The group-nesting and food-hoarding behaviour of the southern flying squirrel, *Glaucomys volans*

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Microsatellite DNA analysis and behavioural experiments on the food-hoarding strategy and mechanisms of cache retrieval were examined in the group-living, scatter-hoarding southern flying squirrel, *Glaucomys volans*. Analysis of 196 individuals from 86 natural nest groups showed that nestmates are typically adult and unrelated (mean ± SE of pairwise relatedness being 0.03 ± 0.05). This result largely precludes any cooperative food-hoarding strategy predicated upon inclusive fitness. The behavioural experiments showed that, under laboratory conditions, food-storing individuals are able to retrieve caches through spatial memory cues alone. Together, these results support a selfish hoarding strategy where nestmates hoard food independently, with a storer receiving a retrieval advantage on the basis of its spatial memory of cache sites. A preliminary conditional evolutionarily stable strategy model is outlined to explain the genetic and behavioural results within the natural history of this species.

Keywords: Coefficient of relatedness, food hoarding, group nesting, scatter caching, spatial memory.

Introduction

IN this paper, I examine the scatter-hoarding and group-nesting behaviour of the southern flying squirrel, *Glaucomys volans*, which is one of two species of flying squirrels in North America. It exhibits a southern and eastern continental distribution that largely overlaps with temperate, deciduous forests. *G. volans* is a well-studied species and much is known of its natural history and ecology[1,2]. Here I attempt to synthesize information regarding the relatedness of nestmates[3] and the proximate mechanisms of scatter cache retrieval[4,5] to explain the food-hoarding strategy of individuals within a nest group.

Natural history

The southern flying squirrel is a small (50–75 g), long-lived (~10 years) nocturnal mammal that nests in groups of 4–7 individuals (mean, range 2–25) during the winter months[1,2,6]. Group nesting in winter is known to provide important thermoregulatory benefits, where the daily energy budget may be reduced by as much as 30% relative to a solitary animal[7]. Its primary food resource is the hard mast of oak *Quercus* spp., hickory *Carya* spp. and beech *Fagus* spp. trees of eastern North America, Mexico and Central America[8,9]. Stomach content analyses document a reliance on hard mast as a primary food resource throughout the year including the winter months when the only source of hard mast is cached food items[10]. It is thought that *G. volans* survives winter, in part, by retrieving scatter caches stored during the previous fall. However, it must do so within the competitive social context of a nest group. Based on radio-telemetry, group members occupy large (~2 ha) home ranges that may overlap by 80%[11–13]. In addition, nestmates must also compete for food and scatter caches with conspecific and heterospecific granivores, including *Sciurus carolinensis, Tamias striatus, Peromyscus leucopus, P. maniculatus* and *Odocoileus virginiaus*[14]. Scatter-caching the ephemeral mast crop is believed to reduce the amount of food lost to most competitors[14,15]; however, its effect among nestmates is unknown.

Scatter-hoarding, group-living animals

Since Audubon and Bachman[16] it has been hypothesized that nest groups are comprised of relatives that practice a communal or cooperative hoarding strategy, where food caches are freely shared. However, the genetic relationships among nestmate squirrels and the proximate mechanisms of cache storage and retrieval have, up to now, been unknown. Field surveys have shown that nearly 90% of *G. volans* groups are comprised of adult individuals, with the remainder being family groups or solitary animals[2]. Furthermore, the temporal scale and longevity of nestmate associations is unknown and could range from long-term social groups to ephemeral aggregations.

These questions led me to investigate the scatter-hoarding and group-nesting behaviour of this unique species and to address the food hoarding strategy of individuals in a nest group. These seemingly disparate topics were first addressed by Andersson and Krebs[17] where they developed a theoretical framework for examining the evolu-

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tionary ecology of such species. They posited two possible evolutionarily stable strategies that mitigate costs of stolen caches in two distinct ways[17]. According to the first hypothesis, group members practice a cooperative hoarding strategy where costs of pilfering incurred by food-storing individuals are recouped through inclusive fitness gains among closely related group members. Conversely, in an independent hoarding strategy, costs are minimized through a storer's retrieval advantage, where food-storing individuals recover their caches more efficiently than a pilfering group member. Either scenario would satisfy the requirements of an ESS where scatter-hoarding nest groups could persist indefinitely. Without a commensurate benefit to food-storing individuals, cache-pilfering individuals would enjoy a fitness advantage due to their reduced foraging costs and drive the entire nest group to extinction. Under a cooperative, communal hoarding strategy, group members could freely pilfer or share caches. However, in an independent hoarding strategy, cache pilfering among nestmates should be minimized through cache storage and retrieval behaviours that provide a storer's retrieval advantage. The storer's retrieval advantage could be based on individuals storing and retrieving scatter caches within unique, defended microhabitats[18–20] or by spatial memory of cache locations[21–26]. I examined each hypothesis by determining the average pairwise relatedness of nestmates and the presence or otherwise of a storer's retrieval advantage.

