

Caching in or Falling Back at the Sevilleta: The Effects of Body Size and Seasonal Uncertainty on Desert Rodent Foraging

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ABSTRACT: Foraging in uncertain environments requires balancing the risks associated with finding alternative resources against potential gains. In arid-land environments characterized by extreme variation in the amount and seasonal timing of primary production, consumers must weigh the risks associated with foraging for preferred seeds that can be cached against fallback foods of low nutritional quality (e.g., leaves) that must be consumed immediately. Here, we explore the influence of resource scarcity, body size, and seasonal uncertainty on the expected foraging behaviors of caching rodents in the northern Chihuahuan Desert by integrating these elements with a stochastic dynamic program to determine fitness-maximizing foraging strategies. We demonstrate that resource-limited environments promote dependence on fallback foods, reducing the likelihood of starvation while increasing future risk exposure. Our results point to a qualitative difference in the use of fallback foods and the fitness benefits of caching at the threshold body size of 50 g. Above this 50-g body size threshold, we observe large fitness gains associated with the maintenance of even a modest-sized cache, whereas similar gains for smaller consumers require maintenance of unrealistically large caches. This suggests that larger-bodied consumers that cache may be less sensitive to the future uncertainties in monsoonal onset predicted by global climate scenarios, whereas smaller consumers, regardless of caching behavior, may be at greater risk.

Keywords: foraging, caching, fallback foods, Sevilleta, stochastic dynamic programming.

Where he can't save a cent and his whole life is spent / Just waitin' for the hard times to go. (Dave Alvin, "Interstate City," 1996)

Introduction

To survive, consumers must take risks as they seek rewards. The strategies they employ must account for both the im-

mediate costs of today and the uncertainties of tomorrow. This entails weighing the costs and benefits of foraging in a temporally and spatially stochastic environment, conditioned on the energetic state of the individual (Mangel and Clark 1986). While the rewards are energetic and ultimately reproductive, the risks include exposure to predation and the potential that resources are not found, such that foraging effort is wasted.

The potential fitness gains provided by specific resources must be weighed in terms of their availability (Caraco et al. 1980), energy density (Emlen 1966), macronutrient content and stoichiometry (Sterner and Elser 2002), and the mechanical and chemical costs associated with processing and digestion (Dominy et al. 2008; Nersesian et al. 2011; Lucas et al. 2014; Yeakel et al. 2014; Machovsky-Capuska et al. 2016). During times of plenty the quality of easily found resources may be prioritized, whereas during times of scarcity resource availability may be expected to play a larger role. While food preference is a well-understood concept, often less appreciated is the importance of those resources targeted during critical use times when preferred high-quality resources are limiting (Wrangham et al. 1998; Laden and Wrangham 2005). During these periods, consumers generally fall back on resources that are otherwise underutilized, which may be due to differences in energy density, abundance, or the direct (e.g., predation) or indirect (e.g., competition) risks associated with acquisition or assimilation. Such foods are sometimes referred to as "keystone resources" (Leighton and Leighton 1983). However, this term is problematic because it has connotations with community stability and the assumption that a keystone resource's outsized role varies inversely with its abundance (Constantino and Wright 2009). To avoid this confusion, we refer to these resources as "fallback foods," a term oft used in primate ecology and paleoanthropology to describe those foods "of low preference and high importance" (Marshall et al. 2009; Lambert and Rothman 2015). While fallback resources may be utilized only rarely, they are vital for ensuring survival during hard times.

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To “save” for a terrestrial consumer means to accumulate energy either endogenously as fat in the form of adipose tissue or exogenously in a cache (Smith and Reichman 1984). Because small mammals can save proportionately smaller amounts of fat on their bodies than larger mammals, they operate closer to the starvation threshold (Lindstedt and Boyce 1985; Dunbrack and Ramsay 1993; Yeakel et al. 2018), meaning that hard times are never far away. In fact, the effects of larger body size on starvation time can be dramatic. If a 10-g organism is expected to last only 12 h before starvation, a 100-g organism would be expected to last two and a half times as long, or ~30 h (Millar and Hickling 1990; McNab 2010). The limited endogenous storage afforded to smaller mammals means that they are more sensitive to spatiotemporal fluctuations in resource availability (Bhat et al. 2020). Caching food resources can buffer against this foraging uncertainty and is a particularly common behavior employed by small mammals and passerine birds (Smith and Reichman 1984; Dunbrack and Ramsay 1993). While many of the advantages of caching have been explored previously (Mangel and Clark 1988; McNamara et al. 1990; Vander Wall 1990; Lucas and Walter 1991; Brodin and Clark 1997; Gerber et al. 2004), how this behavior advantages consumers of different body sizes in highly seasonal environments, particularly when seasonal transitions are uncertain, is not well understood.

Desert ecosystems often support diverse and dynamic small mammal communities in spite of low and unpredictable resource availability (Fox 2011). These communities exemplify how resource-limited ecosystems can support consumers with a diverse range of life-history modes and functional traits associated with resource procurement. In the arid Sonoran and Chihuahuan Deserts of the American Southwest, for example, heteromyid rodents are food-hoarding (caching) granivores that range in body size from ~5 to 150 g and have long gestation times and small litter sizes, but they typically outcompete other species for high-quality seeds. In particular, larger species, such as kangaroo rats (*Dipodomys* spp.), use both scatter- and larder-hoarding strategies to store food in caches that can persist across seasons and even years to provide reliable sources of food during periods of resource scarcity (Schroder 1979; Vander Wall 1990). Smaller heteromyids, such as the silky pocket mouse (*Perognathus flavus*), have highly plastic diets that limit competitive overlap with co-occurring species (Noble et al. 2019).

The highly seasonal and interannual climate variability in desert ecosystems provides an ideal system to quantify the effects of resources on the functional and community ecology of a diverse small mammal community. In the northern Chihuahuan Desert of central New Mexico, precipitation is bimodal, with on average 60% of annual rainfall being delivered by the summer monsoon from

July to October. Monthly averages for more unpredictable winter and spring precipitation are lower than the monsoon, while the driest and hottest period of the year is typically in May and June. Another attribute of this system is interannual variability in both the (annual or seasonal) amount of precipitation and the timing of the transitions between seasons, which impacts foraging strategies of desert consumers (Orr et al. 2015). Overall, environmental variation is a common attribute of precipitation regimes in arid ecosystems, and it is one reason why such environments have served as the backdrop for field-based experiments examining the influence of abiotic factors such as precipitation and temperature on plant (McDowell et al. 2008) and consumer (Meserve et al. 2003; Chesson et al. 2004; Thibault et al. 2004; Kelt 2011) communities. In the future, regional climate models predict rapidly increasing air temperatures, significant decreases of 15%–20% in winter precipitation, increased interannual variability in the strength and onset of the summer monsoon, and higher drought risk (Seager et al. 2007; Gutzler and Robbins 2011; Cook et al. 2015).

These two distinct periods of annual precipitation produce resources of differing quantity and quality that can be traced through the consumer community with carbon isotope analysis of primary consumer tissues and the plant resources they utilize. Highly unpredictable winter/spring rains fuel a spring period of C_3 primary productivity, namely, annual forbs and perennial shrubs. Later in the summer, a second, more reliable period of monsoonal precipitation drives the production of C_4 grasses and limited C_3 growth. C_3 and C_4 plants vary in their nutritional quality, energy content, and persistence in the environment. The leaves of C_3 plants are more nutritious with higher nitrogen and digestible carbohydrate content than C_4 grasses (Caswell et al. 1973; Caswell and Reed 1975, 1976; Barbehenn et al. 2004a, 2004b). In contrast, the leaves of C_4 grasses are harder for consumers to process and digest, but they are more resistant to decomposition (Vanderbilt et al. 2008) and may serve as a fallback food for rodents during periods of resource scarcity.

To what extent are seasonal rodent foraging strategies—what to eat and how much to cache—determined by body size and resource availability? How does increasing uncertainty in seasonal transitions modify expected behaviors, and will such changes to the climate system predispose certain species to increased extinction risk? Here, we explore the influence of resource scarcity, body size, and seasonal uncertainty on the expected foraging behaviors of caching rodents in the northern Chihuahuan Desert in the Sevilleta National Wildlife Refuge. We integrate these elements using a stochastic dynamic program (SDP) to determine fitness-maximizing foraging strategies, where a strategy is defined by the extent to which different resource functional

groups are targeted within a heterogeneous and seasonal landscape.

