Current Opinion in Behavioral Sciences
Volume 45, June 2022, 101139

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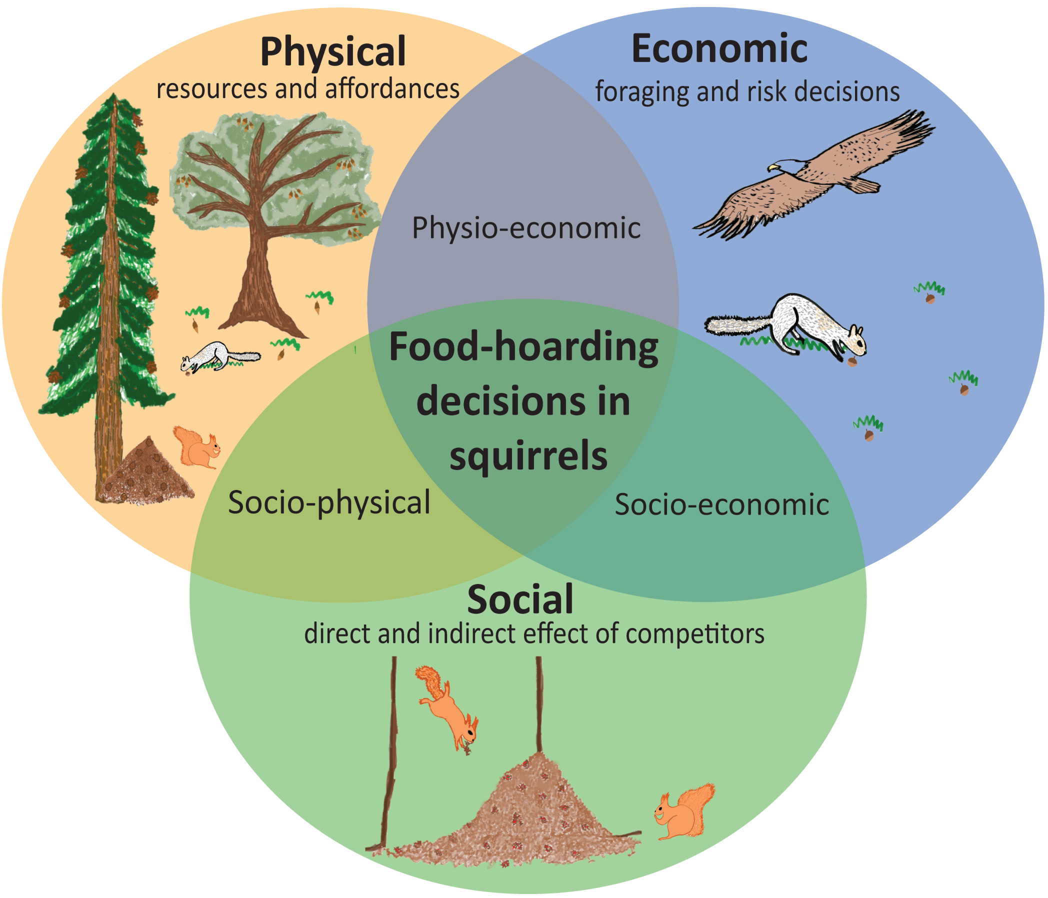
Graphical Abstract



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Highlights

- Wild squirrels are adapted for a diversity of complex food-hoarding economies.
- Economic decisions in apparently solitary species are driven by social interactions.
- Squirrels exhibit suites of behaviors to reduce their risks of predation and cache loss.

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Current Opinion in Behavioral Sciences

The socioeconomics of food hoarding in wild squirrels

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A food-hoarding squirrel reshapes its physical environment through storing food. These changes have ramifications for future economic decisions that cascade into social and reproductive consequences. Food-hoarding strategies exist on a continuum from concentrated caches in a defended larder to scattered caches defended using memory and olfaction. These strategies emerge in response to specific physical environments. Because caches are pilfered, the hoarder must also respond to the competitive social environment. Here, we review recent studies, both from captivity and the field, on the socioeconomics and cognition of hoarding in tree squirrels and chipmunks. As ubiquitous inhabitants of an increasingly urbanized world, these studies illuminate the theoretical and applied research potential of the study of such decisions in squirrels.

