Fluctuations in Density-Dependent Selection Drive the Evolution of a Pace-of-Life Syndrome Within and Between Populations

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Abstract: The pace-of-life syndrome (POLS) hypothesis posits that suites of traits are correlated along a slow-fast continuum owing to life history trade-offs. Despite widespread adoption, environmental conditions driving the emergence of POLS remain unclear. A recently proposed conceptual framework of POLS suggests that a slow-fast continuum should align to fluctuations in density-dependent selection. We tested three key predictions made by this framework with an eco-evolutionary agent-based population model. Selection acted on responsiveness (behavioral trait) to interpatch resource differences and the reproductive investment threshold (life history trait). Across environments with density fluctuations of different magnitudes, we observed the emergence of a common axis of trait covariation between and within populations (i.e., the evolution of a POLS). Slow-type (fast-type) populations with high (low) responsiveness and low (high) reproductive investment threshold were selected at high (low) population densities and less (more) intense and frequent density fluctuations. In support of the predictions, fast-type populations contained a higher degree of variation in traits and were associated with higher intrinsic reproductive rate ($r_0$) and higher sensitivity to intraspecific competition ($γ$), pointing to a universal trade-off. While our findings support that POLS aligns with density-dependent selection, we discuss possible mechanisms that may lead to alternative evolutionary pathways.

Keywords: pace-of-life syndrome, density dependence, life history, trait variation, model, personality.

Introduction

Understanding the evolution of syndromes (i.e., pairs or suites of correlated traits) is a recurrent focus of organismal biology (Agrawal 2020). Syndromes may be proximately mediated by genetic (pleiotropy), endocrine, or developmental pathways and be expressed across different hierarchical levels (Sih et al. 2004). The pace-of-life syndrome (POLS) framework (Réale et al. 2010; Dammhahn et al. 2018) and analogous concepts in human biology (Kaplan et al. 2000; Del Giudice et al. 2015) propose a universal trade-off between current and future reproduction as the ultimate cause of the covariation between traits.

Early works identified reproduction trade-offs as a key to understanding life history evolution (Fisher 1930; Williams 1966). The influential, yet also criticized, $r$- and $K$-selection theory (MacArthur and Wilson 1967; Pianka 1970) hypothesizes that population dynamics select for certain life history strategies. The theory of $r$- and $K$-selection, but also other nonexclusive theories of life history evolution, predicts that life history traits covary (Stearns 1977). This covariation was later termed “slow-fast continuum” (Stearns 1983). The continuum ranges from longer-lived “slow types” that mature and reproduce later to shorter-lived “fast types” that mature and reproduce earlier. Further conceptual developments integrated physiological traits with the slow-fast continuum, yet mainly on an interspecific level (Ricklefs and Wikelski 2002). More recently, the study of animal personalities (i.e., consistent interindividual
behavioral differences) sparked questions of its integration with life history theory (Wolf et al. 2007; Biro and Stamps 2008). For instance, consistently bolder behavior may increase foraging efficiency yet increase predation risk (i.e., mortality), making it a more suitable strategy for early-reproducing fast types (Fraser et al. 2001; Wolf et al. 2007). On the basis of these considerations and empirical evidence, the POLS hypothesis suggests that the slow-fast continuum should extend to the within-population level and include behavioral traits (Réale et al. 2010; Dammhahn et al. 2018). According to the POLS hypothesis, in addition to life history and physiological traits, slow types are more responsive (i.e., reactive toward environmental cues; Wolf et al. 2008) and reduce current risks in favor of future reproduction, whereas fast types are less responsive and bolder.

The connection between animal personality and life history theory and its potential to modify ecological interactions and evolutionary processes (Sih et al. 2012; Wolf and Weissing 2012) made the POLS hypothesis a popular subject. Nonetheless, a decade since the POLS hypothesis has been proposed (Réale et al. 2010), empirical evidence supporting it remains limited and partly ambiguous (Dammhahn et al. 2018; Royauté et al. 2018). This ambiguity can be partially explained by the lack of mechanistic theory that clearly identifies conditions under which POLS would emerge (Dammhahn et al. 2018; Mathot and Frankenhaus 2018). Understanding the emergence of POLS holds the promise to provide heuristic a priori predictions on the interdependency of suites of traits (Côté et al. 2010; Sih et al. 2012).

Only recently, a novel framework suggested that within populations POLS emerges as a result of fluctuations in population density (Wright et al. 2019). The fluctuating density-dependent selection POLS framework is based on recent expansions (Lande et al. 2009; Engen et al. 2013; Engen and Sæther 2017) of classical r- and K-selection theory (MacArthur and Wilson 1967; Pianka 1970) and empirical evidence (Sæther et al. 2016), which suggests that there is a fundamental trade-off between intrinsic reproductive rate (r0; density independent) and the sensitivity to intraspecific competition (γ; density dependent). For instance, fast individuals with large clutch sizes experienced stronger negative density-dependent effects than slow types (Sæther et al. 2016). According to Wright et al. (2019), this trade-off between r0 and γ relates to a trade-off between early and late reproduction, which should evoke a POL axis along a degree of fluctuating density dependence. Fluctuations in population density are ubiquitous owing to recurrent (e.g., seasonal) or stochastic environmental variation; thus, density-dependent selection may pose a general mechanism for the emergence and persistence of POLS at the within- and between-population levels (Wright et al. 2019). Here, we test three key predictions of the framework.