Our approach offers three important insights. First, we show that resource-scarce environments promote consumer dependence on fallback foods that are not cacheable, increasing risk exposure and limiting the ability of a consumer to absorb the effects of future hardship. Moreover, differently sized consumers are shown to adopt similar foraging strategies in these environments, which may be expected to increase competition. Second, we find that while uncertainty in seasonal transitions lowers consumer fitness across the board, maintaining a larger cache can compensate for these effects. Finally, our results point to a qualitative difference in the use of fallback foods and the fitness benefits of caching at the threshold body size of ~50 g, affirming empirical observations of cache use among rodents at the Sevilleta. Above this 50-g body size threshold, we observe large fitness gains associated with the maintenance of even a modest-sized cache. Below this threshold, similar gains in fitness would require maintenance of unrealistically large caches, reducing the value of caching to the consumer.

Methods

We use an SDP (Iwasa et al. 1984; Houston et al. 1988; Mangel and Clark 1988; Clark and Mangel 2000) to quantify the fitness-maximizing foraging strategies of rodent consumers as a function of (i) endogenous energetic reserves stored as body fat $X(t) = x$ and (ii) exogenous energetic reserves stored in a cache $Y(t) = y$. We maintain uppercase notation for random variables and lowercase notation for specific values of all stochastic quantities. The time-step t varies between 1 and the time horizon $t_{\max} = s_{\max} \cdot d_{\max}$, where d_{\max} is the number of days in a season and s_{\max} is the number of seasons in a year. In our framework a year is simplified to three seasons: the premonsoon, the full monsoon, and the postmonsoon. First we will describe how we simulate consumer-resource interactions within a particular foraging bout across heterogeneous resource landscapes. The results from this simulation will be used to numerically estimate a probability distribution describing energetic returns for a consumer implementing a specific foraging strategy. Second, we will show how the energetic returns that result from a particular foraging strategy contribute to the dynamics of the consumer's energetic state, defined by the amount of fat and cache stores accumulated by the consumer over t_{\max} . Third, we will describe how these dynamics are integrated into a fitness equation, which will allow us to determine the fitness-maximizing foraging strategy for a consumer as a function of its energetic state ($X(t) = x$, $Y(t) = y$) and time. See figure 1 for a conceptual illustration of the model framework.

Energetic Returns within a Foraging Bout

In our framework, consumers forage in an environment where there are four resource functional groups— C_3 leaves, C_3 seeds, C_4 leaves, and C_4 seeds—where a resource i has a mean density μ_i characteristic of (i) the full-monsoon season and (ii) the pre- and postmonsoon seasons. Resource mean densities μ_i (g m^{-2}) were estimated from seasonal transects as part of the Sevilleta long-term ecological research monitoring effort (table 1).

Most rodent consumers at the Sevilleta are central place foragers with relatively small home ranges spatially constrained by competition. Because an individual consumer can cover the same ground multiple times within a foraging bout, resource availability is assumed to scale with home range area, such that larger home ranges promote increased resource availability and, by extension, higher effective densities and encounter rates. In contrast, the number of resources intercepted by a forager unconstrained by a central place would be expected to scale with velocity rather than home range area.

To consider central place consumers of different body sizes M (g) foraging over home ranges of different areas, we set the mean encounter rate as $m_i = \rho \mu_i M^{3/4}$ for resource i , where the unitless ρ scales resource availability for all potential foods. We thus assume that home range area scales allometrically with consumer body mass, such that larger consumers have access to more resources during a foraging bout. As ρ scales resource availability, we equate it here with environmental quality. If $\rho = 1$, all observed resource biomass is assumed to be available to the consumer. Because resource availability is limited by productivity, physical access, timing, and competition, we assume that $0 < \rho \ll 1$, although the true value of accessible resource density is not easily measured. We evaluate model results with respect to a range of values of resource availability ρ : the minimum value (poor conditions) was determined by the point at which consumers no longer survive regardless of foraging strategy, and the maximum value (enriched conditions) was determined by the point at which additional resource availability resulted in little or no change to model results (app. A; apps. A–D are available online). Each resource i is distributed according to a mean encounter rate m_i and dispersion α_i , where lower values of α correspond to patchier distributions. Because we are considering resources that are expected to have similar spatial clustering, we set $\alpha = 10$ for C_3 and C_4 leaves and seeds. We show in appendix A that alternative values of α , as well as alternative scalings of home range area with body size, do not have a significant influence on our results.

We estimated energetic return distributions for each foraging strategy. The energetic return distribution describes the probability of gathering $K(t) = k$ kJ of mixed resources

