Scaling the risk landscape drives optimal life-history strategies and the evolution of grazing

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Consumers face numerous risks that can be minimized by incorporating different life-history strategies. How much and when a consumer adds to its energetic reserves or invests in reproduction are key behavioral and physiological adaptations that structure communities. Here we develop a theoretical framework that explicitly accounts for stochastic fluctuations of an individual consumer's energetic reserves while foraging and reproducing on a landscape with resources that range from uniformly distributed to highly clustered. First, we show that the selection of alternative life histories depends on both the mean and variance of resource availability, where depleted and more stochastic environments promote investment in each reproductive event at the expense of future fitness as well as more investment per offspring. We then show that if resource variance scales with body size due to landscape clustering, consumers that forage for clustered foods are susceptible to strong Allee effects, increasing extinction risk. Finally, we show that the proposed relationship between resource distributions, consumer body size, and emergent demographic risk offers key ecological insights into the evolution of large-bodied grazing herbivores from small-bodied browsing ancestors.

foraging | life-history strategies | evolution of grazing

The landscape of risk faced by consumers is determined not only by the mean density of potential foods but also by their variability over space and time (1). Consumer behavioral and life-history strategies are selected for or against over evolutionary time in part to manage these risks (2). At a coarse scale, these strategies involve how and when energy is saved either endogenously or exogenously (3) and when it is spent. For many species, the most substantial metabolic expenditures are those incurred during reproduction (4), and this is particularly true for endotherms, which on average spend more energy per offspring than nonendothermic organisms (5). Both the availability and variability of resources interact directly with the physiological and metabolic constraints of the consumer to give rise to the remarkable diversity of foraging and life-history strategies observed in nature (4, 6–11).

Resource variability scales differently with consumer size and diet, where a single landscape can impart a wide diversity of experiences and challenges to different organisms (9). A savanna is a vast forest to the common African rat (*Mastomys natalensis*), where grass seeds are unevenly dispersed in discrete units across a patch that may represent a sizable fraction of its home range (12). To larger herbivores such as impala (*Aepyceros melampus*), grasses are resources that are more or less homogeneously distributed across discrete patches (13), and to megafauna such as wildebeest (*Connochaetes* spp.), such foods appear even more uniform over space. In contrast, the clustering of fruits, such as wild cucumber or figs, may change less with scale (cf. ref. 14) and the foraging challenges of frugivores may be more similar across body sizes.

Carnivores also specialize on resources that are concentrated in nutritionally rich but spatially distributed units; however, because prey size scales strongly with consumer size, so does its density across the landscape (15). Small-bodied carnivores such as serval (*Leptailurus serval*) face a relatively uniform resource landscape (primarily rodents) compared to leopards (*Panthera pardus*) that face a landscape where resources (larger herbivores) are more clustered. Importantly, the effective richness of the environment also scales with the efficiency of the consumer's metabolic machinery (16). It is the availability of resources relative to the organism's metabolic rate that directly influences consumer risk. For example, because the ectothermic African rock python *Python sebae* has a lower metabolic rate than a similarly sized mammalian carnivore, the availability of resources (small to midsized tetrapods) is effectively greater if the timescale of acquisition is scaled to its energetic needs.

A consumer must enact a fitness-maximizing strategy that differentially allocates energy to somatic growth, maintenance, and reproduction under the constraints imposed by the spatial distribution of available resources (4, 17, 18). The variability of risks and rewards from acquiring these resources is known to have large effects on the expected optimality of life-history strategies (2, 19, 20), as well as implications for population dynamics (21). While the uncertainty associated with foraging payoffs is clearly important, it is the mean effect in lieu of variability that is generally considered when exploring the constraints giving rise to alternative life histories.

Here we explore the effects of both resource availability and variability on the selective advantages of alternative life-history strategies with a mechanistic model of energy allocation coupled to a resource environment with implicit spatial structure. Using stochastic process theory (22), we model the dynamics of a consumer's energetic state over time as a function of the mean and variance of energetic gains, metabolic losses, and reproductive investment. We explore the reproductive fitness of an

Significance

Consumer species assume diverse life-history and foraging strategies in part to mitigate the risks imparted by spatially variable resources. By deriving a mechanistic model of energy allocation, we show how fitness-optimizing strategies are tied to resource variability and that population stability depends on the scaling of resource variability with consumer body size and diet. These relationships offer insight into the evolutionary trend toward larger body size, known as Cope's rule, and the mammalian transition from browsing to grazing following the advent of grasslands in the mid-to-late Miocene.

