

1 **Integrating behavior in life-history theory: allocation versus acquisition?**

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11
12 **Highlights:**

- 13 • Current theory predicts that among-individual variation in behavior is maintained by
14 variation in how individuals resolve life-history trade-offs.
- 15 • Individuals that exhibit 'fast' phenotypes are expected to allocate more into current
16 reproduction and acquire more resources to fuel this investment, while 'slow' phenotypes,
17 with lower acquisition, are predicted to allocate more into future reproduction.
- 18 • Thus, current theory is assuming the presence of behaviorally-mediated among-individual
19 variation in both resource allocation *and* resource acquisition, simultaneously.
- 20 • Here we highlight how explicit considerations of whether behavior is more closely linked to
21 variance in resource acquisition or resource allocation can improve predictions about the
22 observed correlations between behavior and life-history traits, drawing general
23 implications for life-history theory.

26 **Abstract**

27 Central theories explaining the maintenance of individual differences in behavior build on the
28 assumption that behavior mediates life-history trade-offs between current and future reproduction.
29 However, current empirical evidence does not robustly support this assumption. This mismatch might
30 be because current theory is not clear about the role of behavior in an individual's allocation versus
31 acquisition of resources, hindering its empirical testing. The relative importance of allocation
32 compared to acquisition is a key feature of classic life-history theory but appears to have been lost in
33 translation in recent developments of life-history theory involving behavior. We argue that
34 determining the relative balance between variation in resource allocation and acquisition, and
35 behavior's role in this, will help build more robust and precise predictions.

36 **Modern "pace-of-life syndrome" framework: where are we standing?**

37 For the last two decades, understanding the existence of **among-individual variation** (see Glossary) in
38 behavioral expression (i.e. 'animal personality') has been a main focus of behavioral, evolutionary and
39 animal ecology [1,2]. One of the central theories explaining the existence and maintenance of these
40 individual differences in behavior relies on the assumption that behavior mediates a trade-off between
41 resource acquisition and mortality risk: individuals expressing 'riskier' behaviors (i.e. higher aggression,
42 boldness, exploration, activity) are able to acquire and hold more resources, compared to less risky
43 individuals, but in doing so expose themselves to higher mortality risk [2–4]. This modern 'pace-of-life
44 syndrome' (POLS) framework has generated testable predictions about patterns of trait correlations
45 where **'fast' phenotypes** are expected to invest heavily in current reproduction (e.g. faster growth,
46 earlier reproduction, higher metabolic rates) at the expense of survival, whereas **'slow' phenotypes**
47 will prioritize survival and future reproduction. The modern POLS framework has inspired a whole
48 generation of empiricists that put these theories to the test over the last decade, including the use of
49 similar frameworks in human life-history research [5,6, and sometimes abused 7]. However, the
50 accumulating empirical effort has revealed that the predicted patterns of correlations among behavior
51 and other traits are not well supported [8–10].

52 Here, we outline a broader framework for the POLS hypothesis that aims to reconcile the
53 apparent mismatch between theoretical predictions and empirical evidence. We argue that the
54 specific role that behavior plays as a mediator of life-history trade-offs and specifically whether, and
55 what role it plays in influencing an individual's resource **allocation** compared to its resource **acquisition**
56 needs to be further refined in a new POLS framework.

