Acorns were good until tannins were found: factors affecting seed-selection in the hazel dormouse (Muscardinus avellanarius)

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Abstract

Seed selection by forest rodents is based on several factors such as seed palatability, manipulation time and caloric content. The final result of this decision-making process has critical consequences on seed predation and dispersal, and thus on tree demography.

Previous studies on seed selection have mainly focused on non-hibernating terrestrial rodents. Arboreal rodents may be less adapted to cope with seed defences, usually being more frugivorous. Furthermore, hibernating species need to accumulate fat reserves in autumn, which is when acorns are available and may be the only available resource. We selected the hazel dormouse (*Muscardinus avellanarius*, an arboreal hibernating rodent) as model species for our study and focused on three seeds which are an important constituent of the hazel dormouse diet and which are characterized by different defensive strategies.

We here report the results of a series of experiments targeted towards understanding the effects of manipulation time, energy intake and tannin content on seed selection by the hazel dormouse and the effects of such selection on individuals' body condition. Each of these factors was treated separately through a series of coupled food trials. Our results showed a clear order of consumption with first choice biased towards seeds with lower tannin content (*Q. pubescens* vs *Q. cerris*) and/or more caloric seeds (*C. avellana* vs *Q. pubescens*) despite the higher degree of mechanical protection of the former. Seeds with high levels of tannins led to weight decrease, despite the large amounts of seed mass ingested by dormice. Our results suggest that seed selection by the hazel dormouse is targeted towards maximising fat storage, which is pursued despite the cost of higher manipulation time.

Keywords: diet; food choice, Gliridae; *Quercus*; rodents; cafeteria experiments.
**Introduction**

Tree seeds (e.g. acorns, seeds of oaks of the *Quercus* genus) are a fundamental resource for wildlife, especially for forest-dwelling rodents. Rodents have crucial effects on tree demography by contributing to seed predation and dispersal (Hulme, 1998; Velho et al., 2012). Trees need to balance the benefits of dispersal (Steele et al., 2011) with the negative effects of seed loss due to predation (Steele et al., 2005; Zong et al., 2010). As a consequence, many tree species evolved defence mechanisms in order to manipulate rodents’ behaviour and minimize seed predation. Typical seed anti-predatory adaptations consist in harder or thicker pericarps (Zhang and Zhang, 2008), which prolong manipulation time (Jacobs, 1992), and large seed dimensions, which can discourage a rodent to transport the seed (Muñoz and Bonal, 2008). Both these characteristics decrease predation risk by increasing energetic costs for predators. Chemical secondary compounds too can make seeds less palatable, poisonous or at least poorly digestible (Chung-Maccoubrey et al., 1997; Rubino et al., 2012; Shimada and Saitoh, 2003), thus contributing to discourage predation. Acorns in particular are known to have high levels of tannins (Shimada, 2001), a group of polyphenolic molecules which reduce nutrient absorption (Shimada et al., 2006).

Previous studies focused on the interactions between rodents and tree seeds have mainly focused on terrestrial or semi-terrestrial (Buesching et al., 2008) rodents (e.g. *Apodemus* and *Mus* spp.) whose diet is based on acorns over extended periods and have thus developed several strategies to cope with high levels of tannins (Molinari et al., 2006; Shimada, 2006; Takahashi and Shimada, 2008; Xiao et al., 2008). Little has been done on arboreal rodents (but see Rubino et al., 2012 and Smallwood and Peters, 1986). Arboreal rodents are more capable than terrestrial rodents of exploiting the above-ground availability of fruit (which decays quickly on ground); however, they may still have to rely on acorns for extended
periods (Juškaitis, 2008; Moller, 1983). Furthermore, no previous study has focused on hibernating rodents, i.e. species that need to accumulate fat reserves in autumn, which is when acorns are abundant and may be the only available resource. Arboreal hibernating seed consumers are able to consume acorns before they are available to terrestrial species, and may significantly increase their seed consumption before hibernation; therefore they may influence the interactions between trees and seed predators at the community level (Muñoz et al., 2009; Sunyer et al., 2013).