First, according to the framework (Wright et al. 2019), low population densities, which occur in more severely disturbed environments with associated elevated environmental mortality, should select for shorter reproduction cycles and thus favor fast types. Vice versa, slow types would be selected in more stable environments with population density closer to the carrying capacity. Short reproduction cycles of fast-type populations in combination with high environmental mortality would amplify fluctuations in population density. If density-dependent selection gives rise to a POLS, more frequent and more intense density fluctuations selecting for faster types would induce a higher degree of fluctuating selection along the major POL axis compared with the more stable conditions at which slow types are selected. Thus, a second prediction by the framework (Wright et al. 2019) is that fast-type populations show a higher degree of variation in traits (i.e., along the POLS axis). Third, traits selected in slow types at higher (and more stable) population densities should, in contrast to fast types, facilitate a reduced sensitivity to intraspecific competition (γ; population density as a proxy for intraspecific competition) in exchange for a lowered density-independent, intrinsic reproductive rate (r0; i.e., there should be a trade-off between γ and r0).

So far, theoretical studies have discussed this framework only in the context of life history traits (Engen et al. 2020; Wright et al. 2020). Yet in the context of POLS theory (i.e., explicitly regarding multiple traits not restricted to life history and across hierarchical levels, also including the within-population level; Mathot and Frankenhaus 2018), the predictions of the framework remain to be tested. Approaching these predictions through empirical studies is cumbersome, as it requires long-term data sets of repeatedly measured life history traits, behavioral phenotypes, and population density. Although empirical and experimental studies are an essential step to test predictions of the density-dependent POLS framework, exploring its utility first by resorting to modeling appears plausible for informing subsequent experiments. Here, we present a spatially explicit agent-based model that integrates two heritable traits: (1) the responsiveness (as reactivity toward environmental cues sensu Wolf et al. 2008) to differences in resource extractability (harvest rates) in the landscape as a fundamental behavioral trait, which is testable in empirical studies (Oudman et al. 2018; Eccard et al. 2020) and relates to multiple behavioral traits associated with the POLS (Wolf et al. 2008; Zwolak and Sih 2020), and (2) the reproductive investment threshold as a life history trait representing capital breeding (Stephens et al. 2009). The reproductive investment threshold defines the number of resources an animal stores before allocating resources to reproduction.
Our modeling approach allows for associated life history traits (e.g., life span, number of offspring) and behavioral expressions, such as movement rate, to emerge from the animals’ decision-making.

The heritable traits responsiveness and reproductive investment threshold are related to distinct processes of allocating time and resources. First, individuals allocate their time either to foraging at the current resource patch or to moving to a patch where they can gain resources at a higher harvest rate. Second, animals either allocate acquired resources to current reproduction or store resources to avoid starvation (life history trait). These traits are reaction norms representing the relationship between decision-making (behavioral trait: moving/foraging; life history trait: investing/saving resources) and both the external state (perceived resources) and the internal state (available stores), respectively. The higher the perceived positive differences of neighboring resource patches compared with the local resource patch, the more likely an animal will move. If stored resources are sufficiently high, an animal allocates resources to reproduction. We analyzed the selection of these traits under different environmental disturbance regimes, which are defined by the frequency and intensity of stochastic (i.e., environmental) mortality leading to distinct population density fluctuations. Disturbance regimes determined the degree of population density fluctuation in a particular environment.

In summary, according to the predictions of the density-dependent POLS framework (Wright et al. 2019), we formulate the following hypotheses: (H1) optimal levels of responsiveness and reproductive investment threshold covary with the POL along different population densities (intrapopulation) and degrees of fluctuation in population density (interpopulation) forming a POLS as a result of density-dependent selection, (H2) the degree of variation in responsiveness and reproductive investment threshold traits covaries with the POL as it is linked to the degree of fluctuations in population density, and (H3) a trade-off between response and reproductive investment threshold underlies the density-dependent selection of traits associated with the POL (i.e., response and reproductive investment threshold with the POL).

**Methods**

We implemented the model in NetLogo version 6.1.1 (Wilensky 1999). A detailed model description, which follows the ODD (overview, design concept, details) protocol for describing agent-based models (Grimm et al. 2006, 2020; Railsback and Grimm 2019), is available in section S2 of the supplemental PDF (available online). All analyses were done in R version 3.6.1, and scripts are publicly accessible at a code repository (https://doi.org/10.5281/zenodo.5547299). Here, we first provide a summary of the basic features and processes of the model and then of the basic principles underlying our model. The ODD-specific terms in italics refer to those used in the full ODD protocol.

**Model Structure**

The purpose of our model was to test three predictions made by the fluctuating density-dependent selection POLS framework (Wright et al. 2019). The patterns to be reproduced by the model are those made by the three predictions.

The model comprises two types of entities: moving animals and square spatial units (patches). Patches are characterized by a set of state variables, mainly resource density and the number of resources a single animal can extract per time step (i.e., harvest rate), which depends on resource density (table 1). State variables of animals comprise their energetic state (resources available in soma, resources allocated to reproduction), their heritable traits reproductive investment threshold and responsiveness, and their perceived environmental state (table 1). Responsiveness defines the reaction to differences in harvest rates between local and neighboring patches. High values of responsiveness reflect a higher likelihood to respond to resource differences by interpatch movement. The reproductive investment threshold defines the level above which individuals allocate all resources from soma to reproduction. Patches are defined by their resource density and the harvest rate (i.e., the rate at which these resources can be extracted). The spatial extent of the toroidal landscape is 50 units × 50 units.

