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1 **Models of pace-of-life syndromes (POLS): a systematic review**

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10

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19 **Abstract**

20 Variation in life-history (LH) traits along the fast-slow continuum (referred to as pace-of-life, POL) is thought to
21 result from a trade-off between investments in current versus future reproduction. Originally developed for
22 understanding variation in LH strategies at the among-population level, POL theory has more recently been
23 applied towards understanding variation in LH traits at the within-population level, and further extended to
24 address the covariance of LH traits with additional behavioural and/or physiological traits, referred to as pace-of-
25 life syndromes (POLS). The article by Réale et al. (2010; Philos T Roy Soc B 365:4051-4063), which
26 synthesized several earlier reviews and opinions on among-individual covariation between LH, behavioural, and
27 physiological traits, and subsequent research testing POLS in a variety of species, have collectively been cited
28 several hundreds of times—a trend that continues. These works have interdisciplinary impact, informing
29 research in life history biology, behavioural and developmental biology, and the social sciences. In this paper,
30 we review the existing theoretical POLS models that provide adaptive explanations for covariances between LH
31 traits and additional behavioural and/or physiological traits while assuming a trade-off between current and
32 future reproduction. We find that the set of relevant models is small. Moreover, models show that covariances
33 between life-history traits and behavioural or physiological traits can arise even in the absence of a current-future
34 reproduction trade-off, implying that observing such covariances does not provide a strong indication regarding
35 the process generating POLS. We discuss lessons learned from existing models of POLS, highlight key gaps in
36 the modelling literature, and provide guidelines for better integration between theory and data.

37

38 **Keywords:** animal personality, consistent among-individual differences, life history trade-offs, physiology, trait
39 covariance

40 “Science walks forward on two feet, namely theory and experiment ... Sometimes it is one foot that is put
41 forward first, sometimes the other, but continuous progress is only made by the use of both.”

42 - Robert A. Millikan, Nobel Lecture 1924

43 **Introduction**

44 Life-history (LH) traits often vary along a fast-slow continuum, with a fast pace-of-life (POL) characterized by
45 fast development, early age at first reproduction, and low survival, and a slow POL by slow development,
46 delayed reproduction, and high survival (Saether 1988; Stearns 1992; Ricklefs 2000). These patterns of
47 covariation may result from allocation trade-offs (Williams 1966); resources invested in current reproduction
48 cannot be invested in growth, survival, or future reproduction. Ecological conditions can mediate the resolution
49 of this trade-off, resulting in differences in LH traits across populations experiencing different ecological
50 conditions (Stearns 1992). POL theory was later extended to address the coevolution of behavioural and
51 physiological traits with the LH particularities of a species or population (Ricklefs and Wikelski 2002), referred
52 to as pace-of-life syndromes (POLS). For example, organisms evolved towards a slow POL may invest more in
53 traits that increase their probability of surviving long-enough to realize their future reproductive potential (e.g.
54 immunity) (Martin et al. 2006). Similarly, organisms evolved towards a fast POL may accept greater risk while
55 foraging to build assets for immediate reproduction (Stamps 2007).

56 More recently, Réale et al. (2010) suggested that the POLS concept may provide a useful framework for
57 understanding covariation between LH, behavioural and physiological traits among individuals of the same
58 population. Within-populations, individuals exhibit differences in LH strategies (Biro and Stamps 2008), as well
59 as consistent differences in behavioural (Bell et al. 2009) and physiological traits (Holtmann et al. 2016), and
60 LH, behavioural, and physiological traits often co-vary at the among-individual level (Stamps 2007; Biro and
61 Stamps 2008, 2010; Careau et al. 2008). In their paper, Réale et al. (2010) synthesized these previous bodies of
62 work and developed a series of verbal arguments for how and why LH, behavioural and physiological traits may
63 show particular patterns of covariance at the among-individual, within-population level (see also Belsky et al.
64 1991; Ellis et al. 2009 for verbal models of POLS in humans; Del Giudice et al. 2015). For example, if
65 aggressiveness facilitates the acquisition or monopolization of resources, it may have coevolved with high
66 growth rates and early reproduction, but at the cost of increased risk of mortality. Similarly, high metabolic rates
67 may be required to support the rapid growth required for early reproduction and high fecundity, but may
68 simultaneously increase mortality through increased production of reactive oxygen species. Since its

69 publication, the POLS hypothesis at the within-population level has generated a large amount of empirical
70 research (cited over 300 times, see Dammhahn et al. 2017; Royauté et al. 2017).

71 In this paper, we provide a systematic review of the formal (i.e. mathematical) theory of POLS. We review
72 existing models that incorporate a trade-off between current and future reproduction while addressing
73 covariation between LH, behaviour, and physiology at the within-population level. We focus on models that
74 incorporate the current-future reproduction trade-off, which features prominently in verbal POLS theory (e.g.
75 Ricklefs and Wikelski 2002; Réale et al. 2010). We acknowledge, however, that other trade-offs may also
76 produce POLS (see section on Equifinality, below).