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individual consumer, provide predictions on a suite of life-history characteristics, and then extend our methodology to explore population-level implications for terrestrial mammals.

Our results offer 4 fundamental insights into the effects of resource availability and variability in driving the evolution of optimal life-history strategies. First, we show that optimal strategies vary in response to changes in the mean productivity of the resource landscape, where productive environments promote increased investment in future reproductive events and larger litter sizes. Second, we show that both declines in environmental productivity and increases in resource variability promote greater energetic investment in each reproductive event, limiting future fitness and selecting for semelparous strategies. Third, we show that population densities of species foraging for clustered foods such as frugivores or carnivores deviate from the $-3/4$ power scaling of Damuth's law (23, 24) and are prone to strong Allee effects compared to those consuming uniformly distributed foods such as grazers. Finally, we show that the proposed relationship between consumer body size, resource clustering, and the population instabilities arising from Allee effects provides an ecological mechanism for the evolution of large-bodied grazing herbivores from small-bodied browsing ancestors, a well-documented transition in mammalian evolution following the advent of grasslands in the mid-to-late Miocene.

Predicting Optimal Life-History Strategies

We model the dynamics of an individual consumer's energetic state over time as a function of energetic gains from acquiring resources and costs from metabolic losses and reproductive investment. For simplicity, the consumer's energetic state is described by a single state variable (25), $X = x$, which measures the onboard energetic stores available for both metabolic (ontogenetic growth and maintenance) and reproductive expenditures (Fig. 1). Here and henceforth, we use uppercase notation for stochastic variables and lowercase notation for specific values of stochastic quantities. The consumer's energetic state increases by the amount of food it obtains in a day $G = g$, which is stochastic and normally distributed about mean μ with variance σ^2. The consumer's energetic state decreases by a fixed daily metabolic cost associated with somatic maintenance b, regardless of foraging success. The organism dies of starvation when the state drops to zero. Energetic investment in reproduction occurs at the threshold $X = s + r$, where r is the per-litter energetic cost of reproduction and s is the somatic reserves that are maintained during gestation and left to the organism postreproduction. The amount spent on reproduction is equally partitioned among ℓ offspring within the litter with efficiency ϵ. The specific values of the traits $\mathbf{z} = (r, s, \ell)$ thus define the organism's life-history strategy.

We measure the fitness of the organism by the total number of surviving offspring produced during its lifetime, W, which is the generational replacement rate and can be converted to the specific growth rate using the mean lifetime (*SI Appendix*, section A). The values of r, s, and ℓ impact fitness by changing the amount of investment in and timing of each reproductive event. This in turn impacts the number and success of reproductive events in a lifetime (Fig. 1). By accounting for differential energetic allocation in reproductive versus somatic investments, we mechanistically incorporate the trade-offs thought to play a central role in determining life-history strategies. We note that our model does not take into account external mortality, such as predation, or an intrinsic death rate. While these effects could be introduced without difficulty, our approach allows us to isolate the effects of resource-governed dynamics on optimal life-history strategies.

We first treat our framework as an unconstrained optimization problem, where we evaluate the selective landscape with respect to each life-history variable r, s, and ℓ. Fitness as a function of life-history variables is calculated with respect to 4 parameters: 1) the average amount of food obtained per day μ, 2) the variance of food obtained per day σ^2, 3) the daily energetic cost of metabolism b, and 4) the energetic transfer efficiency from parent to offspring ϵ. The dependence of average fitness, $\langle W \rangle$ on the parameters and variables described above, can be solved analytically (*SI Appendix*, section A) to give the expression

$$\langle W \rangle = \frac{\ell \left(1 - \mathrm{e}^{-2(\mu-b)\epsilon r/\ell\sigma^2}\right)}{\mathrm{e}^{-2(\mu-b)s/\sigma^2} - \mathrm{e}^{-2(\mu-b)(s+r)/\sigma^2}}. \quad [1]$$

The relative strength of selection with respect to each life-history trait is thus defined as $\psi(\mathbf{z}) = \partial \log \langle W \rangle / \partial \mathbf{z}$ (26).

