Gradual development and chance beget individuality

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Abstract

Behaviors – and thus behavioral individuality – rarely emerge fully formed but are instead built gradually through development, shaped by processes involving learning, skill formation, and experience. Prevailing theory in behavioral ecology, however, has largely focused on static equilibrium outcomes where behaviors are analyzed only as fully formed traits, often neglecting development. Here, we challenge this tradition by placing gradual development at the center of the emergence of individuality. We show, using a hierarchy of models, that when traits develop incrementally and are subject to even minimal stochasticity, individuality is not a special case but an inevitable outcome. Early chance deviations are preserved and amplified by the path-dependent nature of development, generating high and sustained repeatability across individuals. We demonstrate that this logic holds across neutral processes, directional development toward phenotypic targets, and adaptive, state-dependent decision-making. By integrating stochasticity, developmental dynamics, and optimality theory, our results recast individuality as a generic property of gradual development, not requiring specific adaptive or constraint-based explanations. More broadly, our findings illustrate that understanding biological variation may often require a shift away from static equilibria thinking toward explicitly time-dependent, developmental perspectives.

Introduction

For more than two decades, research in behavioral ecology has employed models to understand consistent among-individual differences in behavior (i.e., individuality, personality) - an almost ubiquitous phenomenon across animal taxa [1–4]. While substantial progress in this area has uncovered a broad range of both adaptive and constraint-based explanations for such variation [2,3,5–10], most of this research – as has been the tradition in behavioral ecology more generally [11,12] – has focused on characterizing and interpreting the static equilibria of 'non-developmental' models, where fully developed behaviors are formed in a single timestep [13,14]. This is in sharp contrast to the fact that many behavioral traits are complex and must be developed incrementally over prolonged periods of time, for example, during learning and skill formation processes [15–19]. Thus, while the field has accumulated a wealth of hypotheses and predictions about the origin of individual differences in situations where individuals can immediately exhibit some static equilibrium behavior, at present, much less is known about the considerably more common and realistic situation where individuals exhibit behavioral traits that are gradually changing, often over extended periods of time [20–23].

Development abounds with examples of gradually changing traits that are not yet at equilibrium – indeed, in real life, many traits may never reach equilibrium [20,24–26]. Generally, individuals start their lives with many phenotypic traits away from some optimal target value for their environment and must then, incrementally and often over an extended period of time, develop traits that progress in the direction of that target value. During skill formation processes, for instance, individuals gradually adjust their behavior in response to incrementally developing experience. When confronted with uncertainty during learning, individuals often gradually – and again often over extended periods of time – acquire new information and adjust their behavior accordingly [13,27–29]. To give a third and equally universally applicable example, whenever environmental conditions change substantially during the lifetime of individuals, individuals will often exhibit trait values that are significantly diverged from optimal as they gradually shift their traits in the direction of the new target value [30–33]. Thus, while gradually changing (i.e. non-equilibrium) behaviors appear to be widespread – arguably even the norm in the real-world – up to now, very few models exist that study the processes and mechanisms governing the emergence of individual differences in such scenarios [34–37].

We here address this knowledge gap. In particular, using a series of models of increasing complexity we show that in scenarios with gradually changing traits, high degrees of individuality emerge as a general phenomenon whenever there is some stochasticity (e.g. environmental or developmental noise) affecting trait expression. The first – and simplest – model conceptualizes behavioral expression as gradually 'diffusing' through development, mimicking the development of incremental traits that are not under selection. We next consider a model where, next to diffusing through development, traits also gradually 'drift' in the direction of a target value. While these first two models are not evolutionary models in the classic behavioral ecology sense (in that we compute optimal developmental trajectories given a set of ecological parameter values and assumptions), they serve as intuition pumps for the key finding of our paper: whenever any among-individual trait differences arise stochastically (at least in part), the incremental nature of the developmental process is predicted to maintain those differences.

We next show that these very same processes generate high degrees of individuality in standard state-dependent behavioral ecology models where developmental trajectories are derived from optimality considerations. To do so, we focus on two variants of an optimal foraging model. In the first variant, individuals gradually learn in which of two environments – high food abundance or low food abundance – they have been born, adjusting their optimal foraging effort accordingly. Importantly, returns from foraging (and thus the cues that animals use to update their estimation of overall, expected foraging returns) are not deterministic but instead probabilistic (i.e., can stochastically vary around an average expected return). In the second variant, rather than learning about expected foraging returns in their natal environment, animals gradually develop foraging skill, which feeds back on the optimal foraging effort. Here, skill is achieved as a function of experience with food items, which again has a stochastic component. Throughout, we use repeatability (calculated in a mixed modeling framework via a developmental sliding window approach) as the standard measure of the degree of individuality in a population [38,39] (see *Supplement 1* for repeatability calculations used in each model). Code for all models is provided in a publicly accessible repository [40].

The basic intuition: gradual development in the Galton board

In the 1870s, Sir Francis Galton conceived of a pedagogical tool – the Galton board – to demonstrate the central limit theorem by directing beads down a vertical board, through rows of interleaved pins (Fig 1a) [41]. Let us now imagine – as inspired by Waddington's developmental metaphor of a ball rolling down an epigenetic landscape (Fig 2b) [42] – that the beads correspond to a population of individuals, and that a bead's progression down the board corresponds to an individual's progress through ontogeny in phenotype space. While simplistic, both the Galton board and Waddington's landscape capture two fundamental aspects of many developmental processes: (1) in each timestep, individuals start where they left off in the preceding timestep (i.e., development is path dependent, proceeding progressively and incrementally), and (2) phenotypes are subject to some degree of stochasticity (e.g., environmental or developmental noise: in both the Galton board and Waddington's landscape metaphors, an individual's phenotypic trajectory emerges from a partly probabilistic process). Intuitively, the combination of both features can be expected to promote the emergence of individuality (i.e., consistent individual phenotypic differences): while chance promotes variation among individuals, the incremental nature of the developmental process is expected to maintain emergent differences. Put slightly more technically, as all individuals are exposed to identical levels of stochasticity, individual differences that are present at any point in time can be expected to be maintained on average. Indeed, in line with this basic intuition, individuals developing through the Galton board exhibit high levels of consistent individual differences (e.g., measured by the repeatability of their 'position' in phenotype space through time; *Supplement 2,* Fig S2), providing the first illustration of the basic logic underlying our key finding: incremental developmental processes with a stochastic component robustly promote individuality.