77 Our results show that *there is in fact little formal theory about POLS*, particularly at the among-individual,
78 within-population level, and *many empirical tests of POLS have no formal bases for their predictions*. We
79 discuss the key assumptions and predictions of existing models, highlighting the mismatch between current
80 empirical tests and model assumptions. Further, we discuss models that predict patterns of covariance between
81 LH, behavioural, and physiological traits via different processes than a current-future reproduction trade-off.
82 Such models are relevant for the evolution of POLS, but are rarely cited in the POLS literature. The mismatch
83 between formal theory and empirical work does not, of course, undermine either; rather, it highlights the need
84 and potential for the development of novel theory addressing the evolution of POLS. Our aim is thus to facilitate
85 better integration of theory and empirical work by highlighting gaps in the current set of models to stimulate the
86 development of further theory and offer guidelines that help in devising tests of extant theory.

87

88 **Models of POLS at the within-population level**

89 In reviewing the literature, we followed the Preferred Reporting Items for Systematic Reviews and Meta-
90 Analyses (PRISMA) protocol (Moher et al. 2009). We searched the Web of Science database (search date
91 08.01.2016) for articles that included the key words “Pace of life” and “Model” or articles that cited Réale et al.
92 (2010). This produced 166 unique references. We read the title and/or abstract for each of these references to
93 assess whether the paper developed a formal model including a life history trait (e.g. age at first reproduction,
94 survival, etc.) and any additional behavioural and/or physiological trait. We considered models that addressed
95 the co-evolution of LH and behavioural and/or physiological traits, as well as the development of POLS over
96 ecological time (e.g. models of phenotypic plasticity). These models tended to address among- and within-
97 individual covariation respectively. We selected papers that met this criteria (N = 7) for reading the full text. We

98 identified an additional 11 articles from the reference lists of these seven articles, and a further 12 articles which
99 were known to the authors or to attendees of the workshop “Towards a general theory of pace-of-life syndrome”
100 (see ESM Fig. S1 for PRISMA flow diagram).

101 We thus selected a total of 30 papers for reading full text based on our search criteria. KJM and WEF
102 independently read each of these 30 papers to evaluate whether they should be included in the systematic review.
103 We established that models should meet all three of the following criteria in order to address the evolution or
104 development of POLS within populations:

105 *1. The study presents a formal model that includes a POL trait.* POL refers to covariances between LH traits
106 resulting from a current-future reproduction trade-off. We considered two ways of capturing this trade-off: (a) as
107 a single trait that allows only for certain combinations of trait values (e.g. the couples of early reproduction/low
108 survival and late reproduction/high survival), and not for others (e.g. early reproduction/high survival and late
109 reproduction/low survival); and (b) as two separable life-history traits (i.e. survival and reproduction), such that
110 all combinations of reproduction and survival were in principle possible. However, a current-future reproduction
111 trade-off was implicit such that within individuals, a higher investment in current reproduction implied a lower
112 investment in future reproduction. We excluded models with discrete, non-overlapping generations (i.e. a single
113 reproductive event per lifetime), because these do not allow for a current-future reproduction trade-off.

114 *2. There was at least one additional trait in the model that could represent a behavioural and/or physiological*
115 *trait.* This criterion was met either when a paper explicitly described a trait as behavioural and/or physiological,
116 or when the assumptions and descriptions of a model parameter were sufficiently general that even when not
117 described as a behavioural or physiological trait, the parameter could be viewed as representing such a trait. For
118 example, a parameter that describes resource level in the environment and whose level can vary could also be
119 taken to represent among-individual variation in the ability to monopolize resources (e.g. due to variation in
120 dominance).

121 *3. The model evaluated the covariance between the POL trait and the behavioural and/or physiological trait.*
122 This criterion was met either if the covariance structure between LH traits and the additional trait was explicitly
123 quantified, or if the covariance structure could be extrapolated based on information provided in the text. For
124 some models, covariances between the LH trait and the behavioural and/or physiological trait were imposed by
125 the model assumptions (i.e. the relationship between the two traits is fixed), rather than evolutionary outcomes.
126 We did not consider that such models address the evolution or development of POLS.

127 KJM and WEF resolved any discrepancies in the evaluation of whether or not a given study met each of these
128 criteria by discussion. Table 1 summarizes each of the 30 full texts evaluated for the three above-mentioned
129 criteria.

130

131 **Within-population models of POLS: within-individuals versus among-individuals**

132 Our systematic review yielded only 8 papers (one of which included two relevant models) of formal models of
133 POLS, i.e. which address the evolution of covariances between LH traits and additional behavioural and/or
134 physiological traits while assuming a trade-off between current versus future reproduction. We summarize each
135 of these models in Tables 2 and 3, highlighting aspects of the model assumptions and predictions that are crucial
136 to developing empirical tests of the models. These models address the evolution of covariance between LH and
137 behavioural and/or physiological traits at two different levels of biological organisation: 1) within-individuals
138 (Houston and McNamara 1989; Clark 1994), and 2) among-individuals within the same population (van
139 Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; Wolf et al. 2007b; van Doorn et
140 al. 2009; Engqvist et al. 2015).

141 The three models addressing POLS (derived from two papers: Houston and McNamara 1989; Clark 1994) at the
142 within-individual level have common features. Both use stochastic dynamic programming (Mangel and Clark
143 1988; Houston and McNamara 1999) to model risk-taking (specifically, a trait that increases resource acquisition
144 at the expense of increased probability of mortality) as a function of residual reproductive value (RRV), where
145 RRV represents the ratio of expected future reproduction to expected current reproduction. Both models involve
146 asset protection, whereby individuals with high assets (i.e. high RRV) are risk averse (i.e. avoid variability in
147 outcomes) to protect their assets. Although neither of these models evaluates the long-term consistency of risk-
148 taking, among-individual variation in RRV and risk-taking would be expected to erode over time given that asset
149 protection is a negative-feedback mechanism (McElreath et al. 2007; Luttbeg and Sih 2010) (but see Wolf et al.
150 2007a for a discussion of why negative feedbacks may not always erode among-individual differences). Thus,
151 the patterns of covariance predicted at the within-individual level by these models cannot be extrapolated to
152 predict patterns of covariance at the among-individual level.