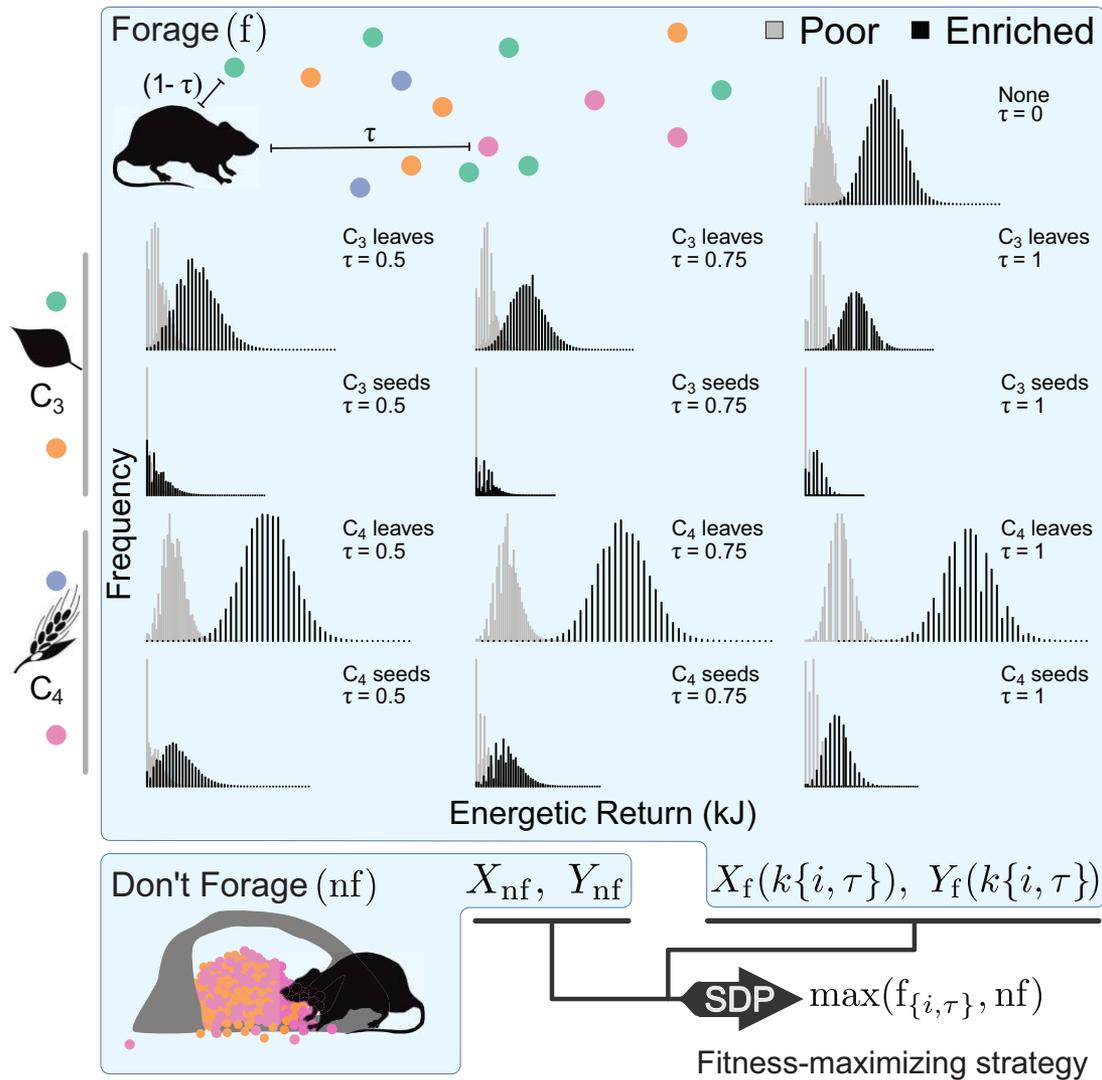


Figure 1: Illustration of the model used to calculate fitness-maximizing foraging strategies. Foraging strategies are defined by targeting different resources i with weight τ ($f_{i,\tau}$) or by not foraging and relying instead on cached reserves (nf). A consumer targeting resource i approaches that resource with probability τ regardless of distance and the nearest resource with probability $(1 - \tau)$. Histograms represent energetic return probability distributions (in kilojoules) given a targeting strategy deployed on a given resource and are numerically determined. Shown here are distributions for the monsoon season in both poor (low ρ ; gray) and enriched (high ρ ; black) environmental conditions. The consumer may also choose to not forage (nf), whereupon it relies on cached reserves. We assess how all possible strategies ($f_{i,\tau}$, nf) change lifetime fitness by altering the consumer's fat stores X and cache reserves Y . The fitness-maximizing foraging strategy is determined by the rules of the stochastic dynamic program (SDP).

during a foraging bout given only the consumer's velocity and foraging strategy. A foraging strategy is defined by the targeting of a preferred resource i with probability τ or the closest resource j with probability $(1 - \tau)$. The distance from the consumer to a resource i is drawn from an exponential distribution with mean $1/\Lambda_i$, where the random variable $\Lambda_i \sim \text{Gamma}(\alpha_i, m_i/\alpha_i)$. A chosen resource is approached by the consumer with body mass M with velocity v , after which the consumer moves on to the next resource on the basis of the next set of independently drawn

distances (fig. 1). This foraging process repeats until the temporal window of the bout has closed. As resources obtained during a foraging bout are assorted, they are added to fat reserves X and/or to the cache Y , where we record the proportional contribution of each resource to the total kilojoule return as π_i , and in particular we record those that are cacheable as $\pi_{\text{cache}} = \pi_{C_3 \text{ seeds}} + \pi_{C_4 \text{ seeds}}$. Importantly, the potential kilojoule return of a bout in season s , $K(t) = k$, is proportional to the energy density g_i of each found resource i (table 1), such that $k = N \sum_i \pi_i g_i$, where

Table 1: Resource mean densities μ_i (g m^{-2}) estimated from seasonal transects as part of the Sevilleta National Wildlife Refuge long-term ecological research monitoring effort as well as associated energy densities and digestibilities

	C ₃ leaves	C ₃ seeds	C ₄ leaves	C ₄ seeds	Units
Mean density $\mu_{\text{pre-/postmonsoon}}$	9,920	1,240	620	78	g m^{-2}
Mean density $\mu_{\text{full monsoon}}$	4,650	581	15,500	1,938	g m^{-2}
Energy density g	15	21	15	21	kJ g^{-1}
Digestibility ϵ	33	75 ^a	25	75 ^a	%

Note: Seed and leaf densities were estimated from plant biomass using allometric relationships in Niklas and Enquist (2002a, 2002b). Resource energy densities were obtained from Karasov and Levey (1990).

^a Also the value of ϵ_{cache} .

N is the grams of resources gathered in a bout. By simulating 10^6 independent replicate bouts, we calculate the probability $p_s(K(t) = k)$ of gathering a potential energetic return of k kilojoules for a given foraging strategy in season s . Minimum and maximum bounds of k ($k_{\text{min}}, k_{\text{max}}$) are determined numerically to capture the range of k where $p_s(k) \gtrsim 0$. See table 2 for a description of parameters used in the model and appendix B for additional notes on parameterization.

Foraging Strategies

The complete set of alternative foraging strategies that we explore includes (1) not foraging and relying instead on cached reserves, (2) foraging without preference for specific resources, and (3) targeting each of the four resource functional groups with increasing preference (fig. 1). Fitness is evaluated across different foraging strategies, where resources i are targeted with weight τ ; if a resource i is targeted with weight τ , the consumer approaches its preferred resource with probability τ regardless of distance; with probability $(1 - \tau)$, the consumer approaches the nearest re-

source. We consider three targeting options for each of the four resource groups, where targeting weights range from partial targeting ($\tau = 0.5, 0.75$) to complete targeting ($\tau = 1$) on each of the resources. If no resources are targeted, the consumer approaches and consumes/gathers the closest resource, and its final cumulative returns will mirror the environmental resource distribution. If a resource is targeted at $\tau = 1$, the consumer ignores all resources except that which it is targeting. Given the targeting weights $\tau = (0.5, 0.75, 1.0)$, the universe of foraging behaviors includes 14 options: stay home and consume cache, forage without targeting, and forage according to the three targeting weights for each of the four resources (fig. 1).

Consumer State Dynamics

A consumer of mass M is assumed to be able to use its fat mass as well as 10% of its muscle mass before starvation results in death (cf. Gannes et al. 1998). A consumer's maximum endogenous storage is thus bounded by the maximum fat mass an organism of mass M can carry plus 10% of its muscle mass, both of which are determined by allometric

Table 2: Parameter definitions, units, and references used in the model

Definition	Parameter	Units	Reference(s)
Consumer fat state	$X = x$	kJ (variable)	...
Consumer cache state	$Y = y$	kJ (variable)	...
Energetic return	$K = k$	kJ (variable)	...
Time	t	days	...
Consumer mass	$M \in [15, 200]$	g	...
Consumer home range	$\alpha M^{3/4a}$	m^2	Calder 1996; Lyons et al. 2019
Consumer velocity	$v = .008 M^{21}$	m s^{-1}	Calder 1996
Time in bout	$h_{\text{bout}} = 5$	h	...
Resting metabolic rate	$b_{\text{basal}} = .065 M^{3/4}$	kJ h^{-1}	Brown et al. 2004
Field metabolic rate	$b_{\text{field}} = .169 M^{3/4}$	kJ h^{-1}	Brown et al. 2004
Energetic cost (nf)	$c_{\text{nf}} = b_{\text{basal}} h_{\text{day}}$	kJ	...
Energetic cost (f)	$c_{\text{f}} = b_{\text{field}} h_{\text{bout}} + b_{\text{basal}} (h_{\text{day}} - h_{\text{bout}})$	kJ	...
Stomach capacity	$x_{\text{stm}} = 1.5 c_{\text{f}}$	kJ	...
Cheek capacity	$x_{\text{chk}} = 1.5 c_{\text{f}}$	kJ	...
Resource availability	$\rho \in 2 [2 \times 10^{-5}, 10^{-4}]$	NA	...
Targeting weight	$\tau \in [0, 1]$	NA	...

Note: See appendix B for additional notes on model parameterizations. NA = not applicable.

^a Intercept determined by ρ .

relationships (Lindstedt and Schaeffer 2002) and assuming an energy density of 20 kJ g⁻¹ (Stryer et al. 1995; Hou et al. 2008; see table 2 and app. B). In contrast, the maximum size of the cache is set to last a consumer one season (100 days) and, unlike fat stores, does not involve a critical value resulting in mortality. For computational feasibility, all energetic variables (fat and cache stores) and parameters are scaled to ensure that the consumer’s endogenous stores are discretized to 20 units. As such, a unit of fat and a unit of cache stores are equivalent for a consumer of a given body size but differ for consumers across body sizes.

When an organism chooses not to forage (denoted by the subscript “nf”) and instead relies on its cache for replenishment, the dynamics of endogenous and exogenous energetic stores respectively are

$$\begin{aligned} X_{nf}(t + 1) &= X(t) - c_{nf} + \epsilon_{cache} \min[x_{stm}, Y(t)], \\ Y_{nf}(t + 1) &= Y(t)(1 - \delta) - \min[x_{stm}, Y(t)], \end{aligned} \quad (1)$$

where x_{stm} is the limit (in kilojoules) of the consumer’s stomach, δ is the decay rate of the cache, ϵ_{cache} is the digestibility of seeds, and the energetic cost c_{nf} is determined by the basal metabolic rate b_{basal} applied across the hours in a day $h_{day} = 24$, such that $c_{nf} = b_{basal}h_{day}$. To state this in words, if the consumer stays home, the energetic cost is low, and it fills its stomach with the digestible portion of its cache, while the cache is depleted by the amount eaten plus per-period decay δ .