For this study we conducted a series of experiments targeted towards understanding factors influencing seed predation by the hazel dormouse (Muscardinus avellanarius, an arboreal hibernating rodent) and the effects of seed selection on individuals’ body condition. We focused on three seed defensive elements, which we expected to affect foraging decisions by the hazel dormice: thickness of pericarp (influencing manipulation time), nutritional composition (directly influencing energy intake) and chemical defences (i.e. tannin content, influencing palatability, digestibility and thus indirectly affecting final energy intake). For this purpose we selected three seeds characterised by contrasting degrees of these defensive characteristics. Specifically we designed our experiments to ask the following research questions:

1) **What is the effect of seed mechanical defence on seed manipulation time?** Answering this question would allow us to quantify the actual time required by hazel dormice to access the resource. We expected manipulation time to be significantly higher for seeds with thicker pericarps. Time spent handling a seed is a relevant trait in the decision-making process by rodents (Wang et al., 2013), thus a quantitative assessment of manipulation time of different seeds is a basic pre-requisite for understanding the process of seed predation.

2) **Which species (and consequently which seed traits) are preferred by hazel dormice for
foraging? The ability of rodents to select seeds of different species, e.g. according to their nutritional or chemical content before consuming them is a fundamental factor affecting the rodent-trees interactions (Rosalino et al., 2013). Seed traits such as tannin concentration or pericarp thickness are known to alter seed selection by rodents (Wang et al., 2013; Xiao et al., 2008). As seed biochemical and mechanical defences are subject to a trade-off (Chen et al., 2012), seed predators can specialize to overtake one kind of protection or the other. We thus expected dormice to act a selection towards seeds that maximize energy intake, i.e. seeds with low tannin content, short manipulation time and high caloric content.

3) What is the effect of seed selection on the body condition of hazel dormice? Different diets can lead to variation in body conditions in rodents (Shimada and Saitoh, 2003). Seeds with different traits can be unevenly available in woodlands, according to tree species composition, relative abundances and masting events (Focardi et al., 2000; Pons and Pausas, 2007). Assessing how diets based on different seeds affect body condition in rodents, particularly in hibernating species, is an important aspect in understanding the relationships between trees and seed consumers. We expected that seeds selected by dormice would lead to a more efficient fat storage and that a tannin-rich diet lead to a weight decrease.

Answering to the three questions listed above will allow us to understand factors affecting foraging decisions by the hazel dormice and contribute to untangling the complex decision-making processes involved in seed predation. Such results may help in providing cues on how to interpret habitat choice, e.g. the different demographic performance of dormice populations in habitat types characterised by different acorn availability (Capizzi et al., 2002; Juškaitis, 2008; Mortelliti et al., 2010; Williams et al., 2013) and thus to improve the accurate parameterisation of distribution modelling (Greaves et al., 2006).
**Materials and methods**

**Choice of the target species**

We chose the hazel dormouse (*Muscardinus avellanarius*, a strictly arboreal and hibernating rodent) as target species for our study for three reasons: 1) it is a species of conservation concern which is declining in parts of its range due to habitat loss and degradation, thus a deeper understanding of its foraging ecology will help guiding conservation actions such as habitat management and reintroduction programs (Bright and Morris, 1996; Mortelliti et al., 2011); 2) the quality of habitat (quality and availability of resources) is a key determinant of its survival and distribution (Mortelliti, 2013). The presence of oaks in fact seems an important factor in determining dormouse presence, at least in the UK, as highlighted by Williams et al. (2013). 3) It has been used as model species for other forest dependent vertebrates due to its life-history and ecological traits (Amici and Battisti, 2009; Bright and Morris, 1996; Greaves et al., 2006; Watts et al., 2010).

**Dormouse housing**

For the duration of the experiments (6 months) naive captive bred dormice (n=7) were housed singly in 45x40x45(h) cm glass tanks with wire-mesh windows for aeration, and each provided with hay bedding, branches and a wooden nest-box. Water was always available. Tanks were housed in a non-heated room and a large window provided a natural day-night cycle. All dormice had no experience with the target species of acorns or nuts at the start of the experiments, being previously fed with commercial rodent seed-mix and fresh fruit.

