL measure is lower than that of fecundity rate, reflecting the stochastic nature of mortality. Generation time performed better in a long-lived species and had a slightly tighter correlation with the simulated allocation trade-off than lifespan, although fecundity rate still performed better. This is partly because, compared to other metrics, generation time accumulates the stochastic variation associated with survival and offspring production, resulting in its performance decreasing more sharply with the average POL of a species (Table 2).

An important aspect to take into account when choosing a POL measure is its dimensionality, because the interpretation of a POL estimate depends on the units it is measured (Galliard et al. 2016). Most of the life-history traits we studied had a time component, which makes intuitive sense as POL is a concept directly related to the timing of life-history events. Hence, age at first reproduction, generation time, and lifespan are measured in units of time, while fecundity rate is measured per unit of time. We also studied fecundity at first reproduction as a potential POL measure, because it could reflect investment in current reproduction, especially in species that reproduce relatively few times in their life. However, fecundity in the first reproduction not only performs poorly in our simulations (Table 2) but is perhaps conceptually not a good measure of POL because it does not have a time component. The units of the measures of an individual's POL are also important when estimating composite measures. For instance, in our PC analysis, most of the measures were related to time; thus, the PCA axis reflects mostly a time axis. However, combining POL measures in different units could lead to incorrect interpretations of the PCA axis (Gailliard et al. 2016); thus, we suggest thinking carefully about the units and transformations of the life-history measures of an individual's POL.

Sources of within-population variation in life-history traits

Our simulation explores only some potential POL measures and presents a simplistic scenario stripped of the many factors that may decrease the accuracy of real life-history trait values as measures of an individual's POL (e.g., age-dependent reproduction and survival). This simulation study is therefore not intended to inform researchers about optimal sampling designs (e.g., power analyses). The aim here was simply to illustrate some basic properties of the different metrics when studying an individual POL within species with different life-history strategies (e.g., fast versus slow). Some specifics of the simulation reflect the patterns of covariation between life histories found in comparative analyses of bird data (see the "Methods" section), but the main conclusions apply more generally. To provide a more general context, in this section, we discuss our simulation results using equations that illustrate the contribution of different sources of variation in the expression of life-history traits within a population.

The sources of variation generating within-population variation in a life-history measure (z_l) can be decomposed into its different components.

$$z_{lhi} = c_l + I_l(p_iR_i) + B_l a_{hi} + d_{lhi} + e_{lhi} \tag{14}$$

where life-history l of individual i at observation h depends upon the population mean value (c_l) and an individual's deviation of the population mean value (I_{li}). An individual's deviation of the population mean value (I_{li}) is determined by its relative allocation to current versus future reproduction (p_i), its ability to acquire resources (R_i), and a coefficient that links the amount of resources invested (p_iR_i) to the measured life-history trait (I_l). Survival probabilities and fecundity can vary deterministically with age (a_{hi}); therefore, B_l is a coefficient that relates the expression of life-history trait l with the age of individual i at measure h. Note that this assumes no among-individual variation in age-dependent reproduction or survival, but this equation can be easily extended to accommodate this complexity. Life-history measures are also affected by stochastic variation in the vital rates of an individual (d_{lhi}; demographic stochasticity). For instance, survival is a probabilistic process containing intrinsic variation and causing stochastic variation in age-related life-history measures. Many different types of environmental variables could affect the expression of a life-history trait; thus, e_{lhi} reflects spatial and temporal variation affecting life-history trait l of individual i on measurement event h. For instance, this may represent spatial variation in resource availability and/or temporal variation in climatic conditions.

From Eq. 14 (above), it follows that variation in the values for a life-history trait (V_l) can be decomposed into variation associated with among-individual variation in allocation (V_{alloc}) and the ability to acquire resources (V_{res}). An underlying assumption of the POLS hypothesis is that there is among-individual variation in p_i, which may be caused by genetic variation and permanent environmental effects. Thus, consistent individual differences in allocation will generate among-individual variation in life-history trait values. Similarly, among-individual variation in quality (sensu Wilson and Nussey 2009), or in other words an individual's ability to acquire resources (R_i), will also generate among-individual variation in life-history traits. Variation in resource acquisition can also vary within individuals, for instance with increasing age (MacNulty et al. 2009) or due to yearly variation in resources, but this will generate within-individual variation in life-history traits. In a similar way, variation associated to demographic (V_{dem}) and environmental stochasticity (V_{env}) will generate within-individual variation in life-history trait values. Assuming no covariance between the different effects affecting a life-history trait, we can describe the variation in a life-history measure l following Eq. 15:

$$V_l = V_{alloc} + V_{res} + V_{dem} + V_{env} \tag{15}$$

From Eqs. 14 and 15, we can infer that the accuracy of a life-history trait as a measure of an individual's POL will be determined by the proportion of variation in a life-history trait value caused by individual variation in allocation (V_{alloc}/V_l) and the degree to which the different sources of variation can be teased apart. For instance, the accuracy of a life-history trait (z_l) as a POL measure will be very low if it is based upon a single measure and if there are large sources of environmental and demographic stochasticity that cannot be controlled for. Our simulations show that a life-history trait based upon repeated measures per individual (e.g., fecundity rate) performs better than a measure based on only one observation (e.g., fecundity at first reproduction). This is because fecundity rate is the average annual fecundity of an individual, and averaging the yearly number of produced offspring decreases the biasing effects of demographic and environmental stochasticity characterizing each breeding attempt. We also found that fecundity rate is a better predictor of an individual's POL in long-lived species. This is because longer-lived individuals have more repeated measures of annual fecundity. Therefore, individual fecundity rates based upon a greater number of repeated measures will suffer less from the biasing effects of demographic and environmental stochasticity.

When among-individual variation in resources strongly affects the expression of a life-history trait, its accuracy as an individual POL measure will decrease. The biasing effects of among-individual variation in resources will depend upon the relative contribution of allocation versus acquisition in the expression of a life-history trait (V_{alloc}/V_{res}). Unfortunately, an individual's allocation to reproduction versus survival (p_i) and its ability to acquire resources (R_i) cannot be measured directly in observational studies. While averaging over many observations of individual life-history trait values may provide an unbiased estimate of an individual's expected value for a life-history trait (I_l), it is not always possible to disentangle how much this value will be influenced by allocation (p_i) versus acquisition of resources (R_i). Only in situations where it is possible to measure or control individual levels of acquired resources will it be possible to partial out the effects of variation in acquisition on life-history trait values. Furthermore, we are assuming that the relative allocation to reproduction versus survival does not depend upon the available resources, which is also an assumption of the conceptual model on life-history trade-offs postulated by van Noordwijk and de Jong (1986). It has been suggested that covariance between allocation and acquisition may be common in nature and affects the ability to detect trade-offs between reproduction and survival (Descamps et al. 2016). Importantly, covariance between acquisition and allocation could be manifested at the within-individual, among-individual, among-population, or among-species level, and its effects on the accuracy of life-history traits as measures of an individual's POL remain to be evaluated.

Sources of covariation between life-history traits

The fast-slow POL continuum at the species level has been inferred from the patterns of among-species covariation in life-history trait values (Stearns 1983; Gaillard et al. 1989; Promislow and Harvey 1990). Similarly, at the within-species among-individual level, the patterns of life-history covariation should support the existence of a fast-slow POL axis. Indeed, our simulations show that PCA scores were among the best performing metrics across all the species, but they were inadequate measures in the presence of among-individual variation in resources (Fig. 3). It is therefore key to study the pattern of correlation between life-history traits to determine if there is support for a within-population fast-slow POL axis. In a similar fashion to partitioning variation in each life-history trait, we can decompose the sources of covariation among the different life-history traits (Cov_{total}) into their different sources:

$$Cov_{total} = Cov_{alloc} + Cov_{res} + Cov_{env} \tag{16}$$

Equation 16 states that the covariance between life-history traits within a population can be caused by covariance induced by individual variation in the proportional allocation to current versus future reproduction (Cov_{alloc}), covariance induced by among-individual differences in resource acquisition (Cov_{res}), plus covariance induced by environmental factors affecting all the life-history traits (Cov_{env}). Composite measures of an individual's POL, such as PCA scores, are based upon the correlation between life-history traits. Therefore, PCA scores are an intuitively good measure of the position of an individual along the fast-slow POL continuum, because they summarize the correlation among different life-history traits. In our simulations, demographic stochasticity results in a weaker correlation among the life-history traits in the faster species, and therefore PCA scores are a less accurate measure, though they are among the metrics that perform best (Fig. 2). The accuracy of a composite measure will also depend upon the relative contribution of variation in allocation in generating covariation among the different life-history traits Cov_{alloc}/Cov_{total}. Therefore, among-individual variation in resources leads to a decreased accuracy of PCA scores as a measure of individual POL, because the relative contribution of allocation in the covariance between traits decreases (Fig. 2 and Table S1). Life-history theory predicts that if allocation has a stronger contribution in the expression of life-history traits, fecundity and age-related measures should be negatively correlated, whereas if resource availability has a stronger influence, the opposite pattern is expected (van Noordwijk and de Jong 1986). Indeed, our simulation results show that the correlation between fecundity and longevity changes depending upon the level of among-individual variation in resources (Fig. 3). Furthermore, in the case of the fastest species, the relative contribution of among-individual variation in resources was higher compared to the contribution of allocation, resulting in a positive correlation between fecundity rate and lifespan. Therefore, it is important and useful to check the patterns of covariation between life-history traits before interpreting PCA scores or any of the other life-history traits as a measure of individual POL.

The adaptive nature of POLS and the multivariate evolution of traits

Estimating variance-covariance matrices of phenotypic traits is a key component of many ecological and evolutionary studies (Houle 1991). These approaches commonly involve partitioning phenotypic variance-covariance matrices into its differences sources. Mixed effect models have been used to partition phenotypic correlations into their among- versus within-individual components (Dingemanse and Dochtermann 2013). Among-individual correlations are a core component of the POLS hypothesis, because it hypothesizes that the proportional allocation of resources to current reproduction should result in among-individual correlations among life-history, morphological, behavioral, and physiological traits. Mixed effect models are very flexible tools that can be used to also control for other factors causing (co)variation in life-history traits, via the inclusion of random and/or fixed effects. Moreover, if pedigree or genetic relatedness information is available, it is possible to estimate the additive genetic (co)variance in life-history trait values using animal models (Wilson et al. 2010), further removing the potential biasing effects of demographic and environmental stochasticity (Reznick 1985), although if among-individual variation in the ability to acquire resources has a genetic component, it will still hinder the ability to aproximate an individual's proportional allocation (Fry 1993). In general, attempting to account for biases using statistical approaches should increase the ability to quantify an individual's POL but requires that the proper factors and the linearity of the relations are correctly modeled.

The variance-covariance matrices estimated from a mixed effect model can be further analyzed to determine whether the covariation between life-history, morphological, behavioral, and physiological traits can be explained by the proportional allocation of an individual to current versus future reproduction. Importantly, the proportional allocation to current reproduction of an individual and its ability to acquire resources are generally not measured directly, and therefore its effect on the different life-history traits should be determined by the pattern of correlation between them. Therefore, the proportional allocation to current reproduction can be studied as a latent variable inferred from the correlation between the different life-history traits. Structural equation modeling (SEM) is a very flexible tool that can be used to study the existence of a latent variable reflecting the proportional allocation to current versus future reproduction based upon the correlation patterns (Grace et al. 2010). Furthermore, this approach can be used to test specific hypotheses regarding the underlying factors generating covariation among other phenotypic traits (Dingemanse et al. 2010; Araya-Ajoy and Dingemanse 2014; Santostefano et al. 2017). However, even when using such an approach, it is still critical to account for the role of among-individual variation in resources in generating the covariation between the different trait values, because this is another latent variable that is difficult to measure directly. It may be possible to control for variation in resources if there is a way to measure it, but if there is a correlation between allocation and acquisition, it may be difficult to disentangle its effects on the different life-history traits. Interestingly, an among-individual correlation between allocation and acquisition will result in selection on allocation, because individuals that allocate resources in a particular way will be the ones that have more resources and therefore a higher reproductive success. This then raises a question concerning the adaptive nature of among-individual variation in allocation and the mechanisms maintaining this variation within populations (Mathot and Frankenhuis 2018 in topical collection on Pace-of-life syndrome).