Calculation of $\psi(\mathbf{z})$ reveals a selection gradient that depends strongly on both resource availability μ and variability σ^2 (Fig. 2). When the average rate of obtaining food is greater than daily metabolic costs (i.e., $\mu > b$), we observe that selection favors 1) increasing per-litter investment in reproduction r with greater μ that saturates as r increases, 2) increased investment in somatic reserves s with greater μ irrespective of the value of s, and 3) increased litter sizes with greater μ that saturates as ℓ increases. In words, more productive environments tend to promote selection for increased per-litter investment in reproduction and litter size when current investment in each is low. The strength of selection for these traits saturates as investment in each grows, whereas the selective benefits of increasing somatic reserves—which will increase future reproductive opportunities—are proportional to environmental productivity. As such, organisms in richer environments are expected to invest more in future fitness (enabled by higher s), thereby promoting the fitness benefits of iteroparity as a life-history strategy. Our model thus predicts that the optimal life-history approach will skew toward an iteroparous "*r*-selection" strategy in rich environments, where investment is partitioned across a larger number of offspring (cf. ref. 27).

When the average rate of obtaining food is less than the metabolic rate (i.e., $\mu < b$), the environment is extremely poor, such that foraging over a given period would result in energetic losses. In this regime, $\psi(\mathbf{z}) < 0$ with respect to each life-history trait, meaning that there is selection for less investment in r, s, and ℓ. Because every reproductive opportunity may be the last in environments where resources are scarce, less investment in future fitness (low s) over a smaller number of offspring (low ℓ) is favored. The directionality of this shift suggests that as resources become more limited, more of an organism's resources are invested into fewer reproductive events, promoting a more semelparous strategy. Interestingly, our model predicts increasingly strong selection for smaller litter sizes with decreasing resources. In depleted environments, this can result in fractional litters $\ell < 1$ (*SI Appendix*, section B), meaning that the optimal strategy is to invest in less than one offspring per capita. In such cases, multiple adults are required to invest in a single offspring, a process mirroring inclusive fitness among social organisms (28). In fact, there is some evidence to suggest that resource limitation may promote the evolution of sociality (29). While our framework is minimal, it is tempting to speculate that the dynamics explored here may contribute to the evolutionary pressures selecting for such cooperative behaviors.

The effects of resource availability on life-history evolution depend on both the environment and the metabolic machinery of the organism. Because ectotherms have lower metabolic rates for a given body size (5, 30, 31), each kilojoule of resource goes farther and the effective richness of the environment is increased. Because $\psi(\mathbf{z})$ is derived generally, the selective landscape shown in Fig. 2 depends only on the difference between resource availability and the organism's metabolic rate $\mu - b$. As such, ectotherms will experience a selective landscape defined