Due to the conservation status of this species (listed in Annex IV of the Habitat Directive) it was mandatory to keep the number of sampled individuals relatively small, but still comparable to other cafeteria experiments on rodents (Ben-Moshe et al., 2001; Shimada, 2001). Required permits for carrying out this research were obtained: permit number 011289.
Seed composition and chemical properties

We used hazel nuts (seeds of Corylus avellana), acorns of the downy oak (Quercus pubescens) and Turkish oak (Quercus cerris) as target species for our study. Nutritional characteristics (lipid, protein, carbohydrates and fiber content), total energy intake and secondary compounds (tannins) of the target seed species are shown in Table 1. Acorns used for chemical analyses were harvested in the same woodlands of those used in the behavioural experiments (see further); hazel nuts used for the experiments were of the same cultivar analysed by Xu and Hanna (2011), from which nutritional data were extracted. All seeds were stored in cloth bags in refrigerated room at 8-10°C until they were used for experiments.

We selected these two oak species for three reasons: a) they are among the most abundant trees in mixed-deciduous woodlands of Mediterranean Italy (Lookingbill and Zavala, 2000; Pons and Pausas, 2007); b) although can occur syntopically, they are the dominant species of different habitat types (Q. pubescens forests are typical of more coastal and drier habitats whereas Q. cerris forests occur more inland (Mohler, 1990), c) they are the most important contributors to the seed bank biomass in such habitats (Focardi et al., 2000). Differences in the biochemical composition of the acorns of these two species are only evident for the tannin content, which is much higher in Q. cerris acorns (almost double compared to Q. pubescens, Table 1). Hazel nuts (Corylus avellana) are considered as a fundamental resource for dormice (Bright and Morris, 1996; Juškaitis and Baltrūnaitė, 2013). Compared to oak acorns, hazel nuts show much higher calorific content mostly due to higher lipid and protein contents (see Table 1) but are also characterised by tannin content comparable to that of Quercus pubescens.

The three target species thus differ in their seed traits (Table 1) such as chemical defences and
pericarp thickness, and thus represent a good combination of traits for evaluating the seed selection decision-making by the hazel dormice.

EXPERIMENT 1: Manipulation time

Ten seeds of *Q. cerris*, *Q. pubescens* and *C. avellana* were offered to dormice, each species separately during different nights, and their nocturnal activity was filmed with a Sony camcorder SR501 with night-shot function (two examples of videos are provided as Supplementary Material).

Foraging activity was later analysed by observing the video-recordings adopting “focal subject sampling” (Altmann, 1974) for recording time spent in the different behaviours, distinguishing between 1) seed manipulation, e.g. holding, rotating and chewing the seed shell, and 2) seed consumption, i.e. fragmenting and ingesting the kernel.

For each video session, we recorded individual dormouse identity and acorn initial weight. We did not include in the analyses the time during which the dormouse was recorded in non-foraging activities such as moving, grooming, alert and vocalising (Ancillotto et al., 2014).

Each individual dormouse was tested for 2-4 nights for each seed species. Seed mass and calories ingested (i.e. energy intake) by dormice per time-unit during each test were calculated as grams or calories / total manipulation time. Only video-recordings during which the focal dormouse completely consumed the acorn were used in the analyses.

EXPERIMENT 2: Cafeteria tests

The seeds of the three species were offered to captive dormice in a series of cafeteria choice tests (Krebs, 1999); during each test, an equal number of acorns of two species was offered in different petri dishes (5 seeds in each dish) positioned inside dormice's cages at around 8 pm. We tested pairs of species as follows: *Q. cerris* vs *Q. pubescens*, *Q. pubescens* vs *C. avellana*. 
Acorns of both species in each test were selected in order to have approximately the same dimensions and weight (5.2±0.2 gr for *Q. cerris* vs *Q. pubescens* tests, 5.8±0.2 gr for *Q. pubescens* vs *C. avellana* tests). After the start of the test, we checked the acorns twice, at 11 pm and 8 am respectively, recording the number of acorns of each species that were totally or partially (¼, ½ or ¾) consumed. Assignment of acorn species to dishes was randomized at each check interval to avoid dormice selecting dish position instead of seed species. We stress that this experiment was the first to be conducted, so that food choices reflect true preferences, not being influenced by habituation of experimental individuals to a type of seed (Experiment 1).

