

REVIEW

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# Food storage in a changing world: implications of climate change for food-caching species

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## Abstract

Food caching is a behavioural strategy used by a wide range of animals to store food for future use. When food is stored, it is susceptible to environmental conditions that can lead to spoilage via microbial proliferation or physical and chemical processes. Given that the nutrition gained from consuming cached food will almost always be less than consuming it immediately upon capture, the degree of degradation will play a central role in determining the ecological threshold at which caching is no longer profitable. Our framework proposes that the degree of susceptibility among caching species is based primarily on the duration of storage, and the perishability of stored food. We first summarize the degree of susceptibility of 203 vertebrate caching species. Thirty-eight percent (38%) of these species are long-term cachers (>10 days) but only 2% are both long-term cachers and store highly perishable food. We then integrate insights from the fields of applied food science and plant biology to outline potential mechanisms by which climate change may influence food-caching species. Four climatic factors (temperature, number of freeze-thaw events, deep-freeze events and humidity) have been shown to affect the degradation of food consumed by humans and are also expected to influence the quality of perishable food cached in the wild. Temperature and moisture are likely important factors influencing seemingly nonperishable seeds. Although we are able to provide broad classifications for caching species at risk of climate change, an improved understanding of how environmental conditions affect the quality and persistence of cached food may allow us to better predict the impact of changing climatic conditions on the fitness of food-caching animals.

**Keywords:** Deep-freeze, Environmental change, Food caching, Food degradation, Food science, Freeze-thaw cycle

## Background

Evidence suggests that climate change is influencing a wide range of biological phenomena, including species distributions [33, 58, 99], population abundance [48, 54], and rates of extinction [26, 73]. Such studies provide important documentation of the potentially serious impacts of climate change on natural systems but, with few exceptions (e.g. [18, 120, 171, 178]), fail to identify the proximate mechanisms by which climate change has influenced fitness and population growth rates [25] and, by extension, community structure [108, 121, 172, 175]. Identifying proximate mechanisms is important for the development of predictive frameworks, permitting an

evaluation of the susceptibility of different species to long-term changes in the environment [19].

Here, we seek to develop such a framework for food-caching animals by integrating insights from the fields of food science and plant biology with knowledge of food-caching behaviours and preferences. Food caching is a widespread behavioural adaptation used primarily by non-migratory species to store food for future use during periods of low resource availability or uncertainty [164]. Once a food item is cached, it is exposed to environmental conditions that can either maintain or degrade its quality over time. Furthermore, the degree of degradation may also depend on a variety of factors, including food type, the duration of exposure and the location where food is stored. Although these factors are well studied in the field of food science, they have not been considered in the context of climate change and caching species.

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Our motivation for understanding the mechanisms behind environmental degradation of cached food stems from our long-term research on a declining population of Gray Jays (*Perisoreus canadensis*) at the southern edge of their range [32, 110, 155, 171, 176]. Gray Jays cache a wide range of perishable food items during the late summer and fall and use this food for over-winter survival and late-winter breeding [154]. Waite and Strickland [171]) proposed that warmer fall temperatures may be leading to the degradation of cached food, which then carries over to influence breeding success. They presented some correlational support for the 'hoard-rot hypothesis' but the effect of fall temperatures on reproductive success was relatively small compared to the steep population declines and there was only weak evidence that fall temperatures increased over the period in which Gray Jays declined. Additionally, a recent experiment using simulated caches did not find a consistent effect of warmer fall temperatures on food quality [140]. Sechley et al. [140]) did, however, suggest that temperature thresholds, such as the presence or absence of deep freeze events, could be driving observed differences in the degree of food preservation over a latitudinal gradient. These lines of evidence lead us to speculate that (a) the persistence of stored food may be influenced by more than a simple linear relationship with temperature and (b) that a deeper understanding of how climate influences food quality may be gained by drawing upon applied research related to the degradation of food stored by humans.

Our three primary goals in this paper are to (1) place the potential effects of climate change on cached food quality in a broader context of the costs and benefits of caching, (2) introduce a framework, based on variation in caching behaviour across species and in the types of food they store, for assessing their susceptibility to climate change and, (3) use insights from the fields of food science and plant biology to identify environmental conditions that could contribute to the degradation or preservation of cached food in the wild. We anticipate that these new perspectives will stimulate future research on a wider range of caching species and improve our ability to understand the potential effects that climate change may have on this subset of animals.

### Relating the potential effects of climate change to the costs and benefits of caching

To put the potential effects of climate change into a broader context, we consider a simple cost-benefit equation [4] in which the fitness (considered here as nutritional gain),  $F$ , of a caching species can be estimated by  $F = Gp - C$ , where  $G$  is the fitness (or nutrition) gained by eating a cached food item at a future date,  $p$  is the probability that that food item is retrieved, and  $C$  is the

cost of deferring consumption of that food item (in other words, the nutrition lost from not consuming it upon capture). Andersson and Krebs [4] argued that, if  $Gp > C$ , then caching would evolve. However, in theory [this principle could also be used to assess how the costs and benefits of caching may change over ecological time and this will be particularly relevant under rapidly changing environmental conditions.

Of course, many species-specific factors will influence  $G$ ,  $p$ , and  $C$ . Past studies have primarily focused on determining what drives  $p$ , for example, by quantifying the frequency of conspecific and heterospecific competitors pilfering cached food [81, 83, 167] and estimating the cognitive ability of a species to recover stored food at a future date [65, 105, 124, 125]. In most cases (particularly for species that cache perishable food), the nutrition gained from consuming a cached item will almost always be less than consuming it immediately upon acquisition and that this is due, in large part, to the degradation of cached food over time. The rate at which a cached food item will degrade is dependent on duration for which it is stored and the type of food that is stored (see detailed discussion in section below).

As an example, we use this equation to estimate the effect of different climatic conditions on caching in Gray Jays. To estimate  $G$ , we use data from Sechley et al. [140] who determined the caloric value of mealworms experimentally cached over a typical storage-retrieval period (fall-winter) at two locations with different climatic conditions. Mealworms are an appropriate food item to use for estimating cached food degradation in Gray Jays because this species only stores perishable food, and arthropods constitute a significant portion of their diet [154]. In the middle of the range in Cochrane Ontario, where temperatures rarely go above freezing beginning in November, mealworms retrieved in March were an average of 0.977 kcal, whereas at the southern edge of their range in Algonquin Park, where temperatures are rarely below zero until November, the average caloric value of mealworms stored over the same period was 0.663 kcal. For  $p$ , we used estimates of cache retrieval from two nutcrackers (0.84; *Nucifraga columbiana*; [160], *Nucifraga caryocatactes*; [70]). Similar to Gray Jays, both species rely on cached food for both over-winter survival and reproduction and, therefore, likely have relatively accurate spatial memories [8]. The cost of caching,  $C$ , can be estimated as the energy it takes an individual to cache a food item and find an additional item that is of equal nutritional quality to the item that was cached. Because the energetic cost of foraging is not known for Gray Jays, we estimated  $C$  by taking an estimate of the daily energetic requirement of an individual Gray Jay (47 kcal; [141]) and multiplying it by the proportion of the day an individual would take to

find a new food item (24 hrs/10 min = 0.007) resulting in  $C = 0.33$  kcal. Using these values, the nutrition gained from caching food at the more southern site is estimated to be >50% lower (0.23 kcal) compared to the more northern site (0.50 kcal). Given temperatures in Algonquin were similar to the Cochrane as early as 1990 [139], this suggests that Gray Jays in Algonquin park have experienced a significant decline in nutritional quality of cached food. Of course, these are crude estimates but they do serve as an example of how this equation can be used to assess the influence of environmental conditions on nutritional benefits of caching.

### Predicting the susceptibility of food-caching species to climate change

Caching behaviour is widely distributed across 30 families of mammals and 15 families of birds and is believed to have evolved independently numerous times within each taxa [30, 57, 145, 164]. Given the repeated, independent evolution of caching behaviour, it is perhaps no surprise that there is also a wide diversity of caching behaviours and types of food that are cached ([164]; Table 1). We believe that the degree to which cached food is influenced by climate change depends primarily on three major axes of variation that we discuss in detail below. In order of importance they are: 1) the duration of time that food is stored, 2) the type of food that is cached, and 3) the location where food is stored (Fig. 1).

#### Duration of food storage

Caching species can generally be divided into two classes based on cache duration. The first is 'short-term cachers' that can be characterized by temporally overlapping and episodic caching and recovery events [164]. These species are primarily motivated by present and/or imminent uncertainty in resource availability and will typically cache food for no longer than 10 days before retrieval. One type of caching species that falls into this class are single-item-surplus cachers that cannot consume all of a prey item in a single sitting and, therefore, attempt to protect the remaining portion of food for future feeding bouts (e.g. Tigers, *Panthera tigris*; [138]). A second type of short-term cacher stores food to protect it from heterospecific and conspecific competitors. For example, Leopards will bring carcasses into trees in order to protect their kills from Lions and Hyenas [35, 39]. Barbados Green Monkeys (*Cercopithecus aethiops*) have been observed to cache food for short periods of time in order to prevent conspecific competitors from accessing their food [15]. A third type of short-term cacher are 'insurance' cachers, such as parids [142] and mustelids [146], who cache food items for hours or days as an apparent hedge against present or imminent uncertainty in the environment.

