

1 ***Title: Cyclical environments drive variation in life history strategies: a general theory of***
2 ***cyclical phenology***

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22

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25

26 **ABSTRACT**

27 Cycles, such as seasons or tides, characterize many systems in nature. Overwhelming evidence
28 shows that climate change-driven alterations to environmental cycles—such as longer seasons—
29 are associated with phenological shifts around the world, suggesting a deep link between
30 environmental cycles and life cycles. However, general mechanisms of life history evolution in
31 cyclical environments are still not well understood. Here I build a demographic framework and
32 ask how life history strategies optimize fitness when the environment perturbs a structured
33 population cyclically, and how strategies should change as cyclicity changes. I show that cycle
34 periodicity alters optimality predictions of classic life history theory because repeated cycles
35 have rippling selective consequences over time and generations. Notably, fitness landscapes that
36 relate environmental cyclicity and life history optimality vary dramatically depending on which
37 trade-offs govern a given species. The model tuned with known life history trade-offs in a marine
38 intertidal copepod *T. californicus* successfully predicted the shape of life history variation across
39 natural populations spanning a gradient of tidal periodicities. This framework shows how
40 environmental cycles can drive life history variation—without complex assumptions of
41 individual responses to cues such as temperature—thus expanding the range of life history
42 diversity explained by theory and providing a basis for adaptive phenology.

43 **INTRODUCTION**

44 Natural populations in all systems must survive environmental fluctuations. Biologists have long
45 known that a particularly common and powerful mode of fluctuations in nature is cyclical, such
46 as seasons. Species around the planet exhibit predictable and sensitive life history transitions that
47 are tightly associated with seasonal cycles, also referred to as phenology. Environmental cycles
48 in fact occur beyond just the timescale of seasons, such as daily, tidal, lunar, flood, fire and
49 decadal oscillations, and life histories of species are often associated with cycles at these
50 timescales as well [1–6]. Despite the ubiquity of cycles in nature, and clear empirical evidence of
51 the importance of cycles for life histories, we lack a general theory of how life history evolution
52 is shaped by cycles.

53 Over the last few decades perturbations to environmental cycles due to climate change
54 have driven dramatic life history changes such as phenological timing in many species [7–15]. In
55 fact, phenological shifts are widely regarded as the most conspicuous and rapid consequence of
56 climate change across marine, freshwater, and terrestrial systems [14]. Notably, different species'
57 phenologies are shifting in different directions, creating phenological mismatches with profound
58 consequences on ecosystem function and health [7,11,16–19]. Disparate case studies of shifts
59 that typically invoke individual-level responses to environmental cues such as temperature may
60 be limited in their potential to explain general evolutionary forces due to system-specific
61 idiosyncrasies. On the trailing edge of rapidly accumulating empirical evidence of shifts,
62 questions regarding general mechanisms of life history evolution in cyclical environments have
63 emerged to the forefront of theoretical population biology, biodiversity, and climate change
64 science [20–22].

65 A first step in understanding the mechanics of life history evolution in cyclical
66 environments may be to conceptualize cycles as sequential arrivals of harsh conditions whose
67 periodicity is not reciprocally affected by local ecological dynamics. An example is the arrival of
68 winter in seasonal systems. A typical consequence of such cyclical events for a population is
69 heightened mortality as well as some perturbation to population structure (e.g. seedling mortality
70 in plants [23]). This consequence not only reduces population size at a given time, but also
71 impacts the long-term trajectory and fitness of the population [24,25]. It follows that, if periodic
72 disturbance is an inherent feature of a habitat, fitness is determined by how well a resident
73 population survives repeated demographic perturbations at regular intervals.

74 Population ecologists have long been interested in demographic dynamics in variable
75 environments, including cyclically variable environments [22,26–31]. Life history theorists, on
76 the other hand, have classically focused on how time-invariant (i.e. constant) perturbations on
77 age-, size- or stage-classes of populations, mediated by trade-offs between biological processes,
78 shape life history strategies broadly [32–36]. For example, theory predicts that heightened
79 juvenile mortality should induce the evolution of reduced reproductive effort. Such predictions
80 have been widely tested empirically, and effects are often strong, rapid, and heritable [37–42]. So
81 far, modern models of life history evolution that do incorporate time-variance in the environment
82 have mainly focused on how optimality predictions are altered by stochasticity (i.e. randomly
83 variable environments), which yield convenient analytical probabilistic conclusions [22,31,43–
84 45]. What is not well understood is how life histories are generally shaped by non-random cycles,
85 despite biological attention to fundamentally cyclical environments such as seasonal systems
86 [22], and the fact that parametric changes to cycles such as season length are repeatedly
87 associated with life history changes across systems.

88 Here I explore the general relationship between periodicity of cycles and evolutionarily
89 optimal life history strategy. Proximate triggers of phenological expression, such as plastic
90 response to temperature cues, mechanistically vary widely across species and habitats [20]. By
91 taking a demographic life history theory approach agnostic to system-specific plastic responses, I
92 address the ultimate selective force behind phenological traits and their shifts, given that
93 phenology is fundamentally a study of how life cycle transitions are fit to environmental cycles.

