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5 **Demographic measures of an individual's "pace of life": fecundity rate, lifespan, generation**
6 **time or a composite variable?**
7

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23 **Abstract**

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

42 **Significance statement**

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

50 **Introduction**

51 Understanding the causes and consequences of variation in life-history strategies in the tree of life
52 has been a central goal of life-history theory (Stearns 1992; Roff 1993). A main axiom of life-
53 history theory is that resource allocation trade-offs (i.e. budgetary compromises) between different
54 aspects of an organism's life-history, such as survival, growth and reproduction, constrain the range
55 of possible optimal life-history strategies that can evolve (Cody 1966; Stearns 1989). One such
56 trade-off is between current and future reproduction. Individuals have a certain amount of resources
57 and they must prioritize either their current or their future reproduction (Williams 1966; Reznick
58 1985). This trade-off can generate a pattern of (co)variation between life-history traits, which has
59 been called the fast-slow continuum (Stearns 1983; Gaillard et al. 1989; Promislow and Harvey
60 1990; Gaillard et al. 2016). At the fast end are organisms prioritizing current reproduction, which
61 have high fecundity rates at the expense of future survival. This results in organisms that will
62 mature early, have high reproductive rates and short life spans. At the other (slow) end of the
63 continuum are the organisms prioritizing survival (future reproduction) versus fecundity, which are
64 characterized by long life spans, high survival rates and low fecundity rates. Comparative analyses
65 support this idea, showing that different species can be placed at different positions along this fast-
66 slow continuum in birds (Saether 1988; Saether and Bakke 2000), mammals (Oli 2004; Bielby et al.
67 2007), fish (Goodwin et al. 2006; Bjorkvoll et al. 2012), reptiles (Bauwens and Diaz-Uriarte 1997)
68 and plants (Salguero-Gómez et al. 2016). The relative allocation of resources to reproduction versus
69 survival reflects how each species resolves the trade-off between current versus future reproduction
70 and determines each species' position in the fast-slow pace-of-life (POL) continuum (Stearns 1992).

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

84 explore whether life-history measures used to study the fast-slow continuum at the species level can
85 be used to characterize individual POL at the within-population level.

86 Life-history measures that have been used to study the fast-slow continuum at the species
87 level can be divided into two broad categories: single indicator variables (e.g. age at first
88 reproduction, lifespan, fecundity rate, fecundity at first reproduction) versus composite measures
89 summarizing different life-history traits. Composite measures can be estimated from multivariate
90 techniques like Principal Components Analysis (PCA: Stearns 1983) or factor analysis (Bielby et al.
91 2007). They can also be estimated as derived quantities, for instance the ratio of fecundity versus
92 age at maturity (Oli and Dobson 2003) or generation time (the mean age of mothers at childbirth;
93 Charlesworth 1994, Gaillard et al. 2005). Such derived quantities can be data hungry and a lack of
94 data on only one of the constituent variables may limit their practical use. Absolute comparisons of
95 a composite measure like PCA scores can also be problematic across studies, because axes derived
96 from a PCA analysis are specific to the data set used to calculate them. In addition, some composite
97 measures compound the sampling or measurement errors from all their separate components. The
98 resulting magnification of error may lead to an erroneous interpretation of the position of an
99 organism on the fast-slow continuum. In comparison, single indicator variables are often easier to
100 estimate and are more broadly available for many study systems, but there is concern that a single
101 measure may not adequately quantify the fast-slow POL continuum within and across populations
102 or species (Oli and Dobson 2003; Dammhahn et al. 2018, this issue).

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

119 Generation time has also been suggested to be a good measure of a species position along
120 the fast-slow POL continuum (Gaillard et al. 2005), because it is a function of all the vital rates
121 describing the life cycle of a population. Species generation time has also been shown to predict the
122 onset of senescence (Jones et al. 2008), supporting the idea that generation time captures important
123 variation in the tempo of life-history strategies. Generation time is a population level concept and is
124 often defined as the average age of mothers of newborns in the population (Charlesworth 1994).
125 The changes in population growth rate can be written as a function of generation time, and Lande
126 (1982) showed that the evolutionary response to selection of a trait per unit time is directly
127 proportional to the inverse of generation time. Therefore, generation time is an appealing measure
128 of POL, because it directly connects measures of life-history with evolutionary theory (Saether et al.
129 2005). We investigated the utility of generation time measured at the individual level as a weighted
130 mean age of reproduction for each individual; the weighted average of individual generation time
131 across all individuals consequently equals the generation time of the population (see methods
132 section for details).