153 We identified six models that address covariances between LH and behavioural and/or physiological traits at the
154 among-individual, within-population level. Four of these models did not address POLS for repeatedly expressed
155 behavioural and/or physiological traits. In the models by van Noordwijk and de Jong (van Noordwijk and de

156 Jong (1986); de Jong and van Noordwijk (1992); de Jong (1993)), the additional trait (resource acquisition) is
157 expressed only once per lifetime. Similarly, in the model by van Doorn et al. (2009), consistency of the trait
158 expression (foraging) is an assumption, rather than an outcome, of the model. Therefore, these models cannot
159 illuminate when individuals would be expected to exhibit consistent among-individual differences in a
160 repeatedly expressed trait, and when the average expression of such traits is expected to co-vary with LH traits.
161 However, most empirical tests of POLS (see reviews by Montiglio et al. 2017; Royauté et al. 2017), consider
162 covariances between LH and behavioural and/or physiological traits that are expressed repeatedly throughout an
163 individual's lifetime (e.g. activity, foraging boldness, parental care, aggression, metabolic rate, etc.).

164 We found only two models that address the evolution of POLS for repeatedly expressed behavioural and/or
165 physiological traits (Wolf et al. 2007b; Engqvist et al. 2015). The model by Engqvist et al. (2015) analyzes the
166 conditions under which males of varying degrees of attractiveness (i.e. reproductive value) should signal for
167 mates (a "risky" behaviour in that it increases access to potential mates at the cost of increased probability of
168 mortality due to predation). The model by Wolf et al. (2007b) analyzes the co-evolution of pace-of-life (early
169 versus late reproduction) and two "risky" behaviours: foraging boldness and conspecific aggression. These
170 models share several key features. Both assume frequency- and density-dependent payoffs to alternative
171 behavioural tactics and both models limit the scope for negative feedbacks to erode among-individual
172 differences in reproductive value. In the model by Wolf et al. (2007b), behavioural actions in the first hawk-dove
173 game (i.e. foraging boldness) influence their reproductive value, which in turn affect their optimal level of
174 aggression in the second hawk-dove game. However, the magnitude of these effects is assumed to be small, such
175 that negative feedbacks between state and behaviour can never negate differences in reproductive value caused
176 by differences in life history strategy. The Engqvist et al. (2015) model does not allow for any negative-
177 feedbacks between state and behaviour; risky-signalling for mates does not produce any lasting effect on male
178 attractiveness independent of the signalling itself. The models both predict that individuals with a fast POL will
179 have consistently higher levels of risk-taking behaviours compared to individuals with a slow POL.

180 These two models also differ in several ways. Wolf et al. (2007b) address covariances between POL and two
181 additional traits, while Engqvist et al. (2015) address covariances between POL and one additional trait. The
182 Engqvist et al. (2015) model emphasizes which changes in parameter values are required to alter the predicted
183 covariance structure. It shows that the predicted covariance between POL and risk-taking reverses when
184 differences in baseline mortality between attractive and unattractive males are small (i.e. when the trade-off
185 between reproduction and survival is weak). Additionally, in the Engqvist et al. (2015) model lifespan varies

186 probabilistically among individuals as a function of their attractiveness, their level of risk-taking, and the
187 frequency of their types in a population. In the Wolf et al. (2007b) model, maximum lifespan is fixed at two
188 reproductive periods (for discussion of developmental modeling of many time periods, including incremental
189 learning about the environmental state, see Stamps and Frankenhuis 2016).

190

191 **What the current models do not teach us**

192 Given the number of empirical studies aimed at testing POLS at the among-individual, within-population level
193 (reviewed in Royauté et al. 2017), the scarcity of formal theory is surprising. Here, we highlight two major gaps
194 in the existing modeling literature.

195 *What types of behavioural and/or physiological traits co-evolve with POL?*

196 The POLS hypothesis predicts covariation between LH traits and multiple, diverse, behavioural, and
197 physiological traits. However, we find that existing models of POLS address covariation of LH traits with a
198 small number of additional traits (one or two), and moreover, these (non-LH) traits share a key characteristic:
199 they directly affect resource acquisition. In some cases, and increase in resource acquisition is traded off against
200 survival (Houston and McNamara 1989; Clark 1994; Wolf et al. 2007b; Engqvist et al. 2015), and in others,
201 there was no direct consequence for survival (van Noordwijk and de Jong 1986; de Jong and van Noordwijk
202 1992; de Jong 1993; van Doorn et al. 2009).