Upon initialization, a resource density in the range of 8–10 is assigned to each spatial unit. Animals are assigned trait values for reproductive investment threshold and responsiveness sampled from a uniform distribution within the range of reproductive investment threshold [0, 2] and responsiveness [0, 2], respectively. We chose a uniform distribution, as it represents an uninformative prior for selection (for initially monomorphic population, see sec. S1.J of the supplemental PDF). Preliminary analyses showed that increasing the ranges any further did not affect the results.

**Model Processes and Scheduling**

**Movement and Foraging.** Each discrete time step, the same sequence of submodels is executed and state variables are updated after each action. First, animals decide whether to move to another patch or to keep foraging at their current patch (fig. 1). This decision is mediated by an animal’s responsiveness as a reaction norm with the average difference between harvest rates at the current patch and
neighboring patches as the external state (i.e., environmental gradient). In the model, responsiveness defines the scale and shape parameter of a gamma distribution. To decide between moving and foraging, an animal samples a value from its gamma distribution. If the value is lower than the external state (average differences in harvest rates), an animal moves to one of the neighboring patches. If instead an animal forages, it extracts resources according to the harvest rate, which follows a saturating type II function. The higher the responsiveness, the lower the sampled values tend to be and, hence, the more likely an animal responds to the external state. Animals assess the resource density of their local patch and surrounding patches only (i.e., gather environmental cues via their foraging and movement decisions).

We chose the difference in harvest rate between local and neighboring patches as movement criterion in reference to the marginal value theorem (Charnov 1976). According to the theorem, moving to another patch is beneficial if the harvest rate at the local patch drops below the average of the habitat. We do not assume, however, that animals can assess averages over the entire habitat but that they sense the average resource density only in the eight neighbor patches. In our model, responsive individuals follow the marginal value movement criterion more closely (i.e., forage more “optimally”). The presence of conspecifics is not an explicit movement criterion, and multiple individuals may forage at one patch.

If an animal stays on its patch, it reduces the resource density of the patch by its harvest rate, and the animal increases its soma by the same amount. If an animal moves to a neighboring patch, it cannot forage in the same time step. The alternation between local-scale foraging and interpatch movement is a common approach (Spiegel et al. 2017) and supported by empirical studies (Michelot et al. 2017; Pohle et al. 2017).

### Resource Allocation, Reproduction, and Trait Evolution

In the next submodel, a fixed amount of resources, which is defined by the global parameter maintenance cost, is deducted from an animal’s soma. If an animal has less than zero resources in soma, it dies. Next, an animal allocates a number of resources from soma to reproduction by which the decadic logarithm soma exceeds the reproductive investment threshold (fig. 1). We chose the decadic logarithm to resolve lower thresholds with a finer resolution. By doing so, small thresholds can result from selection that would otherwise be obscured by intergenerational variation in traits (i.e., heritability; see below). The higher this threshold, the more resources an animal retains in soma. Ecologically, individuals thus represent capital breeders (Stephens et al. 2009; for description and results with income breeding, see secs. S1.G and S2 of the supplemental PDF). Animals reproduce asexually once an accumulated amount of more than 50 resource units (global parameter) was allocated to reproduction, by placing one offspring at a random location in the landscape. Thus, animals need to allocate resources to prevent starvation but also to advance reproduction. Evolution comes into play by assuming that responsiveness and reproductive investment threshold are heritable: they are sampled from trait-specific normal distributions with parental trait values as mean and global parameters to define the heritability as standard deviation. Heritability ($h^2$) of each trait was parameterized to fall within the range of average levels of the heritability of life history and behavioral traits reported by meta-analyses (0.2–0.3; secs. S1.A and S1.B, supplemental PDF; Mousseau and Roff 1987; Stirling et al. 2002).

| State variable          | Entity   | Range                   | Description                                                                 |
|-------------------------|----------|-------------------------|-----------------------------------------------------------------------------|
| Resource-density        | Patch    | [0, …]a                 | Amount of resources per patch                                               |
| Harvest-rate            | Patch    | [0, …]b                 | Amount of resources extractable per time step                              |
| Responsiveness          | Animal   | [0, 2]                  | Trait; probability of interpatch movement based on perceived-current-mean-hr minus current-hr |
| Current-hr              | Animal   | [0, …]b                 | Harvest-rate of local patch                                                |
| Perceived-current-mean-hr | Animal    | [0, …]b               | Mean harvest-rate of neighboring patches (Moore neighborhood, i.e., eight neighbors) |
| Reproductive investment threshold | Animal | [0, 2]                  | Trait; determines the threshold above which resources are allocated from soma to r-buffer |
| Soma                    | Animal   | [0, ∞]                  | Resources available for allocation to maintenance and r-buffer             |
| r-buffer                 | Animal   | [0, ]                   | Resources allocated to reproduction; if ≥50 (default level), the animal reproduces |

Note: See ODD (overview, design concept, details; sec. S2, supplemental PDF) for additional state variables that do not affect the simulation but are relevant to analyze the model.