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

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

154 we discuss how partitioning the sources of life-history (co)variation can be used to study whether
155 individual variation in POL can explain the POLS involving covariation among behavioural,
156 morphological and physiological traits within a population.

157

158 **Methods**

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

167

168 *Individual fecundity rates*

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

171

$$172 \quad r_i = \sum \frac{o_{hi}}{b_i} \quad (1)$$

173

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

178

179 *Individual generation time*

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

183

$$184 \quad \bar{T} = \sum \frac{a_g}{n} \quad (2)$$

185

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

188

189

$$T_i = \sum \frac{a_{gi}}{n_i} \quad (3)$$

190

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

196

197

$$t_i = T_i \frac{n_i}{\bar{n}} \quad (4)$$

198

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

203

204

$$t_i = T_i \frac{n_i}{2\bar{n}} \quad (5)$$

205

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

210

211 *Simulating the trade-off and variation in POL*

212 We simulated a hypothetical community of mythical creatures that behave pretty much like birds, to
213 show how demographic stochasticity and among-individual variation in resources affect POL
214 metrics at the individual level. The trade-off between current and future reproduction is most easily
215 represented when organisms can either allocate their resources to reproduction or survival. We
216 assumed that each individual had a fixed value in its life for the proportion of resources allocated in
217 current reproduction (p). Individual allocation in reproduction will then fully define its allocation in
218 survival (s), and therefore individual allocation in survival was calculated as one minus the
219 proportion of resources allocated to fecundity ($1 - p$). This causes a budgetary trade-off between
220 allocating resources to fecundity versus survival. Based on this simple budgetary compromise (i.e.
221 allocation trade-off), we aimed to create a continuum of species' ranging from those with high

222 allocation in reproduction and a short lifespan to those with long lifespan and low allocation in
223 reproduction. Similarly, within species we created populations and individuals with relatively long
224 lifespans and relatively low fecundity and *vice versa*. We then used simulations based on this
225 allocation trade-off to study how the different life-history measures are able to quantify an
226 individual's proportional allocation to current reproduction in species with different life-history
227 strategies.

228 We use a Beta distribution to simulate the proportional allocation in fecundity versus
229 survival of individuals belonging to different species (Descamps et al. 2016). The Beta distribution
230 is defined by two parameters (alpha and beta) that can be used to generate a distribution of
231 proportional values with defined mean and variance (Ferrari and Cribari-Neto 2004). We specified
232 each species' mean and variance in the proportional allocation in current reproduction (Fig 1A). We
233 simulated 7 hypothetical species with different mean levels of allocation in current reproduction
234 (0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8). Species with low allocation in current reproduction are the
235 "slow" species that allocate more resources to survival, whereas species with high values are the
236 "fast" species that allocate more resources into reproduction. Within these species we simulated
237 populations that varied in their allocation in current versus future reproduction, and within each
238 population we also simulated individuals that varied in their proportional allocation in current
239 versus future reproduction. The proportional allocation in current reproduction (p_j) of population j
240 from species k is drawn from a beta distribution with a species-specific mean allocation (p_k) and
241 among-population variance in allocation (V_{alloc_pop}). Whereas the proportional allocation to
242 reproduction of individual i is drawn from a beta distribution with population mean allocation in
243 current reproduction p_j and among individual variance in allocation (V_{alloc_ind}).

244

$$\begin{aligned} 245 \quad p_h &\sim \text{beta}(p_k, V_{alloc_pop}) \\ 246 \quad p_i &\sim \text{beta}(p_j, V_{alloc_ind}) \end{aligned} \quad (6)$$

247

248 Following the assumption that the allocation trade-off causes that the resources allocated to
249 reproduction cannot be allocated to survival, the survival probabilities s for individual i is
250 calculated as one minus its allocation in reproduction.

251

$$252 \quad s_i = 1 - p_i \quad (7)$$

253

254 Individual i thus survives to the next reproductive event as function of survival probability s_i . This
255 results in a linear relationship between proportional allocation in reproduction and survival

256 probability. Equation 8 describes the relationship between survival probability (s) and the expected
257 lifespan (l) of an individual if survival probability is constant from the age at first reproduction to
258 the oldest age.

$$259 \quad l_i = \frac{s_i}{1-s_i} \quad (8)$$

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

$$269 \quad r_i = p_i + 6p_i^2 \quad (9)$$

270
271
272 The number of offspring (o_{hi}) that individual i produces in breeding attempt h is sampled from a
273 Poisson distribution that has a mean equal to its fecundity rate (r_i).

$$274 \quad o_{hi} \sim \text{pois}(r_i) \quad (10)$$

275 276 277 *Among-individual variation in resources*

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

$$284 \quad R_i \sim N(1, 0.5) \quad (11)$$

285
286
287 Individuals with more resources increase their allocation in reproduction (p_i) and survival
288 probability (s_i) proportionally to their resources (R_i) following equations 12 and 13, respectively.