203 In their paper, Réale et al. (2010) list 13 potential traits for integration within the POLS framework (seven
204 behavioural, six physiological). We suggest that the payoff structures (how the trait value affects fitness-relevant
205 parameters, such as survival probability and resource levels) used in current models of POLS apply to a limited
206 number of these traits. For example, greater foraging boldness may increase resource acquisition at the expense
207 of increased probability of mortality due to predation, and increased metabolic rate may increase access to
208 resources (but see Careau and Garland 2012; Mathot and Dingemanse 2015) at the cost of increased mortality
209 due to higher rates of oxidative damage. However, other traits are likely to have different payoff structures. For
210 example, increased immune function may cost resources but increase the probability of survival. For traits such
211 as sociability or HPA axis reactivity, the probable effects on resource acquisition (or net resource costs) and
212 survival are not obvious. Whether traits with these types of alternative payoff structures will also coevolve with
213 POL is presently unclear.

214 *What processes and conditions favour (or hinder) the development of POLS?*

215 The current models of POLS do not allow for general conclusions about the processes that favour or hinder the
216 development of POLS, in part because this set is small (eight models). Further, only two of these studies
217 addressed POLS at the among-individual, within-population level for repeatedly expressed behavioural traits
218 (Wolf et al. 2007b; Engqvist et al. 2015). In these two models, there is either no (Engqvist et al. 2015) or only
219 limited (Wolf et al. 2007b) possibility for feedbacks between state (reproductive value or assets) and behaviour.
220 They are also the only two studies to assume both frequency- and density-dependent payoffs (Table 2). Whether
221 such assumptions are necessary to evolve POLS at the among-individual level for repeatedly expressed traits is
222 currently unclear, and would require modification of these assumptions.

223 This relates to a general limitation of the current models of POLS: they explore a narrow parameter space.
224 Although each model summarized in Tables 2 and 3 included at least some exploration of changes in parameter
225 values on model outcomes (Table 3), these were limited to modifying values for one or two parameters. A
226 notable exception to this was the model developed by Engqvist et al. (2015), where there was extensive
227 exploration of parameter space for multiple combinations of parameter values. If the goal of studying trait
228 covariances within the POLS framework is to understand the processes that generate particular patterns of
229 covariance, then exploration of parameters space is essential to illuminate when different processes can lead to
230 the same outcome (Equifinality, see below) and when the same process can lead to different outcomes
231 (Multifinality, see below). Explicit consideration of the effects of parameter values on model outcomes will
232 provide more detailed predictions that may enable empiricists to discriminate between alternative processes, and
233 will simultaneously emphasize the importance of matching empirical tests to model assumptions.

234

235 **Equifinality: Different processes, one outcome**

236 Our review shows that POLS can emerge via at least two distinct processes: (1) a direct trade-off between
237 current and future reproduction (Houston and McNamara 1989; Clark 1994; Wolf et al. 2007b; van Doorn et al.
238 2009), or (2) a direct trade-off between current reproduction and survival (van Noordwijk and de Jong 1986; de
239 Jong and van Noordwijk 1992; de Jong 1993; Engqvist et al. 2015). In the former case, the covariance between
240 LH parameters (e.g. age at first reproduction and survival) results from interacting model assumptions. In the
241 latter models, covariance between LH traits is assumed (i.e. fixed combinations of trait values).

242 We also identified three models that involved neither of the aforementioned trade-offs, but which nonetheless
243 predict trait covariances that match predictions from POLS (Stamps et al. 1998; Mangel and Stamps 2001;
244 Mullan et al. 2016). For example in the models by Stamps et al. (1998) and Mangel and Stamps (2001),
245 organisms face a trade-off between growth and survival, which results in covariances between age at first
246 reproduction, survival, and morphological characteristic (see Hämäläinen et al. 2017 for discussion of integrating
247 morphology into the POLS framework). The model by Mullan et al. (2016), in which one trait has positive
248 indirect fitness benefits and the second trait increases pairwise relatedness (i.e. when two individuals that show
249 an increase in the value of a trait have a greater probability of being related than two randomly selected
250 individuals), predicts positive covariances that match POLS predictions (i.e. higher survival associated with
251 lower dispersal and greater helping behaviour). This prediction highlights that observations of particular patterns
252 of covariance between LH and additional traits do not allow for strong inferences about the *processes* generating
253 these patterns. If the same patterns of covariance can arise via multiple processes, how can we increase our
254 understanding of the processes generating patterns of trait covariance observed in biological systems? We
255 suggest that changing the focus of current models from “can POLS evolve?” (i.e. proofs of principle) to “when
256 do POLS evolve?” (i.e. what processes give rise to POLS depending on environmental context and the
257 organism’s state, and in what conditions are these processes likely to eclipse other processes that erode POLS)
258 will help in achieving this aim (see also Montiglio et al. 2017). Ideally, modellers would also stipulate how
259 model assumptions might be tested, and explicitly list suitable empirical systems, which satisfy their models’
260 assumptions.

261

262 **Multifinality: one process, different outcomes**

263 Of the models summarized in Tables 2 and 3, those that involved the most detailed exploration of parameter
264 space (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992; de Jong 1993; Engqvist et al. 2015)
265 also highlight that the same process can lead to different outcomes. For example, the models by de Jong and van
266 Noordwijk (van Noordwijk and de Jong (1986); de Jong and van Noordwijk (1992); de Jong (1993)) illustrate
267 how changing the degree of among-individual variation in resource acquisition can change the covariance
268 between two life history traits linked via a trade-off. When among-individual differences in resource acquisition
269 are small relative to the among-individual variance in allocation, the correlation between LH traits among-
270 individuals reflects the within-individual trade-off (i.e. there is a negative correlation between survival and
271 reproduction). However, when the among-individual differences in resource acquisition are relatively large, the

272 inherent trade-off becomes masked and there is a positive correlation between reproduction and survival at the
273 among-individual level. This insight has been tremendously influential (Metcalf 2016).