Consumer foraging (denoted by the subscript “f”) with a targeting weight τ on resource i obtains a potential energetic return $k\{i, \tau\}$ with probability $p_s(K = k\{i, \tau\})$ in season s . Given this potential return, the fat and cache stores change as

$$\begin{aligned} X_f(t + 1 | k\{i, \tau\}) &= X(t) - c_f + \sum_{j=1}^4 \epsilon_j \pi_j \min[x_{stm}, k\{i, \tau\}], \\ Y_f(t + 1 | k\{i, \tau\}) &= Y(t)(1 - \delta) \\ &\quad + \underbrace{\min[x_{chk}, \pi_{cache}(k\{i, \tau\} - \min[x_{stm}, k\{i, \tau\}])]}_{\text{remainder}}, \end{aligned} \quad (2)$$

where x_{chk} is the kilojoule limit of the consumer’s cheek pouch and the energetic cost c_f is determined by the sum of the field metabolic rate b_{field} applied across the hours in a foraging bout $h_{bout} = 5$, with the basal metabolic rate applied across the remainder, such that $c_f = b_{field}h_{bout} + b_{basal}(h_{day} - h_{bout})$. To state this in words, if the consumer forages, it fills its stomach with its energetic returns and saves the cacheable portion of the remainder, limited by the storage capacity of its cheek pouches. While the found resources fill the consumer’s stomach irrespective of digestibility, only the digestible portion can be added to fat reserves. Moreover,

only the proportion of the energetic return attributable to seeds is cacheable (π_{cache}), and the cache grows by the amount the consumer returns in its cheek after it fills its stomach.

Fitness-Maximizing Foraging Strategies

We consider a nonbreeding interval during which only foraging decisions influence fitness, where the interval has length $t_{max} = d_{max} \cdot s_{max}$, where $d_{max} = 100$ is the length of each season (in days) and $s_{max} = 3$ is the number of seasons in the year. We define the terminal fitness function for the last day/season of the year for a consumer, which is assumed to increase symmetrically with both fat and cache reserves, such that

$$\Phi(x, y, t_{max}) = \begin{cases} \frac{x + \epsilon_{cache}y}{x_{max} + \epsilon_{cache}y_{max}} & \text{if } x > x_{crit}, \\ 0 & \text{if } x = x_{crit}. \end{cases} \quad (3)$$

We scaled the terminal fitness function to unity, so it is easiest to consider it as survival after the terminal time for an individual whose end state is $X(t_{max}) = x, Y(t_{max}) = y$. For times previous to the terminal time, we define the fitness function

$$\begin{aligned} W(x, y, t) &= \max E\{\Phi(X(t_{max}), Y(t_{max}) | X(t) = x, Y(t) = y)\}, \end{aligned} \quad (4)$$

where the maximization selects the foraging behavior that maximizes fitness given fat and cache reserves at time t . For time periods prior to the terminal time, an organism must both survive and select the fitness-maximizing foraging strategy given the stochasticity of energetic gains. Given that the daily mortality probability is m_{nf} for a consumer that stays home and m_f if the consumer forages (where we assume that $m_{nf} < m_f$), $W(x, y, t)$ satisfies the equations of the SDP such that

$$\begin{aligned} W(x, y, t) &= \max \left[\underbrace{(1 - m_{nf})W(x_{nf}, y_{nf}, t + 1)}_{\text{stay home}}, \right. \\ &\quad \left. \max_{(i, \tau)} \left[\underbrace{(1 - m_f) \sum_{k=k_{min}}^{k_{max}} p_s(k\{i, \tau\}) W(x_f, y_f, t + 1 | k\{i, \tau\})}_{\text{target resource } i \text{ with weight } \tau}, \right] \right] \end{aligned} \quad (5)$$

where seasons are coupled such that for seasons prior to the terminal season s_{\max} the consumer's fitness on the last day of season s is a function of the consumer's fitness on the first day of season $s + 1$. In this case, seasonal transitions are deterministic and immediately result in changes to resource distributions.

To implement uncertainty in seasonal transitions, we assume that there is an increased probability that a monsoonal environment will transition to a pre- or postmonsoon environment (or vice versa) as the deterministic seasonal transition is approached. If s' represents the alternative season, we assume that the probability of transition $q(s \rightarrow s'|t, \sigma)$ increases with each day to a maximum value of $q = 1/2$, such that

$$q(s \rightarrow s'|t, \sigma) = \frac{1}{2} \exp\left(-\frac{(t - d_{\max})^2}{2\sigma^2}\right). \quad (6)$$

As such, the uncertainty in transitions between seasons increases with larger σ and is deterministic if $\sigma \ll 1$. With seasonal transition uncertainty, the fitness equation becomes

$$W(x, y, t|\sigma) = \max_{(i, \tau)} \left[(1 - m_{\text{nf}})W(x_{\text{nf}}, y_{\text{nf}}, t), \right. \\ \left. \max_{(i, \tau)} [(1 - q(s \rightarrow s'|t, \sigma))\Omega_{i, \tau}(x_i, y_i, t + 1|s) \right. \\ \left. + q(s \rightarrow s'|t, \sigma)\Omega_{i, \tau}(x_i, y_i, t + 1|s')] \right], \quad (7)$$

where we use the Ω notation defined in equation (5).

Results and Discussion

When to Cache and When to Fall Back

We first assessed general consumer behavioral trends over the course of a year defined by the pre-, full-, and postmonsoon seasonal sequence. This is a simplification of the spring (premonsoon), summer (full monsoon), fall (postmonsoon) transition characterizing the main pulse in primary productivity in the Sonoran and Chihuahuan Deserts each year. Behavioral trends were assessed by calculating the proportion of consumer states resulting in active foraging or relying on cached resources, averaged over both the consumer's fat stores and the cache reserves independently (fig. 2). Assuming deterministic transitions between seasons, we find that consumers employ four primary foraging strategies depending on season and environmental condition. We define these strategies by combinations of two sets of alternative foraging modes: (i) fallback versus replenish (whether foraged foods consist of fallback resources or those that can be used to replenish the cache) and (ii) use versus save (whether cached resources are used or saved against future hardship). We assessed when these strategies were implemented across the pre-, full-, and postmonsoon seasons in response to

poor (low ρ) and enriched (high ρ) resource availability. We note that the qualitative relationships of our model results hold even when multiple sets of seasonal transitions are coupled, suggesting that these findings are generally relevant for systems that cycle between nonmonsoon and monsoon seasons regardless of the number of transitions (app. C).

When resource availability is poor, more conservative strategies are promoted. The strategy in which fallback resources are consumed and cached resources are saved ("fallback and save") is used only when fat stores are very high and when consumption of cached resources is avoided (fig. 2A, 2B). Under these conditions, only fallback foods are targeted (fig. 3A). Fallback foods (leaves) are more common but have lower energy density and are not cacheable, such that they can only replenish body reserves. These qualities mean that such foods are not preferred and in turn are never heavily targeted (fig. 3B), allowing for the opportunistic incorporation of more preferred foods (seeds). We observe this strategy during the premonsoon season in poor environments, where the consumer faces a year of survival in an unforgiving landscape. The "fallback and use" strategy is similar in that foraging for fallback foods is carried out only when consumer fat stores are high but differs in that cached resources are used if available (fig. 2A, 2B). We observe this strategy when resource availability is low during the postmonsoon season, where conserving cache savings carries little reward as the consumer approaches the time at which fitness is assessed (i.e., the terminal time t_{\max}).

When resource availability is high, consumers can either take advantage of food abundance in the present or prepare for future hard times. In enriched environments during the pre- and postmonsoon seasons, consumers adopt a "replenish and use" strategy where the cache is used if it is available and replenished if it is not (fig. 2C, 2D). In these cases, only cacheable seeds are targeted (fig. 3C, 3D). Finally, monsoonal conditions are characterized by not only greater densities of C_4 foods but greater resource abundance overall, such that the risk of foraging and returning with an empty stomach is lower. During the productive monsoon season when resource availability is either low or high, consumers adopt a "replenish and save" strategy where foraging occurs liberally unless fat stores are nearly extinguished, and the cache is not used unless it is full.