289

290
$$\bar{p}_i = p_i R_i \quad (12)$$

291

292
$$\bar{s}_i = 1 - \frac{p_i}{R_i} \quad (13)$$

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

300

301 *Comparing POL metrics*

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

317

318 **Results**

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

320 Our simulation, which incorporates the budgetary trade-off between allocating resources to
321 reproduction versus survival, produced a range of slow (species 1) to fast species (species 7). Fast
322 species had higher values for fecundity rate and fecundity at first reproduction, and lower values for
323 age at first reproduction, generation time and life span (Fig 1). Slow species, on the other hand, had
324 lower values for fecundity rate and fecundity at first reproduction, and higher values for age at first

325 reproduction, generation time and life span (Table 1). Therefore, as expected, allocation in current
326 reproduction was positively related to the species fecundity rate (Fig 1B) and negatively related to
327 its longevity (Fig 1C). Altogether, this generates a negative correlation between fecundity rate and
328 longevity among species, as predicted by the resource allocation trade-off. Importantly, this
329 relationship mimics the covariance pattern of actual avian life histories (Fig 1D, grey circles)
330 presented in Saether and Bakke (2000). We find the same pattern among populations within species,
331 populations that had a relatively higher allocation in current reproduction had relatively higher
332 mean fecundity rates and a relatively lower average life spans (Fig 1D).

333

334 *Individual level correlations between POL and life-history measures*

335 Within all the simulated populations, individual fecundity-related measures (namely, fecundity at
336 first reproduction and fecundity rate) were positively correlated with an individual's proportional
337 allocation in current reproduction, whereas age-related measures (namely, age at first reproduction
338 and lifespan) were negatively correlated with an individual's proportional allocation in current
339 reproduction (Table 2). The correlation with fecundity rate was strongest for the long-lived species
340 and weakest for the short-lived species (Table 2), while the correlation with fecundity at first
341 reproduction did not vary across species. The lifespan of an individual and its age at first
342 reproduction were more strongly correlated to an individual's POL in the slow long-lived species.
343 We find a similar pattern for generation time, where an individual's generation time was negatively
344 correlated with its proportional allocation in current reproduction and that this relationship was
345 strongest for long-lived species. The average correlation between individual PCA scores and the
346 simulated allocation trade-off was stronger for the slow species (Fig 2; also see table S1 for details
347 on the variance explained by PC1). However, correlations changed from negative to positive, for all
348 the species (Table 2). This shows that the direction of the major axis of covariation can sometimes
349 change in relation to the allocation in current reproduction; that is, for some populations higher PC
350 score values reflected a faster pace of life and for others a slower pace of life.

351

352 *Predictive power of individual life-history measures*

353 In general, demographic stochasticity and among-individual variation in resources increased
354 variation in life-history trait values, which as expected, decreased the accuracy of all life-history
355 traits as measures of an individual's POL (Fig 2). Fecundity rate and PC1 scores were the measures
356 that best reflected the simulated allocation trade-off. When there was no among-individual variation
357 in resources, fecundity rate and PC1 scores explained around 60% of the among-individual
358 variation in allocation to reproduction versus survival in the long-lived (slow) species, and around
359 30% in the short-lived (fast species). This contrasts with the correlation between the PCA scores

360 and the simulated allocation trade-off (Table 2), because the R^2 values do not incorporate the
361 directionality of the relationship. Age-related measures performed better in species with a slow POL
362 than in species with a fast POL. As expected, introducing among-individual variation in acquired
363 resources also decreased the predictive power of all the life-history measures.