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Current Opinion in Behavioral Sciences 2022, **45**:101139

This review comes from a themed issue on **Cognition in the Wild**

Edited by **Alexandra Rosati**, **Zarin Machanda** and **Katie Slocomb**

For complete overview of the section, please refer to the article collection, "Cognition in the Wild"

Available online 14th May 2022

https://doi.org/10.1016/j.cobeha.2022.101139

Introduction

A food hoarder converts a seasonal surplus of food to a resource more evenly distributed across time. By altering its physical environment in this way, it also changes its own ecological niche and hence evolutionary trajectory as the new niche demands new adaptations of behavior and cognition [1••]. Because hoarding artificially concentrates a valuable resource, it also increases social competition by attracting intruders and pilferers. Hence food hoarding, even in an apparently solitary species, is a process that emerges from social selection [2]. Because food hoarding instigates this cascade of evolutionary changes, cognition in food hoarders is shaped by interactions between the physical environment, foraging economics, and social competition.

Wild squirrels (Order Rodentia, Family Sciuridae) offer an excellent opportunity to study these phenomena. Squirrels have adapted to urban and non-native habitats [3] and demonstrate diversity and complexity in food-hoarding behaviors. This offers an opportunity to study how socioeconomic decisions adapt over short and longtime spans, not only in hoarding behaviors but also in studies of fear [4], predator responses [5,6•], and problem solving [7•–9].

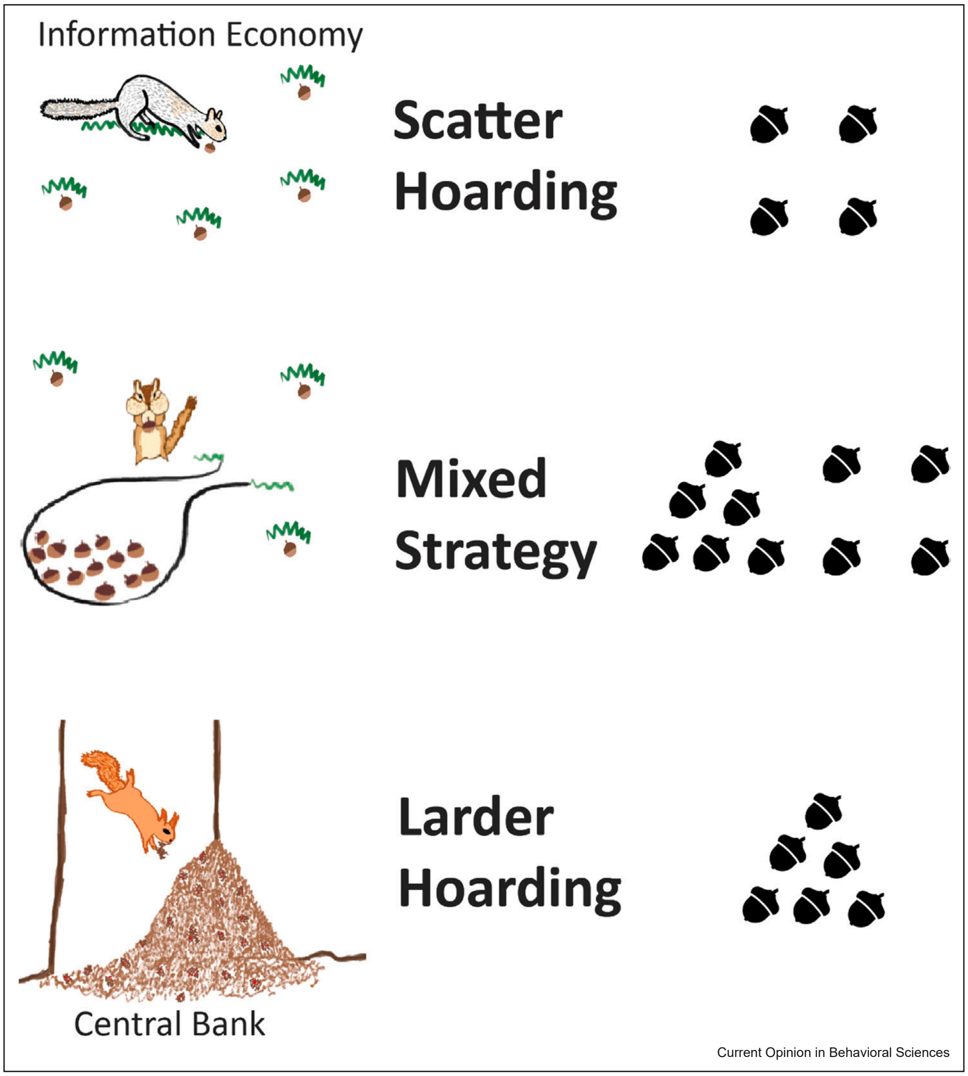
Two strategies anchor the spectrum of hoarding: larder and scatter hoarding. Larder hoarding is the multiple deposition of food items to a single cache site, such as a defended nest. Scatter hoarding is the strategy where each cache is created by a single deposition only, although the single deposition may later be moved to another location. In addition, squirrels may use a mixed strategy, employing both larder and scatter hoarding [10] (Figure 1). A squirrel's economic decisions are constrained both by the physical challenges of foraging for hoardable foods and the social challenges that ensue once the forager has collected and concentrated these valuable food items. And because a scatter-hoarded seed not retrieved may grow into a tree providing future food [1], a squirrel's socioeconomic decisions in turn feeds back upon its physical environment.