* Upper limit defined by parameter resource-growth-limit, default is 15.

* Upper limit defined by parameters resource-growth-limit, handling-time, and encounter-rate.
Dochtermann et al. 2019). We assumed asexual reproduction to keep the number of parameters low and to investigate the emergence of POLS without invoking further complexity due to possible sex-specific POL axes (Hämäläinen et al. 2018).

Disturbances. Besides starvation, the model comprises stochastic, environmental mortality due to disturbances as a source of mortality (i.e., we do not assume an effect of age, and generations are overlapping). With a probability determined by the global parameter disturbance interval, a proportion of the population, sampled from a uniform distribution with the global parameter disturbance intensity as the upper limit, dies (fig. 1). Different disturbance regimes are implemented to modulate density fluctuations and thus facilitate the detection of density-dependent selection. The distinct disturbance events, as implemented in our model, may reflect natural processes (e.g., pulses in abiotic conditions or predation [Bijleveld et al. 2015], disease [Scherer et al. 2020], and anthropogenic processes, such as pesticide exposures [Stark et al. 2004; Debecker et al. 2016] or fishing events [Law 2000]).

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**Figure 1:** Graphical model summary showing submodels and scheduling. (1) Animals decide whether to forage or to relocate on the basis of (a) the difference in harvest rate between the current patch and the average of neighboring patches and (b) their behavioral trait, which varies from responsive (solid line) to unresponsive (dashed line). (2) If an animal forages, it reduces the resource density at the local patch by the harvest rate, which depends only on the patches’ resource density. The animal increases its soma by the same amount. If an animal relocates, it moves randomly to one of the neighboring patches and will harvest resources only in the next time step; this implicitly represents costs of movement. (3) An animal allocates resources to maintenance (fixed, global parameter). If an animal’s soma drops below zero, it dies. Then if resources in soma surpass its reproductive investment threshold, an animal invests all excess resources (i.e., \( \Delta \) between threshold and resources in soma) to reproduction. (4) If the accumulated investment to reproduction surpasses a certain level of resources (global parameter, default is 50), an animal reproduces and a new animal is created; it inherits the parents’ responsiveness and reproductive investment threshold, each modified by a globally defined level of stochasticity mimicking empirical heritability of behavioral and life history traits. (5) With a probability determined by the global parameter disturbance interval, a random proportion of the population with the global parameter disturbance intensity as the upper limit dies owing to environmental mortality; this submodel may generate density fluctuations of different magnitudes. (6) Resource growth: resource density at each patch increases by the growth rate, which is either resource density dependent (logistic function shown by the solid line) or resource density independent (linear function shown by the dashed line).
Resource Growth. At the end of each time step, resource density of patches increases by a fixed amount (secs. S1.H and S1.I of the supplemental PDF show results with logistic growth). The harvest rate of a patch depends on the resource density of a patch (type II) and is updated upon any changes in resource density either due to growth or due to foraging (fig. 1). We parameterized resource growth and maintenance cost so that interpatch movement is required to fulfill energetic demands of reproduction and population density does not increase beyond 1 (for alternative parameterizations, see sec. S1.K of the supplemental PDF).

Scenarios. Simulations were initialized with a population density of 0.1 animals per patch (i.e., 250 individuals), with traits sampled from uniform distributions of responsiveness [0, 2] and reproductive investment threshold [0, 2]. Different ranges of traits did not affect the outcome. We ran 12 combinations (i.e., disturbance regimes) of disturbance interval (100, 125, 150, 200, 300, 500) and disturbance intensity (50%, 80%) with five repetitions each (total of 60 simulations, i.e., populations). Simulations ran for 100,000 time steps. In case simulations stopped because of extinction, they were repeated with the same setting (for parameterization, see also sec. S3.A of the supplemental PDF).

Analysis

Data Processing. We analyzed the trait distributions of responsiveness and reproductive investment threshold of populations throughout a simulation run. We ignored the initial 10,000 time steps to account for initialization effects. To position individuals along the slow–fast continuum (i.e., to measure the POL), we computed the individual generation time ($T_i$) as the average age at reproductive events (Araya-Ajoy et al. 2018):

$$T_i = \sum \frac{a_n}{n_i},$$

with $a_n$ being the age of individual $i$ at the birth of an offspring $g$ and $n_i$ being the total number of offspring of this individual. Higher individual generation times are associated with a slower POL (for details on how generation time is measured in the model, see sec. S2 of the supplemental PDF).

To analyze whether fluctuations in population density select different POLs among and within populations, we calculated two metrics for interpopulation and intrapopulation analysis. For the interpopulation analysis (i.e., among different simulation runs), the coefficient of variation in population density informs about the strength of fluctuations in given disturbance regimes. Higher coefficients of variation correspond to more frequent and/or more intense disturbances. For the intrapopulation analysis (i.e., within simulation runs), we calculated the mean population density that individuals experienced during their life span as a metric of density-dependent selection acting on the individual. We grouped individuals into subpopulations by the decile of this metric such that equal proportions of individuals were in each subpopulation. We applied this grouping to attain a gradient of subpopulations from low to high population density for each population. For each subpopulation, we calculated the median and standard deviation of responsiveness and the reproductive investment threshold as well as their respective behavioral expressions (movement rate, rate of investment to reproduction). In the supplemental PDF (sec. S1.P), we show results for a different generation time metric (mean age at reproduction during reproductive events) and the alignment of traits and population density.