Short-term hoarding strategies used by Carolina chickadees (*Poecile carolinensis*; Paridae) demonstrated that foraging to replenish cache stores is expected to increase as consumer fat reserves decline. When the consumer is near starvation, effort is redirected to restore body fat (Lucas and Walter 1991). Our model supports this expectation but only in the monsoon season, when cacheable foods (seeds) are common. In the pre- and postmonsoon environments,

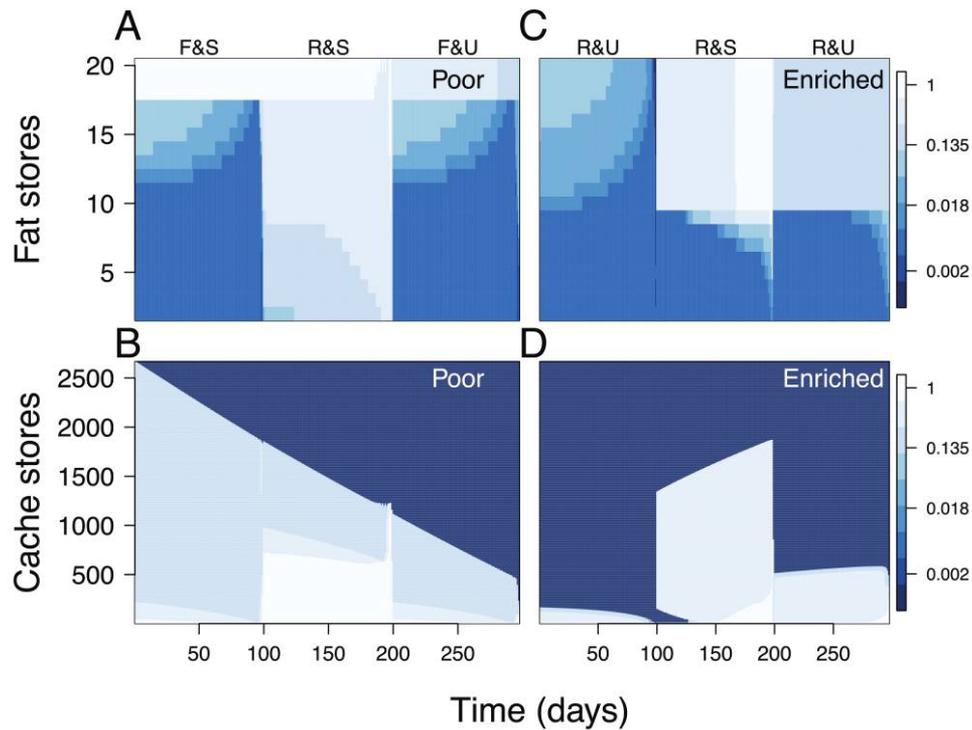


Figure 2: Proportion of states that result in active foraging versus not foraging and relying on cached reserves. Values range from 100% states that result in actively foraging (white) to 0% (dark); 0% active foraging implies 100% relying on cached reserves. To observe the dependence of foraging/not-foraging strategies on consumer fat (X) and cache (Y) states as well as resource availability, values are averaged across cache states in poor environments (A), averaged across fat states in poor environments (B), averaged across cache states in enriched environments (C), and averaged across fat states in enriched environments (D). Fat and cache stores have equivalent units, scaled to bound $x_{\max} = 20$. Note that the color scale is logged to emphasize smaller differences in consumer strategies. R&S = replenish and save; R&U = replenish and use; F&S = fallback and save; F&U = fallback and use.

cacheable foods are rare, and this reverses the expected pattern. During periods of resource limitation, we find that foraging effort increases only when the cache is low or, alternatively, if consumer fat stores are high. In these cases, foraging effort is directed toward fallback rather than cacheable foods.

Body Size and the Nature of Fallback Foods

While fallback foods often appear to play a small role in diet, they may have a contrastingly large influence on the evolution of traits facilitating acquisition (Ungar 2004; Vogel et al. 2008; Marshall et al. 2009) and may have played a prominent role in human evolution (Ungar 2004; Laden and Wrangham 2005; Yeakel et al. 2007, 2014; Constantino and Wright 2009). However, a general theoretical understanding of how and when consumers utilize fallback foods is lacking. At the Sevilleta, fallback foods such as C_3 and C_4 leaves are targeted to replenish fat stores when overall resource abundance is low. Because the monsoon is char-

acterized by overall higher resource abundance, fallback foods are of primary importance during the pre- and postmonsoon seasons. Larger mammals store a larger percentage of their body weight as fat, such that fat mass scales superlinearly with body mass (Lindstedt and Schaeffer 2002; Yeakel et al. 2018). As a consequence, starvation risk differs across body size, suggesting that the role of fallback foods may vary as well.

Rodent species at the Sevilleta vary in body mass by more than an order of magnitude, from ~ 8 – 10 g (e.g., *Perognathus*) to ~ 125 – 200 g (e.g., *Dipodomys* and *Neotoma*). Altering consumer body size influences a number of relationships in the foraging model, including the total amount of fat a consumer can store ($\propto M^{1.19}$), the metabolic costs associated with foraging and resting ($\propto M^{3/4}$), velocity ($\propto M^{0.21}$), and the area used to search for food ($\propto M^{3/4}$; table 2 and apps. A, B). We find that these consumers utilize fallback foods to different degrees during the pre-, full-, and postmonsoon seasons depending on body size and environmental quality, which we suggest has a number of

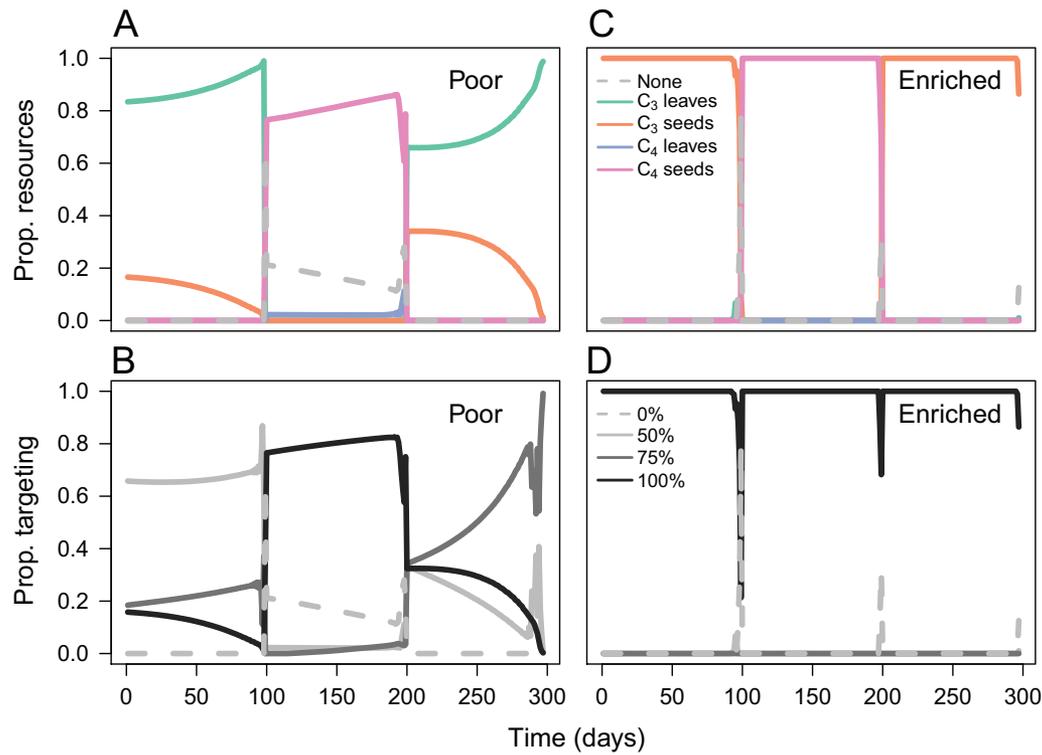


Figure 3: Proportion of foraging states targeting different resources (A) with different targeting weights (B) in poor environments, and proportion of foraging states targeting different resources (C) with different targeting weights (D) in enriched environments. A, C, Resource targets include none (dashed gray), C₃ leaves (green), C₃ seeds (orange), C₄ leaves (purple), and C₄ seeds (pink). B, D, Targeting weights range from none ($\tau = 0$; dashed gray) to partial targeting ($\tau = (0.5, 0.75)$; darker grays) to perfect targeting ($\tau = 1$; black).

important implications for the Sevilleta rodent community in the context of future environmental change.