Here, we ask how these three forces — physical environment, social environment, and economic risk — interact to produce the central bank strategy of the larder hoarder, the information economy of the scatter hoarder and the flexible decision processes in species using a mixed strategy (Graphical Abstract).

The physical environment

Which hoarding strategy is used depends first on the physical world: the distribution of hoardable food (often tree seeds) and the plant's abilities to protect these seeds. Trees increase the cost of predation via chemical defenses (e.g. tannins and resins) and physical defenses (e.g. shell thickness) [1,11]. Tree species may also mast, unpredictably producing large or small numbers of seeds in a given year, a strategy that reduces the seed predator population. If not retrieved in time, cached seeds can escape predation via germination, further constraining

Figure 1



The food-hoarding strategy continuum. Placement of caches exists on a continuum anchored by two extremes: scatter hoarding and larder hoarding. Acorns on the right represent the distribution of stored food items in space ranging from singular scattered caches dispersed across the landscape to defended larders clustered in one location. Illustrations to the left of the listed strategies show exemplar species known to deploy each strategy (top: eastern gray squirrel, middle: yellow pine chipmunk, bottom: North American red squirrel).

the hoarder's options. Finally, the physical environment includes the challenges of winter: chipmunks hoard to survive hibernation and to compete in the spring breeding season, non-hibernating tree squirrels hoard to survive winter and compete in the winter breeding season [1].

The physical properties of multiple seeds packaged into cones allow the North American red squirrel (*Tamiasciurus hudsonicus*) to efficiently utilize a larder-hoarding strategy [12]. Wild red squirrels cut, hoard and consume unripe cones. Their jaw morphology reflects this arms race between conifers and predator: where cones are heavily armored to survive forest fires, the chewing apparatus is more robust [1]. Consuming the cone seeds from a perch, the squirrel creates a midden, a pile of cone scales. The cold, wet midden becomes an ideal microhabitat to preserve cones and it thus increases in value as cone debris accumulates (Figure 1). This multiyear hoard allows the squirrels to survive years when cones are not produced. Female red squirrels appear able to perceive an upcoming mast year and will increase their litter size in anticipation [13,14]. Because midden-stored cone seeds cannot germinate, red squirrels can economically defend territories of even masting trees [10].