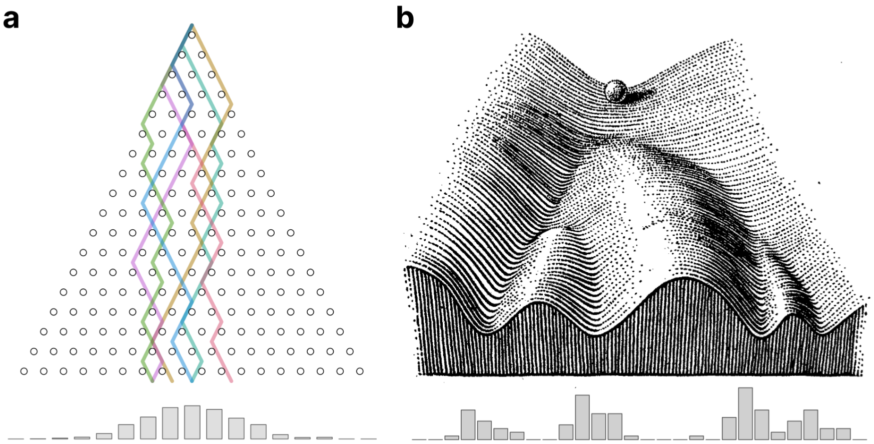

Figure 1. (**a**) A Galton board directs marbles down a chute of interleaved pins: at each pin, a marble passes either to the left or to the right with equal probability. The path dependent, probabilistic process generating a marble's trajectory can be conceptualized as a simple model of gradual phenotypic development, generating consistent phenotypic (i.e., positional) variation across individuals (i.e., marbles). Shown here are trajectories for a random set of six individuals moving through the board. When a sufficiently large number of individuals travel through the

board, a Gaussian distribution of final positions is observed, as shown here. (**b**) Waddington's epigenetic landscape metaphor (reproduced from [42] by arrangement with Taylor & Francis Group). As with the Galton board, movement through this landscape is both probabilistic and path dependent (though, in contrast to the Galton board, the probabilities of movement directions along the landscape depend on a ball's position). Such a process again creates consistent positional variation in a population of balls rolling down the hill – or, in the language of the metaphor – consistent, within-individual phenotypic variation through development.

Selectively neutral development

We further investigate these basic ideas by modeling the developmental process as a Gaussian random walk (Fig 2), corresponding to gradual, 'neutral' development (e.g., development of a selectively neutral or nearly neutral trait [43]). All individuals start their lives with the same trait value. Each timestep, individuals start where they left off in the previous timestep, and their position in behavioral trait space in the following timestep, b_{t+1}, is thus calculated as:

$$b_{t+1} = b_t + \eta_t \qquad \text{where } \eta_t \sim N(0, \sigma^2)$$

in which the variance of the sampled Gaussian distribution, σ^2, represents the diffusion parameter and thus the degree of developmental noise. Simulating a population of 500 individuals for a total of $T = 100$ timesteps yields 500 developmental trajectories through behavioral trait space (Fig 2a); as predicted from our arguments above, in such a population, we see a remarkably high degree of repeatability (~1) achieved shortly after birth and remaining consistently high throughout life (Fig 2b). Note that here, as throughout, repeatability is calculated over development via a sliding window approach (window size = 6 timesteps); this basic pattern is largely robust to the size of the time interval between 'measurements' as well the overall size of the window (*Supplement 1*, Fig S1). This result is also robust to the magnitude of σ^2, given $\sigma^2 > 0$, illustrating how chance and 'developmental drift' in incremental traits is a powerful generator of individuality.

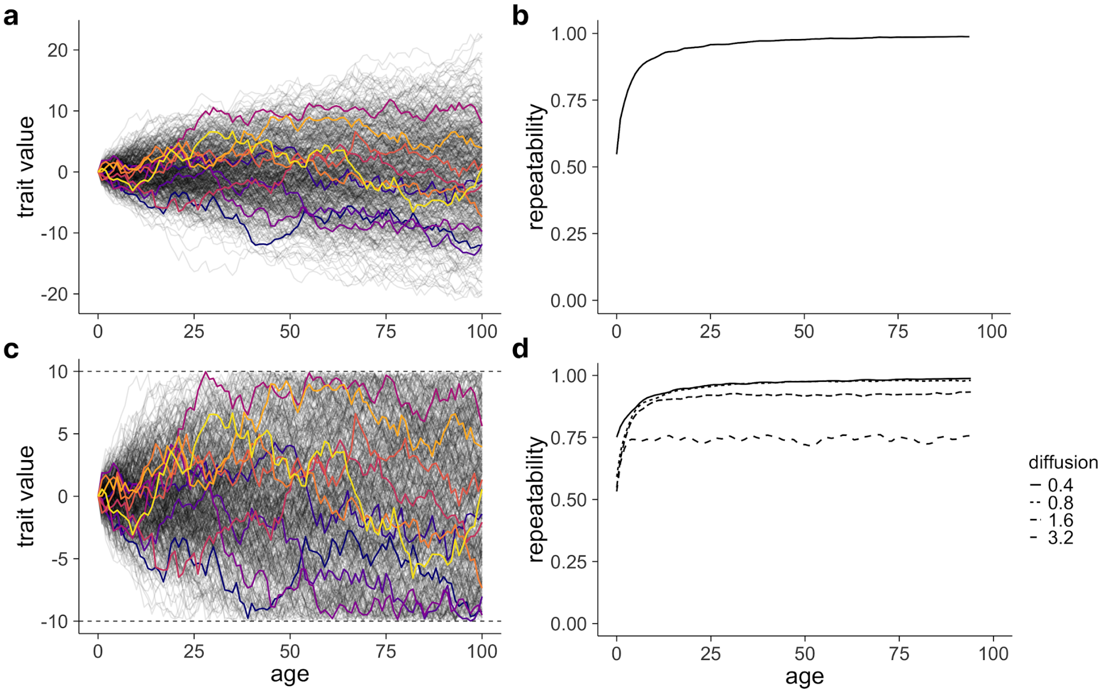

Figure 2. Developmental trajectories of 500 individuals and the corresponding time series of repeatabilities when modelling the developmental process as a Gaussian random walk, corresponding to the gradual development of a selectively neutral trait. (**a**) Trait development, where a diffusion parameter (here, diffusion, $\sigma^2 = 0.8$) describes the degree of stochasticity throughout development. Developmental trajectories for 500 individuals are graphed, with a random subset (n = 10) in colored lines. (**b**) Such trait development leads quickly to a high degree of repeatability that is sustained throughout life; this pattern is observed for all values of diffusion $\sigma^2 > 0$. Here, as throughout, repeatability is calculated using a sliding window approach (window size = 6; see *Supplement 1*). (**c**) Trait development for bounded traits ($\sigma^2 = 0.8$). A random subset (n = 10) of the 500 individuals graphed are in color. (**d**) When traits are bounded (here, between -10 and 10), the degree of repeatability is governed by the degree of stochasticity (diffusion) present in each developmental timestep; the larger the diffusion (resulting in individuals being more likely to stochastically achieve a larger proportion of possible trait space in each timestep), the lower the repeatability.

In contrast to the basic Gaussian random walk model, many behavioral trait spaces are bounded (e.g., due to physical bounds on speed, activity, skill, etc.). We capture this reality by integrating bounds that define the minimum and maximum achievable trait values into the above model by assuming that once individuals reach these bounds, their trajectories reflect off the boundary and then, in the next time steps, continue to develop as before. Such a scenario produces a similar pattern as that achieved in unbounded trait space (Fig 2c and 2d), but here, the magnitude of the diffusion parameter matters: the larger the magnitude of diffusion (i.e., developmental stochasticity), the lower the repeatability both initially and throughout development. This pattern is instructive in that the diffusion parameter corresponds to how much of total (now bounded) trait space can likely be achieved in each timestep: the larger the proportion of total trait space that can likely be achieved (here, stochastically) in a single timestep, the lower the repeatability. This thus highlights again the role of incrementality as a key factor underlying our prediction for the emergence of individuality during development.