The second class of caching species is 'long-term cachers' that are characterized by distinct, non-overlapping storage and recovery periods that are >10 days but are more typically separated by two or more seasons [164]. Long-term cachers store food as a response to a certain lack of food in the future. Species in this class typically engage in intense periods of caching, usually in the late summer or fall [31, 66, 154, 164] and are followed by intervals of limited resources (e.g. winter) during which caches are retrieved. Food stored by long-term cachers will be more susceptible to environmental change simply because it is exposed to the environment for longer periods compared to food stored by short-term cachers. Long-term storage also increases the probability that food will be stored during transitional periods between seasons that are characterized by large fluctuations in environmental conditions that can negatively affect food quality. For example, late summer and fall storage exposes items to potentially damaging freeze-thaw cycles as the year transitions into winter.

Latitude and altitude play an important role in determining the duration that food is stored, particularly for long-term cachers. At high latitudes, periods of limited resources are longer, which means more food must be cached over a comparatively shorter time period [24, 123]. This could imply that populations at higher latitudes are more susceptible to changing climatic conditions because of the presumably higher reliance on cached food compared to populations at lower latitudes. Similarly, along elevation gradients, high elevation population could be at greater risk due to an increased reliance on cached food [168]. Climate warming could benefit caching species by prolonging food availability during the storage season or by reducing the length of low-resource periods in which cached food is relied upon. Both of these examples highlight how caching behaviour changes over temperature gradients, thus, it will be important to consider how changing climatic patterns influence not only food once it is cached, but also how it could influence caching decisions.

#### Type of food stored

A wide variety of food is cached by wild animals [29, 145, 164, 166] and this variation will impact how susceptibility it may be to climate change. At the broadest level, the distinction can be made between perishable and non-perishable food items. Food perishability is primarily a function of its water content, which dictates not only how food will respond to freezing temperatures but also the growth rate of bacteria [64, 96, 102]. Although some species store exclusively perishable (e.g. carnivores, such as canids, felids and raptors; [27, 100], and Gray Jays; [154]) or non-perishable (e.g. tree squirrels *Sciurus spp.* and new world mice *Peromyscus spp.*); [104, 164]) food, many other species store both types of food. For example,

**Table 1** A summary of caching behaviour of 203 vertebrates (adopted and updated from [164]). Caching behaviour includes duration of food storage, the perishability and type of food cached, and the location where food is stored are included within the table. In many cases, information on each of these three categories represent a 'best estimate', as much of the literature consists of anecdotal reports or natural history observations. All species were assigned a susceptibility score from 1-9 based on variation in two major aspects of caching behaviour: duration and food perishability (see text for details). Susceptibility to climate change was predicted to be lowest for short-term cachers of low perishable food item (1) and highest for long-term cachers of perishable food items (9). More research is needed to understand how location of storage may influence degradation of cached food and was, therefore, not included in the susceptibility score

| Species                      | Duration | Perishability | Food cached  | Placement           | Susceptibility |
|------------------------------|----------|---------------|--------------|---------------------|----------------|
| Jackdaw                      | S        | Low           | E, N, Mi, SM | Arboreal Cavity     | 1              |
| <i>Corvus monedula</i>       |          |               |              |                     |                |
| Red tree vole                | S        | Low           | WV           | Arboreal Cavity     | 1              |
| <i>Arborimus longicaudus</i> |          |               |              |                     |                |
| Black-capped chickadee       | S        | Low           | I, N, S      | Arboreal Surface    | 1              |
| <i>Parus atricapillus</i>    |          |               |              |                     |                |
| Boreal chickadee             | S        | Low           | N, S         | Arboreal Surface    | 1              |
| <i>Parus hudsonicus</i>      |          |               |              |                     |                |
| Brown-headed nuthatch        | S        | Low           | I, S         | Arboreal Surface    | 1              |
| <i>Sitta pusilla</i>         |          |               |              |                     |                |
| Coal tit                     | S        | Low           | I            | Arboreal Surface    | 1              |
| <i>Parus ater</i>            |          |               |              |                     |                |
| Eurasian nuthatch            | S        | Low           | N, S         | Arboreal Surface    | 1              |
| <i>Sitta europaea</i>        |          |               |              |                     |                |
| Marsh tit                    | S        | Low           | S            | Arboreal Surface    | 1              |
| <i>Parus palustris</i>       |          |               |              |                     |                |
| Pygmy nuthatch               | S        | Low           | I, S         | Arboreal Surface    | 1              |
| <i>Sitta pygmaea</i>         |          |               |              |                     |                |
| Red-breasted nuthatch        | S        | Low           | N, S         | Arboreal Surface    | 1              |
| <i>Sitta canadensis</i>      |          |               |              |                     |                |
| Siberian tit                 | S        | Low           | S            | Arboreal Surface    | 1              |
| <i>Parus cinctus</i>         |          |               |              |                     |                |
| Tufted titmouse              | S        | Low           | N, S         | Arboreal Surface    | 1              |
| <i>Parus bicolor</i>         |          |               |              |                     |                |
| White-breasted nuthatch      | S        | Low           | N, S         | Arboreal Surface    | 1              |
| <i>Sitta carolinensis</i>    |          |               |              |                     |                |
| Large Japanese field mouse   | S        | Low           | N, S         | Subterranean Ground | 1              |
| <i>Apodemus speciosus</i>    |          |               |              |                     |                |
| Mexican spiny pocket mouse   | S        | Low           | S            | Subterranean Ground | 1              |
| <i>Liomys irroratus</i>      |          |               |              |                     |                |
| Small Japanese field mouse   | S        | Low           | N, S         | Subterranean Ground | 1              |
| <i>Apodemus argenteus</i>    |          |               |              |                     |                |
| Wood mouse                   | S        | Low           | N, S         | Subterranean Ground | 1              |
| <i>Apodemus sylvaticus</i>   |          |               |              |                     |                |
| Yellow-necked mouse          | S        | Low           | N, S         | Subterranean Ground | 1              |
| <i>Apodemus flavicollis</i>  |          |               |              |                     |                |
| Fish crow                    | S        | Mixed         | Mi           | Arboreal Surface    | 2              |
| <i>Corvus ossifragus</i>     |          |               |              |                     |                |
| African striped weasel       | S        | High          | Ca, SM       | Arboreal Cavity     | 3              |

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|                                |   |      |            |                  |   |
|--------------------------------|---|------|------------|------------------|---|
| <i>Poecilogale albinucha</i>   |   |      |            |                  |   |
| Barn owl                       | S | High | SM         | Arboreal Cavity  | 3 |
| <i>Tyto alba</i>               |   |      |            |                  |   |
| Elf owl                        | S | High | I          | Arboreal Cavity  | 3 |
| <i>Micrathene whitneyi</i>     |   |      |            |                  |   |
| Schreech owl                   | S | High | SM         | Arboreal Cavity  | 3 |
| <i>Otus asio</i>               |   |      |            |                  |   |
| American kestrel               | S | High | Bi, Re, SM | Arboreal Surface | 3 |
| <i>Falco sparverius</i>        |   |      |            |                  |   |
| Barred owl                     | S | High | SM         | Arboreal Surface | 3 |
| <i>Strix varia</i>             |   |      |            |                  |   |
| Bat falcon                     | S | High | Ba, Bi     | Arboreal Surface | 3 |
| <i>Falco rufigulais</i>        |   |      |            |                  |   |
| Boreal owl                     | S | High | SM         | Arboreal Surface | 3 |
| <i>Aegolius funereus</i>       |   |      |            |                  |   |
| Broad-winged hawk              | S | High | Bi         | Arboreal Surface | 3 |
| <i>Buteo platypterus</i>       |   |      |            |                  |   |
| Buzzard                        | S | High | SM         | Arboreal Surface | 3 |
| <i>Buteo buteo</i>             |   |      |            |                  |   |
| Crowned eagle                  | S | High | MM         | Arboreal Surface | 3 |
| <i>Stephanoaetus coronatus</i> |   |      |            |                  |   |
| Eagle owl                      | S | High | Bi         | Arboreal Surface | 3 |
| <i>Bubo bubo</i>               |   |      |            |                  |   |
| Eleonora's falcon              | S | High | Bi         | Arboreal Surface | 3 |
| <i>Falco eleonarae</i>         |   |      |            |                  |   |
| Eurasian pygmy owl             | S | High | Bi, SM     | Arboreal Surface | 3 |
| <i>Glaucidium passerinum</i>   |   |      |            |                  |   |
| European kestrel               | S | High | SM         | Arboreal Surface | 3 |
| <i>Falco tinnunculus</i>       |   |      |            |                  |   |
| Goshawk                        | S | High | Bi, SM     | Arboreal Surface | 3 |
| <i>Accipiter gentilis</i>      |   |      |            |                  |   |
| Great horned owl               | S | High | SM, MM     | Arboreal Surface | 3 |
| <i>Bubo virginianus</i>        |   |      |            |                  |   |
| Leopard                        | S | High | LM, MM     | Arboreal Surface | 3 |
| <i>Panthera pardus</i>         |   |      |            |                  |   |
| Little owl                     | S | High | Bi, SM     | Arboreal Surface | 3 |
| <i>Athene noctua</i>           |   |      |            |                  |   |
| Merlin                         | S | High | Bi, SM     | Arboreal Surface | 3 |

