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# Partial Consumption of Acorns by Some Rodents Leads Their Relationship with Oaks Species Towards Mutualism

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**Abstract:** Numerous interactions between plants and animals vary in their outcome between predation and mutualism. Depending on the costs and benefits, the relationship is placed at one end of the scale or the other. A thin line separates both interactions. Acorn consumption by rodent species has been considered a predation relationship. Rodents consume acorns, which is a cost to oaks species as they are prevented from colonizing new places. The aim of this study is to show that part of the costs allocated to depredation due to loss of acorns cannot be allocated to costs. Some attacked acorns are partially consumed, but preserve their embryo and are not lost as they can germinate. This behavior, preserving the embryo, is observed in certain species. We will attempt to verify whether the behavior of conserving the embryo shown by some rodent species during partial consumption of acorns is intended to bring their relationship with oaks species closer to mutualism. To do this, we studied and compared the behavior of two acorns-consuming rodent species (*Apodemus sylvaticus* and *Mus spretus*) with another species that has never used this type of resources (*Microtus arvalis*), during acorns consumption. The results show that only two acorn-consuming species preserved the embryo, and not by species that are incorporating acorns into their diet. Species that have consumed acorns since ancient times show embryo-acorns preserving behavior. These species (*Apodemus sylvaticus* and *Mus spretus*) start consuming the acorns at the basal part, away from the embryo, at a higher energy expense, but they assume it because the mutualistic relationship they seek provides them with food guarantees in the future. This behavior is the contribution made by mutualistic rodents to maintain their relationship with oaks plants within the term of mutualism. Both species benefit from the relationship. Plants seeds are successfully transported to and germinated in suitable places and rodents obtain nutrients and the possibility of providing their offspring with future resources. The species not using acorns as food (*Microtus arvalis*) behaves as a predatory. The most convenient way for it to open the acorn is to devour the embryo, thus posing a threat to oak species.

**Keywords:** Rodents, Oaks, Acorns, Mutualism, Behavior, Partial Consumption, Preserve Embryo

## 1. Introduction

Interaction between rodents and oaks species varies in its outcome [41, 20, 20, 11, 15, 4, 17]. It was first included within an antagonism relationship (predation) [23, 24, 8]. Rodents eat seeds and destroy them by eliminating their ability to germinate and disperse. It was later found that rodents hoard acorns as a reserve for adverse periods and some of them could be forgotten and germinate in caches. The relationship then began to be interpreted as one of collaboration (Mutualism) [42, 43, 18].

Zwolak, Crone and Bogdziewicz proposed a mathematical model to evaluate whether the outcome of this interaction is predation or mutualism [44, 4]. There is a narrow line separating both types of interactions [6, 9]. When the benefits of seed burial and transport exceeds the costs of predation in this scatter-hoarding process, the relationship is considered to be mutualist. Moore and Dittel proposed changes to include variables such as intra-specific competition and feedback between seed production (masting) and seed caching animal populations [18]. Zwolak, Bogdziewicz and Crone argue that

dispersal effects need to be tested for every particular species pair [45].

Subsequently, it was observed that due to the ratio between body size of rodents and acorns, rodents did not ingest them completely [19]. Depending on whether these remains preserve the embryo, some acorns can germinate, although they lack a significant part of their cotyledons. This is a new step in considering the relationship that is closer to mutualism than predation.

We here add a new consideration to the mathematical model of Zwolak and Crone: To evaluate dispersion costs, they include acorn losses due to predation. Nevertheless, not every attacked acorn loses its ability to germinate [44]. These calculations do not include the beneficial effect of partial consumption of acorns in significantly reducing this cost [7].

In any mutualistic relationship, the two intervening species have to contribute something to keep it within these terms [4, 18]. Plants provide abundant resources in the cotyledons of their acorns which they make available to rodents [35, 5, 40, 18]. Rodents contribute to the relationship by transporting seeds to places with conditions suitable for germination, but do they also show embryo preserving behavior? [34, 15, 1, 2] This is the question we will try to answer. If, during the partial consumption of acorns, rodents preserve the embryo, they would be contributing to making the interaction mutualistic.