Directional development towards a target trait value

We next use a simple drift-diffusion model to investigate the common scenario in which individuals begin their lives significantly diverged from a target trait value that they then gradually develop towards. Many traits – complex behavioral traits themselves, or behavior-mediating traits – exhibit this general pattern (e.g., development of foraging and exploration patterns, growth to a terminal size, information acquisition, skill and cognitive development). During the phase of development in which individuals are not yet near their target value, θ, the process of development through phenotype space can be modeled, as before, with a stochastic diffusion parameter, σ^2, but now added to a fixed drift step, μ, up towards the target. We assume that once an individual has developed to within one drift step of the target, individuals express the target trait value in the next timestep, plus some degree of stochastic variance equal to that expressed during development, σ^2. As before, individuals gradually build on developed traits such that trait values at the start of one timestep are those that were achieved at the end of the last timestep; the position *b* in behavioral trait space is thus calculated as:

$$b_{t+1} = \begin{cases} b_t + \mu + \eta_t, & if\ b_t < \theta - \mu \\ \theta + \eta_t, & if\ \theta - \mu \leq b_t \leq \theta + \mu \end{cases} \qquad \text{where } \eta_t \sim N(0, \sigma^2) \qquad (1)$$

Note that in the rare case where b_t overshoots the target value θ by more than μ, behavior in the next timestep, b_{t+1}, thus assumes a drift $-\mu$ (in addition to the typical diffusion) back to θ.

Figure 3 shows a simulation of 500 individuals through $T = 100$ timesteps in which all individuals start life with the same trait value away from some target value (here, $\theta = 30$; $\sigma^2 = 0.8$; $\mu = 0.6$) and then gradually develop towards the target (Fig 3a). As in simulations with Gaussian random walks through development, there is a swift increase in the degree of repeatability during early development. A high level of repeatability is maintained until individuals have achieved the target trait value (Fig 3b). At equilibrium, as expected, repeatability rapidly declines.

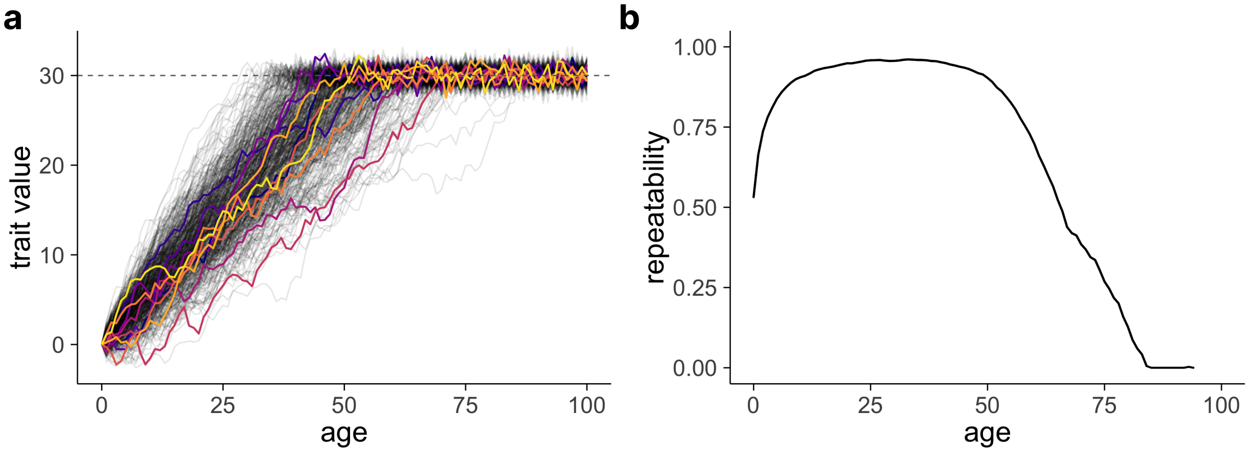

Figure 3. (**a**) Many behavioral or behavior-mediating traits exhibit gradual development towards an optimal target value, which can be modelled with a modified drift-diffusion model, as shown here for a population of 500 individuals, with a random subset (n = 10) in colored lines. All individuals start life with the same trait value ($b_{t=0} = 0$) that they must then develop to some target value, θ (here, $\theta = 30$). Individuals are subject to the same degree of stochasticity ($\sigma^2 = 0.8$) both out of equilibrium (i.e., away from target value) and at equilibrium (i.e., at target value). (**b**) This process results in markedly high degrees of repeatability (calculated via a sliding window approach; window size = 6) during development that reduce to near-zero once a target value is in range.

Information accumulation and skill formation and its behavioral consequences

We now move on from the phenomenological models above and adopt a classic behavioral ecology optimality approach to study the consequences of incrementality and stochasticity during two common processes influencing optimal behavioral expression: information accumulation and skill formation. Both processes often happen gradually and over prolonged periods of time and are subject to stochasticity. Both processes are also often adaptively linked to the expression of gradually developing behavioral traits (i.e., optimal behavior often depends on information and/or skill). Based on our analyses above, we thus expect that, during information accumulation and skill development, the same processes described above act to promote consistent individual differences in both state (i.e., informational state or skill level) and associated behaviors.

To investigate and illustrate these ideas, we present two variants of an optimal foraging model. In variant 1 we focus on gradual information acquisition and its behavioral consequences: we consider a situation where animals accumulate information about the quality of their environment (here, high food return vs. low food return) and optimally adjust their behavior (here, foraging effort) accordingly. In variant 2 we focus on gradual skill formation and its behavioral consequences: animals gradually develop skill with finding or handling food items and optimally adjust their behavior (again, foraging effort) accordingly.

Before proceeding, we note that our phenomenological models above demonstrate how stochasticity and gradual development alone promote individuality (i.e., in the absence of any additional factor affecting the developmental trajectories of variation and individuality). In contrast, the evolutionary models presented below are inherently more complex: rather than behavior at any timepoint following the same time-invariant rules throughout development (as above), state-behavior models in an optimality framework accommodate the reality that behavior at a given timepoint depends on accumulated state, which dynamically affects future behaviors, future state, and their associated expected payoffs in a time-sensitive manner. Such dynamics often create positive or negative state-behavior feedbacks, which are a common and natural feature of many more 'realistic' and internally consistent state-behavior optimality models (see below for details). We note this here since such state-behavior feedbacks have also been implicated in the development of individuality [4,36,37] and thus are additional factors that, together with stochasticity and gradual development, influence the degree of individuality in state-behavior models. Thus, while the effects of stochasticity and gradual development cannot be disentangled from the effects of feedbacks in such models, we will see that the effects of stochasticity and gradual development act to promote the emergence of individuality even when the direction of feedbacks are predicted to constrain individuality (i.e., in the case of negative feedbacks).