In contrast, the seeds of deciduous tree species such as oaks and hickories germinate within months of being cached. Hence, masting deciduous tree seeds are too unpredictable in space and time to be economically defended as a territory. Further, because a scatter-hoarded seed that is not retrieved will have been planted in an advantageous location for its germination and survival, squirrel scatter-hoarding behaviors coevolve in concert with tree reproductive strategies [1,11].

Scatter hoarding is a demanding strategy for squirrels that store their winter food supply but cannot defend a larder; it is 'the best of a bad job'. Scatter hoarding presents new cognitive challenges: hoarders must strategize to retrieve caches more efficiently than their competitors, relying on memory and search strategies. Thus, the physical environment demands an information economy, where resources are defended by cognitive abilities.

Scatter hoarders respond to a specific physical environment by using a range of hoarding strategies. Large tree squirrels adapted to deciduous tree species are often obligate scatter hoarders, such as the North American eastern gray squirrel (*Sciurus carolinensis*) and fox squirrel (*S. niger*) and the Eurasian red squirrel (*S. vulgaris*).

In contrast, chipmunks (small ground squirrels) can utilize a flexible hoarding strategy, using both larder and scatter hoarding. This is possible because of two physiological adaptations: cheek pouches and hibernation. A chipmunk can economically collect a large number of small seeds in its cheek pouches, while a larger tree squirrel cannot. This allows chipmunks to construct multiple scatter hoards from a pouch load or deposit the entire load into a defended larder. Chipmunks further reduce their winter energy budget, compared with that of tree squirrels, using hibernation. However, this strategy also has consequences as hibernation is correlated with smaller brain size in mammals [15].

Hoarding decisions also can be directly influenced by physical factors such as atmospheric humidity, which impacts the accuracy of olfactory search and cache retrieval. A search dog's detection of a faint target odor was significantly more accurate in a warmer, more humid atmosphere [16]. Thus, while wild North American yellowpine chipmunks (*Tamias amoenus*) will pilfer caches in dry soils, they will pilfer more of their competitors' caches when the atmosphere is more humid [17]. In China, captive Siberian chipmunks (*T. sibiricus*) caching in a humid atmosphere will preferentially pilfer other's caches before retrieving their own [18]. Olfaction's role in cache retrieval can be experimentally manipulated. When a native scatter-hoarding rat species is made experimentally anosmic in captivity, they shift retrieval strategies from olfactory search to relying on spatial memory [19•].

Another influence on hoarding behavior that may be adapted to the physical environment is personality, defined as consistent among-individual differences in behavior across time and contexts. More heterogeneous habitats should select for greater variation in behavioral phenotypes [20]. In wild food-storing deer mice (*Peromyscus maniculatus*), personality predicts a suite of foraging and hoarding decisions, including its persistence in search and whether a seed is eaten or cached [21]. In wild Eurasian red squirrels, the survival value of being bolder or shyer varied among habitats: bolder squirrels survived longer when food supplies were unpredictable but shyer squirrels survived longer in habitats where food was stable. Boldness had fitness consequences for both females and males, and the more successful personality depended on resource abundances [22,23]. Similar results might be expected in wild larder-hoarding North American red squirrels, which inhabit not only coniferous but also deciduous forests. This shifts their socioeconomics to a mixed strategy of larder and scatter hoarding [24••], a flexibility of strategy that may well be influenced by personality.