57 **Relative balance of allocation to acquisition: lost in translation?**

58 The classic life-history trade-off between current and future reproduction predicts that the resources
59 an individual allocates to current reproduction comes at the expense of resources available for future
60 reproduction leading to a negative association between the two [11]. There is strong empirical support
61 for this at the among-species level [12,13]. However, van Noordwijk and de Jong [14] critically pointed
62 out that when measured at the within-species level, if individuals differ in their average resource
63 acquisition, this allocation trade-off can be masked at the **'phenotypic' level**. This is because
64 individuals that can acquire more resources overall (either because resource acquisition is genetically
65 or environmentally determined) will be able to allocate more, in absolute terms, to both current and
66 future reproduction compared to individuals who acquire fewer resources [14,15]. It is indeed this
67 relative balance between acquisition and allocation that will determine the appearance of this trade-
68 off at the phenotypic level. If there is comparatively greater variation among individuals in the
69 allocation of resources compared to variation in acquisition, then a negative correlation among life-
70 history traits is expected; if there is greater variation among individuals in the acquisition of resources
71 compared to variation in allocation, a positive correlation can emerge ([14]; Fig 1). This has been a
72 topic of considerable discussion in life-history theory since the 1980s [14,16,17]. It appears however
73 that explicit consideration of this balance, and the role that behavioral expression plays in it, was lost
74 in translation during the development of the modern POLS framework (Box 1: A historical perspective).

75 The modern POLS framework is based on the assumption that selection has favored correlated
76 suites of life-history and behavioral traits to resolve the trade-off between current and future
77 reproduction and that behaviors help mediate this key trade-off [2]. This builds on the hypothesis that

78 individuals that allocate more in current reproduction need a faster metabolic engine requiring more
79 resources for fuel [18]. Individuals with different allocation strategies are predicted to also exhibit
80 differences in behavior and hence resource acquisition abilities, with ‘fast’ phenotypes (greater
81 expression of boldness, activity, exploration, aggression; see Fig 1 in [4]) acquiring more resources
82 compared to ‘slow’ phenotypes. What this means is that the POLS framework is assuming the presence
83 of among-individual variation in both resource allocation *and* resource acquisition, simultaneously.
84 The hypothesis, as it stands now, is not clear about whether we expect an individual’s behavior to play
85 a larger role in their allocation or their acquisition of resources and just as importantly, what we expect
86 the relative balance between among-individual variation in allocation and acquisition to be in a
87 particular system. Therefore, the apparent lack of empirical support for the modern POLS framework
88 may not be because the inherent **within-individual trade-offs** are absent or because behavior plays no
89 role in them. Instead, the POLS framework has not defined its assumptions clearly enough to know
90 exactly how the structure of trait correlations will appear at different **biological levels** and under
91 different environmental conditions. Such clarity will require a better understanding of the relative
92 balance between variation in resource allocation to resource acquisition within a particular study
93 system and then explicit consideration of how we expect individual behavior to be linked to both these
94 processes.

95 **POLS at different levels of biological variation**

96 The relative magnitude of variation in resource allocation compared to in resource acquisition will
97 determine the strength and sign of the observed relationships between costly traits. Comparative work
98 has shown that if species’ estimated allocation to current versus future reproduction was plotted, a
99 negative relationship would emerge whereby ‘slow’ species have longer lives and produce relatively
100 fewer offspring compared to ‘fast’ species that exhibit quicker maturation and production of many
101 offspring [12,13,19,20]. While other axes of life-history variation have been proposed [21,22], this
102 ‘fast-slow’ continuum explains 70% of the variation in life history strategies among species in animals
103 [13].