94 I hypothesize that environmental cycles influence reproductive values of individuals and
95 thus what life history strategy should be evolutionarily optimal in a given cyclical regime.
96 Reproductive value is the expected contribution of an individual at a particular age or stage to the
97 population through current and future reproduction, determined by biological trade-offs and
98 survival through time [36,46]. Reproductive value is a central evaluation for fitness and
99 evolution because it represents the aggregate consequence of trade-offs among many important
100 life history traits [47]. Naturally, the realization of current and future reproduction must depend
101 on current and future environmental conditions for survival experienced by individuals. Thus I
102 expect that, under predictably cyclical environments that periodically incur harsh conditions for
103 survival, the period length of cycles should have a tractable influence on which life history
104 strategy should perform best in a given environment. I analyze this relationship by calculating
105 which life history strategy in a population confers maximum long-term fitness in a given periodic
106 regime, and then studying how optimal life history changes as periodicity changes. I explore how
107 various trade-off assumptions impact these optimality curves to understand how different species
108 in nature—whose life histories are in reality shaped by different sets of trade-offs—may be
109 differentially affected by the same change in periodic regime.

110 Next I test my theoretical predictions in the copepod *Tigriopus californicus* (Copepoda:
111 Harpacticoida), a crustacean found in rock pools in the supralittoral (upper tidal) zone along the
112 North American Pacific coast. Populations are disturbed periodically by wave-wash at high tide,
113 and experience population decline and heightened juvenile mortality periodically. Periodicity of
114 disturbance varies among populations depending on regional tidal patterns and pool height on the
115 shore. *T. californicus* provides an ideal system to study life history variation in cyclical systems
116 across populations due to its short generation time and short disturbance cycles, the rare
117 opportunity to sample from homogenized whole populations, and ease of quick sampling and
118 trait measurements yielding large amounts of within- and across-population data. Across 19
119 natural populations of *T. californicus* in two regions of northern Washington I ask: do
120 disturbance cycle periodicity and known trade-offs together predict life history variation across
121 populations?

122

123 **METHODS**

124 **Model construction.**

125 To uncover general predictions of evolutionarily optimal life history traits in cyclical
126 environments, untied to species-specific idiosyncrasies such as plastic responses to
127 meteorological cues, I describe a hypothetical population in two linked stages of broad
128 applicability: juveniles and reproducing adults. I consider continuous-time demographic
129 dynamics of the stage-structured population and impose stage-specific mortalities at given
130 periodicities (full model description in electronic supplementary material, section 1).

131 First I express constant-environment dynamics as a system of ordinary differential
132 equations

$$\frac{dJ}{dt} = -(\mu + d)J + fA \quad (1)$$

$$\frac{dA}{dt} = \mu J - \gamma A$$

133 which can be expressed as matrix \mathbf{M} :

$$\mathbf{M} = \begin{bmatrix} -(\mu + d) & f \\ \mu & -\gamma \end{bmatrix} \quad (2)$$

134 where J is juveniles, A is adults, μ is the rate at which juveniles mature into reproducing adults, d
 135 is background mortality of juveniles, f is the reproductive rate of adults, and γ is background
 136 mortality of adults. Then, via eigendecomposition of \mathbf{M} , I express the solution at time t as:

$$\begin{aligned} J(t) &= \frac{A(0)v_{(2)1} - J(0)v_{(2)2}}{v_{(2)1}v_{(1)2} - v_{(2)2}v_{(1)1}} v_{(1)1} e^{\lambda_1 t} + \frac{J(0)v_{(1)2} - A(0)v_{(1)1}}{v_{(2)1}v_{(1)2} - v_{(2)2}v_{(1)1}} v_{(2)1} e^{\lambda_2 t} \\ A(t) &= \frac{A(0)v_{(2)1} - J(0)v_{(2)2}}{v_{(2)1}v_{(1)2} - v_{(2)2}v_{(1)1}} v_{(1)2} e^{\lambda_1 t} + \frac{J(0)v_{(1)2} - A(0)v_{(1)1}}{v_{(2)1}v_{(1)2} - v_{(2)2}v_{(1)1}} v_{(2)2} e^{\lambda_2 t} \end{aligned} \quad (3)$$

137 where $v_{(i)j}$ is the j^{th} element of the i^{th} eigenvector corresponding to eigenvalue λ_i of \mathbf{M} . This
 138 solution describes simple structured population dynamics in an undisturbed environment, but by
 139 eigendecomposing the system I isolate the time parameter t which will eventually allow me to
 140 study demographic dynamics as a direct function of period length between disturbances. To
 141 make the solutions explicit with respect to disturbance cycle period T , I let $t = T$, and at time T
 142 multiply the structure by S_J and S_A to impose juvenile- and adult-specific mortality associated
 143 with disturbance. The combined system can be expressed as the matrix \mathbf{P} (S10):

$$\mathbf{P} = \begin{bmatrix} S_J \frac{[(v_{(1)2} e^{\lambda_2 T} v_{(1)2} - v_{(1)1} e^{\lambda_1 T} v_{(2)2})]}{v_{(2)1} v_{(1)2} - v_{(2)2} v_{(1)1}} & S_J \frac{[(v_{(1)1} e^{\lambda_1 T} v_{(2)1} - v_{(1)2} e^{\lambda_2 T} v_{(1)1})]}{v_{(2)1} v_{(1)2} - v_{(2)2} v_{(1)1}} \\ S_A \frac{[(v_{(2)2} e^{\lambda_2 T} v_{(1)2} - v_{(1)2} e^{\lambda_1 T} v_{(2)2})]}{v_{(2)1} v_{(1)2} - v_{(2)2} v_{(1)1}} & S_A \frac{[(v_{(1)2} e^{\lambda_1 T} v_{(2)1} - v_{(2)2} e^{\lambda_2 T} v_{(1)1})]}{v_{(2)1} v_{(1)2} - v_{(2)2} v_{(1)1}} \end{bmatrix} \quad (4)$$