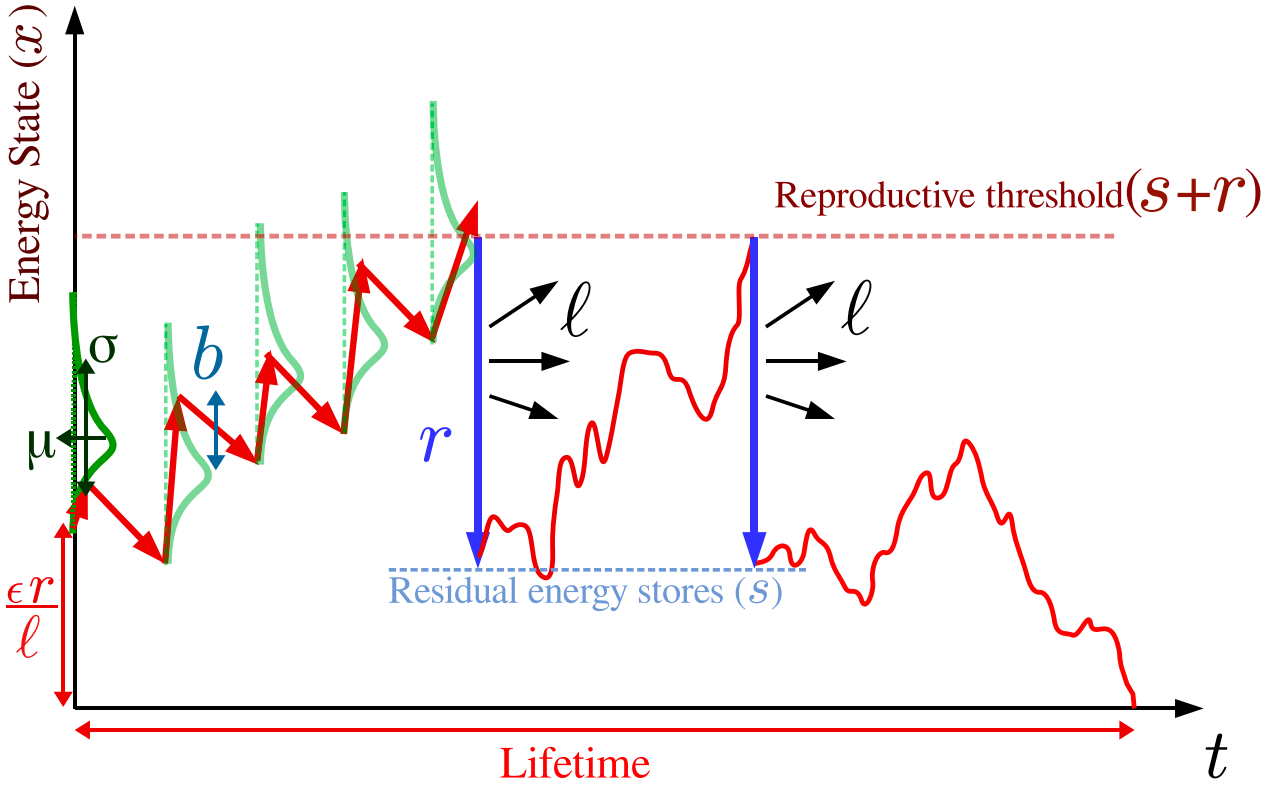

Fig. 1. A schematic of the individual energetic dynamic framework illustrating 1) per-litter energetic investment *r*, 2) investment in somatic reserves *s*, and 3) litter size, ℓ.

by increased resource availability (higher on the y axis in Fig. 2 *A*–*C*) relative to endotherms in the same environment. In this context, the results of our model predict that ectotherms will experience stronger selection for larger somatic reserves (increased s) and litter sizes (increased ℓ), but weaker selection on per-litter energetic investment r. The natural history of iteroparous ectotherms generally supports this notion. For example, many species of snakes, lizards, turtles, and fish tend to distribute resources over larger litters or clutches (31, 32) and conserve somatic reserves to the point where breedings seasons can be skipped entirely (32). Compared to ectotherms, endotherms such as mammals and birds generally show increased energetic investment in smaller litter sizes (2, 30). Moreover, litter sizes are increasing in reptiles $\propto m^{0.46}$ but decreasing in mammals $\propto m^{-0.1}$ (30).

Increasing the variability of resource acquisition σ^2 promotes more conservative life-history strategies. To observe this we compare the relative strength of selection on future reproductive success s versus per-litter investment r, where a value of -1 indicates pure selection toward higher s and a value of $+1$ indicates pure selection toward higher r (Fig. 2*D*). We first observe that selection for s is always stronger than for r. The benefits of retaining the somatic reserves needed to enable future reproduction outweigh investing a larger amount of energy in a single reproductive bout. However, as σ^2 grows so does the relative selection on r, particularly if the current investment in r is low. As the acquisition of energy becomes more uncertain, there will be greater selective benefits for investing in the current reproductive event as it becomes less likely the organism will live to see another one.

Our predictions overlap partially but not completely with classic expectations of optimal life-history strategies (27, 33). Prior life-history models have generally focused on optimal strategies for reproduction given particular survivorship and mortality curves for developing and adult individuals (e.g., refs. 18, 34, and 35 and *SI Appendix*, section B). In contrast, our model allows survivorship and mortality to emerge naturally from the resource dynamics alone. We also predict strong selection for r and weaker selection for ℓ, which is generally expected under resource limitation (27). However, we also predict that poor environments may favor semelparity, which goes against prior expectations (27).

So far, we have ignored the feedback that exists between individual fitness and the resources available to each consumer. As a high rate of reproduction will lead to an increasing population feeding on a finite resource, individual fitness is expected to decline. We next expand our framework to incorporate the effects of a self-limiting consumer population feeding on finite resources and examine to what extent resource availability and variability impact the size and stability of consumer populations.