The basic model

We consider development over T timesteps, say days. On each day, an individual must choose a foraging effort, u (e.g., proportion of time allocated to foraging), which can vary between 0 and 1; the remaining effort, $z = 1-u$, is devoted to other fitness-conferring activities. The payoff from both foraging activities, $k(u)$, and non-foraging activities, $B(z)$, increases with time invested in the respective activities. To be specific, we assume that during foraging, food items are found as a Poisson process with rate λu per day; that is, if effort, u, is devoted to foraging, the probability that k items are found on that day is:

$$p(k,u,\lambda) = \frac{(\lambda u)^k}{k!} e^{-\lambda u}, \quad k = 0,1,2,\ldots \tag{2}$$

If an individual chooses foraging effort u_t in timestep t, the payoff to that individual is thus:

$$k(u_t) + B(z_t) \tag{3}$$

where k corresponds to the food items found in timestep t (which in turn depends on u_t, see above) and B is an increasing function with diminishing returns corresponding to the payoff of the individual from non-foraging activities (which in turn depends on z_t, see above); baseline calculations assume $B(z) = 1.25z - 0.25z^2$ for $0 \le z \le 1$. Further model details are provided in *Supplement 3* (model specifications) and *Supplement 4* (dynamic programming equations), and code used to generate optimal developmental trajectories and plots is publicly accessible (see [40]).

Variant 1: Gradual information acquisition

We first consider a scenario where individuals are born into an environment with either a low or high rate of food returns, λ_A or λ_B respectively. At the start of life, individuals do not know in which environment they are but, as food returns are (probabilistically) related to the quality of the environment (Equation 2), they can use their experience with food returns to form a belief about their environment. As the optimal foraging effort depends on the quality of the environment, individuals adjust their behavior according to their belief about the environment.

More technically, we thus assume that, at the start of any given day, t ($t = 2, 3, \ldots, T$), individuals use Bayesian updating (see *Supplement 4.1*) to calculate the posterior probability $\pi(t)$, that they are in the high food return environment. Optimal state-dependent developmental trajectories for behavior are then determined using stochastic dynamic programming via backward induction such that, the expressed behavioral trajectory (i.e., the sequence of foraging efforts) maximizes the sum of expected total payoffs by the end of development, T (*Supplement*

4.1). Throughout we assume that all individuals begin life with an evolutionarily set prior of $\pi_{t=0} = 0.50$ and that individuals continue to adjust their posterior estimate and thus their behavior until their posterior is close to certainty (here, within $\varepsilon = 0.005$ of either 0 or 1; once within ε of certainty, posteriors are set to certainty).

Figure 4 shows the developmental unfolding of behavior, posterior beliefs, and behavioral repeatability for a simulated population of 100 individuals adopting the optimal developmental trajectories in the environment with a low (Fig 4a-c) and high (Fig 4d-f) rate of food return. As can be seen, in both environments, chance (due to the realistic assumption of probabilistic food returns) creates variation among initially identical individuals, both in behavior (Fig 4a and 4d) and the belief about the environment (Fig 4b and 4e). As predicted from our above arguments and analyses, this initial among-individual variation is stabilized and even increases (due to stochasticity in subsequent timesteps) over developmental time, resulting in consistent among-individual differences and thus high repeatabilities throughout development (Fig 4c and f) – as long as individuals have not reached equilibrium (i.e., certainty about the environment and thus constant optimal behavior). While, as expected, repeatability drops (Fig 4f) or vanishes at equilibrium (at equilibrium, repeatability is expected to be low or even unidentifiable due to low within- and among-individual variation), equilibrium might not be reached in developmental time, as also illustrated in our particular example in the environment with low food returns (Fig 4a-c), resulting in sustained high levels of individual differences and thus repeatabilities throughout development (Fig 4c).

We note that, as discussed above, along with stochasticity and path dependency of gradual development promoting individuality, feedbacks between state (i.e., belief about the quality of the environment) and behavior (foraging effort) are also at play in our model. In particular, in the environment with high food returns, higher foraging effort gives rise to, on average, higher certainty about the high quality of the environment, making higher foraging efforts more advantageous, constituting a positive state-behavior feedback. In contrast, in the environment with low food returns, higher foraging effort gives rise to, on average, higher certainty about the low quality of the environment, making lower foraging efforts more advantageous, constituting a negative state-behavior feedback. The fact that, as predicted from our phenomenological models above, individual differences robustly arise in both environments, illustrates that stochasticity and gradual development are strong promoters of individuality also in the face of other factors affecting variation.

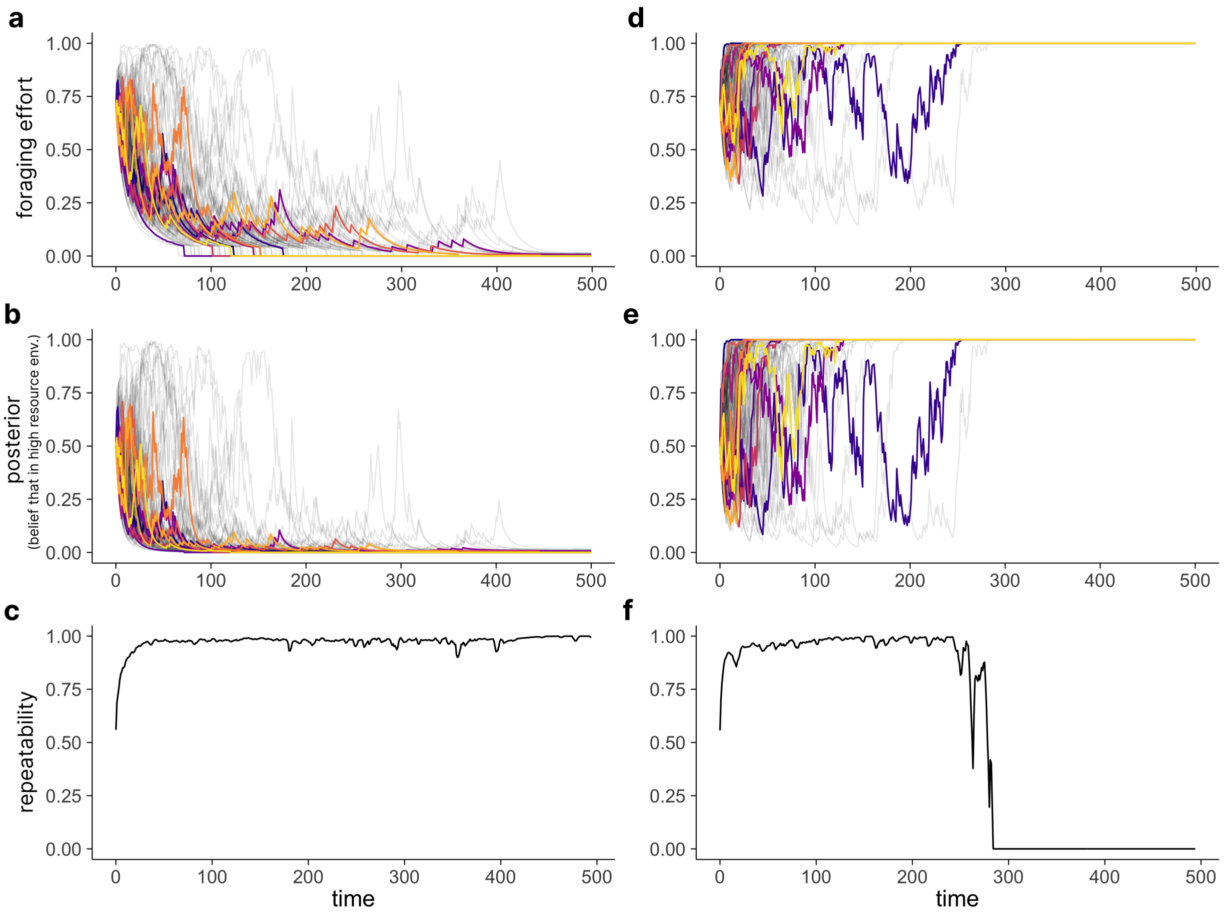

Figure 4. Optimal developmental trajectories of behavior (**a** and **d**), posterior belief that the environment yields a high resource rate (**b** and **e**), and behavioral repeatabilities (calculated via a sliding window approach; window size = 6; **c** and **f**) for a population of 100 individuals; trajectories for a random subset of individuals (n = 10) are shown