144 Matrix-multiplying initial abundances by \mathbf{P} would thus give stage structure after existing in a
145 constant environment for time T and experiencing a disturbance event that incurs stage-specific
146 mortalities. More interestingly, I use this framework to ask: what are the consequences of
147 different combinations of life history traits on the fitness of a population given that it resides in
148 disturbance regime T ?

149

150 **Fitness.**

151 Given the general framework of cyclically perturbed stage-structured population dynamics, I ask
152 how the predicted fitness of the population is influenced by the periodicity of environmental
153 cycles. The dominant eigenvalue (λ) of a population transition matrix is a widely used measure
154 of relative fitness because it represents how well the population will perform in the long run
155 compared to other hypothetical populations with different life history strategies [25,36]. This
156 metric, equivalent to ' r ' in demography and life history theory, does not capture consequences of
157 short-term transient dynamics [48,49], but has been useful for drawing broad life history
158 evolution predictions and conceptualizing relative fitness that match well with empirical
159 observations [24,25,36]. In stochastic environments fluctuations in instantaneous growth rates
160 may lead λ to give inaccurate evolutionary predictions. In systems that can be modelled by
161 periodic switching between environments, however, eigenvalues and eigenvectors of the matrix
162 product of constituent matrices describing the different environmental states can be used for
163 demographic and life history analyses in exactly the same way as they are used in time-invariant
164 theory [25,50]. My matrix \mathbf{P} is equivalent to periodic models since the system switches between
165 an undisturbed phase and disturbance, and the switching periodicity and population matrix
166 elements do not fluctuate randomly (see electronic supplementary material, Fig. S1 for

167 simulation results). Thus, here I use the dominant eigenvalue of \mathbf{P} (hereafter referred to as λ_P) as
168 the measure of relative fitness to compare the theoretical performance of life history strategies in
169 a periodically time-variant framework, and characterize general selective pressures on life
170 history strategies as a function of cycle periodicity.

171

172 **Life history trade-offs.**

173 Life history evolution is a matter of optimization because limited resources must be allocated
174 into various biological processes such as survival and reproduction involving trade-offs [36,51].
175 The exact shapes of trade-off functions in organisms are famously difficult to measure, let alone
176 justify in model assumptions [51,52]. Here I take a conservative approach and assume simple
177 linear trade-offs to investigate general patterns in optimality as a function of the environment
178 without making more complex physiological assumptions. To express a trade-off between any
179 two traits in the construction of a fitness landscape, I computationally set the vector of the range
180 of values of one trait in decreasing order as the other increases, imposing a negative slope
181 between the two traits. When two traits do not trade off, one of the traits remains at the mean of
182 its range as the other varies through its own range. I varied the combinatory inclusions of trade-
183 offs among the four key parameters to create model variants and investigate their relative fit to
184 the data.

185

186 **Fitness landscapes and optimal life history strategies.**

187 All realizations of \mathbf{P} —and thus the construction of fitness landscapes—must be constrained
188 within the space of the interacting life history parameters, μ , d , f , and γ . In this presentation I
189 constrained the space with known *T. californicus* life history ranges and trade-offs to

190 demonstrate one example of the usage of this framework, but constraints can be set flexibly to
191 represent any given species (see electronic supplementary material, section 2.5 for descriptions
192 and citations for parameterization).

193 Using λ_P I construct fitness landscapes for μ and f simultaneously for each model. Here I
194 focus on μ and f because they are life history traits for which I can collect large amounts of
195 paired data in *T. californicus*, but it should be noted that fitness landscapes can be created for any
196 life history trait in the original system of differential equations. For each landscape, I scan across
197 the range of μ or f for a given value of T, while varying all other traits according to trade-off
198 relationships included in the given model. Therefore I construct a vertical gradient of relative λ_P
199 per T. To construct a landscape, I calculate gradients of relative λ_P across the horizontal axis of T.
200 The optimal trait per T is the trait that maximizes λ_P per T. Finally, to get the curve of optimal
201 trait values across the axis of T I track values associated with maximum λ_P across T.

202

203 **Empirical investigation in *Tigriopus californicus*.**

204 *Tigriopus californicus* is a copepod found widely along the North American Pacific coast (see
205 electronic supplementary material, section 2.1 for detailed description of natural history). Dense
206 populations reside in rock pools above the intertidal zone at varying heights [53–55], which
207 accordingly experience tide cycle disturbance at varying periodicities. When tide levels
208 cyclically reach pool heights and waves wash through pools, *T. californicus* cling onto the rocky
209 benthos in order to prevent being flushed down to open water or to the lower intertidal zone [55].
210 If they are washed down, predators that do not occur in *T. californicus* pools feed on them
211 quickly, and re-colonization of *T. californicus* into the pools appear to be low [55,56]. Despite

212 clinging, tidal disturbance was shown to always decrease population size, and in particular, incur
213 heightened juvenile mortality (electronic supplementary material, Fig. S4).