The social environment

No squirrel is an island — hoarding and reproductive strategies are heavily influenced by social factors, even in apparently asocial species. To fill and then to defend its 'central bank', a larder hoarder faces social challenges on which its survival and reproductive success depend. Fitness is relative and the economics of larder hoarding is highly sensitive to social competition. Although solitary, the reproductive fitness of a red squirrel will be influenced by the social environment surrounding their larder. For example, when spruce cones are scarce, a wild red squirrel has lower reproductive fitness if surrounded by highly successful neighbors, though not when cones are abundant [25]. Squirrels must therefore closely monitor social relationships with known individuals to minimize time budgets for defense and vigilance. Wild red squirrels monitor neighbors through their rattle calls, a vocal advertisement used in territory defense. Squirrels can recognize the rattle calls of individuals, and those surrounded by unrelated but familiar neighbors are less vigilant. This 'dear enemy effect' results in squirrels expending less energy on territorial defense, which has positive fitness consequences [26–29••]. Squirrels also use neighbor territorial calls as a proxy for competitor density. As density increases, squirrels initiate breeding earlier in the year, allowing their offspring more time to grow before independence [30,31]. Wild red squirrels also reduce litter size when social competition is high, which increases pup growth rate and competitive ability [13••]. Finally, the social environment may also lead to altruism: if a lactating mother is killed, a female kin member may rescue, adopt and raise some of her orphaned pups [32].

The social environment is also critical to the midden acquisition and hoarding behavior of juveniles. A juvenile North American red squirrel must establish its own territory, fill its midden, and defend both from intruders to survive. Squirrels that acquire a territory before the fall crop ripens are more likely to do so [33]. Territories can be taken over following the deaths of territory owners. Older males have larger middens and the usurper of their midden after their death will breed earlier and achieve higher reproductive fitness [34•]. Offspring can also inherit a midden from kin: red squirrel mothers may even abandon their established territory to bequeath it to a daughter [30]. Thus, the economic food-storing decisions of one individual can have fitness consequences for other squirrels.

Personality also influences social interactions and hoarding behavior [35]. Wild North American red squirrels show trajectories of individual differences in personality that are heritable and stable across an individual's lifetime [36]. These differences interact with social competition and the physical environment: the offspring of more aggressive females are more likely to survive in years when there is greater social competition for physical resources [37]. Finally, red squirrel mothers who are more attentive raise faster growing pups who achieve higher lifetime reproductive fitness [38].

Scatter-hoarding squirrels adjust their caching behaviors in response to their social surroundings [39,40]. Wild eastern gray squirrels employ 'evasive' tactics when caching food in the presence of others by adjusting the spacing of their caches and orienting their backs towards other nearby squirrels [40]. Moreover, as the number of conspecifics in a foraging patch increases, the rate at which squirrels return to a patch between caches increases, indicating that competition decreases the energy expenditure on caching per item [39].

In contexts where climate and resources are more variable, it may be more economically beneficial for hoarders to maintain a mixed hoarding strategy. Like chipmunks, captive kangaroo rats also have cheek pouches and show flexible hoarding strategies, adapting cache distribution in response to pilfer risk [41,42]. Captive Siberian chipmunks shift caching strategy when detecting the sound and/or sight of a conspecific caching. The observer then increases its search for another's caches, which it then both scatter and larder hoards [43], though in other contexts, pilfered seeds are more likely to be larder hoarded [44]. Wild scatter-hoarding Cape ground squirrels are not only sensitive to the presence of a conspecific but also to the conspecific's attentive state. Squirrels cache more when other squirrels are momentarily less attentive to their behavior [45].

The economics of risk

Hoarding entails two categories of existential risk: loss of life to predation and loss of caches, either to competitors or memory loss before retrieval. These risks differ among the three hoarding strategies (Figure 1). Larder hoarders theoretically face the least risk of cache loss via either pilfering or forgetting [46,47]. Scatter hoarders must weigh the additional trade-off between predation and pilferage, as caches are more vulnerable where competitors can search more safely. Additionally, those deploying a mixed strategy must actively track the changing risks and benefits posed by scatter hoarding or larder hoarding in a given context and adjust decisions accordingly.