Relatedness of nestmates

We had earlier collected 196 *G. volans* from 86 natural nest groups and determined their degree of relatedness[3] in order to examine the feasibility of a cooperative hoarding strategy among nestmate flying squirrels based on cache sharing and inclusive fitness gains. Individuals from the same nest group were compared in a microsatellite DNA analysis to determine the average pairwise coefficient of relatedness among group members[3]. This study was conducted during the breeding season and consequently some nest groups were comprised solely of lactating females and neonate young, while the majority consisted of adults in an even sex ratio[2]. I then determined the coefficient of relatedness within the putative family groups for comparison with the adult nest groups. In addition, I used a discriminant function analysis, based on body mass, to independently identify the adult and family nest groups. This analysis resulted in a weight-based age rule where animals less than 25 g were classified as nestlings, animals greater than 55 g as adults and the remainder as subadults[3]. The results showed a low degree of relatedness among adult nestmates (mean ± SE of $r = 0.03 \pm 0.05$) and a high degree of relatedness within the putative family groups ($r = 0.50 \pm 0.08$, Figure 1). Adult nest groups formed the vast majority of naturally occurring nest groups and these results thus largely precluded any cooperative food-hoarding strategy among *G. volans* nestmates that is predicated on inclusive fitness gains. Consequently, I examined the independent-hoarding strategy and the predicted storer's retrieval advantage.

Mechanisms of cache retrieval

Food-storing individuals could possess a cache retrieval advantage provided for by a range of behavioural mechanisms. For example, the defence of unique microhabitats for cache storage and retrieval has been shown in unrelated flocks of willow tits, *Parus montanus*[18,20] and crested tits, *P. cristatus*[19]. Conversely, other granivores have been shown to retrieve caches via private retrieval mechanisms, such as spatial memory, that are available only to the cache-making individual[21–29]. I examined the presence of a storer's advantage and the mechanisms of cache retrieval in *G. volans* by recording the behaviour of animals in an outdoor enclosure that were marked with passive integrated transponders[4]. This study showed that nestmate squirrels do not store and retrieve caches from unique, defended areas and that cache pilfering is minimized among nestmates in support of the independent-hoarding strategy. In addition, I conducted a series of laboratory behavioural experiments to identify the mechanisms of cache retrieval[5]. In the laboratory, I could eliminate all other confounding retrieval mechanisms such as random searching and olfaction- or area-directed searching in order to examine the use of spatial memory cues. Through the use of odourless caches, I was able to show that food-storing individuals from two distinct populations could retrieve their caches through spatial memory alone and

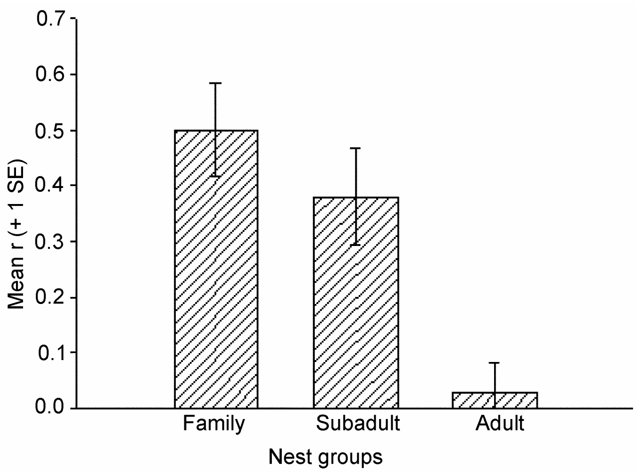

Figure 1. Coefficient of relatedness (mean ± SE) within nest groups. The sample sizes include 14 individuals in four family nest groups of lactating females and neonates, 15 individuals in four subadult nest groups comprising a majority of subadult individuals and 45 individuals in 11 adult nest groups comprising a majority of adult individuals. Originally published in Winterrowd *et al*.[3].

that this tactic was more effective than pilfering (Figure 2)[5]. In the initial baseline experiment, all retrieval cues were eliminated and hungry animals searched for randomly placed caches. These conditions mimicked natural conditions where an animal is forced to pilfer a nestmate's caches. Less than 30% of the caches present were recovered in spite of the animal's high search effort.