214 I sampled 19 isolated populations across two sites in northern Washington, USA (Neah
215 Bay, Friday Harbor) in order to capture a wide gradient of disturbance periodicities (see
216 electronic supplementary material, sections 2.2-2.4 for detailed description of data collection). I
217 quantified the periodicity of tidal disturbance in each pool via timeseries analysis of pool
218 temperature data over 4 months at 5-minute intervals, taking abnormal drops in temperature as
219 signals of wave flush (see electronic supplementary material, section 2.2). I siphoned entire
220 isolated populations out of rock pools, and subsampled individuals after homogenizing them, to
221 get representative population samples. I reared 30 mating pairs captured from each population in
222 common garden settings. In these lines I measured rate of maturity (μ in the model) and rate of
223 reproduction (f in the model) (see electronic supplementary material, section 2.4 for detailed
224 description of trait measurements).

225

226 **Likelihood and model fitting.**

227 I calculated the log-likelihoods of the optimality curves of the two focal life history traits μ and f
228 produced by each model variant given the variance and covariance of the μ and f data. Each
229 model is a different trade-off model (electronic supplementary material, Fig. S2, Table S2).
230 Every model has the same number of estimated parameters because they only differ in how the
231 parameters trade off in the construction of the fitness landscapes, which is included
232 computationally by aligning parameter range sequences in reverse order. Therefore model
233 selection criteria that penalize number of parameters such as AIC were not used. Each model
234 produces optimality curves (dominant eigenvalue of matrix \mathbf{P} across gradient of disturbance

235 period T) of μ and f given trade-off relationships. I searched for the maximum log-likelihood of
236 each model given μ and f data simultaneously within the space of $S_A \geq S_J$ and compared maximum
237 log-likelihoods of the 13 model variants.