Our simulations also show that among-population patterns of life-history covariation are easier to detect, because averaging over many individuals within populations removes the variation caused by demographic stochasticity. In a similar way, at the individual level, metrics based on repeated measures within individuals (e.g., fecundity rate) better predict an individual's POL, because averaging over several observations reduces the biasing effects of demographic stochasticity. The number of individuals in a population does not necessarily affect the accuracy of individual demographic estimates as POL measures (Fig. S1). It is the number of repeats within individuals that affect their accuracy, because as we show, fecundity rate is a better predictor of POL on long-lived species, where estimates are based on a greater number of repeated measures within individuals (slow species Fig. 3). In a similar way, the predictive power of a population's mean life-history trait value reflecting its average allocation to reproduction versus survival tends to increase with the number of individuals sampled in the population (Fig. S1). These results suggest that focusing on populations, or other biologically relevant groups of individuals within populations (e.g., families, flocks, etc.), will improve our ability to study the role of POL, because any estimated life-history measure will be less affected by environmental stochasticity.

Conclusions

In this paper, we explored how to quantify the pace of life (POL) of individuals in the context of pace-of-life syndromes (POLS). We suggest characterizing an individual's POL using demographic measures commonly used in species- and population-level studies (e.g., fecundity rate and generation time). The use of these metrics will allow the connection of any studies of within-population variation in life-history strategies with their among-population and among-species counterparts. The predictive power of the different measures depends upon the relative contribution of individual variation in allocation, stochastic environmental variation, and among-individual variation in resources to the total phenotypic variation in each life-history measure. Our simulations show that metrics like fecundity rate that are based upon repeated measures, and other estimates based upon multiple metrics like PCA, suffer less from the biasing effects of environmental stochasticity. However, the relative contributions of the different sources of variation may differ between metrics and along the fast-slow continuum, making it difficult to find a single individual POL metric that works well across all species. Therefore, we suggest carefully studying the sources of covariation among life-history traits and other phenotypic traits to determine if there is evidence for individual variation in POL, but also because studying the causes of among-individual variation in life-history traits will provide a better understanding of the multivariate evolution of life-history strategies. Our simulations also highlight that focusing on among-population patterns of life-history covariation will increase our ability to study POLS using demographic measures. Moreover, integrating among-population and within-population studies will provide further insights concerning the factors determining the optimal allocation between reproduction and survival of a population and their relationship with the adaptive nature of within-population variation in POL.

Acknowledgements We are grateful to the sponsors, organizers, and participants of the VW-funded workshops 'Towards a general theory of POLS," Hannover 2015-6, which inspired this journal topical collection and provided feedback during discussions of earlier versions of the ideas presented here. We also thank Jean-Michel Gaillard, Melanie Dammhahn, Denis Réale, and one anonymous reviewer for the insightful comments during the reviewing process. This work was supported by the European Research Council (ERC-2010-AdG 268,562) and the Research Council of Norway (SFF-III 223257/F50).

Compliance with ethical standards

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

References

Araya-Ajoy YG, Dingemanse NJ (2014) Characterizing behavioural "characters": an evolutionary framework. Proc R Soc B 281: 20132645

Bauwens D, Diaz-Uriarte R (1997) Covariation of life-history traits in Lacertid lizards: a comparative study. Am Nat 149:91–111

Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CD, Purvis A (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. Am Nat 169: 748–757

Bjørkvoll E, Grøtan V, Aanes S, Sæther B-E, Engen S, Aanes R, Solow AE, Shaw ERG (2012) Stochastic population dynamics and life-history variation in marine fish species. Am Nat 180:372–387

Charlesworth B (1994) Evolution in age-structured populations. Cambridge University Press, Cambridge

Cody ML (1966) A general theory of clutch size. Evolution 20:174–184

Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D (2018) Pace-of life syndromes: a framework for the adaptive integration of behaviour, physiology and life-history. Behav Ecol Sociobiol, topical collection on Pace-of-life syndrome

Descamps S, Gaillard J-M, Hamel S, Yoccoz NG (2016) When relative allocation depends on total resource acquisition: implications fort the analysis of trade-offs. J Evol Biol 29:1860–1866

Dingemanse NJ, Dochtermann N (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol 82: 39–54

Dingemanse NJ, Dochtermann N, Wright J (2010) A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. Anim Behav 79:439–450

Ferrari SLP, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. J Appl Stat 31:799–815

Fry JD (1993) The "general vigor" problem: can antagonistic pleiotropy be detected when genetic covariances are positive? Evolution 47: 327–333