104 The modern POLS framework extends the idea that this trade-off will also shape trait
105 integration at the within-species level (Box 2: Empirical testing across biological levels). The
106 fundamental within-individual trade-off between current and future reproduction is expected to exist
107 at this level: individual animals do not reproduce at a maximal rate immediately at birth and continue
108 to do so throughout their lives. However, for the expected negative correlation among traits to be
109 measurable at the within-species level (i.e., within-population among-individual level), the variation in
110 allocation strategies among individuals would have to be larger than the among-individual variation in
111 resource acquisition (Fig. 1). Many traits will influence both an individual's acquisition of resources and
112 their allocation of those resources to the different fitness goals that animal needs to achieve. For
113 example, resource allocation strategies will be determined by the coordination of many anatomical
114 and physiological traits (e.g. organ size, hormone receptors, metabolism) [23–25]. These traits,
115 particularly the endocrine system, have been suggested to constrain the allocation of resources
116 resulting in well-conserved patterns of covariation among life-history traits [25]. Resource acquisition
117 will certainly be influenced by the anatomy and physiology of an animal but also by cognitive and
118 behavioral traits that will ultimately determine an individual's ability to locate and harvest resources
119 [26,27]. It may be unlikely that a single species would harbor the same order of magnitude of variation
120 in critical anatomical/physiological traits associated with resource allocation among individuals as
121 would be present across a large range of species [28]. Indeed, the fast-slow continuum seems to
122 explain a decreasing amount of life-history variation when approaching the individual level from higher
123 biological levels [5]. If, at the within-species level, there is in fact greater relative among-individual
124 variation in resource acquisition compared to that of resource allocation, this could mask the
125 fundamental within-individual trade-off (Fig 1) and help explain the lack of robust empirical support
126 for the predictions of the modern POLS framework [9,10]. Although quantifying variation in resource
127 acquisition and resource allocation for a given species will carry its own challenges, this information
128 will pave the way for the refinement of the POLS framework to better understand when and at which

129 biological level of variation (e.g. among-species versus among-individuals) we expect to detect the
130 fundamental trade-offs.

131 **Behavior's role in mediating acquisition and allocation**

132 After considering the relative balance between allocation and acquisition in a system, the next step in
133 the refinement of the POLS framework will be to consider whether and how we expect behavior, and
134 which behaviors, to be linked to either (or both) of these processes. Hormones, metabolic physiology,
135 and immune function can play key functional roles in the allocation of resources to reproduction
136 [24,29]. Therefore, if individual behavioral variation is linked to variation in the allocation of resources,
137 then we should expect to find associations between these physiological mechanisms and behavior as
138 well. Metabolic rate, for example, has been assumed to be one of the key physiological traits driving
139 variation in life-history at the among-species level with 'fast' species exhibiting higher metabolic rates
140 [30, but see 31]. The POLS framework has extended this notion to the within-species (and within-
141 population) level. However, theoretical work has shown that the associations between behavior and
142 metabolic rate at the within-species level can be predicted to be positive, null (i.e. not correlated) or
143 negative, depending on the energy allocation model that is used [18,32–34]. For instance, some energy
144 allocation models predict that behavior will be controlled by bottom-up physiology and so will be just
145 one of many traits competing for resources; indeed a recent meta-analysis found greatest support for
146 such 'performance' models [35]. Finally, the current collective evidence does not support an
147 association between metabolic rate and behavior at the among-individual level [8]. Altogether, this
148 suggests that it is unlikely for behavior to play a causal role in determining the allocation of resources;
149 understanding the mechanisms underlying behavioral expression and resource allocation would help
150 to clarify this association. Therefore the key, unresolved question is whether behavior (and which
151 behaviors) causally affects allocation to reproduction via metabolism (or other physiological
152 pathways), or whether behavior is more likely to be one of the passengers, rather than the captain, of
153 the ship when it comes to energy allocation to reproduction [8,35].