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|                               |   |      |              |                  |   |
|-------------------------------|---|------|--------------|------------------|---|
| <i>Falco columbarius</i>      |   |      |              |                  |   |
| New Zealand falcon            | S | High | Bi           | Arboreal Surface | 3 |
| <i>Falco novaehollandiae</i>  |   |      |              |                  |   |
| Northern hawk owl             | S | High | SM           | Arboreal Surface | 3 |
| <i>Surnia ulula</i>           |   |      |              |                  |   |
| Northern pygmy owl            | S | High | SM           | Arboreal Surface | 3 |
| <i>Glaucidium gnoma</i>       |   |      |              |                  |   |
| Northern shrike               | S | High | Bi, SM       | Arboreal Surface | 3 |
| <i>Lanius excubitor</i>       |   |      |              |                  |   |
| Orange-breasted falcon        | S | High | Ba           | Arboreal Surface | 3 |
| <i>Falco deiroleucus</i>      |   |      |              |                  |   |
| Peregrine falcon              | S | High | Bi           | Arboreal Surface | 3 |
| <i>Falco peregrinus</i>       |   |      |              |                  |   |
| Prairie falcon                | S | High | Bi           | Arboreal Surface | 3 |
| <i>Falco mexicanus</i>        |   |      |              |                  |   |
| Prevost's squirrel            | S | High | Fr           | Arboreal Surface | 3 |
| <i>Callosciurus prevosti</i>  |   |      |              |                  |   |
| Saw-whet owl                  | S | High | SM           | Arboreal Surface | 3 |
| <i>Aegolius acadicus</i>      |   |      |              |                  |   |
| South island robin            | S | High | I            | Arboreal Surface | 3 |
| <i>Petroica australis</i>     |   |      |              |                  |   |
| Sparrowhawk                   | S | High | Bi, SM       | Arboreal Surface | 3 |
| <i>Accipiter nisus</i>        |   |      |              |                  |   |
| Tawny owl                     | S | High | SM           | Arboreal Surface | 3 |
| <i>Strix aluco</i>            |   |      |              |                  |   |
| African wild dog              | S | High | LM, MM       | Ground Surface   | 3 |
| <i>Lycaon pictus</i>          |   |      |              |                  |   |
| Barbados green monkey         | S | High | Fr           | Ground Surface   | 3 |
| <i>Cercopithecus aethiops</i> |   |      |              |                  |   |
| Black bear                    | S | High | Ca, MM, SM   | Ground Surface   | 3 |
| <i>Ursus americanus</i>       |   |      |              |                  |   |
| Black-backed jackal           | S | High | LM, SM, MM   | Ground Surface   | 3 |
| <i>Canis mesomelus</i>        |   |      |              |                  |   |
| Black-billed magpie           | S | High | Ca, E, N, Mi | Ground Surface   | 3 |
| <i>Pica pica</i>              |   |      |              |                  |   |
| Bobcat                        | S | High | MM, SM       | Ground Surface   | 3 |
| <i>Lynx rufus</i>             |   |      |              |                  |   |
| Brown bear                    | S | High | Ca, LM, MM   | Ground Surface   | 3 |

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|                                |   |      |                 |                |   |
|--------------------------------|---|------|-----------------|----------------|---|
| <i>Ursus arctos</i>            |   |      |                 |                |   |
| Canadian lynx                  | S | High | MM, SM          | Ground Surface | 3 |
| <i>Lynx canadensis</i>         |   |      |                 |                |   |
| Carrion crow                   | S | High | Ca              | Ground Surface | 3 |
| <i>Corvus corone</i>           |   |      |                 |                |   |
| Common crow                    | S | High | A, E, Fi, N, SM | Ground Surface | 3 |
| <i>Corvus brachyrhynchos</i>   |   |      |                 |                |   |
| Common raven                   | S | High | Ca, E, Mi, SM   | Ground Surface | 3 |
| <i>Corvus corax</i>            |   |      |                 |                |   |
| Coyote                         | S | High | LM, SM, MM      | Ground Surface | 3 |
| <i>Canis latrans</i>           |   |      |                 |                |   |
| European lynx                  | S | High | MM, SM          | Ground Surface | 3 |
| <i>Lynx lynx</i>               |   |      |                 |                |   |
| Fennec fox                     | S | High | E, MM, SM       | Ground Surface | 3 |
| <i>Vulpes zerda</i>            |   |      |                 |                |   |
| Fisher                         | S | High | Bi, MM, SM      | Ground Surface | 3 |
| <i>Martes pennanti</i>         |   |      |                 |                |   |
| Golden jackal                  | S | High | LM, SM, MM      | Ground Surface | 3 |
| <i>Canis aureus</i>            |   |      |                 |                |   |
| Lion                           | S | High | LM, MM          | Ground Surface | 3 |
| <i>Panthera leo</i>            |   |      |                 |                |   |
| MacGregor's bowerbird          | S | High | Fr              | Ground Surface | 3 |
| <i>Amblyornis macgregoriae</i> |   |      |                 |                |   |
| Mink                           | S | High | Bi, MM, SM      | Ground Surface | 3 |
| <i>Mustela vison</i>           |   |      |                 |                |   |
| Mountain lion                  | S | High | LM, MM          | Ground Surface | 3 |
| <i>Felis concolor</i>          |   |      |                 |                |   |
| Northwestern crow              | S | High | Fi, I           | Ground Surface | 3 |
| <i>Corvus caurinus</i>         |   |      |                 |                |   |
| Pine marten                    | S | High | Bi, Ca, MM, SM  | Ground Surface | 3 |
| <i>Martes martes</i>           |   |      |                 |                |   |
| Polar bear                     | S | High | LM, MM          | Ground Surface | 3 |
| <i>Ursus maritimus</i>         |   |      |                 |                |   |
| Snowy owl                      | S | High | MM, SM          | Ground Surface | 3 |
| <i>Nyctea scandiaca</i>        |   |      |                 |                |   |
| Tiger                          | S | High | LM, MM          | Ground Surface | 3 |
| <i>Panthera tigris</i>         |   |      |                 |                |   |
| Wolf                           | S | High | LM, SM, MM      | Ground Surface | 3 |

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|                               |       |      |            |                     |   |
|-------------------------------|-------|------|------------|---------------------|---|
| <i>Canis lupus</i>            |       |      |            |                     |   |
| Arctic shrew                  | S     | High | I          | Subterranean Ground | 3 |
| <i>Sorex arcticus</i>         |       |      |            |                     |   |
| Badger                        | S     | High | Ca, MM, SM | Subterranean Ground | 3 |
| <i>Taxidea taxus</i>          |       |      |            |                     |   |
| Burrowing owl                 | S     | High | I, R       | Subterranean Ground | 3 |
| <i>Athene cunicularia</i>     |       |      |            |                     |   |
| European mole                 | S     | High | I          | Subterranean Ground | 3 |
| <i>Talpa europaea</i>         |       |      |            |                     |   |
| Least weasel                  | S     | High | SM         | Subterranean Ground | 3 |
| <i>Mustela nivalis</i>        |       |      |            |                     |   |
| Long-tailed weasel            | S     | High | SM         | Subterranean Ground | 3 |
| <i>Mustela frenata</i>        |       |      |            |                     |   |
| Masked shrew                  | S     | High | I          | Subterranean Ground | 3 |
| <i>Sorex cinereus</i>         |       |      |            |                     |   |
| Mole-rat                      | S     | High | B, V       | Subterranean Ground | 3 |
| <i>Spalax leucodon</i>        |       |      |            |                     |   |
| Pygmy shrew                   | S     | High | I          | Subterranean Ground | 3 |
| <i>Microsorex hoyi</i>        |       |      |            |                     |   |
| Short-tailed weasel           | S     | High | SM         | Subterranean Ground | 3 |
| <i>Mustela erminea</i>        |       |      |            |                     |   |
| Siberian mole                 | S     | High | I          | Subterranean Ground | 3 |
| <i>Talpa altaica</i>          |       |      |            |                     |   |
| Water shrew                   | S     | High | A, I, SM   | Subterranean Ground | 3 |
| <i>Sorex palustris</i>        |       |      |            |                     |   |
| Spotted hyena                 | S     | High | LM, MM     | Water               | 3 |
| <i>Crocuta crocuta</i>        |       |      |            |                     |   |
| Heather vole                  | Mixed | Low  | WV         | Arboreal Surface    | 4 |
| <i>Phenacomys intermedius</i> |       |      |            |                     |   |
| Eastern gray squirrel         | Mixed | Low  | N, S, Mi   | Ground Surface      | 4 |
| <i>Sciurus carolinensis</i>   |       |      |            |                     |   |
| Eurasian red squirrel         | Mixed | Low  | Co, N, S   | Ground Surface      | 4 |
| <i>Sciurus vulgaris</i>       |       |      |            |                     |   |
| Fox squirrel                  | Mixed | Low  | N, S       | Ground Surface      | 4 |
| <i>Sciurus niger</i>          |       |      |            |                     |   |
| Great basin pocket mouse      | Mixed | Low  | S          | Ground Surface      | 4 |
| <i>Perognathus parvus</i>     |       |      |            |                     |   |
| Hispid pocket mouse           | Mixed | Low  | S          | Ground Surface      | 4 |