In a subsequent experiment, I addressed cache retrieval via spatial memory. Individuals first stored nuts within the sand-filled arena during an overnight, 12-h session. These cache locations were mapped and recorded, and each was paired with a second, experimenter-placed cache in a random location 10 cm from the 'squirrel's' cache. Recovery of both cache types was recorded following a 12-h overnight retrieval session where all retrieval cues, except for spatial memory, were eliminated. In two replicate populations, animals retrieved more of their 'own' caches than the randomly placed caches. The random and squirrel's caches were present in equal numbers and did not differ in any way except whether a squirrel or the experimenter had determined their locations. The results support the presence of a storer's retrieval advantage based on spatial memory and are consistent with an independent-hoarding strategy among *G. volans* nestmates. However, in a separate experiment with odoriferous caches, pilfering was a highly effective means of cache recovery. I thus found that animals use different retrieval mechanisms under different simulated conditions and that

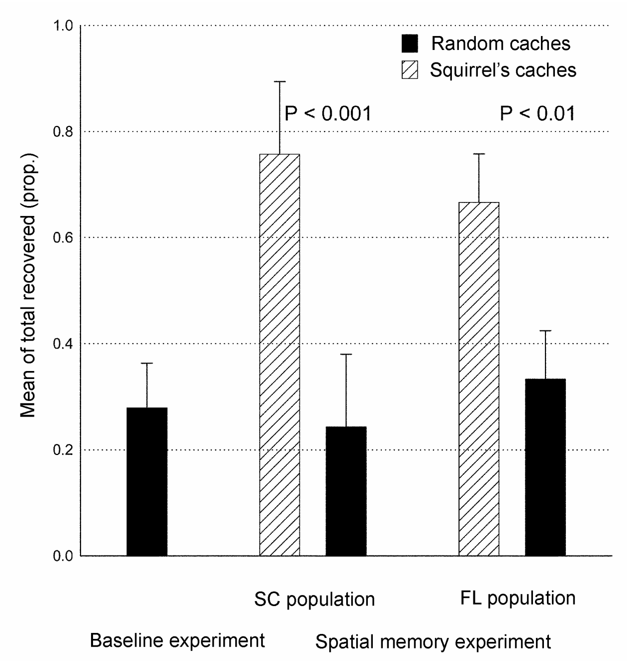

Figure 2. Average proportion of randomly buried caches recovered by *Glaucomys volans* individuals of two populations in 12-h periods. The spatial memory results indicate the proportion of caches recovered from randomly determined locations versus locations determined by food-storing individuals. The null expectation was 0.5 for each cache type. Originally published in Winterrowd and Weigl[5].

the presence of the storer's advantage was equivocal. My initial result was obtained under controlled laboratory conditions and its ecological validity is unclear. It is well known that most granivorous mammals have an acute olfactory sense and it is unlikely that cached items are odourless under natural conditions. In an attempt to solve this dilemma, I have developed a preliminary evolutionarily stable strategy (ESS) model to explain the observed range of caching behaviour and its correspondence to variable environmental conditions.

A conditional ESS model

In addition to the behavioural and genetic results, there is good theoretical support for an independent- or selfish-hoarding strategy in *G. volans*. Various species of granivorous animals use a range of sensory modalities and search mechanisms during cache retrieval[15,23,29] and mammals, in general, can detect buried food items over some distance[30,31]. Furthermore the diverse range of species that make up the guild of granivorous animals in a region shows that food items are stored and retrieved within a competitive intra- and inter-specific environment. Based on sciurid and mammalian natural history and my experimental results, game theory possibly provides an explanation of the myriad interactions among competing granivores for stored food items.

My model is a logical extension of Anderson and Kreb's[17] original model and is based on an assumption of group members being unrelated to one another. Furthermore, it is a conditional, rather than fixed, ESS model, given that the same individuals may retrieve their own or pilfer another animal's caches[4,5]. Thus, *G. volans* individuals possess a flexible capacity to retrieve caches via two distinct tactics, which requires a conditional ESS, where the two tactics result in unequal, long-term fitness payoffs[32]. Animals storing and retrieving their own caches are using the primary tactic that confers the higher long-term fitness, yet all individuals should also practice the secondary tactic of opportunistic pilfering (Figure 3). Individuals should devote a greater proportion of foraging time to retrieving caches via the primary tactic and a smaller proportion of time to opportunistic pilfering, depending on current environmental conditions such as cache density, substrate moisture, temperature and the risk of predation, all of which affect the costs of cache retrieval. The storer's retrieval advantage should cause the primary tactic to be more effective than the secondary tactic under the predominant natural conditions of high search costs. Animals may practice both tactics interchangeably depending on current conditions; however, the primary tactic should result in greater long-term fitness.