with colored lines (the same individuals are shown in corresponding behavior and posterior trajectories for each type of environment). Figures **a**-**c** correspond to an environment with a low resource rate (here, $\lambda_A = 0.75$), and figures **d**-**f** to an environment with a high resource rate (here, $\lambda_B = 1.25$), all individuals begin life with an unbiased prior of 0.50 that the environment exhibits a high resource rate. As can be seen, in both environments, stochasticity and chance generates variation among initially identical individuals in both behavioral traits (**a** and **b)** and posterior beliefs (**d** and **e**). This initial variation, in turn, is maintained and even increased over development, due to the path dependency of gradual developmental processes, resulting in high levels of repeatabilities in both environments when not at equilibrium (**c** and **f**).

Variant 2: Gradual skill formation

We now consider a scenario where individuals can gradually gain foraging skill (e.g., skill with finding or handling food). We assume that foraging skill is gained via past encounters with food items such that the more encounters an individual has with food, the higher the skill. Put more technically, we assume that, at each point in time, the food return λ now increases as a function of the total number of food items *K* encountered up to that point: if K_{t-1} items in total have been found on days 1,2,3, …, *t*-1, then on day *t*, $\lambda_t = S(K_{t-1})$ where *S* is an increasing function with $S(K_{t-1}) = \lambda_A + \frac{(\lambda_B - \lambda_A)K_{t-1}}{0.25T + K_{t-1}}$. Note that this rate is only updated daily, not after each item has been found. As above, optimal state (i.e. skill)-dependent developmental trajectories for behavior are determined using stochastic dynamic programming via backward induction such that, at each point in time, a behavioral decision maximizes the sum of expected total payoffs by the end of development (*Supplement 4.2*).

Figure 5 shows the developmental unfolding of behavior, skill, and behavioral repeatability for a simulated population of 100 individuals adopting optimal behavior at each point in development. While all individuals begin life with identical skill and thus identical foraging effort, since food returns follow a partly probabilistic process, chance events give rise to slight among-individual variation in food returns. Variation in food return causes variation in foraging skill (Fig 5b), which in turn affects optimal foraging effort (Fig 5a). As predicted from our above arguments and analyses, this initial among-individual variation is stabilized and even increases (due to stochasticity in subsequent timesteps) over developmental time, resulting in consistent among-individual differences and thus high repeatabilities throughout development (Fig 5c).

We note that, as presented in the variant 1 model results, we again observe a feedback between state (here, skill) and behavior (foraging effort): those individuals who spend more time foraging tend to encounter more food items, gaining more foraging skill, which then positively affects both current and future expected food return and incentivizes greater foraging effort. Along with stochasticity and gradual development, this positive state-behavior feedback mechanism likely further contributes to the emergence of consistent individual differences (i.e., high repeatability; Fig 5c).

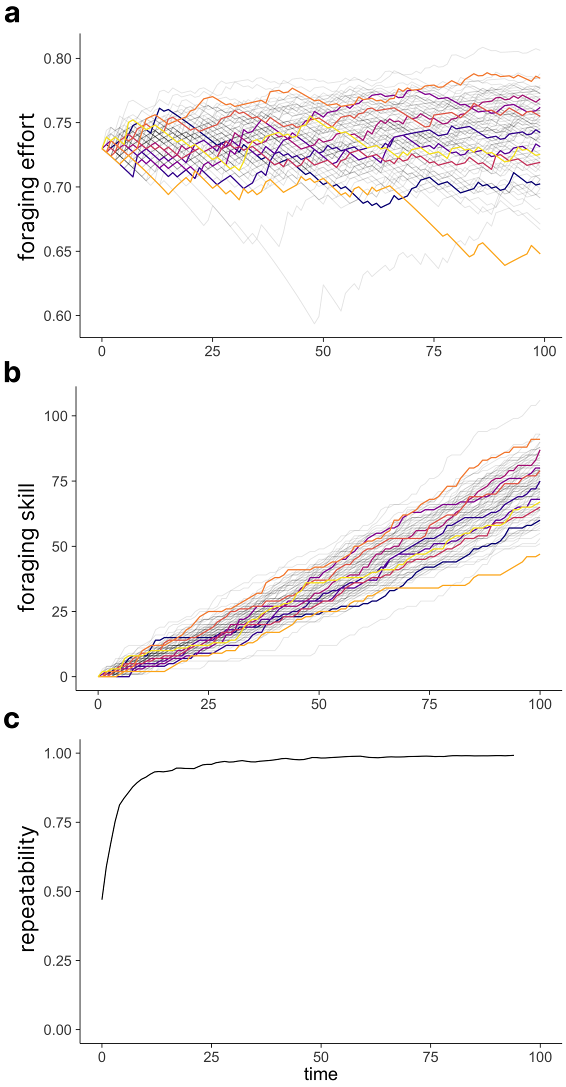

Figure 5. Developmental trajectories of (**a**) optimal foraging effort, (**b**) foraging skill (i.e., the cumulative experience that an individual has with food items), and (**c**) behavioral repeatability (calculated via a sliding window approach; window size = 6). Optimal behavior at each timestep throughout development thus depends on the cumulative experience that an individual has had with food items; in other words, individuals develop foraging skill which then affects future expected payoffs of foraging. Shown in **a** and **b** are trajectories for 100 individuals, where a random subset (n = 10) is shown with colored trajectories (the same individuals are colored in both panels **a** and **b**).

Discussion

For over two decades, theory in behavioral ecology has sought to explain consistent among-individual differences in behavior, focusing on adaptive or constraint-based explanations for behaviors at equilibrium [3,7,44]. Our results suggest that this emphasis has resulted in the neglect of basic, out-of-equilibrium processes that operate in a wide variety of real biological contexts and are themselves strong generators of individuality. By explicitly incorporating gradual development into a diverse set of models – from neutral trait development to directional development towards a phenotypic target to state-dependent optimal foraging – we find that the combination of gradual, path-dependent development and chance robustly produces strong consistent individual differences. We here situate these findings in the context of known drivers of individuality, offer testable predictions and suggest experiments for empiricists, and discuss the implications of this work for out-of-equilibrium perspectives and the role of stochasticity in generating biological variation more broadly.