Gaillard J-M, Lemantre JF, Berge V, Bonenfant C, Devillard S, Douhard M, Gamelon M, Plard F, Lebreton JD (2016) Life histories, axes of variation. In: Kliman RM (ed) Encyclopedia of evolutionary biology. Academic Press, Oxford, pp 312–323

Gaillard J-M, Pontier D, Allainé D, Lebreton JD, Trouvilliez J, Clobert J (1989) An analysis of demographic tactics in birds and mammals. Oikos 56:59–76

Gaillard J-M, Yoccoz NG, Lebreton J-D, Bonenfant C, Devillard S, Loison A, Pontier D, Allaine D (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. Am Nat 166:119–123

Goodwin NB, Grant A, Perry AL, Dulvy NK, Reynolds JD (2006) Life history correlates of density-dependent recruitment in marine fishes. Can J Fish Aquat Sci 63:494–509

Grace JB, Anderson TM, Olff H, Scheiner SM (2010) On the specification of structural equation models for ecological systems. Ecol Monogr 80:67–87

Hamel S, Gaillard J-M, Yoccoz NG, Loison A, Bonenfant C, Descamps C (2010) Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol Lett 13:915–935

Houle D (1991) Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution 45:630–648

Jones OR, Gaillard J-M, Tuljapurkar S et al (2008) Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecol Lett 11:664–673

Kendall B, Wittmann M, Neubert AE, De Angelis ED (2010) A stochastic model for annual reproductive success. Am Nat 175:461–468

Lande R (1982) A quantitative genetic theory of life history evolution. Ecology 63:607–615

Mac Nulty DR, Smith DW, Vucetich JA, Mech LD, Stahler DR, Packer C (2009) Predatory senescence in ageing wolves. Ecol Lett 12:1347–1356

Mathot K, Frankenhuis W (2018) Models of pace-of-life syndromes (POLS): a systematic review. Behav Ecol Sociobiol, topical collection on Pace-of-life syndrome

Montiglio P-O, Dammhahn M, Dubuc-Messier G, Réale D (2018) The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum. Behav Ecol Sociobiol, topical collection on Pace-of-life syndrome

Oli MK (2004) The fast–slow continuum and mammalian life-history patterns: an empirical evaluation. Basic Appl Ecol 5:449–463

Oli MK, Dobson FS (2003) The relative importance of life history variables to population growth rate in mammals: Cole's prediction revisited. Am Nat 161:422–440

Oli MK, Dobson FS, Pfiste AECA, Losos EJB (2005) Generation time, elasticity patterns, and mammalian life histories: a reply to Gaillard et al. Am Nat 166:124–128

Promislow DEL, Harvey PH (1990) Living fast and dying young: a comparative analysis of life-history variation among mammals. J Zool 220:417–437

Réale D, Garant D, Humphrie MM, Bergeron P, Careau V, Montiglio P-O (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos T Roy Soc B 365:4051–4063

Reznick D (1985) Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267

Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. Trends Ecol Evol 15:421–425

Roff DA (1993) Evolution of life histories: theory and analysis. Springer, New York

Saether B-E (1988) Pattern of covariation between life-history traits of European birds. Nature 331:616–617

Saether B-E, Bakke O (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653

Saether B-E, Engen S, Møller AP et al (2004) Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. Am Nat 164:793–802

Saether B-E, Lande R, Engen S et al (2005) Generation time and temporal scaling of bird population dynamics. Nature 436:99–102

Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, de Kroon H, Buckley YM (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. P Natl Acad Sci USA 113:230–235

Santostefano F, Wilson AJ, Niemelä P, Dingemanse NJ (2017) Behavioral mediators of genetic life history trade-offs: a test of the pace-of-life syndrome hypothesis. Proc R Soc B 284:1864

Stearns SC (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. Oikos 41: 173–187

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3: 259–268

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Tarka M, Guenther A, Niemelä, PT, Nakagawa S, Noble DWA (2018) Sex differences in life-history, behavior and physiology along a slow-fast continuum: a meta-analysis. Behav Ecol Sociobiol, topical collection on Pace-of-life syndrome

Wilson AJ, Nussey DH (2009) What is individual quality? An evolutionary perspective. Trends Ecol Evol 25:207–214

Wilson AJ, Réale D, Clements MN, Morrissey MB, Postma E, Walling CA, Kruuk LEB, Nussey DH (2010) An ecologist's guide to the animal model. J Anim Ecol 79:13–26

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690