Overall, the results of my research show that food-storing individuals can retrieve their caches more effectively than can a randomly searching, pilfering nestmate and that a storer's retrieval advantage may be provided for by spatial memory. The storer's retrieval advantage is the basis of a primary food-hoarding tactic that should convey a long-term fitness advantage to storing individuals relative to a cheating, pilfering nestmate. In the wild, this fitness advantage is likely to be conferred by reduced search time during cache retrieval and consequent reduced exposure to nocturnal predators (e.g. owls *Strigidae* spp. and *Tytonidae* spp.) and cold temperatures (ranging to –20°C). The primary tactic should be practised under cold, dry winter conditions when the rapid retrieval of cached food is most critical and could mean the difference between an animal's survival and death. However, while animals are foraging or retrieving caches, they should also take advantage of any opportunistically encountered food caches. Cache pilfering would be most effective under ephemeral environmental conditions; for example, immediately following a rainstorm, when the olfactory cues of caches would be strongest[23] or during early autumn when the mast crop is most abundant and cache density is greatest.

In the literature, there are several experimental studies that support my conditional ESS model. For example, in a study of *Sciurus vulgaris* in an urban park population, scatter-caching behaviour was observed to occur in an environment with a high density each of artificial food, conspecifics and cached food items, and an absence of natural predators[33]. These factors clearly contributed to an environment with very low search costs and the absence of a storer's retrieval advantage. This result led to the conclusion that European red squirrels do not need to recover their own caches and can survive instead by pilfering from those of their conspecifics. Under these conditions, the pilferage rate was so high that there was virtually no chance of an animal retrieving its own caches. This and other similar studies in semi-natural contexts have established the occurrence of scatter-caching behaviour without a storer's retrieval advantages; however, this may be largely artefactual due to the park-like conditions in these habitats, where the costs of pilfering caches were unnaturally low.

In addition, a series of studies by Vander Wall and his colleagues have shown that the hoarding behaviour of many granivorous rodents may also be consistent with such a conditional ESS model. They have shown that some species may retrieve caches via spatial memory under the typically dry conditions of their western North American study site but they may also retrieve caches via olfaction or random searching during ephemeral, mesic conditions[23,28,29]. I would argue that some species, such as *T. amoenus*, might practice the primary retrieval tactic under the typically dry conditions, where the odour cues of buried caches are greatly reduced, but also opportunistically pilfer caches immediately after a rainstorm. The impressive body of work conducted by Vander Wall and his group could be, in part, thus interpreted according to a conditional ESS. They have, however, proposed their own alternative explanation based on the evolutionary mechanism of reciprocal altruism[34]. Regardless of the differences among the proposed models, these should be able to explain the range of behaviours observed in food-hoarding animals, including rampant pilfering under certain conditions, to the use of complex cognitive abilities such as spatial memory among others.

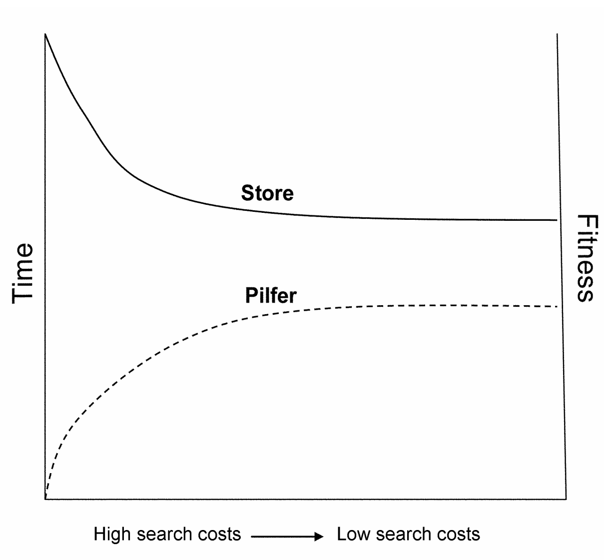

Figure 3. A preliminary conditional ESS model of two cache retrieval tactics: a primary tactic where animals store and retrieve their own food and a secondary tactic of opportunistic pilfering, depending on search costs. The proportion of time an individual devotes to each tactic and the long-term fitness payoffs are plotted on the *Y*-axes.

Conclusion

In conclusion, this work highlights some of the specific results of my research and how they may apply to the food-hoarding strategy of the southern flying squirrel. The proposed conditional ESS model summarizes how these results may also apply more generally to other group-living, scatter-hoarding species. More studies on insect, avian and mammalian food-hoarding systems and their associated plant communities are necessary in both temperate and tropical regions of the world to enable us to fully understand this important area of evolutionary biology. I hope that this work has highlighted some of the important questions regarding the foraging ecology of sciurids and how this may affect their social behaviour. Lastly, I hope that a greater understanding of the complex evolutionary processes unique to wilderness environments can lead to a greater appreciation and preservation of sciurids and forest ecosystems worldwide.

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