364

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

366 At the species level, lifespan was strongly and negatively correlated with fecundity rate (mean = -
367 0.79, 95% confidence interval (CI) = -0.82, -0.76, Fig 1D). At the among-population within-species
368 level the correlations were also negative and strong (Table S2). At the within-population among
369 individual level, lifespan and fecundity were also negatively correlated (Fig 3A-C, left panels).
370 However, these within-population negative correlations were much weaker than the among-species
371 and among-population correlations, despite correlations at different levels being generated by the
372 allocation trade-off between fecundity and survival. This pattern occurred because the individual
373 level correlations were obscured by demographic stochasticity. As expected, introducing among-
374 individual variation in acquired resources further obscured the allocation trade-off between
375 fecundity and survival at the individual level and, in some instances, this even resulted in a positive
376 correlation between lifespan and fecundity rate (Fig 3A, right panel). This scenario is one where
377 most of the variation in life-history traits is caused by differences between individuals in their
378 ability to acquire resources, thus animals with a high fecundity are also the ones that live longer.

379

380 **Discussion**

381 We investigated demographic estimates that can be used to study individual variation in POL.
382 Using a budgetary trade-off between current and future reproduction, measured as allocation in
383 reproduction versus survival, we simulated an among-species pattern of life-history (co)variation
384 consistent with the observed life-history strategies of bird species (Saether and Bakke 2000).
385 Following the hypothesis that variation in the relative allocation in current (fecundity) versus future
386 reproduction (survival) generates variation along the fast-slow POL continuum across different
387 levels of biological organization, we used this same allocation trade-off to create life-history
388 variation among individuals, populations and species. Our simulations show that individual life-
389 history measures are affected differently by demographic stochasticity and that their accuracy as
390 POL measures depends upon the species position along the POL continuum. Our simulations
391 corroborate the results by van Noordwijk and de Jong (1986), showing that among-individual
392 variation in resource acquisition can obscure the relationship between life-history metrics and an
393 individual's proportional allocation to current reproduction. The results of these simulations may
394 also explain the variable and contrasting outcomes of studies intended to relate morphological,

395 behavioral and physiological traits to slow and fast life-history strategies (Montiglio et al. 2018;
396 Tarka et al. 2018; both in topical collection on Pace-of-life syndrome).

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

415 On average, age-related measures prove to be better proxies for the POL of individuals in
416 slow species, as compared to fast species. In short-lived species, lifespan or age at first reproduction
417 are not good predictors of an individual's POL, because there is little scope for variation. For
418 instance, the fastest species in our simulation had an adult survival probability of 0.2, where only
419 20% of the individuals reproduced twice, and less than 5% reproduced three times. Given that
420 short-lived (fast) species have such low survival probabilities, there is a high chance that an
421 individual investing relatively more in survival will nevertheless still die (see Saether et al. 2004).
422 In a similar fashion as with fecundity rate, the within species variance in lifespan is a function of a
423 species' position along the fast-slow continuum, but in this case, it is the variance associated with
424 individual differences in allocation. Species with high survival probabilities will therefore have a
425 higher variance in lifespan, and will therefore be easier to approximate individual variation in POL
426 with age related measures. This agrees with results found in a comparative analysis of mammals,
427 where the chance of detecting a cost of reproduction (allocation trade-off) was lower when the life-
428 history trait studied had a low variance (Hamel et al. 2010). But note that in this paper we explicitly
429 refer to the amount of variation caused by individual differences in allocation in relation to other

430 sources of variation (see below). Even in slow, long-lived species, the accuracy of lifespan as an
431 individual POL measure is lower than that of fecundity rate, reflecting the stochastic nature of
432 mortality. Generation time performed better in a long-lived species and had a slightly tighter
433 correlation with the simulated allocation trade-off than lifespan, although fecundity rate still
434 performed better. This is partly because, compared to other metrics, generation time accumulates
435 the stochastic variation associated with survival and offspring production, resulting in its
436 performance decreasing more sharply with the average POL of a species (Table 2).

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

452

453 *Sources of within-population variation in life-history traits*

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

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

467

468

$$469 \quad z_{lhi} = c_l + I_l(p_i R_i) + B_l a_{hi} + d_{lhi} + e_{lhi} \quad (14)$$

470

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

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

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$$V_l = V_{alloc} + V_{res} + V_{dem} + V_{env} \quad (15)$$

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From equations 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.

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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

535 among-species level, and its effects on the accuracy of life-history traits as measures of an
536 individual's POL remain to be evaluated.