The rest of the contributions are made by rodents for their own benefit. The transport of acorns is carried out to look for safer places of consumption to avoid predation by raptors, and burial, to hide their reserves from intraspecific or interspecific competitors [15, 13, 29, 32, 31]. However, partial consumption and preservation of the embryo benefits the plant rather than the rodent.

So why do rodents practice this behavior? Is it simply the price they must pay to obtain resources? They already provide transport for the acorns. Would it not be easier to open them at the narrower apical end? They would use less energy [7]. Why encourage the plant in this way at the cost of using more energy? Can rodents also benefit from this behavior? Can they be planning the future of their descendants? An acorn that preserves the embryo it totally consumed can germinate with little cotyledons mass [22, 37, 39]. Is it the intention of the rodent that partially consumes an acorn that the preserve embryo should germinate and produce a new tree, thus providing a future source of food for its offspring? During the time it takes to create a new tree, rodents may have produced 100 generations. But from the evolutionary point of view, can this behavior be part of the engagement to which the two species involved in the mutualistic relationship are subjected? [18]. Is this behavior by the rodent the culmination to consider the relationship with oak species already clearly mutualistic?

Our goal is to answer these questions. Firstly, by identifying which rodent species exhibit embryo-preserving behavior, that is, which species are mutualistic with plants and which are predators of acorns. Secondly, verifying what differences exist between mutualistic and predatory species during acorn consumption.

# 2. Material and Methods

### *2.1. Study System*

During the autumn individuals of three different rodent species (*Apodemus sylvaticus* Linnaeus 1758 (wood mouse), *Mus spretus* Lataste 1883 (Algerian mouse) and *Microtus arvalis* Pallas 1778 (common vole) were captured in Palencia, Spain (41° 54'10.51'' N, 4°24'35.00'' W). The wood mouse has inhabited the Iberian Peninsula since ancient times. Acorns of various *Quercus* species are among its food sources and are abundant in the area it inhabits. The Algerian mouse is of North African origin but has been present in parts of the Iberian Peninsula for a long time. It lives practically in the same habitat as the wood mouse except in the Northern Mountains. It also consumes acorns of *Quercus* species. The common vole is abundant in central Europe. Until recently, its distribution area in the Iberian Peninsula has been confined to the Northern Mountains, where it can access fresh food such as soft green herbaceous plants. Due to the increase in the surface of irrigated crops, the common vole has expanded to the central Iberian Peninsula, where it presents periods of overpopulation and is considered a recurrent crop pest [21, 16]. This species does not have coevolution history with *Quercus* species because its distribution area is linked to crops and, therefore, acorns have not been its food source.

Also, acorns of *Quercus ilex* subsp. ballota (Desf.) Samp. (holm oak) were collected during autumn.

### *2.2. Experimental Procedures and Design*

The captured specimens of the three rodent species were placed in terrariums for reproduction. Five specimens from the descendants of each rodent species were selected for the experiment to eliminate any previous acorn consumption experience. The five specimens were placed in isolated terrariums with a layer of soil originating from their capture area. The soil layer was 10 cm thick, so that they could make burrows. We provided them with water and Harlan food Global Diet 2018 until the beginning of the experiment. Lighting was natural, coming through the terrarium windows, in order not to alter their circadian cycle. The rodents were fed only with acorns during the twenty days of the experiment, with an abundant water supply.

Every day, each specimen had available six acorns of *Quercus ilex* (holm oak). Six was the maximum number of acorns consumed in one day by the most voracious species of the three (common vole).