Effects on Population Stability

A population is composed of multiple individuals that partition available resources. Population density determines resource availability and in turn individual fitness. We now examine how differences in the availability and variability of resources impact the steady-state population density as a function of different life-history strategies determined by r, s, and ℓ. We first assume that the mean and variance of resources, μ and σ^2, respectively, are partitioned among n members of a population per area, as $\mu_{\text{ind}} = \mu/n$ and $\sigma^2_{\text{ind}} = \sigma^2/n^{\zeta}$, where resource variance follows a power law (36). As the number of individuals per area n increases, the amount of area foraged by an individual $1/n$ decreases. Larger organisms have lower population densities because individuals require more resources spread across larger areas (23). As such, ζ determines how the resource variance experienced by an individual consumer scales with the population density, and this will

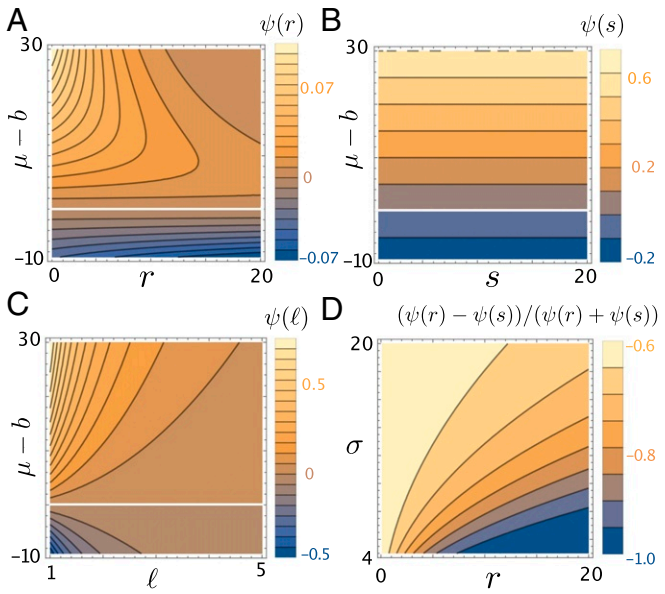

Fig. 2. (*A–C*) The strength of selection ψ with respect to life-history traits $\mathbf{z} = (r, s, \ell)$ as a function of resource availability that is measured relative to metabolic rate $\mu - b$: (*A*) ψ with respect to per-litter reproductive investment r, (*B*) ψ with respect to somatic reserves (investment in future fitness) s, and (*C*) ψ with respect to litter size ℓ. (*D*) The relative strength of selection on r versus s as a function of the SD of resource acquisition σ. A value of -1 indicates pure selection on s; a value of +1 indicates pure selection on r. The horizontal white line in *A–C* shows the location of $\mu - b = 0$.

depend on both the consumer's resource distribution and the area over which it forages.

While resources are partitioned equally on average, the variance of subdivided resources depends on the spatial distribution. At one extreme, resources that are more uniformly distributed (e.g., grasses) are represented by $\zeta = 1$ (Fig. 3, *Left* column). In this case, increasing the foraging area allotted to an individual consumer will lower the coefficient of variation of resource acquisition, $\mathrm{CV}(\zeta = 1) = \sigma\sqrt{n}/\mu$. For $\zeta > 1$, there exists a spatial correlation in the resource distribution with explicit clustering at different spatial scales (Fig. 3, *Center* and *Right* columns). This correlation serves to amplify variance as the spatial scale increases, pertaining to resources that are of intermediate clustering (e.g., fruit or small prey) to those that are highly clustered (large prey). If a resource is clustered, increasing the area foraged per individual (i.e., lowering the population density n) increases acquisition variability, which leaves the coefficient of variation of resource acquisition unchanged: $\mathrm{CV}(\zeta = 2) = \sigma/\mu$. The scaling of resource variability can be estimated empirically from the spatial distribution of resources or connected with previous explorations of home-range scaling (*SI Appendix*, sections D and E).

Incorporating the above assumptions, we obtain an implicit formula to calculate the steady-state population density n^* where $n(t+1)/n(t) = 1$ or $\langle W \rangle^*(\mu/n^*, \sigma^2/n^{*\zeta}|\mathbf{z}, b) = 1$. We numerically solve this equation to obtain the steady-state population density n^* (*SI Appendix*, section C). At steady state, the rate of population growth given as a function of life-history traits $\mathbf{z}$, metabolic rate b, and both the availability and variability of resources (μ, σ^2) is equal to the rate of mortality. In our framework mortality is due solely to starvation, which has a timescale that can be calculated directly using first-passage expressions (*SI Appendix*, section A).