The results presented here complement and extend existing theory on behavioral individuality. State-dependent strategies [45,46], life-history trade-offs [47,48], state–behavior feedbacks [4,36,37], and genetic or developmental constraints [5,49,50] have all been proposed to generate, stabilize, or amplify individual differences. Here, we show that these mechanisms operate on top of a more fundamental baseline: whenever traits involve some degree of stochasticity and develop incrementally, consistent individual differences are predicted to emerge. The first of these requirements (that of some degree of stochasticity) is easily satisfied: indeed, probabilistic or stochastic processes permeate species' ecologies [51], both from external sources (e.g., early life contingencies and chance events [52], imperfect cue reliabilities or environmental uncertainty [53–55]) and internal sources (e.g., stochastic gene expression [56–

58], stochasticity in neurobiological development [23,59,60], etc.). The second of these requirements (that behaviors themselves or their underlying behavior-mediating state variables incrementally develop) is also often satisfied: behaviors that are cumulatively built include learned behaviors [13,18,61,62], motor or cognitive skills [19,63], and social skills [17,64], and the incremental development of internal state variables that often mediate behavior (e.g., information state, energetic state, social rank, etc.) is a widespread biological phenomenon [62,65]. Thus the generality of the perspective uncovered here – as both stochasticity and gradual developmental processes are fundamental characteristics to most ecologies – may help to explain both the ubiquity of individuality and its persistence in systems where there is a lack of strong support for alternative mechanisms (e.g., neither strong feedbacks, clear evidence of adaptive value, pleiotropic constraints, etc.) [3].

The first of our models (i.e., development via Gaussian random walk) shows how neutral 'developmental drift' can create and maintain a high degree of individuality. While not an evolutionary model in the optimality sense, this model demonstrates perhaps the most basic 'out-of-equilibrium' scenario: that in which, in fact, there is no evolutionary equilibrium (e.g., the development of selectively neutral traits). While this basic scenario has been essentially ignored in traditional behavioral ecology theory (which tends to assume, at least as a null hypothesis, that behaviors are adaptive and at equilibrium), many observed behaviors may in fact be 'neutral' (i.e., variation in that trait is selectively neutral) [43]; for such traits, we show that high degrees of repeatability (rather than low repeatability) may be the appropriate null expectation for individuality. As an extension, our findings suggest that whenever behaviors or behavior-mediating state variables incrementally develop, high repeatability should not automatically be interpreted as evidence for adaptive differences or strong constraints, unless it exceeds what might be predicted from stochastic, path-dependent developmental processes alone. This parallels the role of neutral models in molecular evolution and community ecology more broadly, where neutral theory does not deny the importance of selection or niche differentiation, but rather delineates baseline or null expectations for the degree of variation in the absence of selection [66,67].

A second set of two models that we present depict incremental development towards a target value: a simple drift-diffusion process model and an optimality-based learning model. These models generate a set of predictions that are directly amendable to empirical tests. Broadly speaking, when individuals gradually develop toward a target value, repeatability is predicted to be highest during out-of-equilibrium developmental phases (i.e., periods away from the target value). In the case of gradual information accumulation, for example, as animals learn about their environments, individuality is predicted to be strongest during learning phases (given some degree of environmental uncertainty or imperfect cues). As information accumulates and animals approach certainty (they may never do so in many real word scenarios), individuality is predicted to decline as individuals converge on the same optimal behavior. A tailored experiment testing these predictions is easily conceivable measuring, for example, both individual behavior (e.g., foraging or activity) and sequences of experiences through time in environments where food returns are probabilistic. In such a scenario, individuals in the same overall environment (i.e., with the same overall probability of encountering food) will stochastically differ in their sequences of food experiences, which is then predicted to lead to a prolonged developmental period of high individuality until individuals converge on optimal activity or foraging patterns; treatment populations in environments with higher variances in the probability of food returns would be expected to exhibit longer periods through development of high repeatability. In any case, empirical tests that explicitly measure the developmental course of individuality and the state-behavior feedbacks that give rise to behavioral consistency in these ‘out-of-equilibrium’ periods of life are in line with broader calls to move beyond the ‘behavioral gambit’ by explicitly modeling and measuring the developmental mechanisms (e.g., learning) that produce behavior [12,13,68,69].

The skill model demonstrates a related but distinct pattern compared to the learning model. When performance (e.g., expected fitness payoffs) improves through experience, chance differences in early success should generate consistent differences in behavior. In our model, for example, individuals that happen to encounter more food early in life gain more skill; higher skill makes foraging more profitable, further increasing foraging effort and future skill. Rather than convergence at a target equilibrium, as predicted by the learning model, however, the skill model demonstrates that some processes – even assuming optimality – may alternatively lead to behavioral divergence: in either case, stochasticity and incremental development drive high levels of individuality. These results, in which individuality in ‘noisy’ environments is maintained by differences in underlying state, extend a number of important early models of behavioral individuality [46,70] by explicitly modeling the developmental processes through which differences in state may arise and thus feed back on behavior. These results also follow recent calls in behavioral ecology to treat behavioral skill as an important, gradually developing trait that can exhibit important individual-level differences [17,19].

Lastly, our results may help to contextualize a growing literature on so-called stochastic individuality: consistent among-individual differences that emerge even in the apparent absence of genetic and environmental differences. Such individuality has been documented in a broad array of systems from clonal Amazon mollies reared under near-identical conditions [71–74], to genetically identical mice [75,76] and isogenic *Drosophila* lines [59,77] in shared or near-identical environments. These seemingly stochastic differences are often biologically meaningful components of phenotypic variation [23,51,60], and have been shown to correlate with long-lasting differences in growth, reproduction, and fitness [73,78]. Here, our contribution to this growing area of research is to identify a mechanism through which this stochastic individuality might emerge. Indeed, while stochasticity (e.g., environmental or developmental noise) is an important element in the generation of individuality, our results suggest that for this stochasticity to result in consistent individuality, small stochastic differences that arise must be retained, accumulated, and/or amplified. Gradual development satisfies this condition: the path-dependent, time-resolved nature of many developmental processes can maintain initial stochastic differences, developmental state-behavior or behavior-experience feedbacks may amplify these differences, and early life chance events may thus be translated into lasting, repeatable individual differences – even among genetically identical individuals reared in stable, near-identical environments.

We conclude by noting that our models are among only a small minority in behavioral ecology that examine behavioral dynamics away from an evolved, stable equilibrium target value. Classic theory in behavioral ecology has been extraordinarily powerful in identifying the evolutionarily stable strategies (ESS) toward which selection directs behavior [11,79]. Yet often, individuals do not spend their entire lives – or even ever reach – these ESS equilibria. Here, by modeling stochastic development trajectories, rather than just the stable equilibrium trait values themselves, we find that individuality emerges as a simple product of path dependent development. Other, diverse modeling frameworks that consider out-of-equilibrium contexts (e.g., developmental processes, tracking environmental fluctuations, etc.) will provide an important and much needed extension of optimality theory that examines behavior not only at equilibrium targets, but also asks how individuals developmentally achieve these equilibria, helping us to understand the important out-of-equilibrium biology along the way.

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Supplementary material: Gradual development and chance beget individuality

Sean M. Ehlman, John M. McNamara, Ulrike Scherer, Max Wolf

Contents

1 Repeatability calculations

1.1 Calculating repeatability

To quantify the degree of behavioral individuality in the models presented in our manuscript, we rely on repeatability calculated via a mixed-modeling framework in R [1] using the `lmer` package [2]. All code for these calculations applied to the simulations presented in our manuscript can be found in the associated code repository. Here, we briefly outline the model specifications and methods used for all repeatability calculations.