At the end of the experiment, each specimen had consumed 120 acorns, 6 every day, over 20 days. Considering five specimens per rodent species and three rodent species, the total number of acorns managed during the experiment was 1800, 600 by each species. Before being given to the rodents, each acorn was weighed and labelled to estimate the individual mass consumed of each acorn. The

remains of the acorns from the previous day were removed and weighed to estimate their mass after consumption. By calculating the sum of the quantity of each acorn consumed, we estimated the mass ingested daily by each specimen. The way in which rodents handled acorns was analyzed: the place where partial consumption started (basal or apical), embryo presence or absence, acorns completely eaten or intact. Acorns were classified into four categories according to the different forms of consumption: intact (I: acorns were not eaten at all), totally eaten acorns (T), basal (B: partially eaten acorns by the basal end on the opposite side to the embryo), and apical (A: partially eaten acorns by the apical end where the embryo is).

### *2.3. Data Analyses*

The possible effects of rodent species (wood mouse, Algerian mouse and common vole), day (5 levels) and their interactions on the number and mass of acorns eaten per specimen, were analyzed using Linear Mixed Models (LMM) with the Restricted Maximum Likelihood method (REML). The specimens were treated as random factor and the day as repeated factor. Finally, working on the model matrix, contrasts were carried out to test differences between fixed factor levels [26]. Consequently, the Bonferroni correction was used to adjust for the significance level for each t-test [30]. Statistical computations were implemented in the R software environment (version 2.15.3 Core Team R 2013), using the nlme package for LMM [27].

## 3. Results

The results show that the three rodent species studied have different behavior with regard to the treatment of acorns. In Table 1 the LMM analysis showed a highly significant interaction between "category of consumption," "rodent species" and 'number of acorns', suggesting that different rodent species handle acorns in a different way.

***Table 1.*** *The summary results of linear mixed models testing the effects of, Rodent species and Category of consumption, and their interaction on the number of acorns consumed. The F values of the fixed factors and their significance (p) are show.*

| Number of acorns | df | *F* | *p* |
|---|---|---|---|
| Intercept | 44 | 806.8734 | <0.0001 |
| Rodent species | 44 | 0.0000 | 1 |
| Category of consumption | 44 | 69.3021 | <0.0001 |
| Rodent * Consumption | 44 | 31.8104 | <0.0001 |

Preference for different ways of opening acorns can be seen in Figure 1, where we show the number of acorns attacked in different way. We used the Bonferroni test to show significant differences in letters. In particular, the wood mouse and Algerian mouse consumes most of the *Q. ilex* acorns from the basal end, whereas the common vole prefers the apical end (Figure 1). The wood mouse opens more acorns at the basal end, far from the embryo, than does the Algerian mouse, and the common opens only a very small number in this way.

The wood mouse is the species that does not open the acorn from the apical end, where the embryo is located. The Algerian mouse opens very few acorns in this way, whereas the common vole is the specie that opens most acorns from the apical end, destroying the embryo.

The number of intact acorns shows that the Algerian mouse leaves many acorns unused. It is also the species that consumes the fewest whole acorns.