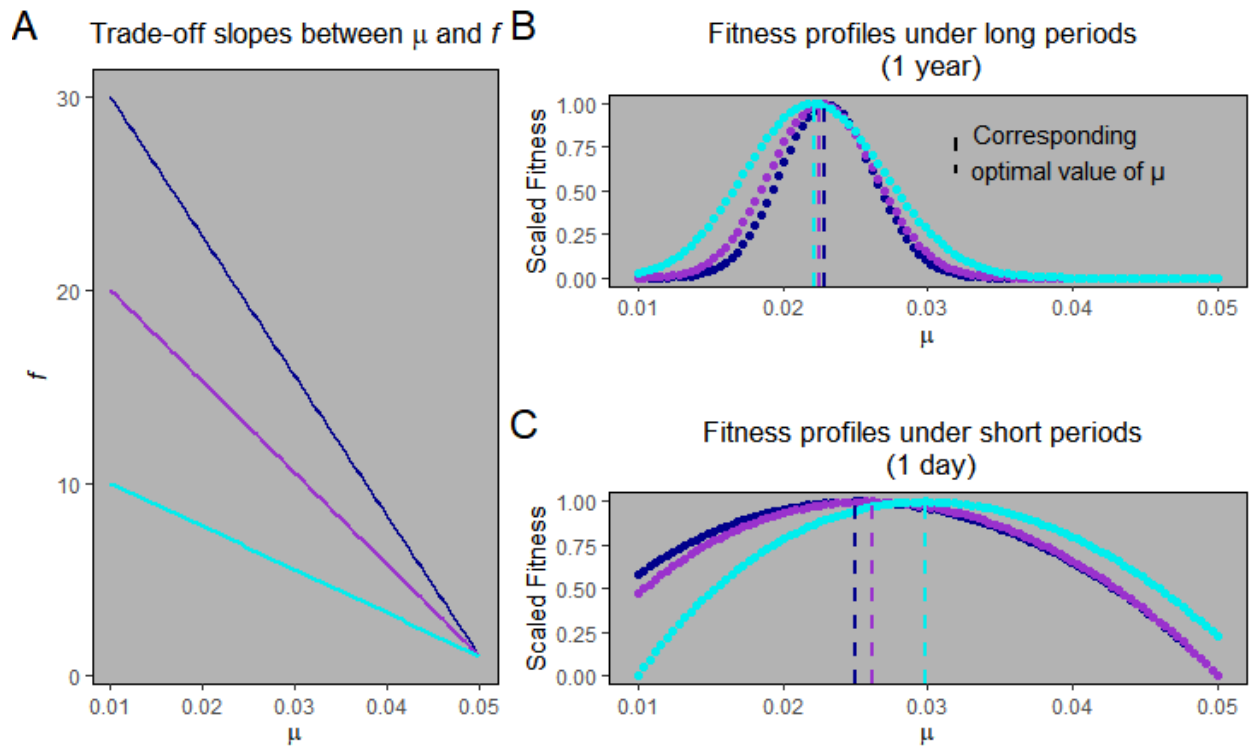
238

239 **RESULTS**

240 **Cycle periodicity alters optimal life history predictions.**

241 Classic life history theory balances costs and benefits of key biological investments such as
242 development, reproduction, and survival to predict fitness profiles of life history traits [36,57,58].
243 Here I incorporated these classic balance considerations but imposed cyclical perturbations to
244 population structure and asked if the fitness predictions change as a function of environmental
245 cycle periodicity. Using this framework, I analyzed the role of cost (slope of trade-off, Fig. 1A)
246 on the fitness profile of a life history trait (maturation rate) in two scenarios: one in which period
247 length is long enough (e.g. to fit more than 10 generations in a period) that the effect of discrete
248 cycles on the evolution of life history rates should be small (Fig. 1B), and another in which
249 period length is at a similar timescale to generation time (Fig. 1C). The former approaches
250 classic formulations of optimal life history predictions based on trade-offs alone [57]. The latter
251 shows that external periodic perturbations significantly change optimality predictions. In the
252 latter scenario all trade-off cost assumptions predict higher optimal values of maturation rate
253 compared to the former. The shape of fitness profiles is also flatter in the latter scenario, which
254 may suggest weaker selection or that larger variance of maturation rate can be maintained within
255 a population under shorter disturbance cycles. Lastly, the relationship between trade-off cost and
256 optimality is reversed between the two scenarios: the lowest cost case produces the lowest
257 optimal maturation rate under long periods but the highest optimum under short periods, and vice

258 versa. These results show that the periodicity with which harsh environmental conditions arrive
 259 and affect survival modifies the expected reproductive value of individuals, and significantly
 260 alters relative fitness of strategies with which individuals invest biological resources into life
 261 history traits. This effect can reshape classic predictions of optimal life history that are solely
 262 based on internal trade-offs.



263

264 **Figure 1.** Three hypothetical cost functions between μ —rate at which juveniles mature into reproducing
 265 adults—and f —adult fecundity—are analyzed while setting linear trade-offs between μ and f , and
 266 between those two traits and their respective stage-specific background survival rates (d and γ). Stage-
 267 specific survival terms associated with cyclical disturbance are set at $S_A = 0.9$ & $S_J = 0.6$. Colors of cost
 268 functions in A correspond to colors of fitness profiles of μ in B and C. Dashed lines in B and C show
 269 peaks of fitness profiles which correspond to optimal values of μ . Periodicity of cyclical perturbation to
 270 population structure is set to be much greater than generation time in B ($T=365$), and at a relevant time
 271 scale ($<$ generation time) in C ($T=1$). Under short periods (C), all cost functions produce higher optimal
 272 μ values, wider fitness profiles, and an exactly reversed relationship between cost and optimality
 273 compared to long periods (B).

274

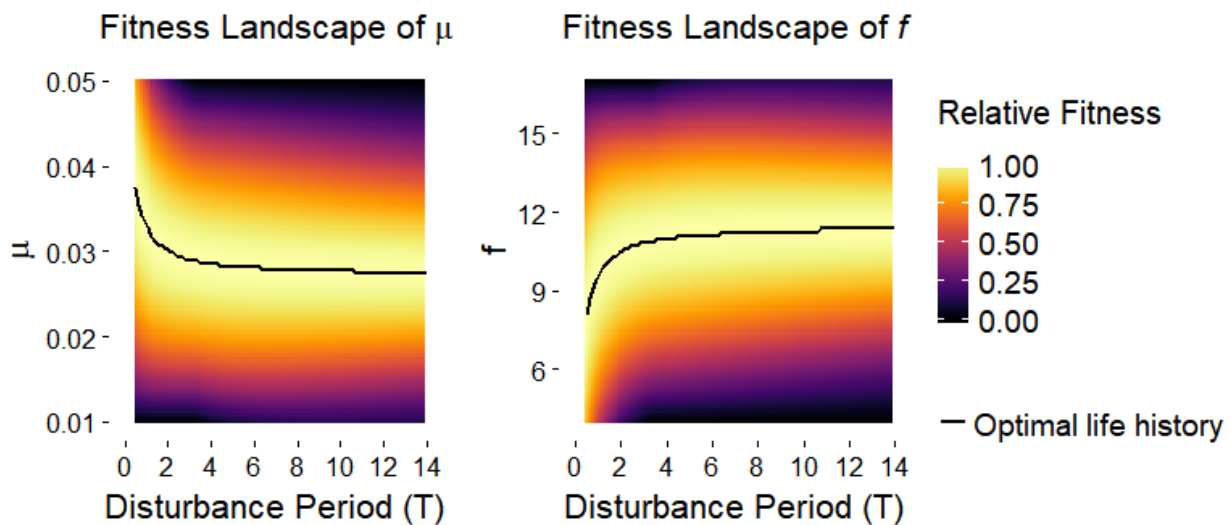
275 **Periodicity and trade-offs interact to produce diverse life histories.**

276 Optimal life history varies nonlinearly as a function of disturbance cycle period, even with
277 assumptions of simple linear trade-offs between traits (Fig. 2). This nonlinearity implies that
278 changes in the evolutionary optimum of a life history trait can be of very different magnitudes
279 even with the same magnitude change in periodicity, depending on the initial period length.