154 In resource acquisition, the role of behavior is likely to be more direct. By definition, animals
155 must “behave” (e.g. search, sample, move) in order to gain energy. Indeed, optimality models of
156 energy acquisition played a large role in initiation of behavioral ecology as a study field (i.e. optimal
157 foraging theory; [36]). All else being equal, differences in resource acquisition can then increase an
158 individual’s quality through, for example, increased growth rates or lipid storage [3]. This could allow
159 increased allocation to several traits in absolute terms, leading to a positive correlation between costly
160 traits at the among-individual level [15] (Fig 1). For example, in male three-spine sticklebacks
161 (*Gasterosteus aculeatus*) which perform parental care, a trade-off between nest care and nest
162 defense is expected as both traits are costly. However, Stein and Bell [37] instead found a positive
163 correlation whereby some male sticklebacks exhibited both greater nest care and greater defense
164 compared to other males. These males also occupied higher quality territories suggesting that these
165 males were intrinsically of higher quality and so could better gain such a territory, or once their
166 territory was established, access to the resources on that territory increased the individual’s overall
167 quality. There is now considerable evidence that more active, aggressive and/or explorative individuals
168 (i.e., ‘fast’ phenotypes) are able to acquire more resources (or acquire territories holding more
169 resources) [reviewed in 3,38]. Therefore, the current evidence suggests a stronger direct functional
170 link between behavior and resource acquisition as compared to between behavior and resource
171 allocation. Importantly, even though the current POLS hypothesis assumes that many behaviors, e.g.
172 boldness, aggression, exploration, activity, parental care, sociability, are integrated into POLS [4], it is
173 not clear which behaviors actually are functionally associated with resource acquisition, allocation
174 and/or life-history and whether we should expect the same directionality in all the relationships.
175 Moreover, the functional role of a specific behavior probably depends on both the species (i.e. biology)
176 and/or the environment (i.e. ecology) [39]. Thus, a major goal moving the field forward will be to
177 determine not just whether behavior is linked with life-history trade-offs, but exactly which behaviors
178 and in which environments this linkage is most likely to exist.

179 If individual behavioral variation is more likely to be functionally linked to resource acquisition,
180 and there is greater variation among individuals in resource acquisition compared to allocation, then
181 this can mask or reverse the expected negative correlation between behavior and other life-history
182 traits at the among-individual level (Fig 1). The current POLS framework is built on the assumption that
183 individuals that express ‘fast’ phenotypes should suffer higher mortality [2–4]. But if behaviors
184 expressed by fast phenotypes allows individuals to harvest more resources then this could compensate
185 for the potential survival costs associated with such behavior. Indeed, some state-dependent models
186 predict that individuals in relatively good condition or that are structurally larger are better able to
187 avoid predation [40,41]. Moreover, a recent meta-analysis demonstrated that riskier individuals,
188 contrary to POLS predictions, had higher survival, but only when measured in wild conditions, where
189 presumably individuals could better express variation in their resource acquisition abilities compared
190 to lab conditions and where extrinsic mortality plays a role [10]. Finally, classic life-history trade-offs
191 are more likely to be revealed when animals are measured in stressful, e.g. resource-depleted,
192 conditions [11], indicating that trade-offs can be masked by acquisition. While the presence of
193 variation in energy acquisition is briefly mentioned in the modern POLS literature as one explanation
194 for the absence of a trade-off between current and future reproduction [39], it does not appear that
195 the field has comprehensively considered how the relative importance of acquisition versus allocation
196 will modulate predictions of trait associations. Indeed, these considerations go beyond POLS and
197 behavior as they raise questions on how best to measure any type of trade-off at different levels of
198 biological organization. If within-individual constraints, e.g. the resources an individual allocates to
199 current versus future reproduction, can be masked by among-individual differences in other traits, e.g.
200 resource acquisition via behavioral expression, then this will make the observation of any expected
201 negative relationship between traits very difficult at the among-individual level. Indeed, this is the
202 most frequent explanation for the non-detection of reproductive costs [15], and likely contributes to
203 problems with the phenotypic gambit [42] and comparisons between populations. Such considerations
204 are critical though, and here we show how they can help researchers to make much-needed

205 predictions about under which conditions negative versus positive relationships between life-history
206 traits and behavior are expected to be observed (Fig 1).

207 **Concluding Remarks**

208 The modern pace-of-life syndrome framework can still learn important lessons from revisiting classic
209 life-history theory while also placing more emphasis on developing formal modeling [43] and carrying
210 out more experimental work, to push the field forward. Considering the relative balance of among-
211 individual variation in resource allocation compared to resource acquisition in a system, and how we
212 expect behavioral variation to be linked to either or both of these processes, is a good first step
213 (Outstanding Questions). Such considerations have the potential to transform the modern pace-of-life
214 syndrome framework into a more predictive framework about the integration of life-history,
215 physiological and behavioral traits, and go even beyond POLS, providing clarifications for general life-
216 history research.