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|                                  |       |     |            |                                 |   |
|----------------------------------|-------|-----|------------|---------------------------------|---|
| <i>Perognathus hispidus</i>      |       |     |            |                                 |   |
| Japanese squirrel                | Mixed | Low | Co         | Ground Surface                  | 4 |
| <i>Sciurus lis</i>               |       |     |            |                                 |   |
| Little pocket mouse              | Mixed | Low | S          | Ground Surface                  | 4 |
| <i>Perognathus longimembris</i>  |       |     |            |                                 |   |
| Long-tailed pocket mouse         | Mixed | Low | S          | Ground Surface                  | 4 |
| <i>Perognathus formosus</i>      |       |     |            |                                 |   |
| Plains pocket mouse              | Mixed | Low | S          | Ground Surface                  | 4 |
| <i>Perognathus flavescens</i>    |       |     |            |                                 |   |
| Red-tailed squirrel              | Mixed | Low | N          | Ground Surface                  | 4 |
| <i>Sciurus granatensis</i>       |       |     |            |                                 |   |
| Rock pocket mouse                | Mixed | Low | S          | Ground Surface                  | 4 |
| <i>Perognathus intermedius</i>   |       |     |            |                                 |   |
| Tassel-eared squirrel            | Mixed | Low | N, S, Mu   | Ground Surface/Arboreal Surface | 4 |
| <i>Sciurus aberti</i>            |       |     |            |                                 |   |
| Alaska ground squirrel           | Mixed | Low | S, V       | Subterranean Ground             | 4 |
| <i>Spermophilus undulatus</i>    |       |     |            |                                 |   |
| Arctic ground squirrel           | Mixed | Low | S, V       | Subterranean Ground             | 4 |
| <i>Spermophilus parryii</i>      |       |     |            |                                 |   |
| Botta's pocket gopher            | Mixed | Low | S          | Subterranean Ground             | 4 |
| <i>Thomomys bottae</i>           |       |     |            |                                 |   |
| Djungarian hamster               | Mixed | Low | N, S       | Subterranean Ground             | 4 |
| <i>Phodopus sungorus</i>         |       |     |            |                                 |   |
| Golden-mantled ground squirrel   | Mixed | Low | N, S       | Subterranean Ground             | 4 |
| <i>Spermophilus lateralis</i>    |       |     |            |                                 |   |
| Lesser bandicoot rat             | Mixed | Low | N, S, T    | Subterranean Ground             | 4 |
| <i>Bandicota bengalensis</i>     |       |     |            |                                 |   |
| Mountain pocket gopher           | Mixed | Low | V          | Subterranean Ground             | 4 |
| <i>Thomomys monticola</i>        |       |     |            |                                 |   |
| Muskkrat                         | Mixed | Low | B, R, T, V | Subterranean Ground             | 4 |
| <i>Ondatra zibethicus</i>        |       |     |            |                                 |   |
| Northern pocket gopher           | Mixed | Low | R, T       | Subterranean Ground             | 4 |
| <i>Thomomys talpoides</i>        |       |     |            |                                 |   |
| Pouched mouse                    | Mixed | Low | N, S       | Subterranean Ground             | 4 |
| <i>Saccostomus campestris</i>    |       |     |            |                                 |   |
| Richardson ground squirrel       | Mixed | Low | S, V       | Subterranean Ground             | 4 |
| <i>Spermophilus richardsonii</i> |       |     |            |                                 |   |
| Rock squirrel                    | Mixed | Low | N, S       | Subterranean Ground             | 4 |

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|                                      |       |       |               |                     |  |   |
|--------------------------------------|-------|-------|---------------|---------------------|--|---|
| <i>Spermophilus variegatus</i>       |       |       |               |                     |  |   |
| Syrian golden hamster                | Mixed | Low   | S, R, T       | Subterranean Ground |  | 4 |
| <i>Mesocricetus auratus</i>          |       |       |               |                     |  |   |
| Thirteen-lined ground squirrel       | Mixed | Low   | S, V          | Subterranean Ground |  | 4 |
| <i>Spermophilus tridecemlineatus</i> |       |       |               |                     |  |   |
| Desert woodrat                       | Mixed | Mixed | V             | Ground Surface      |  | 5 |
| <i>Neotoma lepida</i>                |       |       |               |                     |  |   |
| Eastern woodrat                      | Mixed | Mixed | V             | Ground Surface      |  | 5 |
| <i>Neotoma floridana</i>             |       |       |               |                     |  |   |
| White-throated woodrat               | Mixed | Mixed | V             | Ground Surface      |  | 5 |
| <i>Neotoma albigula</i>              |       |       |               |                     |  |   |
| Bushy-tailed woodrat                 | Mixed | Mixed | V             | Subterranean Ground |  | 5 |
| <i>Neotoma cinerea</i>               |       |       |               |                     |  |   |
| Mexican woodrat                      | Mixed | Mixed | S, V          | Subterranean Ground |  | 5 |
| <i>Neotoma mexicana</i>              |       |       |               |                     |  |   |
| Mountain beaver                      | Mixed | High  | V             | Subterranean Ground |  | 6 |
| <i>Apodontia rufa</i>                |       |       |               |                     |  |   |
| Arctic fox                           | Mixed | High  | E, MM, SM     | Ground Surface      |  | 6 |
| <i>Alopex lagopus</i>                |       |       |               |                     |  |   |
| Red fox                              | Mixed | High  | Bi, E, MM, SM | Ground Surface      |  | 6 |
| <i>Vulpes vulpes</i>                 |       |       |               |                     |  |   |
| Short-tailed shrew                   | Mixed | High  | A, Fi, I, SM  | Subterranean Ground |  | 6 |
| <i>Blarina brevicauda</i>            |       |       |               |                     |  |   |
| Agouti                               | L     | Low   | N, S          | Ground Surface      |  | 7 |
| <i>Dasyprocta punctata</i>           |       |       |               |                     |  |   |
| Alipne chipmunk                      | L     | Low   | N, S          | Ground Surface      |  | 7 |
| <i>Tamias alpinus</i>                |       |       |               |                     |  |   |
| Blue jay                             | L     | Low   | N, Mi, S      | Ground Surface      |  | 7 |
| <i>Cyanocitta cristata</i>           |       |       |               |                     |  |   |
| Clark's nutcracker                   | L     | Low   | S             | Ground Surface      |  | 7 |
| <i>Nucifraga columbiana</i>          |       |       |               |                     |  |   |
| Cliff chipmunk                       | L     | Low   | N, S          | Ground Surface      |  | 7 |
| <i>Tamias dorsalis</i>               |       |       |               |                     |  |   |
| Eastern chipmunk                     | L     | Low   | I, N, S       | Ground Surface      |  | 7 |
| <i>Tamias striatus</i>               |       |       |               |                     |  |   |
| Eurasian jay                         | L     | Low   | Co, N, S      | Ground Surface      |  | 7 |
| <i>Garrulus glandarius</i>           |       |       |               |                     |  |   |
| Eurasian nutcracker                  | L     | Low   | S             | Ground Surface      |  | 7 |

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|                                  |   |      |            |                                 |   |
|----------------------------------|---|------|------------|---------------------------------|---|
| <i>Nucifraga caryocatactes</i>   |   |      |            |                                 |   |
| Flat-headed vole                 | L | Low  | V          | Ground Surface                  | 7 |
| <i>Alticola strelzowi</i>        |   |      |            |                                 |   |
| Green achouti                    | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Myoprocta acouchi</i>         |   |      |            |                                 |   |
| Least chipmunk                   | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Tamias minimus</i>            |   |      |            |                                 |   |
| Lodgepole pine chipmunk          | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Tamias speciosus</i>          |   |      |            |                                 |   |
| North American pika              | L | Low  | V          | Ground Surface                  | 7 |
| <i>Ochotona princeps</i>         |   |      |            |                                 |   |
| Pinyon jay                       | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Gymnorhinus cyanocephalus</i> |   |      |            |                                 |   |
| Red achouchi                     | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Myoprocta exilis</i>          |   |      |            |                                 |   |
| Red-tailed chipmunk              | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Tamias ruficaudus</i>         |   |      |            |                                 |   |
| Western scrub jay                | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Aphelocoma coerulescens</i>   |   |      |            |                                 |   |
| Siberian chipmunk                | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Tamias sibiricus</i>          |   |      |            |                                 |   |
| Siberian pika                    | L | Low  | V          | Ground Surface                  | 7 |
| <i>Ochotona alpina</i>           |   |      |            |                                 |   |
| Steller's jay                    | L | Low  | N, Mi, S   | Ground Surface                  | 7 |
| <i>Cyanocitta stelleri</i>       |   |      |            |                                 |   |
| Yellow pine chipmunk             | L | Low  | N, S       | Ground Surface                  | 7 |
| <i>Tamias amoenus</i>            |   |      |            |                                 |   |
| Douglas'squirrel                 | L | Low  | Co, Mu, S  | Ground Surface/Arboreal Surface | 7 |
| <i>Tamiasciurus douglasii</i>    |   |      |            |                                 |   |
| Red squirrel                     | L | Low  | Co, Mu, S  | Ground Surface/Arboreal Surface | 7 |
| <i>Tamiasciurus hudsonicus</i>   |   |      |            |                                 |   |
| African giant rat                | L | Low  | N, S, T    | Subterranean Ground             | 7 |
| <i>Cricetomys gambianus</i>      |   |      |            |                                 |   |
| Alaska vole                      | L | Low  | V          | Subterranean Ground             | 7 |
| <i>Microtus miurus</i>           |   |      |            |                                 |   |
| Bank vole                        | L | High | V (Lichen) | Arboreal Cavity/Surface         | 7 |
| <i>Clethrionomys glareolus</i>   |   |      |            |                                 |   |
| Banner-tailed kangaroo rat       | L | Low  | S          | Subterranean Ground             | 7 |