The availability and variability of resources directly influence the profitability of different life-history strategies and ultimately determine fitness. To gain insight into the influence of resource distributions on the expected population steady states for mammals, we assume known allometric scaling relationships for the life-history parameters r, s, and ℓ, as well as metabolic rate b (30, 37, 38) (*SI Appendix*, section C). We then numerically solve for $\langle W \rangle^*$ to obtain the steady-state population densities n^* as a function of mass m and the resource parameters μ, σ, and ζ.

We can now directly assess the fitness trade-offs associated with alternative foraging strategies for consumers of different body sizes: from grazing on homogenously distributed foods to browsing or predating on clustered foods. We observe that there is one stable population steady-state n^* for $\zeta = 1$ and both a stable and an unstable steady state for $\zeta > 1$ (n^* and n°, respectively). When the resource SD σ is much smaller than the mean μ, the steady-state population densities follow the $-3/4$ power scaling predicted by Damuth's law (23), given that $n^* = \mu/b_0 m^{3/4}$ for all values of ζ (Fig. 4*A*). As variance increases, n^* is diminished, and this reduction disproportionately affects consumers of smaller body size (Fig. 4*A*). When resource acquisition is more variable, the populations of larger-bodied consumers better absorb the negative effects of variable foraging success, whereas the populations of smaller-bodied consumers do not. This finding agrees with expectations from the fasting endurance hypothesis (39) and recent perspectives on the fitness benefits associated with the evolution of larger body size (4).

When resources are uniform ($\zeta = 1$), a consumer population decline will ensure that more resources are available to the existing members of the population, increasing the growth rate and allowing the population to recover to the stable state. When resources are clustered ($\zeta > 1$), we observe the appearance of a strong Allee effect where there exists a critical consumer population density n° below which growth rates are negative and population collapse is inevitable (Fig. 4*B*). Thus the model also predicts a lower bound on body size given by $n^*(m_{\min}) = n^\circ(m_{\min})$ as a function of the resource distribution, complementing previous work (41).

Steady-state solutions as a function of body size reveal that increased variability in resource acquisition is expected to disproportionately affect smaller-bodied consumers that feed on clustered resources (Fig. 4). This suggests that if a consumer is smaller bodied, specialization on foods that are spatially

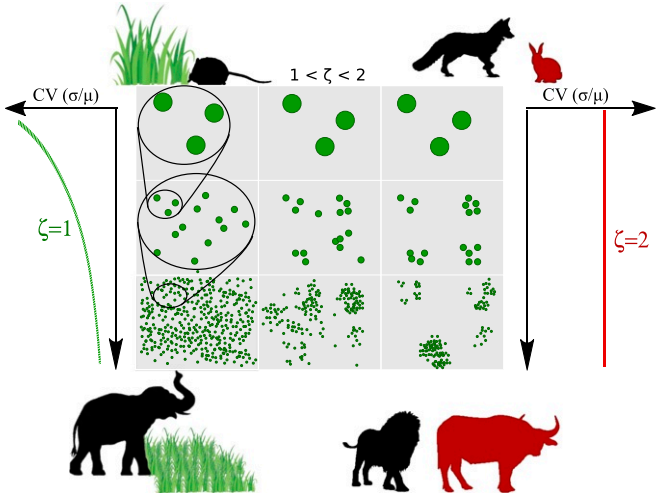

Fig. 3. A visual representation of resources with different variance-scaling exponent, ζ. (*Left*) At $\zeta = 1$, resource distribution is homogeneous; i.e., larger consumers face less spatial stochasticity (smaller CV) compared to smaller consumers. (*Right*) Whereas at $\zeta = 2$, resource distribution is highly clustered. This could be due to spatial distribution of food or due to size of individual units being proportionally larger for a larger consumer.

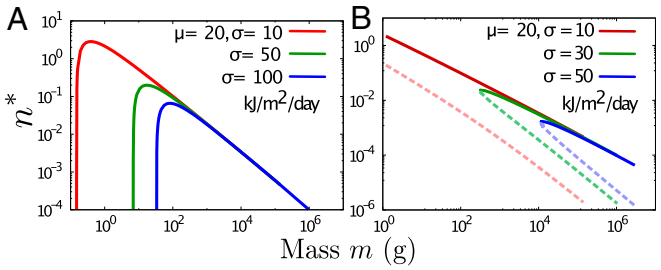

Fig. 4. (*A* and *B*) Steady-state population densities as a function of species size for a fixed resource density (μ), across various values of SD (σ), (*A*) for $\zeta = 1$ and (*B*) for $\zeta = 2$. The dashed lines denote unstable critical population size n°.

clustered carries with it larger demographic risks, whereas targeting more evenly distributed resources may provide certain selective advantages. For small mammals such as rodents, these risks may be expected to promote the evolution of behaviors such as caching (42). Foraging for more clustered resources such as larger fruit may require larger body sizes or locomotive adaptations such as flight, which serve to reduce the spatial variability of resources (43, 44). Similarly, small carnivores tend to specialize on smaller more evenly distributed prey, whereas larger carnivores target larger spatially clustered prey (45).