280 Shapes of optimality curves (optimal traits vs. period) can vary dramatically depending
281 on which life history trade-offs are included (electronic supplementary material, Fig. S2). For
282 example, when maturation trades off with background juvenile survival and fecundity (Fig. S2G),
283 optimal maturation rate is expected to decrease and optimal fecundity is expected to increase as
284 period length increases; on the other hand, if maturation trades off with background adult
285 survival and fecundity instead (Fig. S2I), directions of expected trends in both optimal traits as
286 period length changes are the opposite of the former case. Similarly, when maturation trades off
287 with background adult survival, optimal maturation rate and fecundity are both expected to
288 increase with period length (Fig. S2C), but both are expected to decline with period length if
289 background juvenile survival trades off with background adult survival (Fig. S2E) or if fecundity
290 trades off with background adult survival (Fig. S2F); on the other hand, both optimal maturation
291 and fecundity are insensitive to change in period length if maturation trades off with background
292 juvenile survival (Fig. S2A). Collectively, this broad range of cases examined demonstrates that
293 the way in which external environmental cycles determine what combination of life history traits
294 is evolutionarily optimal depends heavily on how traits trade off of one another internally. In the
295 next section I show that the model that includes known trade-offs in *T. californicus* has the
296 highest likelihood given *T. californicus*-specific life history data; but it is important to note that

297 no one model is necessarily better than another in a general sense because different species in
298 nature will have different levels of complexity and rank order of trade-offs between life history
299 traits [57,51,59].

300 A long-accepted tenet in life history evolution theory is that the mean and variance of
301 population structure perturbations shape life history variation [24,34,35,39]. Results here show
302 that the temporal nature of such perturbations, such as the period length of environmental cycles,
303 should interact strongly with general life history trade-off architectures in determining
304 evolutionarily optimal traits. Trade-off patterns realistically vary widely among species due to
305 variations in physiological and developmental mechanisms [51]. Periodicity of environmental
306 cycles, such as growing season length across latitudes, varies widely across habitats as well. The
307 interactive effect of environmental cycles and life history trade-offs is a previously unexplored
308 cause of variability in optimal life history which can drive diverse strategies in nature.



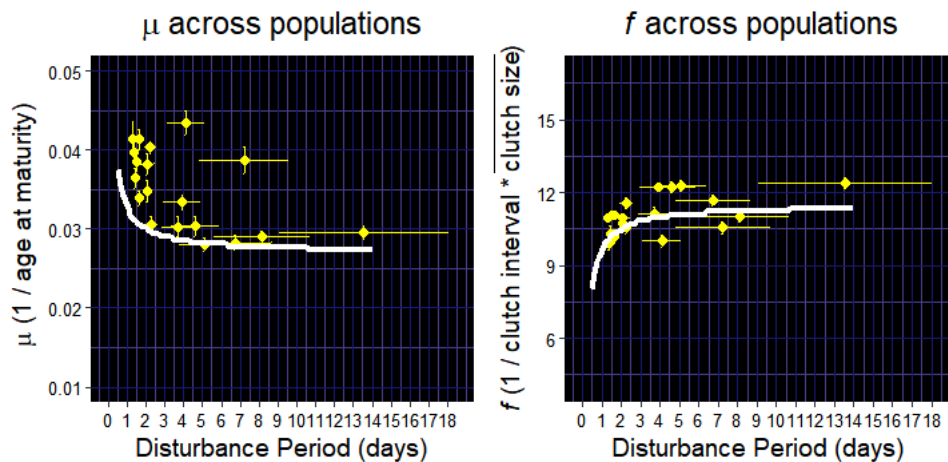
310 **Figure 2.** Example fitness landscapes of two focal life history traits, μ (rate of maturity) and f
311 (reproductive rate) which assumes lower juvenile survival with each disturbance event ($S_A = 0.9$, $S_J =$
312 0.6), and trade-offs between μ and f , between μ and d , and between f and γ . Heat shows normalized
313 fitness of a life history strategy compared to all other strategies in a disturbance regime (T). Curves track
314 the optimal (maximum fitness) life history trait across T .

315

316 ***Tigriopus* trade-offs predict life history variation across a periodicity gradient.**

317 Temperature time series analyses confirmed that there is a broad range of disturbance cycle
318 periodicities across *T. californicus* pools across the two regions (electronic supplementary
319 material, section 2.1; Fig. S4A, B; Table S1). These sampled pools provided a gradient of
320 periodic regimes against which I tested optimal life history predictions. Daily temperature
321 regimes, which may contribute to life history differences [60,61], were not significantly different
322 among pools of varying periodicity regimes across the two regions (Fig. S5). Disturbance always
323 caused higher juvenile mortality than adult mortality in subsampled disturbance events, with
324 mean juvenile mortality of 41% and mean adult mortality of 6% (Fig. S4C).

325



326

327 **Figure 3.** Mean ($\pm se$) values of the two focal life history traits μ and f across 19 *T. californicus*
328 populations, against mean ($\pm se$) disturbance period determined by timeseries analysis of wave
329 disturbance signals in each pool. Curves are optimal life history functions across periodicity (T) fit
330 simultaneously to μ and f .