Emergence of a POLS and Its Alignment to Density-Dependent Selection (H1). We checked for the covariation of median traits and their respective behavioral expressions (movement rate, rate of investment to reproduction) in subpopulations with POL (i.e., generation time). We analyzed whether this axis of variation covaried with density-dependent selection (i.e., along different levels of population density) and with the degree of population density fluctuations. Furthermore, we analyzed whether intrapopulation and interpopulation POL axes were aligned. Therefore, we determined the overall interpopulation POL axis via quadratic linear regression (responsiveness as dependent variable, reproductive investment threshold as independent variable). Next, for each population, we determined the local slope of the interpopulation POL axis at the median reproductive threshold of a population and compared it with the slope (i.e., the regression coefficient of a simple linear regression) of the intrapopulation POL axis of that population (illustration: sec. S1.D, supplemental PDF).

Relation between the Degree of Phenotypic Variation and Pace of Life (H2). To test whether greater phenotypic variation occurs in faster populations, we analyzed the relationship between generation time and (1) the scaled standard deviation of responsiveness and reproductive investment threshold and (2) the scaled standard deviation of movement rate and rate of investment to reproduction. Standard deviation was appropriate, as traits and behavioral expressions were normally distributed at the subpopulation level. We scaled the standard deviation to make variation more comparable between traits.

Trade-Off between $r_0$ and $\gamma$ along Different Paces of Life (H3). A higher sensitivity to intraspecific competition ($\gamma$) should
become more adverse at increasing population densities (i.e., slower types should be selected). We tested whether a trade-off between \( r_0 \) and \( \gamma \) occurred by analyzing the relationship between reproductive rate and population density for fast-type and slow-type populations.

**Robustness Analyses.** To test whether density fluctuations affect the emergence of POL axes, we analyzed simulations without disturbances (sec. S1.E, supplemental PDF) and with highly frequent disturbances of low intensity, which led to stable population sizes below the carrying capacity defined by resource growth (sec. S1.F, supplemental PDF). Additionally, we varied the parameterization via a one-at-a-time approach with each parameter shifted toward its minimum and maximum value. For all parameter sets, we compared the evolution of responsiveness, reproductive investment threshold, and POL under contrasting disturbance regimes (labile vs. stable conditions) with the default parameterization (secs. S1.K and S3.B, supplemental PDF). We also studied the emergent POL axes if interpatch movement was not required to reproduce (i.e., maintenance costs were below the resource growth rate and carrying capacity was >1; secs. S1.L–S1.N, supplemental PDF).

**Results**

We found that disturbances drive fluctuations in population density (fig. 2B), which feeds back on resource density and thus harvest rates (fig. 2A). To test the three key predictions of the fluctuating density-dependent selection POLS framework (Wright et al. 2019), we analyzed traits at the level of subpopulations. Subpopulations were grouped by the deciles of mean population density experienced by individuals (fig. 2B). The term “subpopulation" always refers to this aggregation level.

**Emergence of a Pace-of-Life Syndrome and Its Alignment to Density-Dependent Selection (H1)**

Traits covered only a small fraction of the initial trait space (fig. 3A). Among populations, responsiveness and reproductive investment threshold were correlated with POL (i.e., generation time) forming an interpopulation POL axis (fig. 3B). Populations composed of responsive foragers with a high reproductive investment threshold were positioned at the slow end, whereas populations composed of less responsive foragers with a low reproductive investment threshold were located at the fast end.

Within and between populations, generation time was positively correlated with population density (fig. 4A; secs. S1.F–S1.J, supplemental PDF). Thus, the intrapopulation POL axes covaried with different levels of population density and populations arranged along a gradient of different degrees of density fluctuations (fig. 4B). Movement rate was reduced, whereas the rate of investment to reproduction was elevated at lower population densities and higher degrees of density fluctuations (fig. 4C). While the association between traits was similar across hierarchical levels, intrapopulation POL axes emerging in severely disturbed environments did not fully align with the interpopulation POL axis (fig. 4D). If—in robustness analyses—we chose parameters so that carrying capacity increased beyond one individual per patch on average, the POL axes became nonmonotonic with selection for lower levels of responsiveness and movement rate in slower types (secs. S1.L and S1.M, supplemental PDF).

**Relation between the Degree of Phenotypic Variation and Pace of Life (H2)**

Because of stronger density fluctuations, the degree of trait variation in fast-type populations is predicted to be higher. We related the degree of variation (measured by the scaled standard deviation) in responsiveness and reproductive investment threshold and their behavioral expression (movement rate, rate of investment to reproduction) with POL (i.e., generation time). The degree of variation was negatively correlated with POL for all traits except for movement rate (fig. 5). Here, slower subpopulations showed a higher degree of variation. So despite a higher degree of variation in responsiveness, behavioral expression movement rate did not show higher levels of variation, as it was possibly modified by a lower degree of relative variation in harvest rates at lower densities (sec. S1.N, supplemental PDF).