537

538 *Sources of covariation between life-history traits*

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

549

$$550 \quad Cov_{total} = Cov_{alloc} + Cov_{res} + Cov_{env} \quad (16)$$

551

552 Equation 16 states that the covariance between life-history traits within a population can be caused
553 by covariance induced by individual variation in the proportional allocation to current versus future
554 reproduction (Cov_{alloc}), covariance induced by among-individual differences in resource
555 acquisition (Cov_{res}), plus covariance induced by environmental factors affecting all the life-history
556 traits (Cov_{env}). Composite measures of an individual's POL, such as PCA scores, are based upon
557 the covariance between life-history traits. Therefore, PCA scores are an intuitively good measure of
558 the position of an individual along the fast-slow POL continuum, because they summarize the
559 covariation among different life-history traits. In our simulations, demographic stochasticity results
560 in a weaker correlation among the life-history traits in the faster species, and therefore PCA scores
561 are a less accurate measure, though they are among the metrics that perform best (Fig. 2). The
562 accuracy of a composite measure will also depend upon the relative contribution of variation in
563 allocation in generating covariation among the different life-history traits Cov_{alloc}/Cov_{total} .
564 Therefore, among-individual variation in resources leads to a decreased accuracy of PCA scores as
565 a measure of individual POL, because the relative contribution of allocation in the covariance
566 between traits decreases (Fig. 2, Table S1). Life-history theory predicts that if allocation has a
567 stronger contribution in the expression of life-history traits, fecundity and age-related measures
568 should be negatively correlated, whereas if resource availability has a stronger influence, the
569 opposite pattern is expected (van Noordwijk and de Jong 1986). Indeed, our simulation results show

570 that the correlation between fecundity and longevity changes depending upon the level of among-
571 individual variation in resources (Fig. 3). Furthermore, in the case of the fastest species, the relative
572 contribution of among-individual variation in resources was higher compared to the contribution of
573 allocation, resulting in a positive correlation between fecundity rate and lifespan. Therefore, it is
574 important and useful to check the patterns of covariation between life-history traits before
575 interpreting PCA scores or any of the other life-history traits as a measure of individual POL.

576

577 *The adaptive nature of POLS and the multivariate evolution of traits*

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

595 The variance-covariance matrices estimated from a mixed effect model can be further
596 analyzed to determine whether the covariation between life-history, morphological, behavioral and
597 physiological traits can be explained by the proportional allocation of an individual to current
598 versus future reproduction. Importantly, the proportional allocation to current reproduction of an
599 individual and its ability to acquire resources are generally not measured directly, and therefore its
600 effect on the different life-history traits should be determined by the pattern of correlation between
601 them. Therefore, the proportional allocation to current reproduction can be studied as a latent
602 variable inferred from the correlation between the different life-history traits. Structural equation
603 modeling (SEM) is a very flexible tool that can be used to study the existence of a latent variable
604 reflecting the proportional allocation to current versus future reproduction based upon the

605 correlation patterns (Grace *et. al* 2010). Furthermore, this approach can be used to test specific
606 hypotheses regarding the underlying factors generating covariation among other phenotypic traits
607 (Dingemanse *et al.* 2010; Araya-Ajoy and Dingemanse 2014; Santostefano *et al.* 2017). However,
608 even when using such an approach, it is still critical to account for the role of among individual
609 variation in resources in generating the covariation between the different trait values, because this is
610 another latent variable that is difficult to measure directly. It may be possible to control for variation
611 in resources if there is a way to measure it, but if there is a correlation between allocation and
612 acquisition it may be difficult to disentangle its effects on the different life-history traits.
613 Interestingly, an among-individual correlation between allocation and acquisition will result in
614 selection on allocation, because individuals that allocate resources in a particular way will be the
615 ones that have more resources and therefore a higher reproductive success. This then raises a
616 question concerning the adaptive nature of among-individual variation in allocation and the
617 mechanisms maintaining this variation within populations (Mathot and Frankenhuis 2018 in topical
618 collection on Pace-of-life syndrome).

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

634

635 *Conclusions*

636 In this paper, we explored how to quantify the pace of life (POL) of individuals in the context of
637 pace-of-life syndromes (POLS). We suggest characterizing an individual's POL using demographic
638 measures commonly used in species and population level studies (e.g. fecundity rate and generation
639 time). The use of these metrics will allow the connection of any studies of within-population

640 variation in life-history strategies with their among-population and among-species counterparts. The
641 predictive power of the different measures depends upon the relative contribution of individual
642 variation in allocation, stochastic environmental variation and among-individual variation in
643 resources to the total phenotypic variation in each life-history measure. Our simulations show that
644 metrics like fecundity rate that are based upon repeated measures, and other estimates based upon
645 multiple metrics like PCA, suffer less from the biasing effects of environmental stochasticity.
646 However, the relative contributions of the different sources of variation may differ between metrics
647 and along the fast-slow continuum, making it difficult to find a single individual POL metric that
648 works well across all species. Therefore, we suggest carefully studying the sources of covariation
649 among-life-history traits and other phenotypic traits to determine if there is evidence for individual
650 variation in POL, but also because studying the causes of among-individual variation in life-history
651 traits will provide a better understanding of the multivariate evolution of life-history strategies. Our
652 simulations also highlight that focusing on among population patterns of life-history covariation
653 will increase our ability to study POLS using demographic measures. Moreover, integrating among-
654 population and within-population studies will provide further insights concerning the factors
655 determining the optimal allocation between reproduction and survival of a population and their
656 relationship with the adaptive nature of within-population variation in POL.