**EXPERIMENT 3: Monospecific diet effects**

Acorns of the same species were available ad libitum to each dormouse and were replaced with new ones once every four days for the entire duration of the experiment (24 days for each treatment); total seed weight was recorded before and after each check in order to quantify the effective mass consumed by dormice. Weight and conditions of each dormouse were recorded once every 4 days. Each dormouse was tested consecutively with three different treatments (*C. avellana*, *Q. cerris* and *Q. pubescens*) and the order of treatment administration to each individual was randomized.

**Data analysis**

For experiments 1 and 3 we adopted repeated-measures ANOVAs testing the effects of seed species on manipulation times, mass and calories ingested in the time-unit (grams/min; Kcal/min) during each test (experiment 1) as well as on individual weight variation, mass of seed consumed and ingested calories (experiment 3). Data were tested for normality with Shapiro-Wilk tests. We used Holm's post-hoc tests to assess significant differences among
treatments. For experiment 2 we adopted exact binomial tests on choice data upon first species tasted and seed species most consumed. Results were considered significant when $p < 0.05$; all tests were run in R 2.13.2 (R Core Team, 2005).

**Results**

**EXPERIMENT 1: Manipulation time**

We obtained 45 complete video-recordings of dormice consuming seeds (*C. avellana* n = 15, *Q. pubescens* n = 15, *Q. cerris* n = 15; see video S1 and S2 in Supplementary Material). The following results are reported as mean ± standard deviation (see also detailed dataset in Table S1 in Supplementary material). We found no significant difference in the consumption times (i.e. fragmenting and ingesting the kernel) of the kernels of the three species examined (Figure 1a). Dormice spent significantly different times in manipulating seeds of different trees ($F_{2,43} = 118.51$, $p<0.001$), with longer times for *C. avellana* (76.0 ± 16.4 min) than acorns (*Q. pubescens*: 14.5 ± 2.6 min, *Q. cerris*: 16.5 ± 4.0 min); no significant difference was detected between *Quercus* species (Holm's test $p>0.05$; Figure 1b).

Dormice ingested significantly different seed mass per time-unit ($F_{2,43} = 57.65$, $p<0.001$) between hazelnut (0.034 ± 0.04 grams/min) and acorns (*Q. pubescens*: 0.133 ± 0.04 grams/min; *Q. cerris*: 0.117 ± 0.06). Differences were only significant between hazel nuts and the two oaks (Holm’s test $p<0.01$) but not between oak species (Holm’s test $p>0.05$). However, the amount of ingested calories per time unit (*Q. pubescens*: 0.22 ± 0.06; *Q. cerris*: 0.23 ± 0.04; *C. avellana*: 0.22 ± 0.03) was not significantly different between different treatments ($F_{2,43} = 0.36$, $p=0.70$).

**EXPERIMENT 2: Cafeteria tests**
We recorded a total of 42 trials (21 *Q. cerris* vs *Q. pubescens*; 21 *Q. pubescens* vs *C. avellana*). Acorns of *Q. pubescens* were preferred by dormice when compared to *Q. cerris* ones, with most individuals selecting the former as first choice (Binomial $z=40.29$, $p<0.01$) and consuming more overall quantity (Binomial $z=40.48$, $p<0.01$). Dormice selected hazelnuts during *Q. pubescens* vs *C. avellana* tests for the first choice (Binomial $z=23.81$, $p<0.01$) but not for the total quantity consumed (Binomial $z=7.14$, $p>0.05$). We infer an order of selection for the three species as follows: *C. avellana* > *Q. pubescens* > *Q. cerris*, with hazelnuts and downy oak acorns being equally selected when considering the total amount of seed consumed.