**Trade-Off between \( r_0 \) and \( \gamma \) along Different Paces of Life (H3)**

Fast types occurred at levels of lower intraspecific competition (low population density), where \( r_0 \) mainly defines the reproductive rate, whereas slower types occurred at higher levels of intraspecific competition (high population density) with reproduction rates modified by \( \gamma \) (fig. 6). This pattern pointed to a correlation of generation time (POL) with \( r_0 \) and \( \gamma \); hence, populations of responsive types with low investment to reproduction, which were associated with a slow POL, have a lower \( r_0 \) but also a lower \( \gamma \) (i.e., their reproductive rate was less sensitive to higher population densities compared with populations at the fast end).

**Discussion**

In our study we approached the fundamental question of whether and how observed correlations between suites of traits (i.e., syndromes) may emerge and be maintained
by variation in population density that leads to fluctuations in density-dependent selection, as proposed by a novel framework (Wright et al. 2019). We tested three key predictions of the framework using an eco-evolutionary, generic, agent-based model. The parsimonious model design integrates fluctuations in population density via disturbance regimes, foraging, and reproduction, resulting in selection pressures on responsiveness (behavioral trait), reproductive investment threshold (life history trait), and further traits as emergent properties (sec. S1.0, supplemental PDF). Our model supports all tested key predictions by the framework, yet results highlight potential difficulties in determining POL axes in real ecological systems. In the following, we discuss these results and the mechanisms induced by population density and its fluctuations that have led to the emergence of POL axes.

**Emergence of a Pace-of-Life Syndrome and Its Alignment to Density-Dependent Selection (H1)**

We found that responsiveness and reproductive investment threshold formed a common axis of variation along
slow-fast continua within and between populations; hence, a POLS evolved at two hierarchical levels of biological organization. Selection of responsiveness and reproductive investment threshold are both linked to mechanisms induced by population density and density fluctuations. Density-related variation in behavior has been demonstrated by several empirical studies. Common voles exhibit seasonal variation in behavior, with bolder individuals in low-density spring populations compared with high-density summer populations (Eccard and Herde 2013). Another prominent example is western bluebirds, where individuals with higher dispersal propensity and aggressiveness are more prevalent in newly founded low-density populations (Duckworth 2006, 2008). Duckworth and Aguillon (2015) synthesize that aggressiveness in western bluebirds impairs parental care, which becomes more pronounced in dense populations and thus reduces fitness of aggressive individuals. For our simulated populations we can explain the covariation of responsiveness and reproductive investment threshold with the POL along a density gradient by density-dependent fluctuations in mortality risks and resource distributions.

Two sources of mortality exist in the model: density-independent environmental mortality and density-dependent risk of starvation. Density-dependent risk of starvation emerges from patterns of resource use and increases with population density (sec. S1.R, supplemental PDF) as resource availability and harvest rates decrease (fig. 2; sec. S1.N, supplemental PDF). Individuals with low somatic resources (offspring, individuals with low reproductive investment threshold) are more prone to density-dependent starvation (sec. S1.R, supplemental PDF). Hence, as population density increases, individuals with higher reproductive investment threshold can contribute more to population growth (fig. 4; sec. S1.P, supplemental PDF).

The effects of population density on the resource layer explain the selection for different levels of responsiveness. As harvest rates decreased with population density, the relative costs (in terms of resources) of moving to another patch instead of foraging in a given patch decreased; consequently, moving required lower positive interpatch differences to be beneficial. Also, as the coefficient of variation in harvest rates increased with population density (sec. S1.N, supplemental PDF), moving to another a patch became more often rewarding. Furthermore, with elevated population density, increasing interference and exploitation competition favored an earlier response to more subtle interpatch differences. These factors contributed to the selection of higher responsiveness and thus higher movement rates at higher population densities. This relates to empirical observations of density-dependent movement activity, as intraspecific competition enforces resource scarcity, for instance, in elephant and opossum populations (Young and Van Aarde 2010; Almeida et al. 2015).

The acquisition of resources (mediated by responsiveness) and the allocation to reproduction (mediated by the reproductive investment threshold) affect the generation time. In line with optimality models, shorter generation
times are beneficial in environments with elevated environmental mortality (Michod 1979; Engen and Sæther 2016). As population density increases, slower individuals with reduced allocation to current reproduction can reduce the density-dependent mortality due to starvation and contribute to population growth. Similarly to Araya-Ajoy et al. (2021), we found that environmental mortality limits the maximum range of generation times (sec. S1.R, supplemental PDF). Comparing between hierarchical levels, POL axes were overall aligned yet differed systematically. The slope of the POL axes (i.e., the variation of responsiveness) was steeper at the intrapopulation level compared with the interpopulation level in more frequently and intensely disturbed environments (fig. 4D, secs. S1.G–S1.L, supplemental PDF). As outlined above, traits aligned to POL axes as environmental properties and population density covaried. Yet this covariation is not fixed (i.e., differences between environmental contexts) and may thus result in POL axes that do not fully align across hierarchical levels. This observation highlights that POL axes between hierarchical levels are not necessarily aligned. Instead, in contrast to most conceptual POLS figures (as in Wright et al. 2019), intrapopulation POL axes may rather systematically deviate from the major axis at the interpopulation level.