217

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228 **Outstanding questions**

229

230 Within a species, what is the magnitude of among-individual variation in allocation? Do aspects of a
231 species' ecology or biology predict whether allocation or acquisition will exhibit greater variation? For
232 example, are species that exhibit variation in mating strategies (e.g. sneaker versus territorial males)
233 more likely to exhibit greater variation in allocation strategies? Or are species that live in resource-
234 poor (e.g. deserts) versus resource-rich (e.g. tropical forests) environments more or less likely to show
235 greater variation in resource acquisition?

236

237 Are traits correlated due to constraints imposed by developmental plasticity or shared pathways (e.g.
238 physiology, pleiotropy)? Experimental manipulations of physiological traits can be used to test for
239 correlated responses in behavior and life-history. For example, in poikilothermic animals, will
240 increasing metabolic rate (e.g. by manipulating temperature) result in 'fast' life-histories and 'riskier'
241 behavior? Will artificial selection experiments with direction selection on certain physiological,
242 behavioral or life-history traits result in correlated responses in other traits?

243

244 How can we use environmental manipulations to test POLS predictions, e.g., by constraining
245 individuals' abilities to acquire resources within a laboratory environment? How widespread is the
246 existence of genotype by environment interactions in allocation and acquisition strategies? Is the
247 relationship between behavior and allocation and/or acquisition stable throughout an animal's life?
248 How is behavioral plasticity related to POLS; do individuals with relatively 'slow' phenotypes exhibit
249 relatively greater behavioral plasticity?

250

251 How often do POLS patterns at the additive genetic level resemble patterns at the unpartitioned
252 phenotypic level? What is the role of permanent environmental effects (e.g., due to developmental
253 plasticity from early life environmental conditions) in the expression of POLS? Could the mixed support

254 for the POLS hypothesis be related to mismatch in trait correlations generated by permanent
255 environmental and additive genetic effects?

256

257

258 **Box 1. A historical perspective**

259 The modern POLS framework [2,4] is built on classical *r/K*-selection theory [44–46]. The latter
260 postulates that phenotypes or genotypes characterized by fast growth, early maturation and rapid
261 reproduction are selected for at low population densities while the opposite phenotypes/genotypes
262 are favored at high population densities [45]. The modern pace-of-life framework differs from the *r/K*-
263 selection framework in that it i) includes more traits (behavior and physiology) and ii) focuses
264 exclusively on variation among individuals within populations. Thus, the POLS hypothesis integrates
265 life-history, evolutionary biology, behavioral ecology and animal physiology research under one
266 framework.

267 Similar to the *r/K*-selection framework that evolved through time to be more complex and
268 realistic [45], the POLS framework has also seen important development towards acknowledging the
269 biological and ecological complexity in the expression of pace-of-life syndromes [2,39]. One of the key
270 differences in the development of the *r/K*-selection and the POLS framework is that the former is
271 strongly linked to population dynamics and ecology, and has evolved through formal mathematical
272 modeling while the latter is largely based on verbal models inspired by formal slow-fast continuum
273 hypotheses [43,45] and population dynamics or strong ecological elements were only involved in very
274 recent, mostly verbal, models [39,47,48]. The lack of formal models might be one of the reasons for
275 the phenomenological nature of the empirical work testing the POLS framework: solid testable
276 predictions about the conditional expression of pace-of-life syndromes are still largely missing. The
277 general scarcity of formal models leads to 1) few detailed predictions that may enable empiricists to
278 discriminate between environmental-specific processes and 2) limited ability for empiricists to match
279 their study system and experimental designs to particular model assumptions [43]. The lack of formal

280 models in pace-of-life syndromes research is in line with a general declining trend in formal models in
281 life-history related research [49]. Life-history research has also become more fragmented through
282 time, potentially reducing the exchange of ideas across closely related sub-fields [49].