274 Engqvist et al. (2015) similarly show that the specific combinations of parameter values can have large effects
275 on predicted trait covariances. When the POL-related differences in baseline mortality are large, the predicted
276 covariance between POL and risk-taking is consistent with the prediction of Réale et al. (2010) that fast POL
277 will be associated with greater risk-taking. However, when the POL-related differences in baseline mortality are
278 small, individuals with a slow POL are predicted to be more risk-taking. This result arises because when
279 differences in baseline mortality are large, the cost to individuals with high reproductive value (attractive males)
280 of signaling in the presence of predators is relatively small, and therefore, attractive males signal. In contrast,
281 when the differences in baseline mortality are low, the cost of signalling for mates in the presence of predators is
282 large (relative to baseline mortality). As attractive males have more reproductive assets to protect, there is
283 selection against signaling by attractive males in the presence of predators. This trade-off results in a relaxed
284 competitive environment for unattractive males which favours greater signalling for mates by unattractive males
285 under predation risk. By highlighting that model assumptions and parameter values influence predicted trait
286 covariances, these papers provide more detailed predictions for empiricists (e.g. positive covariance expected
287 under condition x , but negative covariance under condition y). They also provide a reminder of the critical
288 importance of matching empirical tests to model assumptions.

289

290 **Guide for empiricists**

291 Scientific progress depends on a good fit between theory and data. In Table 2, we highlighted several aspects of
292 model assumptions that are relevant in devising sound empirical tests of theory, such as the type of trait
293 represented, whether payoffs are frequency- or density-dependent, the level of biological variation, etc. Here, we
294 discuss some assumptions of existing models in order to provide guidelines that can aid in the development of
295 empirical tests that are well matched to theory. Predictions arising from the existing set of POLS models are
296 summarized in Table 3.

297 The POLS concept develops verbal predictions for covariances between POL and a range of behavioural and
298 physiological traits. However, the formal models of POLS are relevant for only a subset of the traits outlined in
299 Réale et al. (2010). Empiricists should be careful to ensure that the traits they study are likely to show the type(s)
300 of relationships and payoff structure(s) assumed by the models. In other words, before testing model predictions,

301 empiricist should first examine, and ideally test, model assumptions in their system. For all existing models, the
302 additional non-LH trait increases access to resources, and either decreases survival or has no effect on survival.
303 Thus, for many behavioural and physiological traits (e.g. immune function, HPA axis reactivity, sociability,
304 etc.), there are in fact no formal predictions regarding their expected covariance with LH traits, and therefore,
305 quantification of their covariance with LH traits does not constitute a test of extant formal POLS theory.

306 Focusing on the payoff structures incorporated into models when selecting traits will help empiricist avoid so-
307 called ‘jingle-jangle fallacies’, when a single trait label describes two functionally different traits or when two
308 different labels actually describe the same trait (Carter et al. 2013). For example, in the model by Wolf et al.
309 (2007b), the POL trait is called ‘exploration’, and the model predicts covariance between ‘exploration’ and risk-
310 taking behaviours. However, in the animal personality literature, exploration is typically a measure of how an
311 organism moves through a novel environment (Réale et al. 2007), not a measure of their life-history strategy. In
312 fact, a recent meta-analysis reveals that exploration does not reliably co-vary with measures of reproductive
313 performance or survival (Smith and Blumstein 2008). Thus, the validity of using exploration as a proxy for POL
314 requires testing on a system-by-system basis. Testing for covariation between exploration (of a novel
315 environment) and risk-taking does not constitute a test of the Wolf et al. (2007b) model, nor does a positive
316 covariation constitute support for it, unless the assumption that exploration reflects POL has been tested.

317 In addition to choosing traits whose payoffs structures are properly captured by existing models, assumptions
318 related to the timing of their effects on resource (acquisition or allocation) and survival should be matched to the
319 biology of the empirical system. For example, in the Engqvist et al. (2015) model, resources gained by risky
320 mate signalling behaviour are converted instantly to reproductive output, reproductive assets do not accrue. In
321 the Wolf et al. (2007b) model, resources gained by risk-taking behaviour can accrue between year 1 and year 2,
322 but the potential increase in asset is small compared with differences caused by differences in life history
323 strategy. These may be valid assumptions when considering the risk-taking behaviour of income breeders during
324 the reproductive period, where the entire energy requirements for current reproduction are met by current energy
325 intake. It may similarly apply to risky-signalling for mates, as described in the Engqvist et al. (2015) model:
326 signalling for mates now increases access to mates now, but has no carry-over effect on access to mates in future
327 reproductive bouts. In contrast, behaviour outside of the reproductive period by definition is not converted
328 immediately to reproductive output, and therefore, should be expected to affect reproductive assets in ways that
329 feedback to influence risk-taking (McElreath et al. 2007).