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|                                 |   |     |          |                     |  |   |
|---------------------------------|---|-----|----------|---------------------|--|---|
| <i>Dipodomys spectabilis</i>    |   |     |          |                     |  |   |
| Black-bellied hamster           | L | Low | T, V     | Subterranean Ground |  | 7 |
| <i>Cricetus cricetus</i>        |   |     |          |                     |  |   |
| Brandt's vole                   | L | Low | V, WV    | Subterranean Ground |  | 7 |
| <i>Microtus brandti</i>         |   |     |          |                     |  |   |
| California ground squirrel      | L | Low | S, V     | Subterranean Ground |  | 7 |
| <i>Spermophilus beecheyi</i>    |   |     |          |                     |  |   |
| Cape mole-rat                   | L | Low | B, R, T  | Subterranean Ground |  | 7 |
| <i>Georchus capensis</i>        |   |     |          |                     |  |   |
| Cape dune mole-rat              | L | Low | T        | Subterranean Ground |  | 7 |
| <i>Bathyergus suillus</i>       |   |     |          |                     |  |   |
| Common mole-rat                 | L | Low | B        | Subterranean Ground |  | 7 |
| <i>Cryptomys hottentotus</i>    |   |     |          |                     |  |   |
| Common vole                     | L | Low | B        | Subterranean Ground |  | 7 |
| <i>Microtus arvalis</i>         |   |     |          |                     |  |   |
| Coruro                          | L | Low | B, T     | Subterranean Ground |  | 7 |
| <i>Spalacopus cyanus</i>        |   |     |          |                     |  |   |
| Daurian pika                    | L | Low | V        | Subterranean Ground |  | 7 |
| <i>Ochotona daurica</i>         |   |     |          |                     |  |   |
| Deer mouse                      | L | Low | S        | Subterranean Ground |  | 7 |
| <i>Peromyscus maniculatus</i>   |   |     |          |                     |  |   |
| Desert kangaroo rat             | L | Low | S        | Subterranean Ground |  | 7 |
| <i>Dipodomys deserti</i>        |   |     |          |                     |  |   |
| Diurnal sand rat                | L | Low | S, V     | Subterranean Ground |  | 7 |
| <i>Psammomys obesus</i>         |   |     |          |                     |  |   |
| Edible doormouse                | L | Low | B, N, S  | Subterranean Ground |  | 7 |
| <i>Myoxus glis</i>              |   |     |          |                     |  |   |
| Forest dormouse                 | L | Low | Co, S    | Subterranean Ground |  | 7 |
| <i>Dryomys nitedula</i>         |   |     |          |                     |  |   |
| Giant kangaroo rat              | L | Low | S        | Subterranean Ground |  | 7 |
| <i>Dipodomys ingens</i>         |   |     |          |                     |  |   |
| Great basin kangaroo rat        | L | Low | S        | Subterranean Ground |  | 7 |
| <i>Dipodomys microps</i>        |   |     |          |                     |  |   |
| Greater long-tailed hamster     | L | Low | V        | Subterranean Ground |  | 7 |
| <i>Cricetulus triton</i>        |   |     |          |                     |  |   |
| Hazel doormouse                 | L | Low | Co, N, S | Subterranean Ground |  | 7 |
| <i>Muscardinus avellanarius</i> |   |     |          |                     |  |   |
| Heermann's kangaroo rat         | L | Low | S        | Subterranean Ground |  | 7 |

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|                                |   |     |            |                     |   |
|--------------------------------|---|-----|------------|---------------------|---|
| <i>Dipodomys heermanni</i>     |   |     |            |                     |   |
| Indian gerbil                  | L | Low | S, V       | Subterranean Ground | 7 |
| <i>Tatera indica</i>           |   |     |            |                     |   |
| Meadow vole                    | L | Low | R          | Subterranean Ground | 7 |
| <i>Microtus pennsylvanicus</i> |   |     |            |                     |   |
| Merriam's kangaroo rat         | L | Low | S          | Subterranean Ground | 7 |
| <i>Dipodomys merriami</i>      |   |     |            |                     |   |
| Mexican jay                    | L | Low | N, S       | Ground Surface      | 7 |
| <i>Aphelocoma ultramarina</i>  |   |     |            |                     |   |
| Mid-day gerbil                 | L | Low | N, S, T, V | Subterranean Ground | 7 |
| <i>Meriones meridianus</i>     |   |     |            |                     |   |
| Mole-rat                       | L | Low | B, R, T, V | Subterranean Ground | 7 |
| <i>Spalax microphthalmus</i>   |   |     |            |                     |   |
| Mole vole                      | L | Low | B, T       | Subterranean Ground | 7 |
| <i>Ellobius talpinus</i>       |   |     |            |                     |   |
| Mountain pygmy possum          | L | Low | N, S       | Subterranean Ground | 7 |
| <i>Burramys parvus</i>         |   |     |            |                     |   |
| Namaqua gerbil                 | L | Low | S          | Subterranean Ground | 7 |
| <i>Desmodillus auricularis</i> |   |     |            |                     |   |
| Nothern grasshopper mouse      | L | Low | S          | Subterranean Ground | 7 |
| <i>Onychomys leucogaster</i>   |   |     |            |                     |   |
| Pale kangaroo mouse            | L | Low | S          | Subterranean Ground | 7 |
| <i>Microdipodops pallidus</i>  |   |     |            |                     |   |
| Pallas' pika                   | L | Low | V          | Subterranean Ground | 7 |
| <i>Ochotona pallasi</i>        |   |     |            |                     |   |
| Plains pocket gopher           | L | Low | B, T       | Subterranean Ground | 7 |
| <i>Geomys bursarius</i>        |   |     |            |                     |   |
| Prairie vole                   | L | Low | S          | Subterranean Ground | 7 |
| <i>Pitmys ochrogaster</i>      |   |     |            |                     |   |
| Reddish-gray vole              | L | Low | V          | Subterranean Ground | 7 |
| <i>Clethrionomys rufocanus</i> |   |     |            |                     |   |
| Rook                           | L | Low | Co, N, S   | Ground Surface      | 7 |
| <i>Corvus frugilegus</i>       |   |     |            |                     |   |
| Santa Cruz kangaroo rat        | L | Low | S          | Subterranean Ground | 7 |
| <i>Dipodomys venustus</i>      |   |     |            |                     |   |
| Social vole                    | L | Low | B, R       | Subterranean Ground | 7 |
| <i>Microtus socialis</i>       |   |     |            |                     |   |
| Southeastern pocket gopher     | L | Low | B, T       | Subterranean Ground | 7 |
| <i>Geomys pinetis</i>          |   |     |            |                     |   |

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|   |   |       |               |                     |   |
|---|---|-------|---------------|---------------------|---|
| Spiny pocket mouse<br><i>Heteromys desmarestianus</i> | L | Low   | Fr, N, S      | Subterranean Ground | 7 |
| Taiga vole<br><i>Microtus xanthognathus</i>           | L | Low   | V             | Subterranean Ground | 7 |
| Tamarisk gerbil<br><i>Meriones tamariscinus</i>       | L | Low   | N, S, T,      | Subterranean Ground | 7 |
| Tree mouse<br><i>Beamys major</i>                     | L | Low   | S, N          | Subterranean Ground | 7 |
| White-footed mouse<br><i>Peromyscus leucopus</i>      | L | Low   | N, S          | Subterranean Ground | 7 |
| American beaver<br><i>Castor canadensis</i>           | L | Mixed | V, WV         | Water               | 8 |
| Dusky-footed woodrat<br><i>Neotoma fuscipes</i>       | L | Mixed | N, S, V       | Subterranean Ground | 8 |
| Eurasian beaver<br><i>Castor fiber</i>                | L | Mixed | V, WV         | Water               | 8 |
| Bull-headed shrike<br><i>Lanius bucephalus</i>        | L | High  | Bi, I, SM     | Arboreal Surface    | 9 |
| Gray jay<br><i>Perisoreus canadensis</i>              | L | High  | Ca, Fr, I, Mi | Arboreal Surface    | 9 |
| Siberian jay<br><i>Perisoreus infaustus</i>           | L | High  | Ca, Fr, I     | Arboreal Surface    | 9 |
| Wolverine<br><i>Gulo gulo</i>                         | L | High  | LM, MM        | Ground Surface      | 9 |