283 **Box 2: Empirical testing across biological levels**

284 The POLS framework posits that past selection have favored particular associations among traits [4].
285 How do we best identify these patterns and test their evolutionary and ecological implications? The
286 signatures of past selection pressures are best identified at the additive genetic level, and assessing
287 genetic constraints (or lack thereof) can provide information about the short-term evolutionary
288 potential of trait correlations [11,50]. Quantitative genetic breeding designs coupled with appropriate
289 statistical models (e.g. ‘animal models’ [51]) allow researchers to partition phenotypic variance among
290 its additive genetic, permanent environmental and/or maternal components. Using such methods,
291 Santostesfano et al. [52] found a positive genetic correlation between developmental time and lifespan
292 in field crickets (*Gryllus bimaculatus*) as expected by POLS predictions; however this effect was masked
293 at the phenotypic level due to a negative correlation imposed by permanent environmental effects.
294 Boulton et al. [53] used similar quantitative genetic designs to test for correlations in social dominance
295 and growth rates in swordtails (*Xiphophorus birchmanni*); here, the underlying genetic associations did
296 largely follow the patterns occurring at the among-individual level. These two empirical studies
297 illustrate how trait correlations can differ between biological levels. Accordingly, empiricists must
298 design experimental studies that test for POLS at the appropriate biological level for the question at
299 hand [16]. Ideally, empiricists should also plan to test POLS at multiple biological levels, as each level
300 will provide essential insights to further our understanding of POLS and its underlying mechanisms.

301 Permanent environmental effects can alter the appearance of trait correlations within an
302 animal’s lifetime. Manipulating early-life environments would allow researchers to better investigate
303 the role of developmental plasticity in generating or breaking trait associations; a promising area of
304 empirical research that is still building a formal modeling foundation [5]. Importantly, the expression

305 of genetic correlations itself is not immune to environmental effects [11,54,55]. Genetic correlations
306 can differ, for example, across environments, across samples within same population, between ages,
307 between animal groups, between populations, between species and between laboratory and wild
308 environments [11]. The mechanisms for such “instability” of genetic correlations include, for example,
309 variation in gene frequencies within and across animal groups and genotype by environment
310 interactions [11]. Therefore, a better understanding of the ecological and evolutionary factors affecting
311 expression of POLS would require studies where genetic correlations are estimated at multiple
312 different environments [56].

313 **Glossary**

314 **Acquisition:** Collection and consumption of resources from the environment.

315 **Allocation:** Division of resources between two or more physiological processes within an individual.

316 **Among-individual variation:** Variation in a labile trait, e.g. behavior, in a sample of individuals caused
317 by individual differences in their average trait expression (measured across multiple observations).
318 This variation is caused by a combination of additive genetic effects and (permanent) effects of the
319 environment on phenotypes. This level differs from the phenotypic level (see below) in that the
320 residual variance is not included.

321 **Biological levels:** Trait expression varies across hierarchical levels of biological organization. For
322 example, behavioral expression can vary among observations (within individuals), among individuals,
323 among genotypes, among populations and among species.

324 **Fast phenotype:** Correlated suite of traits typically characterized by fast growth, quicker time to
325 maturity and shorter lifespans. These individuals are predicted to also express relatively high activity,
326 boldness, exploration and aggression and have higher metabolic rates.

327 **Phenotypic level:** Variation among phenotypes expressed within a population and that has not been
328 partitioned among the contributing components. This level of variation will include the influence of
329 additive genetic, permanent environmental and/or residual effects on trait expression.

330 **Slow phenotype:** Correlated suite of traits typically characterized by slower growth, delayed
331 maturation and longer lifespan. These individuals are also predicted to express relatively low activity,
332 boldness, exploration and aggression and have lower metabolic rates.

333 **Within-individual trade-off:** Constraint within an individual (i.e., intra-individual); typically mediated
334 by physiological processes. For example, division of limited resources between two “competing”

335 physiological processes, underpinning investment between current (e.g. allocation to offspring) and
336 future (e.g. allocation to growth) reproduction.