657

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665

666 **Conflict of Interest**

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

668

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829 **Figure captions**

830

831 **Fig. 1** Simulated variation in the allocation in current reproduction, fecundity and longevity for 7
832 species, each with a different pace-of-life (POL). Red colours are associated with a fast POL, and
833 green colours with a slow POL. Grey dotted lines represent the expected relationships. (A)
834 Distributions of individual allocation in current reproduction for the different species. (B) Mean
835 (circles) and 95% confidence interval (lines) for the fecundity rate for each species as a function of
836 their mean allocation in current reproduction. (C) Mean (circles) and 95% confidence interval
837 (lines) for fecundity as a function of lifespan for each species. (D) The resulting relationship
838 between fecundity rate and lifespan at the among-population and among-species level. Filled
839 colored circles represent species means, unfilled colored circles represent populations means and
840 grey circles represent the values for bird species extracted from Sæther and Bakke (2000)

841

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

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

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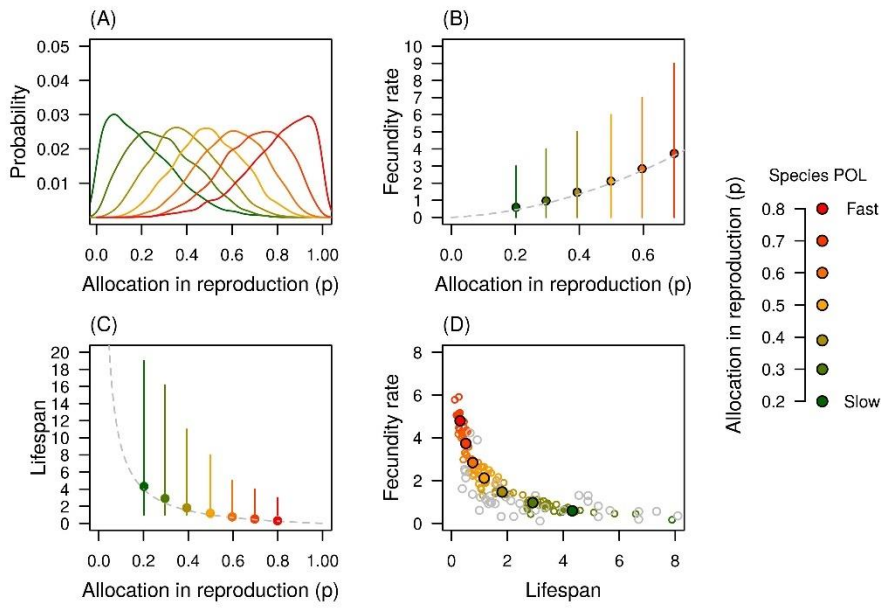
Tables and figures