First, we find that reliance on fallback foods is nonlinear across consumer body size (fig. 4). Smaller consumers

rely on fallback foods heavily, regardless of environmental quality ρ . This is due to the unaffordable risk of starvation associated with foraging for higher-quality seeds. However, this reliance is lessened for the smallest (15-g) consumer in

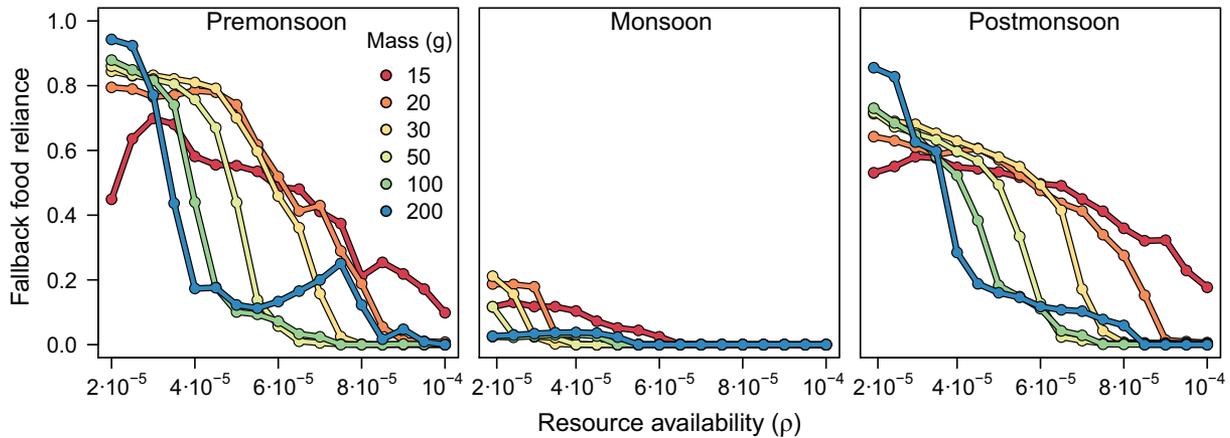


Figure 4: Proportional reliance on fallback foods (noncacheable C₃ and C₄ leaves) as a function of resource availability ρ , averaged over both fat and cache states as well as days for each premonsoon (left), full-monsoon (center), and postmonsoon (right) season. Colors corresponds to consumers with different body mass, ranging from 15 to 200 g.

the poorest environment, where it targets a larger proportion of higher-quality seeds than expected. In fact, the smallest member of the northern Chihuahuan desert community, *P. flavus*, is a granivorous food-caching heteromyid (Noble et al. 2019), whereas other species <40 g are noncaching cricetids. That high-quality yet risky returns maximize fitness for consumers near starvation—and small consumers are closer to starvation than larger consumers—supports both theoretical and empirical expectations for risk-sensitive foraging (Caraco et al. 1980; Craft 2016). For all but the poorest environments, a greater reliance on fallback foods means that fewer fat/cache states result in foraging behaviors that promote cache maintenance and replenishment. Greater reliance on more ubiquitous foods lowers the uncertainty associated with maintaining adequate energetic reserves, and this becomes more important for smaller consumers with a lower percentage of body fat. Given that smaller consumers have a limited energetic tolerance and cannot afford to conserve a substantial cache, it is likely that additional sources of uncertainty may disproportionately impact these species.

Intermediate to large consumers (30–200 g) tend to target preferred foods for a greater proportion of energetic states but increase their reliance on fallback foods as environmental conditions deteriorate. That smaller consumers rely more on fallback foods over a larger range of environmental conditions is in general agreement with recent work showing that resource homogeneity provides greater fitness gains to smaller consumers, whereas larger consumers can more readily target resources that are harder to find without high fitness costs (Bhat et al. 2020). In very poor environments, larger consumers that have a higher proportion of their body mass devoted to fat storage (e.g., *Neotoma*) are expected to be less risk sensitive. In these cases, our model affirms general expectations that such consumers target the lower-quality, more ubiquitous fallback foods. Specifically to Southwest desert ecosystems, this prediction is in line with observations of *Neotoma* dependence on lower-quality leaves (Thompson 1982; Kohl et al. 2014).

The rodent communities of the American Southwest have long inspired ecologists to ask, How do so many species with seemingly overlapping niches coexist in stochastic resource-limited environments (Brown 1975)? We suggest that diverse use of fallback versus preferred foods among consumers of different body sizes may, over the course of a year, point to an important axis of differentiation that separates consumer niches. While some species are expected to target C_3 or C_4 seeds, others are expected to target leaves or rely on their caches, and these proclivities vary with fat and cache state in addition to body size and time of year. When fallback foods are targeted, consumers prioritize their fat stores over cache maintenance and replenishment. It follows that lowering reliance on fallback foods promotes a greater proportion of energetic states devoted to targeting

seed resources, which by extension results in cache maintenance and larger cache sizes. That larger species maintain larger caches is a well-known phenomenon in diverse rodent communities and may promote coexistence of many species that share similar resources (Price et al. 2000). Indeed, the two largest species at our field site, *Dipodomys spectabilis* and *Neotoma albigula*, are known to rely heavily on large caches (Koontz and Simpson 2010).

Competition impacts resource availability and directly structures rodent communities in the American Southwest (Lemen and Freeman 1983; Heske et al. 1994; Brown et al. 2002) and elsewhere (Kelt 2011). Although we assess the effects of resource availability on expected foraging strategies, we do not include the dynamic feedback between consumers and their foods because of the computational limitations of our approach. Such feedback, both from the consumer itself and from intra- and interspecific competitors, would serve to limit access to certain resources if the cumulative rate of acquisition exceeded the rate of leaf or seed regeneration. Regardless, we can estimate the expected competitive overlap of differently sized consumers by comparing the similarity of fitness-maximizing foraging strategies between consumers as a function of resource availability.

We observe that resource availability has a large effect on the similarity of foraging strategies employed by consumers across a range of body sizes, where it is expected that increased similarity between two consumers promotes competition. When resources are scarce (low ρ), strategy similarity is maximized, particularly for consumers of similar body size (fig. 5). That similarly sized consumers are expected to utilize similar foraging strategies and compete more strongly is supported by observed patterns of competitive exclusion in desert rodent communities (e.g., Bowers and Brown 1982). In resource-limited environments, fallback foods are prioritized for nearly all consumers. As ρ increases to intermediate values, strategies become more diverse—particularly for consumers of different body sizes—suggesting that intermediate resource availability serves to lower competitive overlap.

In environments with abundant resources, foraging strategies once again converge, as all consumers opt for nutritionally dense and cacheable seeds (figs. 4, 5). Interestingly, while empirical observations of rodent populations in controlled removal experiments reveal a strong competitive limitation between certain species, competitive effects do not appear to increase during periods of resource scarcity (Heske et al. 1994) or so-called ecological crunches (Wiens 1977). While our model does predict that competition increases in environments where resources are severely limiting, the predicted similarity of foraging strategies between consumers is shown to vary widely with body size and nonlinearly across resource availability. This suggests that