331

332 Life history traits shift as disturbance period changes across *T. californicus* populations

333 (Fig. 3), mirroring the shape predicted by the model (Fig. 2). The best model (likelihood

334 maximizing when μ and f are fit simultaneously, represented by Fig. 2) was the one that assumed
335 trade-offs between maturation rate and fecundity, between maturation and juvenile survival, and
336 between fecundity and adult survival, consistent with known trade-offs in *T. californicus*
337 (electronic supplementary material, section 2.1). Raw data collected for μ and f per maternal line
338 in my populations also support a general negative relationship between μ and f (electronic
339 supplementary material, Fig. S6). Finally, model variants with double or tertiary trade-off
340 assumptions generally fit better than ones with only single trade-offs (see electronic
341 supplementary material, Fig. S2 and Table S2 for the full list of models). These comparisons
342 among model variants suggest that multidimensional trade-off relationships—which are typically
343 avoided in empirical measurements or model assumptions of life history evolution [51,52], but
344 gaining some attention [62,63]—may actually be important in predicting life history optimization
345 in cyclical environments because trade-off consequences change as a function of cycle period.

346

347 **DISCUSSION**

348 Ecologists have long assumed that environmental cycles are important for life cycle-related traits.
349 But growing knowledge of phenological shifts has generated confusion regarding how
350 environmental cycles shape life history strategies and thus transition rates of life cycle phases.
351 One unresolved paradox in phenology is that various species in the same community (e.g. those
352 in different trophic levels) undergoing the same change in seasonal cycles often exhibit
353 phenological shifts in opposite directions. Here my results suggest that an interaction between
354 environmental cycles and general biological trade-off relationships among fitness-related traits
355 might contribute to life history and phenological divergence: the long-term consequence of trade-
356 offs, a fundamental driver of life history strategy, is modified by environmental cycle periodicity,

357 and significantly alters traditional predictions of optimal life history that are based on
358 assumptions of population structure perturbations and trade-offs alone. A version of the model
359 tuned with known *T. californicus* trade-offs successfully predicted the shape of life history
360 variation across natural periodicity regimes, demonstrating the power of this interactive effect.

361 A fundamental question in ecology and evolution is why life histories are so diverse in
362 nature. Divergent trends in phenological shifts among species in fact offer a current, global
363 opportunity to study the production of life history diversity. Here I show that the interaction
364 between environmental cycles and life history trade-offs is a simple mechanism that can account
365 for large variations in life histories. First, due to the non-linear relationships between cycle
366 period and optimal traits, the same magnitude of period change can induce different magnitudes
367 of life history evolution between two populations of a species that are in different cyclical
368 regimes (Fig. 2). Second, different trade-offs produce varying shapes of optimality curves
369 (electronic supplementary material, Fig. S2), and thus the same change in period can induce an
370 increase, decrease, or no change in a life history trait for different species in the same system
371 depending on what trade-offs are biologically important for those species. Environmental cycle
372 periodicity is diverse across systems (such as growing season lengths across a latitudinal
373 gradient), and trade-off architectures among populations and species vary widely due to
374 physiological constraints, environmental conditions, and reaction norms [51]. Combined, cycles
375 and trade-offs can produce a wide array of predicted life history strategies. Testing this
376 mechanism in species that are controlled by different trade-offs, either across populations in
377 different cyclical regimes or within a single population through time in a habitat undergoing a
378 change in cycle periodicity—for instance due to climate change—will provide fruitful avenues
379 for further exploring this perspective.

380

381 **Stochasticity, ESS models, and gene flow.**

382 Cycles in nature, of course, are not perfectly periodic. The present study focuses on the
383 consideration of period, or interval length between autocorrelated events. The mechanistic
384 influence of fundamentally cyclical environments on life history evolution is noticeably
385 understudied compared to probabilistic expectations in stochastic environments [22], even
386 though regular cycles on various time scales are common in nature. Periodic models can be used
387 to address a real aspect of nature that is difficult or impossible to address explicitly with
388 stochastic models: cyclicity. Here, I take advantage of the fact that periodic models allow the
389 use of matrix properties such as the dominant eigenvalue to infer relative fitness within a
390 fluctuating system [25,50] and analyze conditions for optimization. By doing so I uncover a novel
391 mechanistic relationship between cyclicity and life history evolution. However, cyclicity and
392 stochasticity are both important aspects of nature. For instance, stochastic fluctuations in
393 instantaneous population growth rate can significantly modify evolutionary trajectories predicted
394 by time-invariant or periodic theoretical assumptions [48,49,64]. Studying the relative influences
395 of periodicity and stochasticity on optimal strategy, and on how quickly a population evolves to
396 its predicted optimal strategy, are the obvious next steps that will add more richness to the
397 perspective offered here.

398 Optimality curves in my model framework represent variations in evolutionary stable
399 strategies (ESS) because I take the long-run growth rate of populations (dominant eigenvalue of
400 **P**) as the measure of fitness as is commonly done in demography and life history theory. ESS
401 models are useful for the purpose of predicting general directions of selection over a long term.
402 ESS models take a non-genetic perspective on broad selective forces, although a genetic

403 justification for optimization of a quantitative trait is given by the fact that a mutation can invade
404 the population if it confers a higher r on its carriers [24]. Optimization models and quantitative
405 genetics models are approximately equal for constrained multivariate systems [65]. Nonetheless,
406 results found here are inconclusive with respect to what a population's evolutionary trajectory
407 from one optimum to another should look like in an environment undergoing change in cycle
408 periodicity. Antagonistic selection on correlated traits imposed by different environmental
409 variables associated with seasonal fluctuations, such as photoperiod and temperature, might
410 cause deviations from ESS predictions. Evolutionary trajectories could be altered if bottlenecks
411 are created by a sequence of disturbances and constrain the standing genetic variation subject to
412 selection. In *T. californicus*, selection on optimal life histories may be obscured if high gene flow
413 among nearby populations exists due to wave transport. However, colonization rates and genetic
414 exchange have been repeatedly observed to be low in this system [66–68], and demographic
415 dynamics given high mortality rates caused by tidal disturbance likely overwhelm population
416 genetic dynamics on the time scale of tide cycles. In this study I deliberately chose populations
417 that were deemed to be well isolated given field observations. But the level of gene flow may
418 vary depending on locality due to habitat characteristics, and may contribute to some of the
419 variance within populations and deviations of population means from ESS predictions.
420 Nonetheless, my model fitting results suggest that ESS assumptions predict *T. californicus* life
421 histories reasonably well given a population's periodic regime.