330 Similarly, the assumption that the accrued assets will be small relative to differences in assets associated with
331 life-history decisions (Wolf et al. 2007b) may be unrealistic for behaviours that are expressed repeatedly
332 between reproductive bouts (e.g. foraging boldness). For example, the assets that might be gained from a single
333 expression of foraging boldness may reasonably be expected to have small effects on assets relative to
334 differences in assets associated with life history strategy. However, the cumulative effect of hundreds of
335 instances of risk-taking decisions between two reproductive bouts may be more reasonably expected to have
336 potentially large effects on assets. In fact, many empirical “tests” of POLS involve traits where the assumption
337 of no (or limited) feedback between behaviour and assets is unlikely to be upheld (e.g. foraging boldness during
338 the non-breeding season).

339

340 **Conclusions**

341 We conclude that there is, at present, little formal theory about POLS. Further, the only two models of POLS at
342 the within-individual, among-population level for repeatedly expressed traits (Wolf et al. 2007b; Engqvist et al.
343 2015), although pioneering and insightful, shared numerous characteristics that limit the range of empirical
344 applications. Both models address covariance between POL and a trait that increases access to resource at the
345 cost of increased probability of mortality (e.g. due to predation) (or two additional traits in the case of Wolf et al.
346 2007b). At the same time, they explicitly do not allow (Engqvist et al. 2015) or limit (Wolf et al. 2007b)
347 feedbacks between behaviour and reproductive value. We discuss scenarios where these assumptions are likely
348 to be met and which, therefore, would constitute the best possible tests of the existing theory. However, we also
349 point out that many studies that aim to test POLS do not satisfy these model assumptions, hence it is unclear how
350 much support exists for current theory. Future modelling work can contribute to our understanding of POLS by
351 shifting focus from demonstrating that POLS *can* evolve, to demonstrating *when* POLS evolve (providing a
352 flashlight for empiricists), and by modelling a wider range of traits (e.g. immunity, sociability, etc.).

353

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465

466 **Table 1** Overview of papers that were evaluated in the context of POLS

Reference	POLS criteria			Model attributes summarized in Tables 2 & 3 ^d
	POL ^a	Additional trait(s) ^b	Covariances evaluated ^c	
Baldauf et al. (2014)	N (D)	Y (1)	NA	N
Baldini (2015)	Y (A)	N	NA	N
Chan and Kim (2014)	Y (A)	Y (1)	I	N
Charlesworth (1990)	Y (A)	N	NA	N
Clark (1994)	Y (RRV)	Y (1)	Y	Y
de Jong and van Noordwijk (1992)	Y (A)	Y (1)	Y	Y
de Jong (1993)	Y (A)	Y (1)	Y	Y
Delaguerie et al. (1991)	Y (A)	N	N	N
Engqvist et al. (2015)				
I. All else being equal model	N ^h	Y (1)		N
II. higher baseline mortality for attractive males	Y	Y (1)	Y	Y
Frankenhuis et al. (2013)	Y (A)	N	NA	N
Houle (1991)	N (D)	Y (1)	NA	N
Houston and McNamara (1989)	Y (RRV)	Y (2)	Y	Y
Jonsson et al. (1998)	Y (A)	N	NA	N
Luttbeg and Sih (2010)	N (D)	Y (1)	NA	N
Mangel and Stamps (2001)	N (E)	Y ^g (1)	Y	N
Mallpress et al. (2015)	Y (A)	Y (1)	N ^f	N
McElreath and Strimling (2006)	N (D)	Y (1)	NA	N
McNamara and Houston (1996)	Y (RRV)	N	NA	N
Mullon et al. (2016)	N (E)	Y (1)	Y	N
Riska (1986)	Y (A)	N	NA	N
Sibly and Calow (1984)	Y (A)	N	NA	N
Stamps et al. (1998)	N (E)	Y ^g (1)	Y	N
Teriokhin (1998)	Y (A)	Y (1)	N	N
van Doorn et al. (2009)	Y	Y (1)	Y	N
van Noordwijk and de Jong (1986)	Y (A)	Y (1)	Y	Y
Wolf and McNamara (2012)	N (D)	Y (2)	NA	N
Wolf et al. (2008)	N (D)	Y (1)	NA	N
Wolf et al. (2011)	N (D)	Y (2)	NA	N
Wolf et al. (2007b)	Y (ST)	Y (2)	Y	Y
Worley et al. (2003)	Y (A)	N	NA	N

467

468 a. Is the trade-off between current and future reproduction implicit in the model assumptions? Yes (Y) or No
469 (N). The implicit trade-off can be modelled either as a single trait that captures the trade-off (ST) (e.g. trait
470 values are either early reproduction/low survivals or late reproduction/high survival), residual reproductive
471 value (RRV), or as an allocation decision (A). Allocation decision can be directly between current and future
472 reproduction, or between current reproduction and survival as these are nested within current/future
473 reproduction trade-offs (i.e. if you die, you necessarily cannot reproduce). Note however that current/future
474 reproduction trade-offs do not necessarily imply differences in survival. Models did not meet the LH trade-off
475 criteria if they did not allow for variation in investment to current versus future reproduction because models
476 were structured with discrete non-overlapping generations (D), or because there was no implicit trade-off

477 between current and future reproduction. However, even in the absence of an implicit trade-off, variation
478 timing of reproductive events can arise as an emergent property of a model (E)

479 b. Additional trait(s): were additional traits considered in the models that can be interpreted as either
480 behavioural and/or physiological traits. Number of additional traits is provided in parentheses