We assume here that foragers encounter and consume resources stochastically. Previous work has focused on how a broad range of specific foraging strategies and behaviors interact with landscape structure to explain various ecological processes (46–54). Our framework is currently agnostic to these strategies. Different modes of foraging within different environments and spatial dimensions (55) will result in changes to resource acquisition parameters (μ, σ, ζ). This mapping would enable an exploration of the impact that more complex interactions between foragers and their environment have on model predictions.

The Adaptive Benefits of Grazing

Our framework provides a mechanistic link between resource distributions, a consumer's life-history strategies, and emergent demographic risks. Thus we predict that a shift in the resource landscape will have direct consequences on consumer evolution. The advent and global expansion of grassland ecosystems in the Miocene (ca. 10 My BP) represents a fundamental shift in the resource landscape that led to large and long-lasting effects on mammalian communities. These effects manifested in changes to morphology, body size, and diet for multiple herbivore guilds that largely define Mio-Pliocene savanna–woodland ecosystems (56). We next use our framework to explore the underlying ecological drivers that shaped mammalian communities during this period.

The viability of a population requires that perturbations away from the stable steady state decay over time. The perturbation decay rate λ is thus a measure of dynamic stability and is determined by the slope of population growth near the steady state, such that perturbations change over time as $\propto e^{-\lambda t}$. If λ is large such that perturbations decay quickly, the residence time of fluctuations following a disturbance is short. This is particularly important if the stable state (n^*) is near the critical steady state (n°), as fluctuations that fall below n° result in population decline. High values of λ thus indicate that the system is more resistant to collapse. Changes in λ as a function of consumer mass and resource clustering thus represent a fitness surface for consumers of different sizes foraging on resources with different spatial distributions (Fig. 5*A*).

Overall, we find that consumer populations foraging on homogeneous resources (low ζ) have a higher λ than those foraging on clustered resources (high ζ) and that populations of larger-bodied consumers have greater tolerance for resources that are increasingly clustered. Populations of smaller-bodied organisms foraging on clustered resources are also positioned closer to the critical population density n° (*SI Appendix*, section C). These populations both reside closer to the tipping point and have fluctuations with longer residence times, putting them at a disadvantage and serving to emphasize the fitness gains of alternative strategies. The fitness surface across (m, ζ) thus points to a selection gradient favoring larger-bodied consumers specializing on resources that are more homogeneously distributed.

The results of our population-level analysis suggest that differences in population stability may have contributed to the selective pressures that shaped the evolution of grazing. To test this hypothesis, we examine whether the evolution of multiple mammalian guilds in East Africa and North America may have followed evolutionary trajectories in line with the adaptive advantages predicted by λ. Specifically, we examine suids, equids, rhinos, deinotheres and giraffids, and elephantids and gomphotheres in Lake Turkana, East Africa (57, 58), as well as equids from North American grasslands spanning the grassland expansion beginning at 10 My BP (59). We gathered estimates of body size for fossil genera both from published sources and in some cases estimated directly from allometric relationships of body size and published tooth measurements (see *SI Appendix*, section F for details) (60, 61). We calculated the scaling of herbivore resource clustering based on estimated reliance on graze vs. browse from the published $^{13}C/^{12}C$ carbon isotope ratios of fossil and modern teeth, the latter corrected for the global decrease in ^{13}C of atmospheric CO_2 (57–59). We assumed that a diet of 100% graze would result in a resource $\zeta \approx 1$, whereas a diet of 100% browse would result in a resource $\zeta = 1.72$, which we estimated from distributions of browse resources in contemporary savanna–woodland environments (*SI Appendix*, section D).