Predation and pilferage risk together shape hoarding strategy. Wild eastern gray squirrels cache preferred foods in open habitats where the predation risk is greater and pilferage risk is lower, while caching less preferred foods under the safety of the canopy [11,48]. In England, wild eastern gray squirrels were found to make these decisions based on prior heuristics rather than dynamic cues indicating current risks [49] and in China, Siberian chipmunks also preferentially cached in open forest gaps [50]. Here again, the physical and social environment shape the hoarding strategy.

Increases in space use increase risk of predation [48,51]. Arboreal scatter hoarders potentially face higher predation pressure than arboreal larder hoarding species, as they must forage, store, and later retrieve caches from much larger spatial areas. While scatter hoarding on the ground, they must also escape terrestrial predators. On the ground, wild eastern gray squirrels quickly calculate the distance of potential trees and the angular degree between the squirrel, predator, and tree when choosing escape routes [52•]. While foraging in trees, they must escape pursuit by flying and arboreal predators, such as owls, hawks, and small carnivores, such as pine martens [5]. On rods of different diameters, captive eastern gray squirrels increase half-bounds and galloping as the branch diameter decreases [53]. Wild fox squirrels can adapt their launch position and force to the changing compliance of the launch branch while also maintaining the flexibility to incorporate parkour maneuvers to add additional control points mid-leap [54••]. To further manage risk, wild eastern gray squirrels eavesdrop on bird chatter [55].

The next risk emerges from the social environment — a scatter hoarder must combat loss of caches by employing strategic caching, deciding what to eat, what to cache and where to cache it. Captive eastern gray squirrels decide what seeds to eat or cache not by seed species but by a combination of seed traits. They also chose to cache seed species that they had not already cached, increasing the nutritional diversity of stored foods [56]. In the field, wild fox squirrels assess nut weight using specialized paw and head movements [57]. Fox squirrels then invest effort proportionately to nut value, carrying heavier nuts farther and caching preferred nuts at lower densities [58]. Squirrels must also strategically place stored items to mitigate the risk of forgetting the cache location. Wild scatter-hoarding Cape ground squirrels employ a sun compass to orient both during caching and retrieval, to reduce this risk [45]. Wild fox squirrels employ the mnemonic strategy of spatial chunking. Such a hierarchical organization of cached food items (e.g. spatial segregation of caches by nut species) should theoretically improve recall, based on studies in laboratory rodents. Given a pseudorandom series of different nut species, fox squirrels organized the scatter hoards into species-specific clusters [59]. Studies of captive Siberian chipmunks also reveal the potential risk of memory loss with males more likely than females to place caches near tall vertical landmarks [60]. Such a sex difference could emerge from the female advantage for spatial array memory, as in wild scatter-hoarding fox squirrels and captive kangaroo rats [61,62].

These examples capture only the initial decision of cache placement. In the field, radio-tagged acorns, presumably cached by wild eastern gray squirrels, were moved several times after initial caching. Hence, many studies probably underestimate the complexity of a scatter hoarder's strategy as such recaching would create a more recent memory of the cache's location [63]. As squirrels continually deplete their caches, such recaching may also allow the squirrel to rearrange its remaining caches to optimize the dispersion of nuts to reduce cache pilferage by its competitors.

Thus, in physical environments where larder hoarding is not an economic option, squirrels must suffer the multiple increased risks of scatter hoarding (e.g. predation, forgetting, and pilferage). In chipmunks, these risks can be managed flexibly according to context and physical environment. During the summer, wild North American yellow pine chipmunks range more widely in space, scatter hoard seeds and do not defend a larder. As winter approaches, the chipmunks transport and concentrate their scattered caches as a larder in their hibernaculum. The wild Siberian chipmunk, which relies heavily on scatter hoarding during nonhibernating months, will also larder hoard when costs and benefits shift. In captivity, a Siberian chipmunk experiencing high rates of cache loss from its larder will shift to scatter hoarding [64]. After pilfering, a captive chipmunk will store pilfered seeds in its larder [44]. This may reflect the energetic value of a pilfered item, which may be counted as higher value as the owner, not the pilferer, paid for the initial search and handling costs.