481 c. Was the covariance between the LH traits and the additional trait(s) evaluated? Not applicable (NA) if either
482 LH trait or additional trait is absent, yes (Y) if the model directly evaluates covariance structure between LH and
483 additional trait, or covariance structure can be directly extrapolated based on information provided in the text,
484 no (N) if the model neither directly evaluates covariance structure nor is information directly available in
485 current results, or imposed (I) if covariance between traits is imposed by the model assumptions in such a way
486 that only a single covariance is possible (e.g. trait A ~ trait B + constant)

487 d. Model attributes summarized in Table 2, predictions outlined in Table 3: Yes (Y) or No (N). Models were
488 selected for more detailed summaries if they met all four criteria for POLS at the within-population level. We
489 additionally included models that met all criteria except for evaluating the consistency in trait expression over
490 the lifetime of individuals as these may be relevant for understanding POLS at different levels of variation (e.g.
491 among-populations or within-individuals) (see Table 2)

492 e. Analyses predict fixation of trait R (allele for resource acquisition), therefore, no possibility for genetic
493 covariance between resource acquisition and allocation (C) between reproduction and survival. Phenotypic
494 variance in R is all due to stochastic processes

495 f. Consistency and/or covariances not evaluated for the traits relevant for POLS (e.g. consistency of POL or
496 additional trait, or covariance between POL and additional trait)

497 g. additional trait is body size (morphological, not behavioural or physiological)

498 h. In the model version where only attractiveness (i.e. reproductive value, RV) differs among males, variation in
499 survival comes about because less attractive males are expected to be more risk-taking. This is not a POLS trait
500 however, because there is no implicit trade-off between current and future reproduction, and the covariance
501 between RV and survival that emerges from the model is opposite to the covariance that would be expected
502 given the trade-off

503 **Table 2** Subset of papers summarized in Table 1 that met the three minimum criteria laid out for a model to address POLS. Additional details on model structure are provided
 504 to facilitate interpretation of model applicability

Ref	Source of initial variation ^a	Model attributes									
		Model type ^b	Environment structure ^c	Social environment ^d	Feedbacks ^e	Lagged effects ^f	Additional factors	Inheritance system ^g	Consistency evaluated	Applicable levels ^h	
Clark (1994) ^j	Continuous reproduction	NA	Stochastic dynamic	No	No	Yes (-)	No	No	NA	No	WI
	Growth and episodic reproduction	NS	Stochastic dynamic	No	No	Yes (-)	Yes	No	NA	No	WI
de Jong (1993)	NS	Deterministic	No	No	No	No	No	NA	NA ^k	AI ^m	
de Jong and van Noordwijk (1992)	NS (genetic) S(phenotypic)	Genetic	No	No	No	No	No	Diploid, single locus	NA ^l	AI ^m	
Engqvist et al. (2015)	NS	Stochastic dynamic	No	FD, DD	No	No	No	NA	Y (can be inferred from information given in text)	AI	
Houston and McNamara (1989)	NS	Stochastic dynamic	No	No	Yes (-)	No	Yes (metabolic rate)	NA	No	WI	
van Doorn et al. (2009)	M	Individual-based simulation	Yes (discrete habitat patches)	FD	Yes (explore both + and -)	Yes	No	Diploid, multilocus	NA	AI	
van Noordwijk and de Jong (1986)	NS	Deterministic	No	No	No	No	No	NA	NA ^l	AI ^m	

Wolf et al. (2007b)	M (POL trait) NS (behavioural traits) Later variation in behavioural traits also arises via mutation	Individual-based simulation	No	FD, DD	Yes (-), but effect is constrained to be small relative to differences arising from LH variation	Yes ⁱ	No	H-ML, D-ML	Yes, but under restrictive conditions (traits expressed only twice in lifetime)	AI
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506 ^a**Source of initial variation:** Assumed, but origin not specified (NS), mutation (M), stochasticity (S), not applicable because no among-individual differences taken to exist (NA)

507 ^b**Model type:** Genetic (G), Deterministic state-dependent, stochastic dynamic state-dependent, (co-)evolutionary

508 ^c**Environmental structure** refers to attributes of the environment that affect all individuals simultaneously (e.g. high versus low resource availability, different patches, stochastic environmental fluctuations) but not to attributes that affect individuals singly (e.g. stochastic variation in prey encounter rates). Variation in these attributes must
509 exist either within the lifetime of an individual (within-generation, WG), or of the lineage (among-generation, AG)
510

511 ^d**Social environment:** Is there social environment structure? Yes: Frequency dependent payoffs (FD), or density dependent payoffs (DD), or No

512 ^e**Feedbacks:** Yes: the output of trait A affects the input for trait B, and vice versa. When the effect of A on B and of B on A are in the same direction (e.g. higher value of A
513 increases B, higher value of B increases A), the feedback is positive (+), when they are in opposite directions, the feedback is negative (-)

514 ^f**Lagged effects** Yes: the consequences of behaviour for reproduction are delayed; No: the consequences are immediate. Y/N indicates that both lagged and non-lagged effects
515 were explored

516 ^g**Inheritance system:** Not applicable (NA, non-genetic model), haploid (H), diploid (D), single locus (SL), multi-locus (ML)

517 ^h**Applicable levels:** what level of variation was the model constructed to explain? Among –populations (AP), among-individuals within the same population (AI), within-
518 individuals (WI)