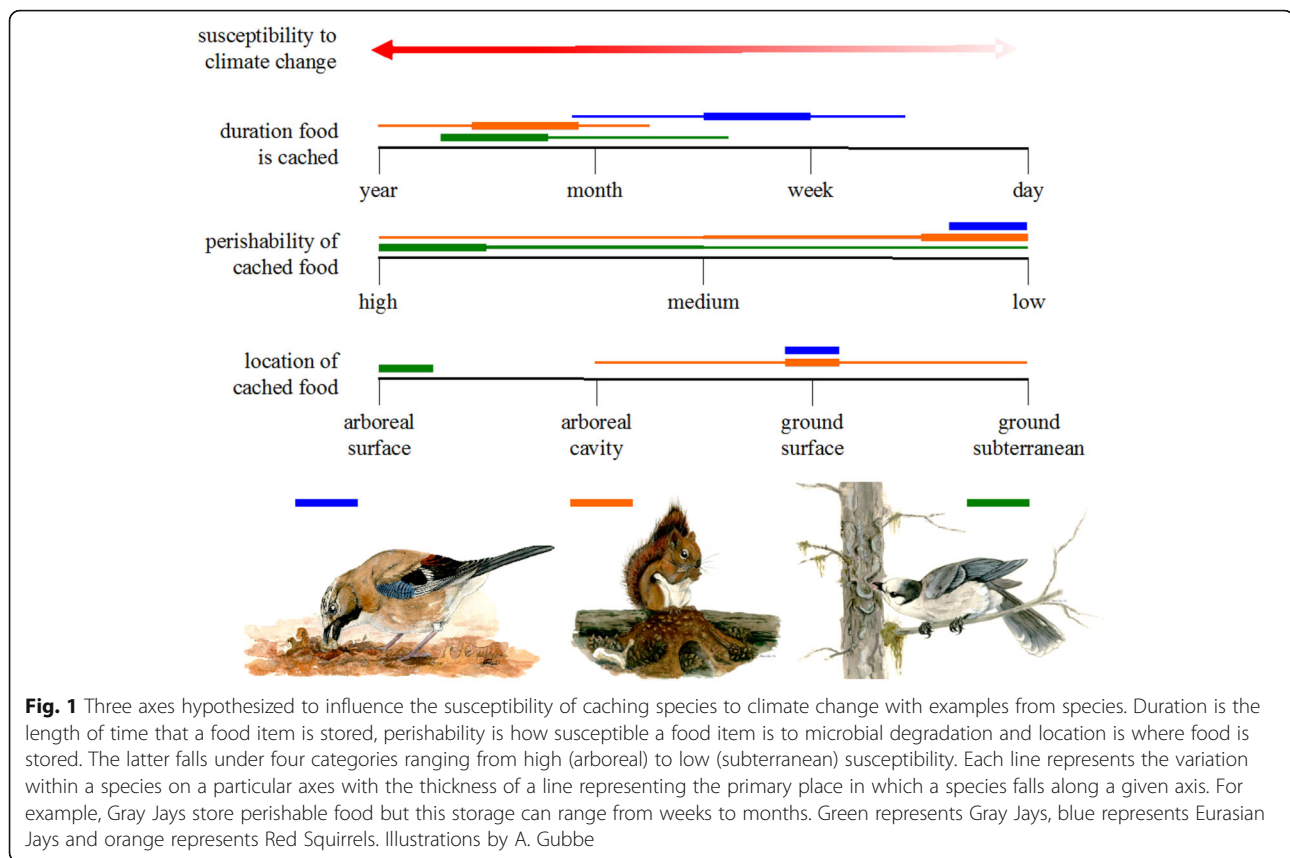
Legend: A amphibian, B bulb, Ba bat, Bi bird, Ca carrion, Co cone, E eggs, Fi fish, Fr fruit, I invertebrates, LM large mammal, N nuts, Mi miscellaneous human foods, MM medium mammal, Mu mushroom, R roots, Re reptiles, S seeds, SM small mammal, T tuber, V vegetation, WV woody vegetation. Note that mammal classifications are based off of Vander Wall [164]

herbivores, such as Collared Pikas (*Ochotona collaris*), and Agoutis (*Dasyprocta punctata*) have been documented to store both non-perishable nuts, and seeds, and perishable fruit [38, 71, 92, 134, 165].

Below, we discuss how the field of food science can be used to develop an understanding of conditions that maintain and degrade perishable food items. Although there are few studies in food science that examine the influence of the environment on seeds and nuts, we also discuss how the field of plant biology may offer some insight into how variation in climate could influence germination rates and reduce the functional quality of stored seeds.

### Location of food storage

With the exception of Beavers (*Castor canadensis* and *Castor fiber*) and Spotted Hyenas (*Crocuta crocuta*) which cache food in water, caching species store food in two types of locations: in the ground or in trees [164]. When food is stored below ground it will tend to be more buffered from environmental conditions compared to food that is stored above ground. For example, when air temperatures are below zero, temperatures remained above freezing in underground burrows of Alpine Marmots (*Marmota marmot*; [5]). When food is stored during the temperate zone winter, snow accumulation of 30-40 cm can decouple soil and air temperature [156].



In contrast, when food is cached above ground, it is more likely to be directly exposed to environmental conditions. For example, White-breasted Nuthatches (*Sitta carolinensis*) store food caches in exposed bark crevices on the trunk and limbs of trees [75, 116, 179], while Jays of the genus *Perisoreus* cache food under pieces of bark or lichen on branches [36, 154]. Other species, such as Leopards, leave food items conspicuously on branches where it is difficult for competitors, such as Lions and Spotted Hyenas, to access them ([35], Eltringham SK. The ecology and conservation of large African mammals. [39]). In contrast, some species, such as Boreal Owls (*Aegolius funereus*), store food in tree cavities [79], which likely offers greater protection from environmental conditions compared to food stored on the exterior of a tree.

Regardless of whether species store above or below ground, some species may also exploit different microhabitats. For example, Banner-tailed Kangaroo Rats (*Diopdomys spectabilis*) store food in multiple chambers within their complex subterranean burrows [134]. Storage chambers can vary in both humidity and temperature, resulting in differential microbial activity between chambers [133]. Banner-tailed Kangaroo Rats prefer seeds with intermediate levels of mould and, therefore, exploit differences in microhabitats by moving

seeds with high mould levels to low humidity chambers, and seeds with low mould levels to high humidity chambers [133]. Differences in cache placement (subterranean burrows, ground surface, tree cavities and tree surfaces) mean that food items will be exposed to different climatic conditions, which could lead to variation in the degree of degradation. It is clear that additional research is required to better understand the extent to which exposure to environmental conditions differ between caching locations.

#### Summary of trends and susceptibility estimates

We compiled a list of 203 caching species for which there is information on both the duration of storage and perishability of cached food (Table 1). From this information, we developed a susceptibility score for each species using a hierarchical classification system. Species were first divided into three categories based on the duration of food storage (short, mixed or long) and then, within each of these three categories, further divided into three groups according to the degree of perishability of cached food (low, mixed or high). We considered what are typically called 'non-perishable' food (nuts, seeds) as low perishability because climate may influence germination rates (see food science and plant biology

discussions below). For both storage duration and perishability, species were defined as 'mixed' when there was evidence in the literature for both 'high' and 'low' storage duration or perishability. This classification created nine possible categories, [1] short-term, low-perishability, [2] short-term, mixed-perishability, [3] short-term, high-perishability, [4] mixed duration, low-perishability, [5] mixed duration, mixed-perishability, [6] mixed duration, high-perishability, [7] long-term, low-perishability, [8] long-term, mixed perishability, and [9] long-term, high-perishability food. High scores represent the greatest predicted susceptibility to climate change. Storage location was not used to determine susceptibility scores because there is not yet enough empirical evidence about how food cached at these different locations (e.g. subterranean vs. arboreal surface) is influenced by environmental conditions.

Because of the short-term nature of their caching behaviour, the largest proportion of caching species (44%) were assigned to the three lowest susceptibility scores (1-3). Of the 38% of species in the three highest susceptibility categories (score of 7-9), 91% relied on low-perishability food (score of 7). Seven percent (7%) stored both high- and low-perishability food and only 2% (four species: the Bull-headed Shrike *Lanius busephalus*, Gray Jay, Siberian Jay *Perisoreus infaustus* and Wolverine *Gulo gulo*) were both long-term cachers and relied exclusively on high-perishability food (susceptibility score of 9). Population declines at the southern edge of ranges have already been documented for both Gray Jays [171] and Wolverines [6] and studies on both of these species also suggest that climate change could be contributing to population declines [62, 139, 171].

A smaller proportion of species (18%) were classified as mixed duration cachers (e.g. Arctic Foxes, *Alopex lagopus* and Red Foxes, *Vulpes vulpes*, susceptibility scores of 6). The reason why some species are classified as mixed duration cachers may partly reflect geographic differences in caching behaviour within a species [43, 90, 168]. However, most species or populations likely cache a variety of food items with different degrees of perishability (Fig. 1). In such cases, food that is more perishable may also be of higher nutritional value (e.g. meat), which implies that species in this category may be more susceptible to climate change than we have estimated here. Nevertheless, it is clear that, for many species, more information is required to quantify how long food is stored, as well as the proportion of specific food items that are stored and their degree of perishability. Such information will improve our estimates of susceptibility and will, therefore, be important for understanding how climate change could influence their abundance.

### **Integrating concepts from food science to understand the susceptibility of perishable food to climate change**

Understanding how environmental conditions influence food quality is a major focus of the field of food science [107, 122]. A number of conditions have been identified that can degrade or preserve a wide range of perishable food consumed by humans [16, 86, 97, 107]. At the most general level, food can be degraded in three ways. First, even in the complete absence of bacteria or fungi, food may lose nutritional quality through a breakdown in structure due to a number of physical and chemical processes [10, 16]. Second, microbial proliferation in food leads to losses of the nutrients and energy originally available to non-microbial competitors (e.g., humans) as these resources are diverted into the growth of indigestible bacteria [51, 59, 60]. Third, even when food still contains energy and nutrients potentially useful to non-microbes, these resources may be rendered inaccessible as many bacteria (e.g., *Staphylococcus aureus* and *Clostridium botulinum*) produce toxins or noxious substances that induce vomiting, diarrhea or otherwise render food inedible for humans [51, 52]. Although spoilage is fundamentally different from the physical or microbial degradation of a food item, in nature the three processes can be considered tightly linked. For example, the physical degradation of a food item (e.g. through freeze-thaw cycles) may accelerate microbial proliferation, which could then enhance the production of toxins that render food inedible. Thus, these processes will likely have to be considered together as they will be difficult to separate in the wild. Here, we focus on four classes of environmental factors that are recognized to influence perishable food stored by humans and that we believe are relevant to natural systems.

#### **Temperature**

Temperature has long been the subject of study in the field of food science because it influences microbial growth, with different temperature thresholds responsible for facilitating or inhibiting microbial growth depending on the food item and species of bacteria [107]. Generally, warm temperatures act to facilitate microbial growth, whereas cold temperatures inhibit growth [23]. Humans have manipulated temperature for centuries to extend the duration for which food can be stored [107, 151]. Lowering temperature is extremely effective because it acts to retard microbial growth across a range of food groups, such as meat, fruit and vegetative matter [22, 23, 129].