Repeatability was calculated using a sliding-window approach (window size = 6), in which data from all simulated individuals from six consecutive timepoints (see *Supplement 1.2* for a robustness analysis with different time interval lengths between measured timepoints) were used to assess the degree of within- and among-individual variation:

$$\text{Behavioral trait value} \sim 1 + (1|\text{ID}), \tag{1}$$

where ID is an individual's identity and (1|ID) allows for the estimation of a random intercept for each individual. Note that in the case of models in which the mean trait value changes as a function of time (i.e., all models except Gaussian random walk and bounded Gaussian random walk), `age` was included as an additional fixed effect, and repeatabilities were thus adjusted for individual age.

From these models, variance components were extracted and used to calculate repeatability adjusted for time. Specifically, among-individual variance was estimated from the variance of the random intercepts, denoted V_{among}, and within-individual variance was estimated from the residual variance, denoted V_{within}. Repeatability was then calculated as

$$R = \frac{V_{\text{among}}}{V_{\text{among}} + V_{\text{within}}} \tag{2}$$

1.2 Robustness of repeatability results to sliding window intervals and sizes

Throughout the main text analyses, repeatability was calculated with a sliding window approach using a window size, w, of 6 consecutive timepoints as 'measurement points' and the window sliding one time point at a time, ending at $t = T - w$ timepoints, with T being the maximum age. Below, we present two additional analyses that demonstrate the effects of (1) the time interval between measurement points (Figure S1a) and (2) the size of the window (Figure S1b). Shown is the case of development via Gaussian random walk (corresponding to Figure 2 in the main text), though the general pattern is consistent across cases. As can be seen, in both the case of increased time interval between measurements and window size, the general pattern of high, sustained repeatability as observed in the main text analyses is shown. The effect of increasing time intervals between measurements acts to depress repeatability, as expected.

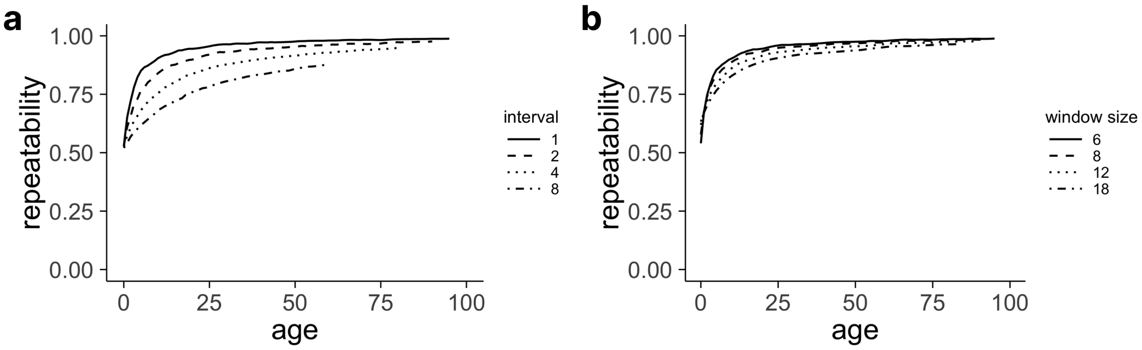

Figure S 1: Repeatability calculated via a sliding window approach applied to trait trajectories of $n = 500$ individuals developing via Gaussian random walk (e.g., compare to Figure 2 in the main text; all other parameter values besides those toggled here, are the same as in the main text). (**a**) Though still elevated, repeatability decreases as the interval between measurements increases. (**b**) Increasing the window size (here, measurement point interval is set back to 1) results in slightly decreased repeatability, mostly towards the beginning of life. In both cases, the general pattern of repeatability through development resembles that presented in the main text.

2 Galton board repeatability

Figure 1 in the main text presents the metaphor of marbles moving through a Galton board as a simple abstraction of phenotypes developing through trait space (*sensu* Waddington's epigenetic landscape). While simply a device for shaping intuitions around the general consequences of stochasticity and gradual development on phenotypic individuality, we here formally plot the trajectory of repeatability through development for $n = 1000$ marbles moving through the depicted Galton board with $n = 18$ interleaved layers of pins, where, at each pin, a marble either moves to the left or to the right of a pin with a binomial draw of probability 0.5 (Figure S2).

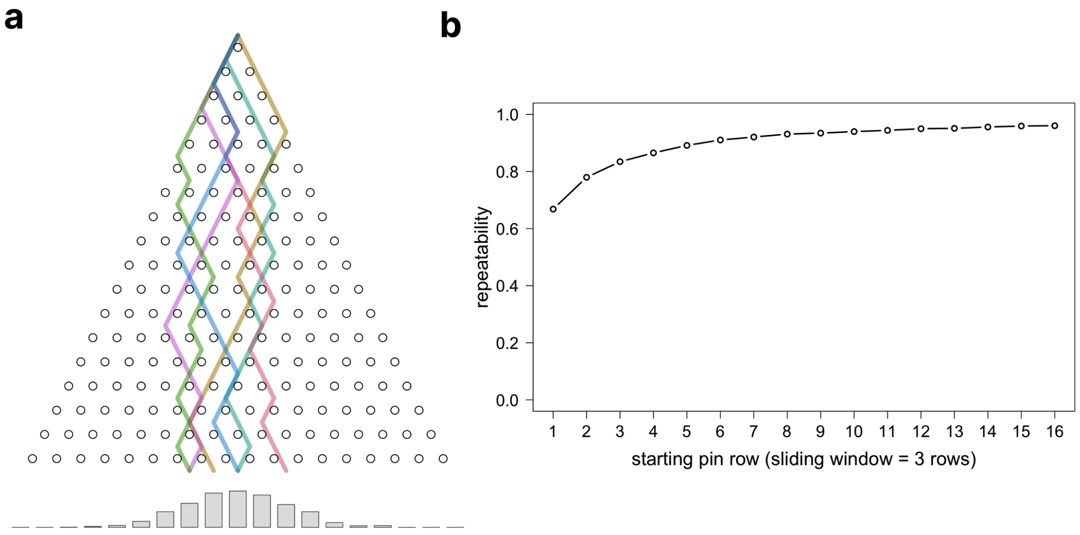

Figure S 2: (**a**) A reproduction of Fig1a from the main text of a Galton board: marbles move through a chute of interleaved pins, where the movement of marbles around a given pin follows a probabilistic process (e.g., a binomial draw with probability 0.5 of moving either to the left or right of the pin). Shown here is a random subset of 6 trajectories of marbles through Galton board space, corresponding to 6 individuals developing through a simple phenotype space, according to the metaphor (see main text). Shown at the bottom of the Galton board is the distribution of final positions for a population of $n = 1000$ marbles (individuals). (**b**) Repeatability (calculated via a sliding window approach; window size $= 3$) for a population of $n = 1000$ marbles throughout Galton board space.

3 Optimal foraging models

We analyze behavior under two optimal foraging models. Both models assume a stochastic food supply. In the first variant, individuals learn about the mean food availability. In the second, they acquire foraging skills as a result of finding food items.

3.1 The food supply

We consider behavior over a period of T days. On each day, an individual must choose the proportion of time allocated to foraging. The remaining time is allocated to other fitness-conferring activities.