We observe that transitions in body size and the spatial clustering of dietary resources follow a general trend toward increased population stability (increased λ) over evolutionary time for multiple herbivore guilds (Fig. 5*B*). For suids, rhinos (with the exception of the contemporary black rhino *Diceros bicornis*), and both North American and African equids, the trajectory from smaller-bodied browsers to larger-bodied grazers follows the calculated fitness gradient. This suggests that reducing population instabilities induced by the joint effects of body size and uncertainties in acquiring adequate resources may have served as a catalyst for the evolutionary trends observed within these clades. For the larger herbivore guilds that include deinotheres

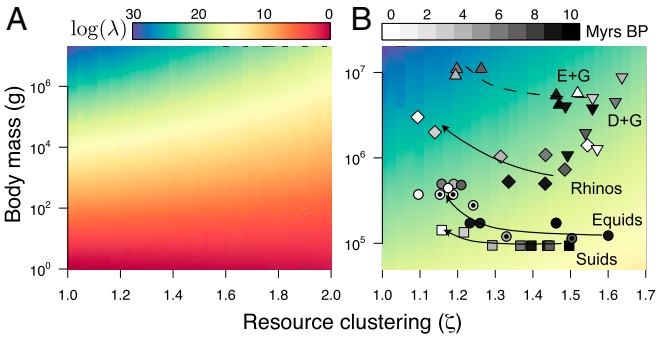

Fig. 5. (*A*) Perturbation decay rate λ as a function of consumer mass m and resource clustering ζ given $\mu = 20$ kJ · m^{-2} · d^{-1} and $\sigma^2 = 2{,}500$ kJ^2 · m$^{-2\zeta}$ · d^{-1} (40). (*B*) Body mass and dietary ζ (symbols) of different clades across East Africa and North America: □, suids; ◯, equids; ⊙, North American equids; ◇, rhinos; ▽, deinotheres and giraffids (D + G); and △, elephantids and gomphotheres (E + G). Arrows follow evolutionary trajectories; dashed lines denote ambiguous trajectories.

and giraffids and elephantids and gomphotheres the temporal trend is less clear, with elephantids and gomphotheres showing high variability in dietary ζ, whereas deinotheres and giraffids remain browse specialists. That these guilds do not reveal a clear temporal trend is in line with the predictions of our model, where larger body sizes are associated with a milder selective gradient over ζ.

Once homogeneous grasslands became a dominant feature in Miocene environments (62), mammalian lineages evolved to capitalize on this relatively new resource, but did so at different rates (57, 58, 63). While the correlation between the evolution of larger body size and increased grazing during the Miocene and Pliocene is well known (64, 65), the ecological drivers promoting this association are less well understood. The broad agreement between our model and the diverse herbivore guilds considered here suggests that the demographic risk arising from the exploitation of clustered resources is a strong candidate driver for the observed macroevolutionary trends following the advent of grasslands. Moreover, the positive relationship between λ and body size lends additional theoretical support for the idea that the dynamics of starvation and recovery may fuel the evolutionary trend toward larger body size known as Cope's rule (4).

The risk landscape experienced by consumers specializing on different resource types largely depends on body size. However, body size also influences the risk landscape by determining the area over which resources are foraged and, consequently, the spatial clustering of those resources experienced by the consumer. As we have shown, the availability and variability of resources are expected to have a large influence on the evolution of life-history strategies and population stability. Explicitly incorporating variability into models of resource acquisition reveals ecological constraints that may have played an important role in observed evolutionary trends associated with correlated changes in consumer body size and resource type. In the future, accounting for the dynamics of individual state with more detailed foraging strategies may provide additional insight into the ecological constraints influencing the evolutionary trajectories of species.

Materials and Methods

Estimating ζ from Resource Landscape Satellite Image. We estimate the value of ζ for a clustered resource such as browse by sampling the spatial distributions of trees and shrubs from satellite images of the Serengeti (*SI Appendix*). We use the 2 extreme values measured ($\zeta = 1$ and $\zeta = 1.72$) as the values of ζ for all grazing and all browsing behaviors, respectively. Paleontological dietary compositions for horses are estimated by using $\delta^{13}C$ isotope measurements from ref. 59. A pure C_3 diet is assumed to correlate with $\zeta = 1.72$, which describes the distribution of trees and shrubs we measure in the Serengeti. A pure C_4 diet is assumed to correlate with $\zeta = 1$, which describes a uniform distribution of resources. Mixed diets are assumed to have a linearly interpolated value of ζ between 1 and 1.72.

Data Availability. The data supporting the findings of this study are available within the main text and *SI Appendix*.

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