422

423 **Trade-off functions.**

424 Trade-offs between traits can be nonlinear, and multidimensional architectures of trade-offs can
425 be extremely difficult to measure [51,59,52]. Here I have taken the conservative approach of

426 assuming linear trade-offs among modeled life history variables, which biologically equate to
427 strictly substitutable energetic currencies divided between different traits, to focus on the
428 demonstration that consequent optimality curves across periodicity are nonlinear, and that a
429 diverse set of optimality curves can be produced with different trade-offs. The simple linear
430 assumption still performs well, at least with *T. californicus* life history data from my sample
431 populations. However to test this framework further in different species, different functions can
432 and should be used if the relationship between two traits is known to be nonlinear.

433

434 **Links to evolution of seasonal phenologies.**

435 In seasonal environments cyclical arrival of harsh meteorological conditions (e.g. winter) can
436 incur large demographic perturbations and thus strongly influence population dynamics [69,70].
437 Here I show that if periodic arrivals of disturbance incur significant demographic perturbations,
438 individuals and their lineages that have life history strategies that are non-optimal in the context
439 of their environment's cyclicity will have lower long-term fitness; thus, cyclical perturbations
440 play an important role in driving the evolution of life history transition rates.

441 Period is not the only parameter of cycles, however. Particularly for seasons, cycle
442 amplitude may also shape phenologies in important ways, and is shifting with climate change in
443 many natural systems (e.g. seasonal CO₂ cycle amplitude [71,72]). Amplitude of seasonal cycles
444 may play two roles for evolution. First, amplitude is associated with intensity of disturbance,
445 which can be explored with survivorship functions in my theoretical framework. If the pattern of
446 stage-specific mortality associated with cyclical disturbance is clear, such as in *T. californicus*
447 and many seasonal species, then heightened intensity of cyclical disturbance will likely increase
448 strength of selection. Second, amplitude reflects the rate of environmental change within cycle

449 phases. Rate of change may be important for cue-detection and plastic responses. For example
450 many plants in seasonal environments are well known for tracking growing degree-days as a way
451 of taking cues on the passing of the seasons [73]. In my theoretical framework, cyclical
452 disturbances arrive without warning and simply incur repeated penalties on individuals and
453 cohorts that had non-optimal life history strategies for the given regime. In reality there may be a
454 number of continuously changing environmental variables in *T. californicus* pools such as
455 salinity, and I cannot exclude the possibility that, like plants, birds, or many aquatic invertebrates,
456 *T. californicus* possess biological mechanisms to use cues from continuously changing
457 parameters to plastically alter their phenotypes. Nonetheless, I was able to predict variation in *T.*
458 *californicus* life histories across a periodicity gradient in the environment without accounting for
459 plasticity, suggesting that plastic responses might not have a strong effect on life history
460 evolution in response to cyclicity. Future phenological work should directly compare the
461 relative roles of demographic influences such as those discussed here and plastic response to
462 cues that can be tracked along continuous cycles.

463 When considering phenological evolution in cyclical environments, the relative scaling of
464 life cycles and environmental cycles becomes important. For instance, a perennial species must
465 endure multiple seasonal cycle periods per generation. An annual species' generation on the
466 other hand fits within a single cycle period. In both cases, consequences of fitness-related
467 phenotypes in one generation carry over to subsequent generations via intergenerational trade-
468 offs in life histories [36], but the trajectory of evolution may differ between the two because of
469 the number of cycle periods a generation experiences. Further, the model framework presented
470 here assumes overlapping generations but many annual organisms have non-overlapping
471 generations and synchronous phenologies. The evolutionary consequences of non-overlapping

472 generations and synchronization in a population in cyclical environments should be explored
473 further.

474 Phenology is the study of how life cycle schedules are fit to environmental cycles. A
475 phenological trait is a manifestation of the aggregate life history strategy of a species [16], and
476 expression timings of traits are ultimately controlled by transition rates between life history
477 stages [20]. Phenological studies typically measure one representative phenotype such as
478 flowering time in association with proximate drivers such as temperature or precipitation. But
479 phenotypes covary and therefore one must consider trade-offs and competing selective forces
480 with a whole-life perspective in order to understand the evolution of cyclical phenological traits.
481 Here I placed such connections in the general context of environmental cycles, of which the
482 annual seasonal cycle is one example, and tested mechanistic predictions on the relatively short
483 timescale of tide cycles which yielded large amounts of data across many cycle periods and
484 generations quickly. This framework provides a basis for analyzing, comparing, and predicting
485 adaptive phenological shifts in changing seasonal environments.

486

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494

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