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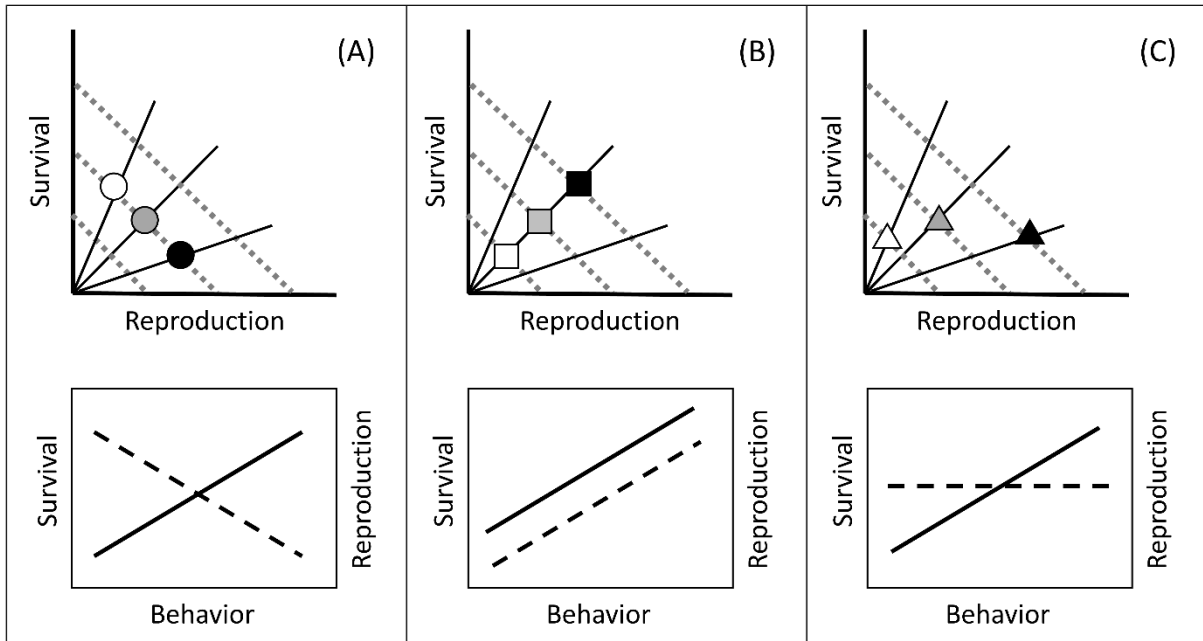
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472 **Figure 1.**

473 The relationship between behavior and resource allocation versus resource acquisition can generate
 474 different correlations between behavior and survival and between behavior and reproduction. Top
 475 graphs show a potential trade-off between survival and reproduction (though this could be generalized
 476 to other costly life-history traits as well); dotted lines indicate different levels of resources available
 477 for allocation (driven by resource acquisition) whereas solid lines indicate differential allocation into
 478 either trait. Shape color indicates individual behavior with darker colors indicating greater expression,
 479 'fast' phenotypes (e.g. greater boldness). Bottom graphs illustrate the resulting expected correlation
 480 between behavior and survival (dashed lines) and between behavior and reproduction (solid lines). In
 481 panel A, all individuals have similar acquisition and among-individual variation in behavior relates most
 482 closely to variation in allocation, with e.g. bolder individuals allocating more into reproduction at the
 483 cost of survival, as implicitly assumed in the original pace-of-life-syndromes hypothesis. In panel B,
 484 among-individual variation in behavior is most closely related to variation in resource acquisition so
 485 that bolder individuals have more resources to allocate to both survival and reproduction. In panel C,
 486 among-individual variation in behavior is related to variation in both resource acquisition and resource

487 allocation whereby bolder individuals reproduce more but with no apparent survival costs. Figure
488 inspired from [14].