The risk of cache loss due to pilfering also entails other species. Wild yellow pine chipmunks hoard in competition with other sympatric scatter hoarding species, including another chipmunk species and deer mice. All three of these species engage in reciprocal pilfering [65], losing approximately 30% of their caches to heterospecific pilferers. At the same time, all three species pilfer from the larders of the larger golden-mantled ground squirrel (*Callospermophilus lateralis*), which neither scatter hoards nor pilfers [66]. This is also seen in studies from China, where in the field and in captivity scatter-hoarding rodent species are more efficient cache pilferers than larder-hoarding species [67].

Conclusion

Hoarding strategies emerge from the affordances of the physical environment, in particular the adaptations of plants to reduce seed predation. These properties dictate the spatiotemporal distribution of surplus food, limiting the hoarding strategies that a squirrel can economically sustain. These physical factors in turn constrain the social environment, which is predicated on the need to reduce the risks of predation and cache loss (Graphical Abstract). Squirrel cognition in the wild appears adapted to minimize risks, such as showing innovative motor learning during locomotion. Other losses — memory loss and pilfered caches — are driven by social competition, which may select for further cognitive traits, such as the ability to orient to celestial cues or to create a hierarchical organization of caches. Hoarding is thus a context-specific response to diverse factors — physical, social, and economic.

The impact of the interaction amongst the physical, social, and economic environments on behavior and cognition is evident across the food-hoarding strategy continuum (Figure 1). The packaging of conifer seeds in cones, where scale debris creates a long-term repository for seeds, creates a context where a nonhibernating tree squirrel can economically defend a territory, even surviving years where no cones are produced. The ability to defend this central bank then reverberates into adaptations for social competition among neighbors and within kin lineages. In contrast, the packaging of seeds by deciduous masting trees into acorns and nuts precludes this hoarding solution and instead instigates the information economy of the nonhibernating scatter hoarder. Because scatter hoarders are both predators and seed dispersers, this plant–animal relationship has led to the coevolution of seed morphology and squirrel cognitive traits necessary to assess, invest, and profit by their hoarding investments. Scatter hoarding also greatly increases the need to monitor and respond to social competitors. The costs of social competition, and its impact on hoarding decisions, are even more prominently displayed in the mixed-strategy hoarding of chipmunks. Here, too, the physical environment — the need to use scatter hoards to prepare a larder hoard for winter hibernation — is critical to understanding the chipmunk's social environment. And this in turn drives the cognitive traits required by such a mixed strategy.

As squirrels continue to adapt themselves to the human landscape, the study of hoarding offers the potential to understand how socioeconomic decisions flexibly adapt to new physical and social environments. It offers a unique opportunity to study perception, motor learning, spatial memory, and decision making in diurnal wild rodents. Urbanization is a potent selective force on wild squirrel behavior and cognition, where complex differences in response to cognitive challenges emerge between rural and urban squirrels, and native versus introduced squirrel species [4,7–9]. Hoarding strategies in such squirrels can be studied to tease apart the selective pressures arising from the physical and social environments. Thus future studies of cognition in the wild of even a city squirrel, living in our increasingly cosmopolitan and carpentered world, can contribute significantly to our understanding of the evolution of socioeconomic behaviors.

Author contributions

Amanda N. Robin: Conceptualization, Writing – original draft, Writing – review & editing, Visualization (figure creation and preparation). Lucia F. Jacobs: Conceptualization, Writing – original draft, Writing – review & editing.

Conflict of interest statement

Nothing declared.

Acknowledgements

We would like to thank artist CL Frausto for creating the illustrations of squirrel species and thank two anonymous reviewers for their helpful and constructive comments. ANR was supported by a National Science Foundation (NSF) Graduate Research Fellowship Program (GRFP): 2017238448 and LFJ was supported by Army Research Office MURI Fund 574723.

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- • of special interest
- •• of outstanding interest.

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