**EXPERIMENT 3: Monospecific diet effects**

Dormice treated with diets of different seed species showed different weight responses ($F_{2,10} = 5.264$, $P<0.05$), with significant differences between *C. avellana* and *Q. cerris* (Holm's test $p<0.01$) and between *Q. pubescens* and *Q. cerris* (Holm's test $p<0.05$) but not between hazelnut and downy oak (Holm's test $p>0.05$). Dormice eating only *Q. cerris* acorns faced a weight decrease whereas *C. avellana* seeds lead to an increase in weight (Figure 2a). A monospecific diet of *Q. pubescens* acorns determined no weight fluctuations. The amount of ingested seed mass (Figure 2b) also differed among treatments ($F_{2,10} = 192.08$, $p<0.001$), with lower values for *C. avellana* compared to acorns of *Q. pubescens* (Holm's test $p<0.001$) and *Q. cerris* (Holm's test $p<0.001$) oaks. Energy ingestion (Figure 2c) differed among treatments ($F_{2,10} = 32.350$, $p<0.001$) with significant higher values for oaks (Holm's test $p<0.001$ for both species).

**Discussion**

The hazel dormouse clearly acts a selection when different seeds are available. Acorn
selection is made by this rodent upon specific seed characteristics, balancing the effects of chemical compounds (e.g. tannins) and seed mechanical defence (i.e. pericarp hardness) on the final energy intake. The use of naïve captive individuals suggests that the ability to evaluate such seed characteristics is innate in this species (but see Muñoz and Bonal, 2008), and is presumably mediated by the use of sensorial cues such as odour and taste. Hazel dormice show a clear order of consumption when seeds with different characteristics are offered. First choice is biased towards seeds with lower tannin content (\textit{Q. pubescens} vs \textit{Q. cerris}) and/or more caloric seeds (\textit{C. avellana} vs \textit{Q. pubescens}) despite the higher degree of mechanical protection of the former. Once found and opened, a more caloric seed like the hazel nut ensures a high intake, minimizing costs of seed “search” and thus exposing the rodent to lower predation risk. This is also confirmed by the smaller amounts of hazel nuts ingested by dormice during monospecific diet experiments. Dormice selectively chose hazel nuts as first choice, but subsequently consumed similar amounts of low-tannin acorns. This non-significant difference between consumed mass of \textit{Q. pubescens} and \textit{C. avellana} may be due to the low predation risk perceived in captivity, thus allowing dormice to relax food selection and consume both species indifferently. \textit{M. avellanarius} need significant more time to open hazel nuts than acorns (more than one hour for hazel nuts compared to about 15 minutes for acorns), thus confirming the predicted effectiveness of mechanical defences by \textit{C. avellana}, at least against small seed predators like the hazel dormouse. Prolonged manipulation of hazel nuts leads to a lower mass ingestion per time/unit by the dormouse, but the higher nutritional values of such highly defended seed compensate this. Increased manipulation times due to harder and thicker pericarps constitute a complementary defensive strategy that makes seeds less attractive to predators (Yang et al., 2012; Zhang and Zhang, 2008). Moreover, a rodent is, presumably, visually and acoustically more evident to potential predators when engaged in opening a seed. In addition, seed
defences are subject to a trade-off between biochemical and mechanical mechanisms (Chen et al., 2012) so that seed predators may specialize to overcome one mechanism or the other. Monospecific diet experiments indicate that dormice eating seeds of different tree species do show differences in their capability of gaining weight, with preferred species allowing an actual benefit in terms of fat storage. Seeds with high levels of tannins led to weight decrease, despite the large amounts of seed mass ingested by dormice, comparable to the tannin-free *Quercus* acorns. This result is in line with Shimada and Saitoh (2003), who found that Japanese wood mice (*A. speciosus*) showed a marked decrease in their body weight when subjected to monospecific diets of the high tannin-content acorns of *Q. mongolica*. Even species in the same genus may show different degrees of tolerance to tannins (e.g. *Sciurus* spp.: Kenward and Holm, 1993), a trait potentially affecting interspecific competitive dynamics.