Another level of complexity is added if environmental patterns do not vary monotonically along a gradient of population density. We parameterized our model according to the assumption that interpatch movement is required to meet energetic demands for reproduction. Yet if we relaxed this assumption and population density (i.e., carrying capacity) could increase beyond 1, we observed a shift in foraging regimes. If all patches were, on average, occupied by at least one individual, resources

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**Figure 4**: Along a gradient of density fluctuations (A), different intrapopulation pace-of-life (POL) axes between median responsiveness and reproductive investment threshold (B) and between median rate of investment to reproduction and movement rate emerge (C). A–C show the slow and fast ends (i.e., fastest/slowest subpopulation; ends are distinguishable by shape) of each intrapopulation POL axis (12 populations, one per unique disturbance regime; sec. S1.C of the supplemental PDF shows repeats). A, POL (i.e., generation time) of the fast and slow ends aligned to population density with the fast type located at lower population densities. B, Covariation of median responsiveness and reproductive investment threshold along intrapopulation POL axes and different degrees of density fluctuation (expressed by the coefficient of variation) between populations. C, Covariation of median movement activity (rate of moving instead of foraging) and median rate of resources invested to reproduction along intrapopulation POL axes along different population densities and degrees of density fluctuation. D, Comparison between slope of intrapopulation axes (n = 60 populations) and local slope of interpopulation POL axis (fig. 3B). Slopes between hierarchical levels are similar (close to dashed line) yet differ systematically with disturbance regimes.
were more homogeneously foraged, resulting in a negative correlation of coefficients of variation in harvest rates with population density (opposite to situations with population density $<1$). Now fast types (with lower reproductive investment thresholds) occurring at lower population densities were more responsive and moved more than slower types, resulting in a nonmonotonic selection along density gradients.

The integration of traits along a slow-fast continuum, as proposed by Réale et al. (2010), has so far yielded limited evidence (Royauté et al. 2018). Some studies of behavioral correlations along population density gradients, though, have shown correlations of traits, such as dispersal propensity and sociability (Duckworth 2006, 2008; Cote and Clobert 2007), as well as exploratory behavior and investment to current reproduction (Nicolaus et al. 2015, 2016), which are in line with POLS theory. Yet this may not be general (Vanden Broecke et al. 2021), and the presence of nonmonotonic responses of environmental properties and interactions to density fluctuations could obscure underlying POL axes in studies of fluctuating density-dependent POLS. Furthermore, nonmonotonic POL axes emphasize that conceptual associations between traits along a slow-fast continuum (Réale et al. 2010) may not be taken as a universal prediction. Instead, an intimate knowledge of the study system is required (Montiglio et al. 2018; Royauté et al. 2018; Agrawal 2020).

**Relation between the Degree of Phenotypic Variation and Pace of Life (H2)**

In disturbance-free scenarios (sec. S1.E, supplemental PDF), traits evolved to high responsiveness and low reproductive investment threshold. With increasing fluctuations in population density, POL shifted to the fast end, and the degree of variation in responsiveness and reproductive investment threshold increased. Our observations are thus in support of the hypothesis that fluctuations in population density increase the variation in traits. Yet lowered intraspecific competition at lower population densities

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**Figure 5:** Relationships between pace of life (POL; i.e., generation time) and scaled standard deviation of median responsiveness and reproductive investment threshold (top) and behavioral expressions (bottom) along different subpopulations (points; $n = 600$). Standard deviation was scaled to make traits and behavioral expressions comparable. Fast-type subpopulations show a higher degree of variation in traits and behavioral expression except for movement rate.
may be associated with relaxed selection, which may also contribute to a higher degree of trait variation (sec. S1.Q, supplemental PDF). Furthermore, in case the environmental variation correlates positively with population density, higher variation in traits (i.e., wider reaction norms) in fast types may not be associated with a higher variation in behavioral expressions. In our study we observe this case as harvest rates become more similar at low-density conditions. This resulted in differences between patches too small for, on average, less responsive foragers to react to, which led to a more uniform response. Thus, when testing this prediction based on the variation in a behavioral expression, environmental effects need to be appropriately attributed (Hertel et al. 2020).

Temporal fluctuations in population density as a source of trait variation may have some vital implications for ecological research, as consequences of trait variation scale up to the community level (Bolnick et al. 2011; Sih et al. 2012; Violle et al. 2012; Wolf and Weissing 2012; e.g., by affecting coexistence mechanisms [Hart et al. 2016; Banitz 2019; Crawford et al. 2019; Milles et al. 2020] or mobile link functions [Brehm et al. 2019; Schlägel et al. 2020; Shaw 2020]). Studying the effect of fluctuations in population density on trait variation adds another perspective to anthropogenic effects on trait diversity. For instance, resource provisioning in wildlife management, albeit increasing foraging efficiency and thus fitness, alleviates density fluctuations, which may negatively affect trait diversity and its associated functions.

Figure 6: Relationship between population density, as a proxy for effects from intraspecific competition, and reproductive rate of subpopulations (n = 600) with different pace of life (POL; i.e., generation time; color gradient).

Trade-Off between $r_0$ and $\gamma$ along Different Paces of Life (H3)

Following the fluctuating density-dependent selection POLS framework (Wright et al. 2019), traits should reflect a trade-off between the sensitivity to intraspecific competition ($\gamma$) and intrinsic reproductive rate ($r_0$). Elevated levels of responsiveness increase the chance to be the first to react to interpatch differences and thus succeed in exploitation competition, which becomes more prominent if population density approaches the carrying capacity. Furthermore, a low reproductive investment threshold reduces the density-dependent risk of starvation. So responsiveness and reproductive investment threshold affect the sensitivity to intraspecific competition ($\gamma$; i.e., the observed negative effect of increased population density on reproductive rate). Similarly, lower responsiveness maximizes resource uptake in the absence of competition, and a high reproductive investment threshold facilitates a rapid conversion of resources into offspring (i.e., their intrinsic reproductive rate, $r_0$, increases). Thus, the covariation between responsiveness and reproductive investment threshold along the interpopulation POLS axis directly translates into a trade-off between $r_0$ and $\gamma$.