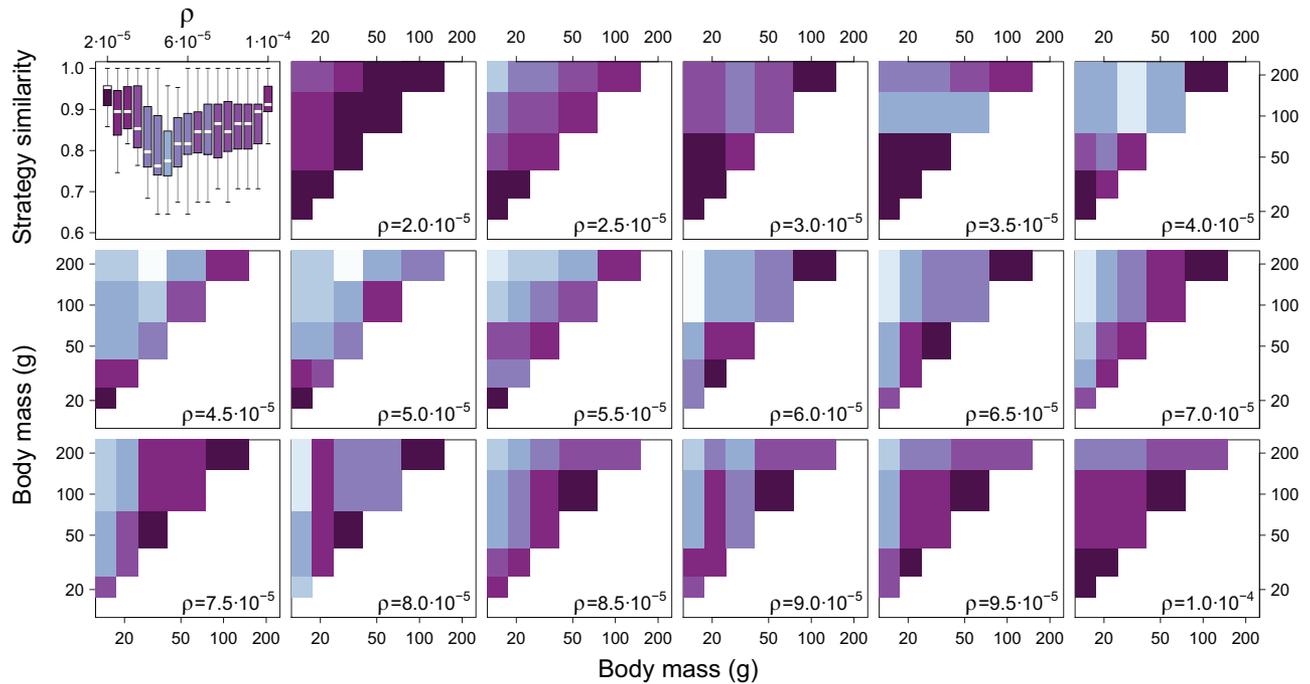


Figure 5: Similarity in foraging strategies for consumers of different body mass (g) as a function of resource availability ρ . Similarity is calculated from the cosine similarity index given by $\theta_{ij} = (\vec{v}_i \cdot \vec{v}_j) / (\|\vec{v}_i\| \|\vec{v}_j\|)$, where \vec{v}_i and \vec{v}_j are normalized vectors of fitness-maximizing foraging strategies for species i and j , respectively. Upper left: box plots of similarity values for all species pairs as a function of resource availability ρ . All others (left to right, top to bottom): pairwise similarity values for each consumer body size pair for ascending values of ρ . Dark tones denote similar pairwise strategies, while lighter tones denote increasingly dissimilar pairwise strategies.

the competitive effects between a particular pair of species at the Sevilleta may be multidimensional and therefore difficult to anticipate, which may explain why species' responses to altered competitive landscapes are often surprising (Heske et al. 1994).

Uncertain Seasons

We next examine how uncertainty in seasonal transitions, which is predicted to increase with climate change, impacts the expected foraging behaviors of rodent consumers. We find that elevated uncertainty in the timing of seasonal transitions ($\sigma = 20$) has three important effects on the expected foraging strategies of rodent consumers. First, as the uncertainty in predicting the resource landscape increases, the transitional periods between seasons (e.g., May–June) promote nontargeted foraging. Specifically, we find that foraging without targeting a specific resource maximizes fitness in poor environments once the uncertainty in the monsoonal onset begins (ca. day 80; app. D) and remains an important strategy until uncertainty in the onset of the postmonsoon season ends (ca. day 220). In enriched environments, this foraging strategy is observed to maximize fitness only when seasonal uncertainty

is highest (app. D). Foraging without a targeted resource means that the forager scans the environment only for the nearest resource, thereby minimizing travel costs without regard to resource quality or cacheability. In environments without seasonal transition uncertainty, this strategy is rarely fitness maximizing (fig. 3), indicating that it is worthwhile only when resource distributions are unpredictable.

Second, seasonal transition uncertainty lowers the relative importance of fallback foods. For consumers of all body sizes, the targeting of fallback foods averaged over energetic and cache states declines with increasing seasonal transition uncertainty (fig. 6). During the premonsoon, the decline in fallback food utilization is the most extreme, especially for smaller consumers in intermediate environments. During the postmonsoon, the decline in fallback food utilization is greatest for larger consumers in poor environments. This change in the use of fallback foods with increasing seasonal transition uncertainty means that more effort is spent foraging for cacheable resources that can be used to maintain larger caches. Previous modeling efforts focused on daily timescales have shown that increasing uncertainty in foraging returns leads consumers to build fat rather than cache reserves (Pravosudov and Lucas 2001). In contrast, our results show that longer-term uncertainty

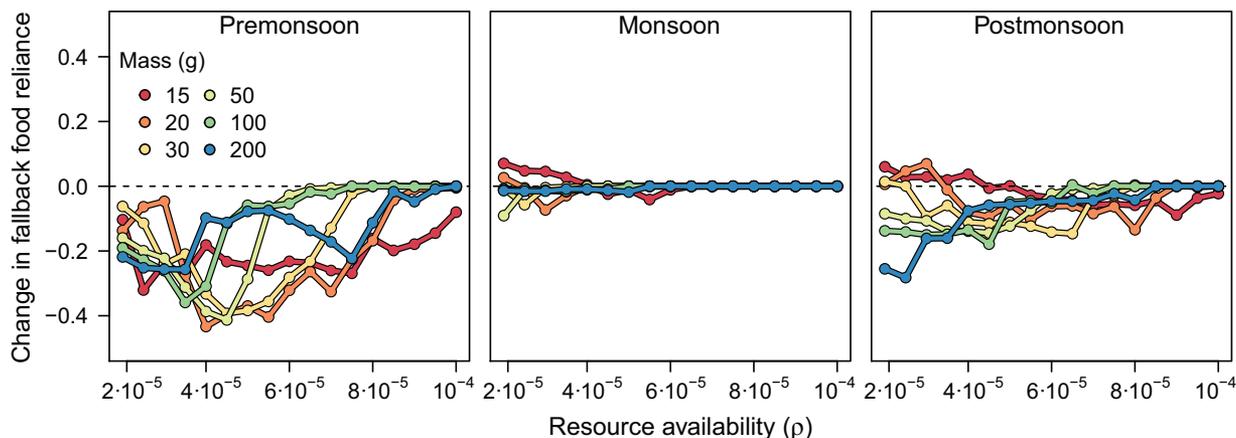


Figure 6: Difference in fallback food reliance (as measured in fig. 4) between environments with uncertain seasonal transitions ($\sigma = 20$) and those with deterministic seasonal transitions ($\sigma \approx 0$). Reliance is averaged over both fat and cache states as well as days for each premonsoon (*left*), full-monsoon (*center*), and postmonsoon (*right*) season. Positive values mean that consumer states in environments with uncertain seasonal transitions target more fallback foods; negative values mean that consumer states in environments with uncertain seasonal transitions target fewer fallback foods. The dashed line denotes zero change. Colors corresponds to consumers with different body mass, ranging from 15 to 200 g.

associated with seasonal transitions leads to strategies promoting cache maintenance. That the largest redirection in effort is realized by smaller species during the premonsoon season suggests that it is these consumers most impacted by seasonal uncertainty; however, as we show next this can be measured directly.

Third, seasonal transition uncertainty reduces consumer fitness, but the extent to which fitness is reduced largely depends on both the body size of the consumer and the size of its initial cache. To measure the effect of seasonal uncertainty on expected fitness, we compare the probability of survival for a consumer foraging in an environment with deterministic seasonal transitions at the beginning of the year, $W(x, y, t = 1 | \sigma \approx 0)$, to that of a consumer foraging in an environment with uncertain seasonal transitions, $W(x, y, t = 1 | \sigma = 20)$.