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

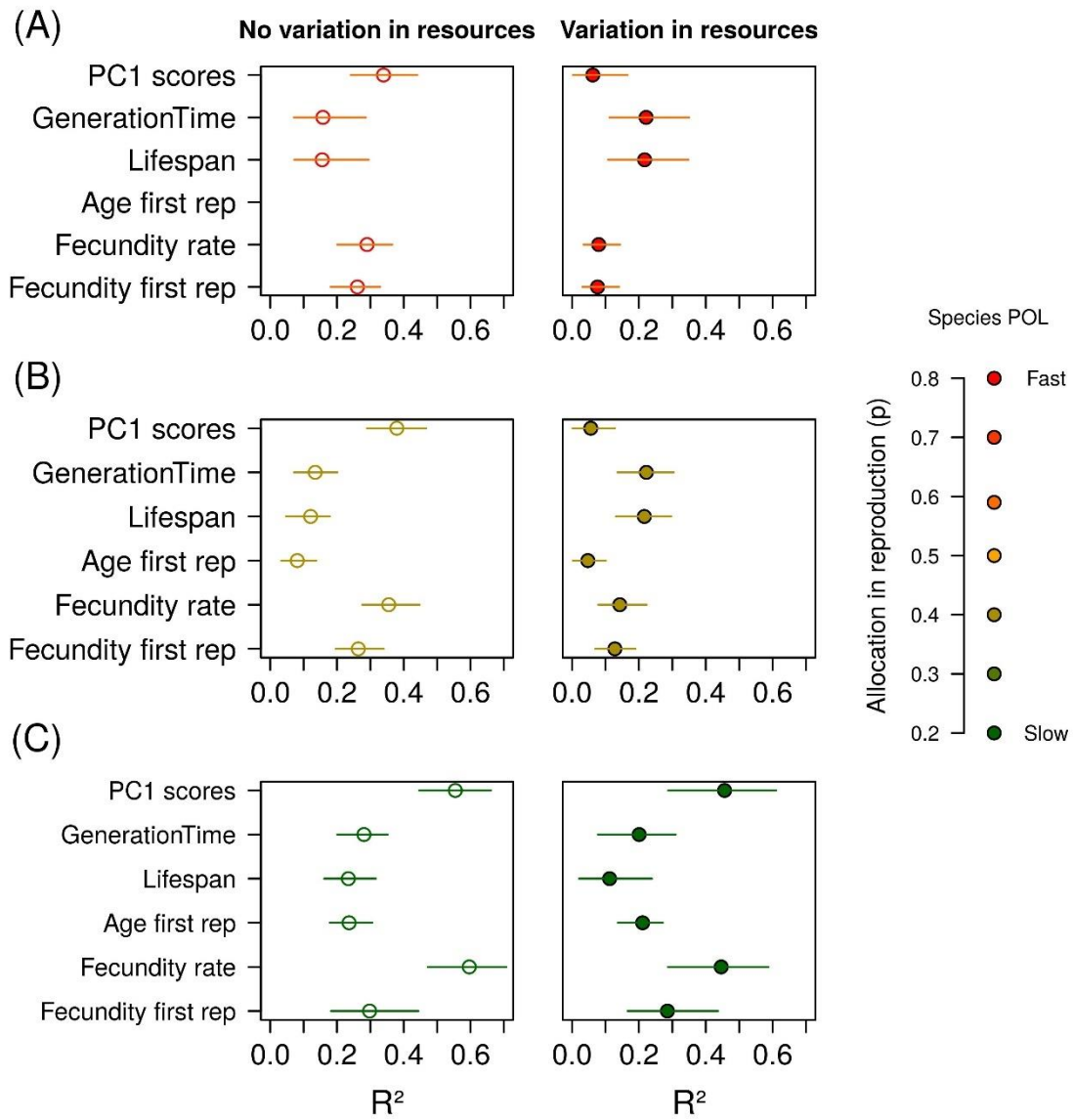
866 **Table 2** The correlation between the different derived life-history traits and the simulated
867 proportional allocation to fecundity versus survival for 7 species with different POL. Species 1 is
868 the species with the slowest POL and species 7 is the species with the fastest POL. The estimates
869 are based on 100 populations consisting of 300 individuals for each of the 7 species. We present the
870 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 (0.4, 0.64) | 0.77 (0.72, 0.81) | -0.49 (-0.55, -0.44) | -0.48 (-0.55, -0.41) | -0.53 (-0.59, -0.48) | -0.4 (-0.74, 0.71) |
| 2 | 0.51 (0.42, 0.6) | 0.71 (0.64, 0.77) | -0.44 (-0.5, -0.37) | -0.44 (-0.52, -0.35) | -0.49 (-0.55, -0.4) | -0.27 (-0.71, 0.66) |
| 3 | 0.5 (0.42, 0.58) | 0.67 (0.6, 0.73) | -0.39 (-0.44, -0.31) | -0.4 (-0.49, -0.32) | -0.44 (-0.51, -0.35) | 0 (-0.66, 0.64) |
| 4 | 0.51 (0.44, 0.58) | 0.62 (0.56, 0.68) | -0.33 (-0.42, -0.24) | -0.36 (-0.45, -0.25) | -0.39 (-0.48, -0.29) | 0 (-0.65, 0.62) |
| 5 | 0.51 (0.44, 0.57) | 0.59 (0.51, 0.64) | -0.27 (-0.38, -0.17) | -0.35 (-0.45, -0.25) | -0.37 (-0.46, -0.28) | -0.1 (-0.64, 0.61) |
| 6 | 0.53 (0.45, 0.58) | 0.57 (0.51, 0.63) | -0.24 (-0.35, -0.1) | -0.36 (-0.46, -0.25) | -0.37 (-0.48, -0.26) | -0.08 (-0.65, 0.63) |
| 7 | 0.52 (0.45, 0.59) | 0.55 (0.49, 0.62) | -0.2 (-0.33, -0.02) | -0.39 (-0.51, -0.26) | -0.39 (-0.53, -0.24) | -0.21 (-0.65, 0.64) |