519 ⁱModel involves many iterations in each of the two years of an individual's life, but the consequences of POL (exploration) in year 1 for resource level only emerge in year two.
520 The survival effect however, is immediate

521 ^jnote that (Clark 1994) involves multiple models 1) continuous reproduction (included because it addresses WI covariation), 2) growth and episodic reproduction included
522 because it explores lagged effects

523 ^kR (resource acquisition) is expressed only once in an individual's life, no within-individual variation possible. However, consistency of allocation decisions was evaluated

524 ^lR (resource acquisition) and c (allocation decision) each expressed only once in an individual's lifetime

525 ^mAlthough predicted covariances between LH and additional behavioural and/or physiological trait are applicable at the among-individual level, the additional trait is not
526 expressed repeatedly in an individual's lifetime, and therefore the model does not address the stability of repeatedly expressed traits (i.e. animal personality)

527 **Table 3** Subset of papers summarized in Table 1 with details on model predictions

Reference	POL	Additional trait(s)	Predicted covariance	Conditions
	<i>i.e. how POL is modelled</i>	<i>i.e. how the paper describes the additional trait</i>	<i>Between POL and additional trait</i>	<i>i.e. parameter space explored</i>
Clark (1994)				
Continuous reproduction	RRV ^a	Risk-taking while foraging (implicit trade-off between gaining resource and survival)	Risk-taking increases with decreasing RRV. Animals become more risk-taking as they age. Stability not directly analyzed, but not expected based on negative feedback	Changing T (maximum number of time steps).
Growth and episodic reproduction)	RRV ^a	Risk-taking (foraging tactics: implicit trade-off between gaining resources and survival)	Stability of syndromes not analyzed Generally, higher RRV favours lower risk-taking.	Explore consequences of different levels of starting body mass
de Jong (1993)	Allocations (successive)	R (resource availability) Can be thought of as a behavioural or physiological trait that influences access to resources	Predicted covariance between fecundity and survival at different points in time depend on mean acquisition, variance in acquisition, and initial allocation decision (see Figures 3 and 4 from de Jong (1993)	Explore consequences of varying R, and varying allocation decisions at different times in life
de Jong and van Noordwijk (1992)	Allocation	R (resource availability) Can be thought of as a behavioural or physiological trait that influences access to resources	When there is large among-individual variance in R, among-individual covariation between reproduction and survival is positive, and both co-vary positively with R When there is little among-individual variation in R, reproduction and survival are negatively correlated. There is no covariance with R (because R does not vary, or varies little, among-individuals)	Explore consequences of varying R among-individuals
Engqvist et al. (2015)	Parameter values for two traits set to encompass	Risky-signalling (signalling behaviour to attract mates,	When signalling costs are relatively low, fast POL covaries positively with risky-signalling (boldness)	Explore consequences of varying differences in

	trade-off (baseline mortality greater for males with high reproductive value)	increases mating success but increases predation rate)	When differences in baseline mortality are low, slow POL individuals are more risk-taking	baseline mortality, explore consequences of varying predation costs of signalling
Houston and McNamara 1989 ³	RRV ^a (note that term used in paper is expected future reproductive success)	g (gross rate of gain while foraging, could reflect food availability, or variation in energy assimilation rates) u (proportion of time allocated to foraging, considered “risky” in the sense that it increases risk of predation relative to non-foraging)	Stability of syndromes not analyzed Generally, higher RRV favours lower risk-taking.	Explore consequences of variation in gross energy gain and energy reserves for the relationship between risk-taking and RRV
van Doorn et al. (2009)	Choice between current versus future reproduction (decision to breed immediately or queue for a territory)	Foraging. Individuals can choose between foraging under predation risk (risk declines with age), or under low risk (risk does not vary with age) Decision taken only once in an individual’s lifetime, switching is not possible.	Variation in POL and behaviour evolve first via frequency-dependence. Then correlation evolves such that individuals with a slow POL (those that queue for reproduction) are expected to forage under predation. When negative feedbacks between assets and risk-taking are allowed, the among-individual differences erode	Explore consequences of + versus – feedbacks between assets and risk-taking
van Noordwijk and de Jong (1986)	Allocation	R (resource availability) ¹ Can be thought of as a behavioural or physiological trait that influences access to resources	When there is large among-individual variance in resource acquisition (R), higher R is associated with higher fecundity and higher survival When there is low-among-individual variance in resource acquisition, higher fecundity is associated with lower survival, but there is no covariance with R (because R shows little variance)	Explore consequences of varying R among-individuals
Wolf et al. (2007b)	Single trait encompassing trade-off ^c	Two separate risk-taking behaviours:	Covariation between POL and risk-taking behaviours arise due to state (POL)-dependent payoffs. Mix of	Explore different payoff combinations in anti-

		Boldness/shyness Aggressiveness (hawk/dove)	types maintained in populations via frequency- and density-dependence	predator and hawk-dove game
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528 ^aRRV = residual reproductive value, the ratio of expected future reproduction to expected current reproduction

529 ^bIndividuals have a total finite resource amount available, which they can allocate to current reproduction (fecundity) or future reproduction (survival)

530 ^cPOL capture by life history trait encompassing trade-off between current and future reproduction. Trait is called "exploration". Higher exploration = lower current
531 reproduction but higher future reproduction, lower exploration = higher current reproduction but lower future reproduction. Other combinations of current/future
532 reproduction (e.g. high-high, low-low) are not possible