Many studies have investigated the relationship between temperature and microbial growth (e.g. [9, 20, 21, 49, 184]). Zwietering et al. [184] focused on modelling



the relationship between temperature and bacterial growth rate. Simple models, including a linear relationship between temperature and growth rate and constant growth at all temperatures were not supported. Instead, the best fitting models were derived from a square root model originally proposed by Ratkowsky et al. [131]. Part of the reason why simpler models show a lack of fit is that asymptotes exist to bacterial growth, particularly at extreme temperatures [184]. These studies also highlight the importance of both bacterial species and the food substrate in determining rates of bacterial growth at different temperatures. For example, Bovill et al. [21] demonstrated that the proliferation of *Listeria monocytogenes* and *Salmonella* spp. at the same temperature depended on substrate (milk vs. broth vs. meat) and bacteria species. This dependence is likely the result of competition between the existing bacterial flora of a food item and novel bacteria [119]. In natural systems, local bacterial communities could prevent additional harmful bacteria from colonizing a food item, preventing food spoilage due to the accumulation of noxious substances.

The majority of studies on the effects of climate change in wild animal populations have focused on the effect of temperature (e.g. [40, 77]) and temperature is certainly the most common environmental predictor variable used in studies of caching species as well (e.g. [106, 171]). The advantage is that temperature is the most commonly recorded long-term environmental variable and, where it is not recorded, several models are available to estimate past temperature values on either a monthly or annual basis [94]. Using mean temperature values over a specific time period is clearly convenient, but we argue, perhaps not always the only ecologically relevant factor for caching animals because it may not capture other environmental conditions that are associated with different mechanisms known to influence the quality of stored food.

### Deep freezing

It may be useful to separate deep freeze from the general effects of temperature because it represents a specific threshold below which microbial growth is halted rather than simply retarded. The specific temperature associated with a deep freeze event will depend on the microbe in question as cold tolerance varies across species [69]. As microbial activity is a major cause of food spoilage, stopping this process to preserve food over long time periods has been a major focus in the field of food science [17, 41]. One study suggested that temperatures as low as  $-55^{\circ}\text{C}$  represent ideal storage conditions for meat [55] because enzymatic reactions and oxidative rancidity cease completely, removing most of the key processes that would degrade food quality [182]. However, temperatures do not necessarily need to be this

extreme to halt microbial activity over time. A number of studies have found that bacteria and fungi on frozen food generally cease growth at  $-8^{\circ}\text{C}$  [45] and other research has provided evidence that the growth of some microbes halts at around  $-12^{\circ}\text{C}$  [42, 98].

Perhaps more importantly, deep freeze events can also cause cell death or injury to microbial cells [113]. If microbes are killed when exposed to deep freeze temperatures, it means that subsequent degradation will occur at a slower rate, as fewer bacteria will be present to deplete nutritional resources or render a food item inedible through spoilage when temperatures increase [91, 174]. However, if not all bacteria are killed, deep freeze events can also act as a selection agent to promote cold tolerance [174]. Many bacterial species can also enter a 'viable but nonculturable' (VBNC) state, characterized by a large reduction in metabolic activity in response to extreme temperatures and other environmental stressors [74, 113]. Once in the VBNC state, bacteria remain dormant until conditions facilitate resuscitation. Some studies suggest that an increase in temperature can result in resuscitation of cells in the VBNC state [114, 115, 177]. This highlights the importance of understanding the relationship between temperature and the activity of microbes present on cached food. In particular, understanding relevant thresholds that inhibit bacterial growth or kill bacteria will be key to interpreting the influence of climatic variables on food quality over time.

For caching species, deep freeze events could play a significant role in preserving the quality of stored food, in particular for species that store food for use over the winter. For example, in a study of the caloric content of simulated Gray Jay caches at three different latitudes in Ontario, Canada, Scheley et al. [139] found that the mass loss and caloric content of cached food (mealworms and raisins) was similar between low- and mid-latitude sites even though these sites differed in mean fall temperatures. However, food caches from the high-latitude site lost less weight and caloric content, leading Scheley et al. [139] to speculate that 'deep freeze' events may be driving this pattern as the high-latitude site was the only site that reached an average of  $-16^{\circ}\text{C}$  during the winter. In Finland, bacterial activity was halted in two different decomposer communities in soil at  $-16^{\circ}\text{C}$ , suggesting that this may be an important threshold in natural systems [157]. Despite these indirect lines of evidence, there have been no studies that have experimentally examined whether deep freeze events contribute to the preservation of perishable cached food of a wild animal.

### Humidity

Another influence on microbial growth is the amount of water in the surrounding environment [1, 7]. Humidity,

a measure of the moisture content of air, influences the transfer of moisture between the air and surface of adjacent substrates [76]. It is well known that increases in moisture around a food item leads to increased microbial growth and proliferation [161]. For example, lower environmental moisture content has been found to decrease microbial growth on rice and flour and, consequently, increase the length of time these food items can be stored [1, 47].

Since high ambient humidity facilitates microbial degradation and spoilage [1], pronounced seasonal fluctuations in rainfall and ambient humidity may mean that during large portions of the year it is likely not profitable to store perishable food, particularly at low latitudes. In contrast, high-latitude ecosystems have lower ambient humidity levels, punctuated by increases in moisture in the form of rain and snow. This reduction in humidity favours long-term storage and could also allow species to store at multiple time points throughout the year.

At high latitudes, humidity is likely to influence food caches primarily in the spring, summer, and fall because warm air can hold a larger quantity of water vapour [162] and this means that more water is available to microbes [82]. Conversely, in winter, much of the moisture is present as a solid (i.e. ice), which means that it cannot be easily accessed by microbes, thus inhibiting growth.

#### Freeze-thaw events

Freeze-thaw events cause phase changes of bound water within a cell (e.g. ice crystal formation) and the associated rapid expansion and contraction of water can result in damage to cellular structures [10, 86, 87, 170]. As a result of the degradation of cellular structures, freeze-thaw events can affect multiple aspects of food quality and several studies in applied food science have been conducted to understand the mechanisms behind these processes.

Microstructure is one major component of food quality that is heavily influenced by freeze-thaw events [3, 10]. The denaturation of proteins, particularly within meat and fish products, has been linked to changes to the microstructure of a food item [3, 16]. Associated with these changes in microstructure is a process known as 'drip loss' [182]. As a food item undergoes a freeze-thaw cycle, damaged cells leak an exudate containing soluble nutrients, vitamins, minerals and protein [10, 86]. In addition to siphoning nutritional content away from the cell, this exudate also produce favourable conditions for microbial growth by increasing nutrient and moisture available around a food item [86].

The number of freeze-thaw events that a food item experiences can also influence the amount of damage that is caused. Multiple freeze-thaw events can have strong additive effects that can cause food to degrade more rapidly [16, 68, 128, 148, 150, 180, 181]. Srinivasan et al.

[150] documented an increase in mechanical damage sustained by freshwater prawns (*Macrobrachium rosenbergii*) exposed to repeated freeze-thaw events and this damage was caused by repeated melting and reformation of ice-crystals within a cell. Boonsumrej et al. [16] found similar mechanical damage to Tiger Shrimp (*Penaeus monodon*) characterized by torn muscle fibres, an increase in distance between adjacent muscle fibres, and a breakdown of the subcuticular membrane surrounding muscle fibres. This mechanical damage was associated with increased thawing loss (the weight lost by a sample when comparing frozen and thawed weight), a decrease in protein concentrations and an increase in thiobarbituric acid, a compound associated with food decomposition [16].

In the field of food science, studies have typically examined the effect of up to five consecutive freeze-thaw events on food quality (e.g. [68, 148, 180, 181]). However, one study demonstrated that meat might continue to degrade after 15 freeze-thaw cycles [128]. Further studies are needed to determine if various food types have different threshold numbers of freeze-thaw cycles beyond which no further damage can be inflicted. Such studies would be important in order to determine if possible increases in the number of freeze-thaw events resulting from long-term changes in climate could decrease survival of food caches in the wild.

#### Integrating concepts from plant biology to understand the susceptibility of non-perishable food to climate change

Although cached seeds are typically considered non-perishable, seed become inedible when they germinate and therefore, may also be influenced by climate change. The field of plant biology has identified a number of regulatory processes and environmental conditions that influence the likelihood of germination [11]. For example, dormancy, the failure of a seed to germinate when conditions are otherwise favourable to promote germination [34, 46], ensures that seeds will only germinate when conditions are favourable for growth [34, 169] and is greatly influenced by a number of environmental variables including temperature and moisture.

#### Temperature

The effect of temperature is generally related to the life history of the plant species or taxa [11]. For example, winter annuals require periods of warm temperatures preceding cold temperatures in order for their seeds to germinate [12], whereas summer annuals require periods of cold weather followed by warm temperatures in order to germinate. Patterns of temperature fluctuations can also be important to stimulate germination, with many

species responding favourably to alternating temperatures [84, 109, 144, 149].

Freeze-thaw cycles may also influence the germination of seeds that are stored by many food-caching species. Soil temperature regimes, which can be influenced by freeze-thaw events, have a strong bearing on the occurrence and timing of germination [126, 127], however this relationship is highly variable between plant species [14]. Several studies indicate that exposure to low soil temperatures is necessary for germination to occur [78, 143] and other studies have shown that freeze-thaw cycles can lead to scarification, a necessary precondition for germination in some plant species [183]. Van Assche *et al.* [163] proposed that freeze-thaw cycles could interact with cold winter temperatures in a two-step process to promote germination. First, low winter temperatures make seeds sensitive to freeze-thaw cycles. Second, freeze-thaw cycles cause seeds to become water permeable, facilitating germination. For such species, warming winter temperatures could lead, in the short term, to prolonged availability of food caches, as seeds would fail to germinate and, in the long term, to eventual local extinction of the trees/plants producing the seeds favoured by food-caching species. On the other hand, for plant species whose seeds germinate independently of exposure to cold temperatures or freeze-thaw cycles, warmer and shorter winters could shorten the availability of seeds to any animals that cached them [93].