If a proportion of time u is devoted to foraging and a proportion $z = 1 - u$ to other activities on a day, then the payoff to the individual is $k + B(z)$ where k is the number of food items found during foraging and B is an increasing function with diminishing returns. Baseline calculations assume

$$B(z) = 1.25z - 0.25z^2 \quad \text{for } 0 \leq z \leq 1. \tag{3}$$

During foraging, food items are found as a Poisson process at rate λ per day. Thus, if a proportion of time u is devoted to foraging, then the number of items found has a Poisson distribution with parameter λu. This means that the probability k items are found on that day is

$$p(k, u, \lambda) = \frac{(\lambda u)^k}{k!} \exp(-\lambda u), \quad k = 0, 1, 2, ... \tag{4}$$

In numerical implementation we constrain the number of food items found during a day to not exceed $k_{max} = 20$. Let

$$S = \sum_{k=0}^{k_{max}} p(k, u, \lambda) \tag{5}$$

Then we assume that the probability of finding k items is

$$\tilde{p}(k, u, \lambda) = \frac{p(k, u, \lambda)}{S} \quad k = 0, 1, ..., k_{max}. \tag{6}$$

3.2 Model variant 1. Learning about the food supply

The rate λ is constant over the T days, and the environment takes one of two possible values for λ, denoted by λ_A and λ_B, where $\lambda_A < \lambda_B$. Baseline calculations assume $\lambda_A = 0.75,\ \lambda_B = 1.25$. At the start of day 1 of the period it is not known which of these two values holds, with the prior probability that $\lambda = \lambda_B$ equal to $\pi(1)$.

At the start of day t ($t = 2, 3, ..., T$) the individual uses the posterior probability at the start of the previous day $\pi(t-1)$, the value of u on the previous day, and the number of items found on the previous day to obtain $\pi(t)$: the posterior probability that $\lambda = \lambda_B$.

A strategy specifies how the value of u on each day depends on t and the posterior at the beginning of that day. We consider behavior under the strategy that maximizes the sum of the payoffs over the T days.

3.3 Model variant 2. Acquiring foraging skill

In this model variant, λ can increase as the forager finds more food items. Initially $\lambda = \lambda_A$.

If a total of K items has been found on days $1, 2..., t-1$, then on day t we have $\lambda = S(K)$ where S is an increasing function. Note that this rate is only updated daily, not after each item has been found. Computations assume that

$$S(K) = \lambda_A + \frac{(\lambda_B - \lambda_A)K}{K_0 + K}, \tag{7}$$

Where K_0 is a constant. Again, baseline calculations assume $\lambda_A = 0.75,\ \lambda_B = 1.25$.

4 The dynamic programming equations

4.1 DP for the learning model

Posteriors. Suppose that the posterior probability that $\lambda = \lambda_B$ at the start of day t is π $(1 \leq t \leq T)$ and that the proportion of the day spent foraging is u. Then the probability that k food items are found is

$$q(k,u,\pi) = (1-\pi)p(k,u,\lambda_A) + \pi p(k,u,\lambda_B) \quad k = 0,1,2,.... \tag{8}$$

If k items are found, then the posterior at the start of day $t+1$ is

$$\pi'(k,u,\pi) = \frac{q(k,u,1)}{q(k,u,\pi)}\pi. \tag{9}$$

The value function. Let $V(\pi, t)$ be the expected total future payoff for an individual with posterior π at the start of day t, given that future behavior is optimal. We formally set $V(\pi, T+1) = 0$.

The DP step. Let

$$H(\pi,t,u) = B(1-u) + \sum_{k=0}^{\infty} q(k,u,\pi)\left[k + V(\pi'(k,u,\pi), t+1)\right]. \tag{10}$$

Then

$$V(\pi,t) = \max_{0 \leq u \leq 1} H(\pi,t,u). \tag{11}$$

These equations can be solved iteratively by working backwards from $t = T$.

The optimal strategy. The optimal proportion of time spent foraging on day t given posterior π at the start of the day is $u_t^*(\pi)$ where

$$H(\pi,t,u_t^*(\pi)) = \max_{0 \leq u \leq 1} H(\pi,t,u). \tag{12}$$

Numerical implementation of DP. Following equation 8 we set

$$\tilde{q}(k,u,\pi) = (1-\pi)\tilde{p}(k,u,\lambda_A) + \pi\tilde{p}(k,u,\lambda_B) \quad k = 0,1,2,...k_{max}, \tag{13}$$

where $\tilde{p}$ is given by equation 6. In calculating posteriors in the numerical implementation we use equation 9 with $\tilde{q}$ replacing q. Let $P_{max} = 10000$ and set $\delta = 1/P_{max}$. We take posterior probabilities to lie on the grid $\{0, \delta, 2\delta, ..., 1\}$. We use linear grid interpolation. Specifically, for given posterior $\pi'(k, u, \pi)$ set

$$\pi'_0(k, u, \pi) = \frac{|P_{max}\pi'(k, u, \pi)|}{P_{max}}, \tag{14}$$

where $|v|$ denotes the integer part of v. Let $\pi'_1(k, u, \pi) = \min\{\pi'_0(k, u, \pi) + \delta, 1\}$. Set $p_1(k, u, \pi) = P_{max}(\pi'(k, u, \pi) - \pi'_0(k, u, \pi))$ and set $p_0(k, u, \pi) = 1 - p_1(k, u, \pi)$. Then in the DP step, equation 10 becomes

$$H(\pi, t, u) = B(1 - u) \tag{15}$$

$$+ \sum_{k=0}^{k_{max}} \tilde{q}(k, u, \pi)\left[k + p_0(k, u, \pi)V(\pi'_0(k, u, \pi), t + 1) + p_1(k, u, \pi)V(\pi'_1(k, u, \pi), t + 1)\right]. \tag{16}$$

Equation 11 is then as before.

Numerical implementation of forward iteration. Individuals start with a prior probability that $\lambda = \lambda_B$ of 0.5 . They then follow the optimal strategy, so that for each time t and posterior π the action chosen is that derived in the dynamic programming part. In calculating posterior probabilities, grid interpolation is used, as above. We do, however, make a small modification. If the derived posterior is less than very small ϵ then it is set to 0, while if the posterior is greater than $1 - \epsilon$ it is set to 1. Computations are based on the value $\epsilon = 0.005$.

4.2 DP for the skill model

The value function. Let $V(K, t)$ be the expected total future payoff for an individual at the start of day t that has previously found a total of K food items, given that future behavior is optimal. We formally set $V(K, T + 1) = 0$ for all K.

The DP step. Note that if a forager has found a total of K food items on days $1, 2, ..., t - 1$ and forages for a proportion of time u on day t, then the probability of finding k items on day t is $p(k, u, S(K))$ where p is given by equation 4.

Let

$$H(K, t, u) = B(1 - u) + \sum_{k=0}^{\infty} p(k, u, S(K))\left[k + V(K + k, t + 1)\right]. \tag{17}$$

Then

$$V(K,t) = \max_{0 \leq u \leq 1} H(K,t,u). \tag{18}$$

These equations can be solved iteratively by working backwards from $t = T$. As in the learning model, numerical computations replace the probabilities p by $\tilde{p}$.

The optimal strategy. The optimal proportion of time spent foraging on day t given K items before that day is $u_t^*(K)$ where

$$H(K,t,u_t^*(K)) = \max_{0 \leq u \leq 1} H(K,t,u). \tag{19}$$

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