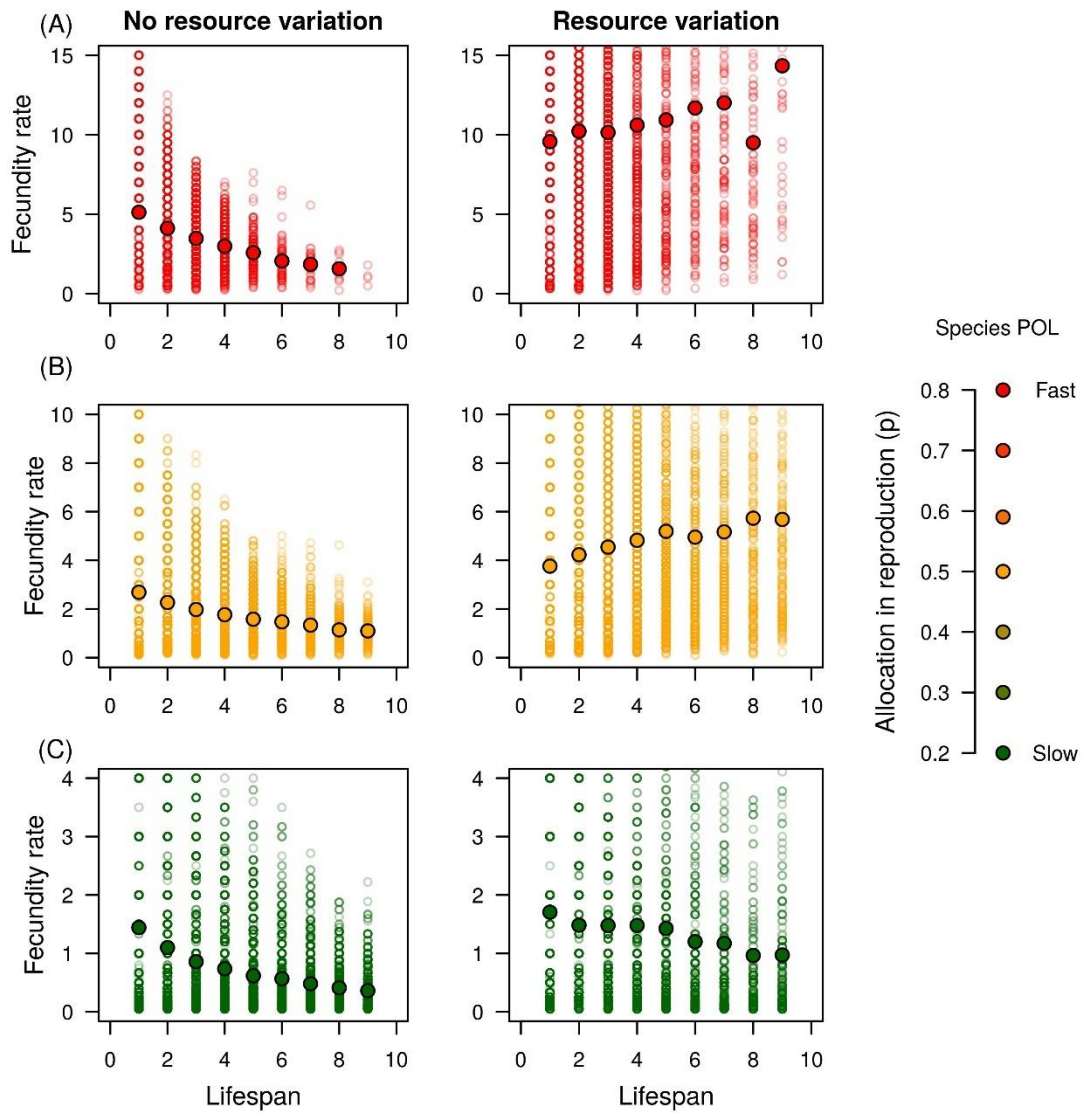


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Figure 1



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 874 **Figure 2.**



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876 **Figure 3.**