Future Directions

We observed a persistent covariation between responsiveness (behavioral trait) and reproductive investment
threshold (life history trait). Yet in systems where resource availability is not (solely) driven by density in the upper trophic level or where mortality risk from disturbance across the trait space is anisotropic because of trait-dependent adaptive strategies (Mathot et al. 2012), the relationship between these traits may be altered, as they do not have a common causal link to population density fluctuations. The identification of mechanisms induced by fluctuations in population density is thus vital to formulate testable predictions about the emergence of a POLS and the directionality of the covariation between traits. Such mechanisms may induce a directionality that deviates from the classical association between traits in POLS or to nonmonotonic POL axes. In stark contrast to most conceptual figures of POLS (as in Wright et al. 2019), we observed a systematic difference in the slopes of POLS axes between hierarchical levels (interpopulation vs. intrapopulation level). Slopes of intrapopulation POL axes in more severely disturbed environments were steeper than suggested by the interpopulation POL axis. We could explain this by the distinct effects of population density and fluctuations in population density, which act differently across the hierarchical levels. Hence, differences in mechanisms across hierarchical levels and variation in mechanisms associated with population density fluctuations should be accounted for when generating hypotheses to test the fluctuating density-dependent selection POLS framework and the POLS hypothesis in general. This adds to suggestions by other studies (Montiglio et al. 2018; Royauté et al. 2018) that relaxing core assumptions (e.g., by regarding relationships between traits more adapted to the specific context; Montiglio et al. 2018) would allow for more general applicability and may partly resolve the issue of an unclear state of evidence.

Future studies, both in vivo and in silico, might test the fluctuating density-dependent selection POLS framework in a less generic system with population density fluctuations induced by specific anthropogenic, biotic, or abiotic sources. In our study, environmental mortality imposed on individuals by disturbances was isotropic (i.e., traits did neither mitigate nor amplify the mortality risk during a disturbance event). Yet individuals with higher responsiveness may reduce their mortality risk as they observe their environment more closely and may thus perceive environmental cues of disturbances earlier and react accordingly. Despite the apparent absence of a general relationship between behavioral traits and mortality risk (Moiron et al. 2020), adaptive strategies to reduce mortality risk (Mathot et al. 2012) may be an important element of specific systems. For instance, such adaptive strategies may arise if disturbances become less predictable and may facilitate the persistence of plastic slow types at more severe disturbance regimes (Hämäläinen et al. 2021). This would change not only the relationship between POL and other traits but also the general association between POL and density-dependent selection. As a first step our study provides evidence for the fluctuating density-dependent selection causing a POLS with a null model of interaction between traits and mortality risk; further studies in specific systems with certain sources of density fluctuations will help to further explore limits of the framework and POLS hypothesis itself.

Conclusions

Our study provides support for key predictions of the fluctuating density-dependent selection POLS framework. Both at the intrapopulation level and at the interpopulation level a POLS emerged. The selection of responsiveness and the reproductive investment threshold were mediated by distinct mechanisms induced by population density (i.e., competition for resources) and fluctuations in population density (i.e., environmental mortality). Because of differences in the expression of these distinct mechanisms, the POLS axes did not fully align and instead differed systematically between hierarchical levels. This observation adds nuance to hypothesis making in POLS compared with assuming equal inclination across hierarchical levels. While our study is in support of the framework, further studies may apply predictions to specific sources of population density fluctuations (i.e., disturbance types). Such studies would shed light on whether adaptive strategies (i.e., anisotropic mortality risk across the trait space) or reversible plasticity may alter or even obscure the emergence of POLS along a gradient of density-dependent selection.

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Statement of Authorship

Conceptualization, development, and analysis of the model were done by A.M.; M.D. and V.G. gave feedback on the model development and concepts; A.M. visualized the results and wrote the first draft; and all authors reviewed and edited the draft and contributed substantially to revisions and the final version of the manuscript.
Data and Code Availability

To reproduce the data and main text/supplemental figures, the analysis scripts and the model code are available at Zenodo (https://doi.org/10.5281/zenodo.5547299). Data and code are generated via the model code.

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“I once found a mocking-bird (Mimus polyglottus) which by some awkward stroke in his rapid flight, had fractured his right wing... After dressing and securing the little songster’s wing, I turned over some old rails in search of something for him to eat. There were plenty of crickets and scorpions concealed under the rails, for the latter of which he showed the greatest preference. He would peck at them, and by bruising and thus stunning them a little, readily swallow them whole. After he had swallowed seven of them, I thought, as I had volunteered my services as surgeon and physician for him, it would not be prudent for me to suffer him to indulge farther at this time; so I placed him in a large cage with some canary birds, where he remained feasting on nine scorpions a day, until he had recovered the use of his wing, when I set him free.” From “Scorpion of Texas” by G. Lincecum (The American Naturalist, 1867, 4:203–205).