### Moisture

In general, some moisture is required to facilitate germination but the optimum water content varies across species [111]. Soaking seeds is a common commercial method used to “prime” seeds for germination, leading to a higher percentage of germination for many species [2, 118]. Similar to temperature, variability in moisture is necessary for many species to promote germination. However, for some species, variability in moisture levels can result in a decreased germination rates or have no effect at all [13, 89, 159]. There may also be strong interactive effects between moisture and temperature. For example, in seeds without sufficient water content, dormancy will not be broken by temperature alone [11].

### Linking food-degrading environmental conditions with climate change

The environmental variables outlined above are particularly relevant to natural systems as they are rapidly shifting due to climate change [63]. Already mean temperatures across the globe have increased [63, 173], precipitation patterns have shifted resulting in altered moisture regimes [147, 152] and an increase in unpredictable weather patterns, such as mid-winter thaws and late frosts, have been documented [63, 173]. The shift in these environmental

variables suggests that the relationship between caching species and their environment is changing and potentially altering the benefits of caching food. However, it is important to note that not all of these environmental variables will necessarily shift in the same way or with similar magnitudes.

### Extracting climatic variables from historical weather data

Historical weather records are valuable for quantifying how climatic variables may influence long-term changes in abundance of caching species. Even when data are sparse, minimum, maximum and mean temperatures can be used to estimate other climatic variables, such as freeze-thaw events and the duration of deep freeze events. Natural history characteristics, such as when a species begins caching food and when it retrieves cached food, should be used to determine relevant time points to extract data from historical records.

### Freeze-thaw events

Extracting information on freeze-thaw events from historical records requires knowledge of food-specific initial freezing point [103]. Initial freezing points are directly related to the concentration of solutes in a food item and its water content [130] and are known for a variety of food items. Many of these estimates could be used as surrogates for food items cached by wild species. Missing from the existing literature, however, are estimates of arthropod initial freezing points, which are relevant to a number of food-caching species that regularly store this taxa. Once initial freezing points have been determined by experiments or estimated from the literature, the numbers of freeze-thaw events can then be extracted from historical weather records by determining the point when the temperature drops below and then rises above the initial freezing point.

### Deep-freeze Events

Although deep-freeze events can be easily extracted from historical temperature records, the use of minimum, mean or maximum daily temperatures has an important bearing on how deep-freeze events are interpreted. For example, extracting deep-freeze events based on minimum daily temperature implies, in most cases, that temperatures will drop below the deep-freeze threshold for only part of the day. Alternatively, using maximum daily temperatures implies that temperatures will remain below the given deep freeze threshold for the entire day. Maximum daily temperatures allow for the estimation of deep-freeze days, which is the number of complete days that microbial activity is inhibited. However, without hourly weather records it is difficult to estimate exactly how long deep freeze events would inhibit microbial growth. To better

predict deep-freeze thresholds, it is also important to understand the species or groups of microbes that are present in a food caching system. An understanding of the microbial diversity present on a food item could provide better estimates on the temperature at which microbial activity is halted, rather than relying on estimates obtained from the literature.

### Humidity

Estimates of humidity from historical records can be difficult to obtain, as many weather stations have not recorded daily humidity [44]. In spite of this, proxies can be used to provide estimates of humidity or moisture levels in the environment. Rainfall and snowfall are climatic variables that are commonly found in historical weather records and can be used to provide a crude estimate of moisture in the environment. However, predictive models based on precipitation in combination with minimum daily temperature have been shown to provide better estimates of humidity in both North America and Europe. However, in more arid environments, such as parts of Africa, this relationship does not seem to be robust [44] and it is necessary to use more complex models [76].

## Characteristics of caching species that could mitigate the impact of climatic change

### Behavioural strategies

Caching species have developed a number of behavioural strategies that retard cache degradation [37, 67, 95, 135, 158] and, therefore, may mitigate the effects of changing climate. These strategies include handling techniques, exploitation of chemical properties in the environment, and exploitation of certain climatic factors to decrease food perishability.

Several species have been documented to use specific handling techniques that lessen degradation of a cached food item. For example, incapacitating, rather than killing prey at the time of capture can serve to inhibit spoilage or reduce the rate of degradation. Burrowing Owls (*Athene cunicularis*) have been shown to incapacitate long-horned beetles to facilitate storage [135], while Elf Owls (*Micrathene whitneyi*) have been observed to damage the thorax and remove the legs from live sphinx moths [88]. Other animals, such as the Short-tailed Shrew (*Blarina brevicauda*), produce toxins in their saliva that immobilize prey by rendering them comatose [95]. Once in this state, prey can remain alive for several days after capture.

Some species may exploit antimicrobial compounds in the environment to preserve cached food. Elgmork [37] suggested that Brown Bears (*Ursus arctos*) cover carcasses with *Sphagnum* moss to aid in long-term preservation because *Sphagnum* is known to contain phenolic

compounds that have antimicrobial properties. Arboreal caching species may exploit similar antimicrobial compounds of coniferous trees (e.g. spruce *Picea spp.*), which have been proposed to preserve cached food better than deciduous trees. In Gray Jays, evidence suggests that territory quality at the southern edge of their range is related to the percentage of conifers on their territories [110, 155], which appears to be partly due to the superior ability of conifers to preserve food [155]. Willow Tits (*Parus montanus*) have also been observed to preferentially cache food on conifers rather than deciduous trees [81], which could also be related to the antimicrobial properties of conifers.

A third method that caching species use to retard microbial degradation over time is to exploit microhabitats and climatic conditions. Tigers have been documented to cache prey in areas with increased brush and cover prey items in debris. Schaller [138] suggested that these tigers did this to lower the temperature experienced by a food item to reduce microbial activity. Many rodents dry grass and berries [145] and Red Squirrels hang mushrooms in trees [56]. This drying process is analogous to freeze-drying human food, which increases the length of time food can be stored [132, 137]. Cones, however, are susceptible to disintegration through drying which may explain why squirrels place cones in terrestrial middens, where moisture levels are higher than above the ground or snow [158].

Species that have developed behavioural strategies to mitigate the influence of exposure to the environment may be less susceptible to the effects of climate change. For example, dried food will likely be less influenced by freeze-thaw cycles, as damage due to the phase change of water will be reduced. However, it is important to note that examples of species exploiting the environment to enhance preservation are largely anecdotal and, therefore, require more rigorous study.

### Physiological adaptations

To our knowledge, no studies have explicitly investigated potential physiological adaptations of caching species to cope with microbial proliferation on cached food items but studies of scavengers could help to inform future research on this subject. Recently, Roggenbuck et al. [136] characterized a variety of adaptations in the digestive tracts of two New World vultures, *Coragyps aratus* and *Cathartes aura*. Both species were found to have low pH in their digestive systems that destroyed most bacterial species before they could reach the hindgut. Additionally, the intestinal microbiome of both species had a high prevalence of both Clostridia and Fusobacteria [136], which are commonly found on carrion. Their abundance in the hindgut likely benefits vultures by further breaking down carrion, allowing for the more

complete digestion of food [136]. Both Clostridia and Fusobacteria have been demonstrated to cause a variety of negative effects in both wildlife and humans [53, 61, 80]. Their presence in vulture intestinal tracts suggests that they tolerate bacterial toxins, a finding also documented in other scavenging birds [112]. It is possible that food-caching species also possess similar physiological adaptations to eliminate harmful microbes that colonize stored food.

Specialized gut microbiomes could also allow caching species to cope with microbial colonization of a cache or digest rotting food. These adaptations could be particularly important for species that cache perishable food items, which are more likely to be colonized by bacteria. Such adaptations could buffer the impact of increased degradation arising from climate change. Investigations of gut microbiomes have been undertaken for a diverse range of species, including amphibians, reptiles and mammals (e.g. [72, 85, 101]), including one caching species (Red Squirrel; [153]).

## Conclusions

We outline a novel approach to address how changes in the environment may influence food-caching species by synthesizing information from the fields of food science and plant germination ecology and then classifying the vulnerability of species based on caching behaviour. As caching species rely on stored food for survival during periods of limited food availability and, in some cases, for reproduction, factors that influence food quality could have major downstream effects on fitness and population dynamics.

Studies on both the Gray Jays [171] and Wolverines [6, 62] highlight how climate could be influencing population abundance but detailed demographic studies on caching species remain limited. It will also be important to consider what cached food is being used for during periods of low resource availability. For example, both Gray Jays and Wolverines use cached food not just for survival but also for reproduction [28, 154], meaning that multiple demographic vital rates may be linked to changes in cached food quality over time. Identifying the vital rates driving population dynamics will help to identify how the downstream effects of climate change on cached food quality may influence population growth rates.

In addition to demographic studies, understanding the influence of climate change on caching species will require experimental work on how specific environmental variables may influence cached food. Such studies could take place in the field (e.g. [139]) or in the laboratory by borrowing many of the approaches used in the field of food science (e.g. [16, 50, 117]). Ultimately, a combination of experimental and demographic studies will be the most rigorous approach for identifying specific

mechanisms by which climate change could influence this fascinating group of animals.

## Abbreviations

IPCC: Intergovernmental Panel on Climate Change

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## Authors' contributions

AOS, DS and DRN conceived of the review and contributed to drafting the manuscript. All authors read and approved the final manuscript.

## Competing interests

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## Ethics approval and consent to participate

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