Tannins are known to alter palatability (Spalinger et al., 2010) and digestibility (Hagerman et al., 1992) of seeds and other plant parts, and thus can influence food choice of herbivore/granivore animals like rodents (Wang et al., 2013; Xiao et al., 2008). However, many herbivore mammals evolved a class of tannin-binding proteins, that is a family of proteins which reduces the detrimental effects of tannins on digestion (Hagerman and Robbins, 1993; Shimada, 2006). Acclimation, i.e. an increase in the production of tannin-binding proteins, by means of gradual exposition to tannins is known to occur in some acorn-eating rodents (Shimada et al., 2004; Takahashi and Shimada, 2008), but no study reports such proteins for glirids (Shimada, 2006). The higher values of seed mass consumed by dormice when eating acorns compared to hazel nuts may also be another response to the impoverished nutrient acquisition due to tannins. Rodent species which lack tannin-binding proteins may compensate the diminished energy intake by increasing the amount of seed mass ingested, albeit being potentially exposed to the detrimental effects of high tannin
intake. This strategy though does not seem to efficiently compensate the effects of tannins, as dormice eating only acorns of the highly tannin-content *Q. cerris*, generally decreased in weight.

Both acorns and hazel nuts play a consistent role in the diet of the hazel dormouse in its whole range (Bright and Morris, 1996; Juškaitis and Baltrūnaitė, 2013) as well as of other forest-dwelling rodents (Kollmann and Schill, 1996); tree species composition of woods along the hazel dormouse distribution may thus result in different levels of suitability, e.g. woods dominated by tannin-rich acorns could be less suitable, because of a lower weight gain efficiency during the critical time before hibernation.

Our study indicates that *M. avellanarius* forages selecting seeds by balancing net energy intake with seed manipulation times, suggesting that dormouse is a seed predator specialized on seeds with thick and/or hard pericarps. We acknowledge that further studies, both in captivity and in nature, with larger sample size and dealing with a larger number of tree species are needed to generalize our findings on hazel dormouse foraging ecology. In addition, we also acknowledge that we conducted our experiments with cultivated hazel nuts, which may slightly differ from seeds of wild *C. avellana* in their biochemical composition.

Studies on other species in the wild also report strong selection by seed predators, with seeds characterized by low net energy intake (due to low caloric content, large dimensions and/or high chemical defence) being generally avoided by seed-caching rodents (Molinari et al., 2006; Yang et al., 2012). Furthermore we stress that seed choice in natural habitats is highly affected by extrinsic factors such as the presence of conspecifics and predators (Sunyer et al., 2013), competitor species (Kenward and Holm, 1993; Muñoz et al., 2009; Wauters et al., 2001) and even seed parasites (Muñoz and Bonal, 2008; Perea et al., 2012).

Forest-dwelling rodents have a relevant effect on dispersal and survival of tree species (Hulme, 1998; Vander Wall, 2010; Velho et al., 2012; Yang and Yi, 2012), so that
understanding the mechanisms underlying seed selection by seed predators at a fine scale (Wang et al., 2013) is fundamental. The study of the interactions between plants and rodents in forests may also lead to guidelines for the conservation and management of both forests and forest-dwelling rodents.

Acknowledgements

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**References**


**Figure legends**

**Figure 1.** Seed consumption. Seed consumption (a) and seed manipulation (b) times (Mean ±SD, in minutes) for single seeds of three different tree species by captive hazel dormice *Muscipinus avellanarius*. CA = Hazel - Corylus avellana; QP = Downy oak - Quercus pubescens; QC = Turkish oak - Quercus cerris. Significant differences among species are indicated on bars: * = p<0.01; n.s. = p>0.05.

**Figure 2.** Effects of seeds on body condition. Weight gain/loss (g) (A), ingested mass of acorn (g) (B) and ingested energy intake (Kcal) (C) by captive dormice after each monospecific diet. CA = hazel - Corylus avellana; QP = downy oak - Quercus pubescens; QC = Turkish oak - Quercus cerris.
Tables

Table 1. Biochemical composition of seeds from three different tree species. Data on acorns was kindly provided by the Ethoikos foundation (Fondazione Ethoikos, Gasperini et al. in prep).

<table>
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<th>Species</th>
<th>Kcal / 100 g</th>
<th>Tannins mg / Kg</th>
<th>Lipids %</th>
<th>Carbohydrates %</th>
<th>Proteins %</th>
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<tr>
<td>Quercus cerris</td>
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<td>13200±</td>
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<td>21.50</td>
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<tr>
<td>Corylus avellana *</td>
<td>437</td>
<td>7500±</td>
<td>3.50</td>
<td>40.40</td>
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*data from Xu and Hanna, 2011.