Our results reveal that while seasonal uncertainty lowers consumer fitness, a large enough initial cache can compensate for these negative effects (fig. 7). The cache size at which fitness gains compensate for seasonal transition uncertainty depends on both consumer body size and environmental quality. In poor environments, the probability of survival is so low that when seasonal transitions are uncertain, compensation is accomplished only if the cache is $>60\%$ the maximum value, or the amount needed to survive a single season (100 days; fig. 7, solid lines). Above this threshold, additional cache reserves have an exponential effect on fitness, fully compensating for the effects of seasonal uncertainty. In contrast, the cache stores needed to compensate for the detrimental effects of seasonal uncertainty for consumers of $M < 100$ g must be much larger than the maximum allowed in our framework. Because

such a cache is unrealistically large for these consumers, we suggest they will be most likely to suffer the fitness costs of seasonal uncertainty.

In enriched environments, the cache threshold required to compensate for the negative effects of seasonal uncertainty is much lower (fig. 7, bubble lines). In this case, the fitness advantage of a larger cache is more gradual but again

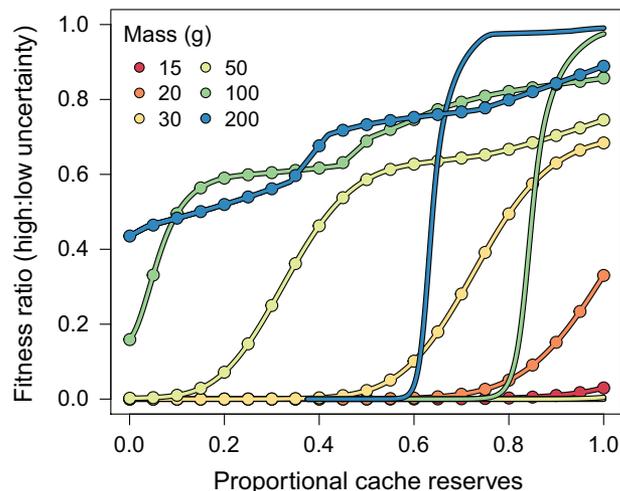


Figure 7: Ratio of fitness values for consumer states in environments with uncertain ($\sigma = 20$) versus deterministic ($\sigma \approx 0$) seasonal transitions as a function of the initial size of the consumer's cache at the beginning of the year. A value of 1 means that the uncertain and deterministic environments result in the same fitness values. Values < 1 mean that uncertain environments result in consumer fitness values lower than those in deterministic environments. Solid lines indicate poor environments, and bubble lines indicate enriched environments.

primarily benefits larger consumers. Consumers of $M < 50$ g require close to maximum cache reserves for compensation. Together, our findings suggest that while caches can compensate for seasonal transition uncertainty, they will provide a greater advantage to larger consumers. While increased resource availability is expected to increase the range of body sizes over which the compensatory effects of a cache are realized, the smaller consumers remain most prone to the fitness costs of seasonal transition uncertainty.

Brodin and Clark (1997) showed in a related model for willow tits (*Poecile montanus*; Paridae) that even small amounts of cached resources are expected to have a large impact on survival during hard times. Parids are scatter hoarders and store seeds in both short-term and long-term stores that require costly memorization and recall (Brodin 1992). While we focus here on the dynamics of central place caching (larder hoarding), the rodents in the American Southwest practice both forms (Schroder 1979), and which strategy is utilized may depend on the ability of a species to defend its cache (Daly et al. 1992). Multiple models of hoarding behaviors for birds in the family Paridae have shown that during resource-depleted seasons, consumers redirect their efforts toward maintaining greater body fat stores (Brodin and Clark 1997; Clark and Mangel 2000). While the risks and demands associated with memorizing hidden caches are less important for central place foragers, our results support both of these findings. Seasons that bring hard times require consumers to focus on body fat rather than cache maintenance, and it follows that those species that can endogenously store greater proportions of energy in the form of body fat are expected to have a survival advantage, which we show is magnified when seasonal transitions are uncertain.

Our model predictions point to a qualitative difference in the use of fallback foods and the fitness benefits of caching at the threshold body size of $M \approx 50$ g. Below this threshold fallback foods play a significant role even in enriched environments, whereas above this threshold fallback foods are utilized only in very poor environments, where resources are scarce (fig. 4). Moreover, for consumers below this threshold caches must be very large—equivalent to the energy needed to survive half a season—to compensate for uncertain seasonal transitions. Above this threshold, the fitness benefits of smaller caches are greater (fig. 7). This prediction affirms empirical observations of cache use among rodents at our Sevilleta field site in the northern Chihuahuan Desert. For example, nearly all of the four species of commonly caught food-caching granivorous heteromyids have $M \geq 50$ g in body size, including three species of kangaroo rats (*Dipodomys* spp.). The only exception is the small (8–10 g) silky pocket mouse (*Perognathus flavus*). In contrast, the noncaching Cricetids that include members of the *Peromyscus*, *Onychomys*, and *Reithrodon-*

tomys genera are well below this threshold and range in size from ~20 to 35 g. Body condition data show that the Cricetids have body fat mass ranging from 8% to 12% of their body weight, while the larger caching heteromyids have body fat estimates of only 4%–6%. Interestingly, *Perognathus* have body fat estimates (8%–10%) that are similar to those of the slightly larger noncaching Cricetids, suggesting that the smallest species in the community use a combination of stored fat and cached reserves to persist in this uncertain resource landscape. Overall, our results support a size-dependent energetic basis for observed patterns in caching versus noncaching foraging strategies among members of the small mammal community in the northern Chihuahuan Desert.

Beyond the Sevilleta

Here, we consider only the fitness differences between alternative foraging strategies during a nonbreeding interval, where fitness is defined in terms of survival after the terminal time. However, organisms must invest in both somatic growth and maintenance as well as reproduction. Given the varying nature of reproductive schedules among rodent species in the Chihuahuan Desert (Brown and Zeng 1989), we do not include these effects in our model. As survival after the terminal time is expected to increase with both endogenous and exogenous stores (eq. [3]), reproductive output after the terminal time may be expected to correlate similarly. Inclusion of reproductive investment within the considered time interval may promote riskier behaviors, such as foraging for seeds when they are rare. Moreover, increased body fat may expose consumers to greater predation risk (Houston and McNamara 1993), and it is well known that predation is a major cause of mortality among desert rodents (Sullivan et al. 2001). How these correlated risks and rewards integrate with the foraging dynamics explored here will be the subject of future investigations.

Desert rodent communities outside the American Southwest exhibit strategies that reveal diverse responses to aridity and seasonal resource availability. For example, many mole rat species throughout southern Africa are underground storage organ specialists that maintain caches in shared burrows (Lovegrove and Jarvis 1986; Lovegrove and Painting 1987). And while caching behavior among mole rats is more common in arid regions (Davies and Jarvis 1986; Bennett et al. 2000), such strategies are often mixed with cultivation of living tubers (Jarvis and Sale 1971). Seed specialization is a dietary strategy of central importance to desert rodent species across multiple continents, although caching behaviors vary. Scatter-hoarding and larder-hoarding behaviors are found among arid-land granivores in South America and the Old World (Kelt

2011) but are absent in Australia (Mares 1993). A better understanding of the diversity and utility of such strategies would require a careful examination of resource availability and the uncertainties governing acquisition in these different environments, in addition to consumer traits (see Mares 1993). While we do not consider it here, we submit that our framework could be adopted to explore the fitness advantages of different foraging strategies in these diverse desert ecosystems.

Hard times are expected to become not only “harder” in a future defined by climate change but more uncertain as well. We have shown that consumers in a highly seasonal stochastic environment, characteristic of many temperate regions around the world, enact foraging strategies that utilize less available, nutrient-rich, and cacheable (preferred) foods differently from those that are more ubiquitous and noncacheable (fallback), depending on consumer body size and resource availability. Our framework suggests that it is the smaller-bodied consumers that benefit least from maintaining cached reserves and are subject to the largest fitness detriments associated with seasonal uncertainty. Moving into an uncertain future where hard times are all too common, there is much value in knowing which species are most prone to the fitness costs of additional uncertainty. In the northern Chihuahuan Desert, it may be those species that cannot save a cent.

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Statement of Authorship

J.D.Y. and S.D.N. conceived of the study; J.D.Y., S.D.N., and U.B. developed the theoretical framework; J.D.Y. and U.B. performed the analyses; and all authors participated in writing the original draft and multiple revisions of the manuscript.

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