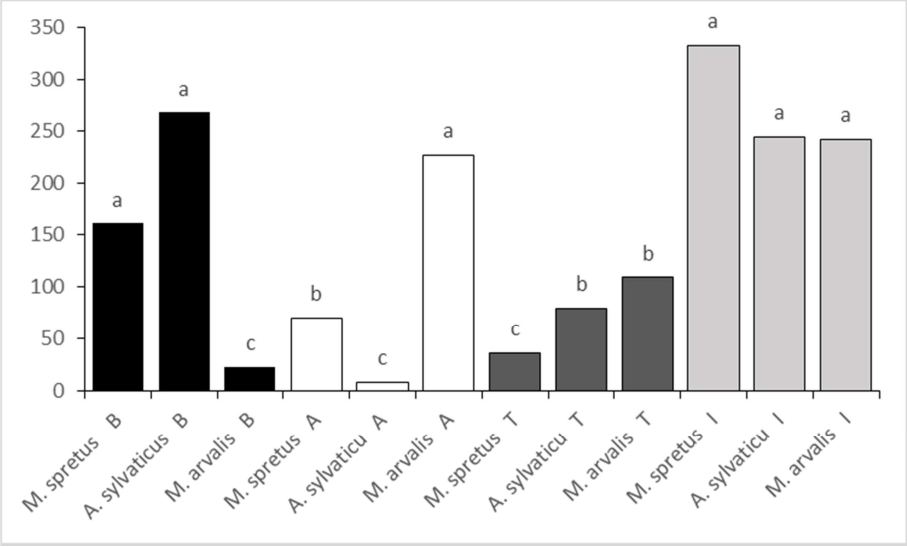


***Figure 1.*** *Number of Q. ilex acorns attacked in different ways by three rodent species (M. spretus, M. arvalis, Asylvaticus). Categories consumed B = Basal: acorns partially eaten from the basal end, A = Apical: acorns partially eaten from the apical end where the embryo is located, T = Totally eaten acorns, I = Intact: acorns not eaten. Different letters above the bars indicate significant differences (p < 0.05).*

We also studied the weight consumed of each acorn attacked by each species of rodent. The LMM analysis showed a highly significant interaction between "category of consumption," "rodent species" and 'mass consumed of acorns' (Table 2), suggesting that rodent species show preference for some kinds of acorns. The three species of

rodents also show differences in the amount of each acorn ingested. In all three, the largest mass consumed per acorn corresponds to those consumed completely (Figure 2), but the wood mouse consumes more mass of the acorns that it opens from the basal part than the few it opens at the apical part. The common vole consumes more mass of the acorns that it opens at the apical part, the usual starting point of these acorns in this species, than from the few it opens from the basal part. The Algerian mouse consumes similar amounts of all types of acorns regardless of the starting end. This is the species that consumes the least mass of the three types of acorns attacked (Figure 2). This species also ingests the least mass of totally consumed acorns, which indicates that the acorns it selects for consumption are lighter in weight.

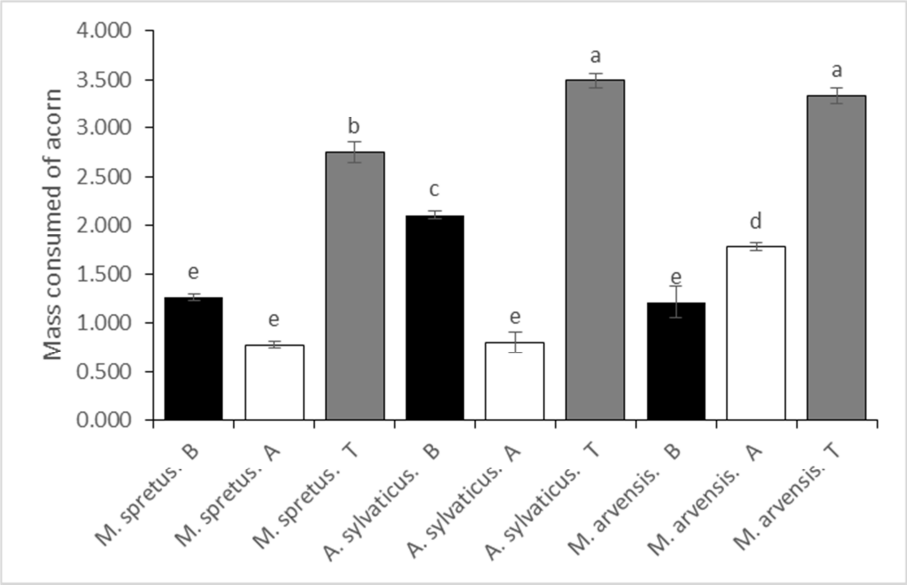


***Figure 2.*** *Mass consumed per acorn attacked by three rodent species (M. spretus, M. arvalis, A. sylvaticus). Categories consumed B = Basal: acorns partially eaten from the basal end, A = Apical: acorns partially eaten from the apical end, where the embryo is, T = Totally eaten acorns, I = Intact: acorns not eaten. Different letters above the bars indicate significant differences ($p < 0.05$).*

***Table 2.*** *The summary results of linear mixed models testing the effects of, Rodent species and Category of consumption, and their interaction on the mass of acorns consumed. The F values of the fixed factors and their significance (p) are show.*

| Number of acorns | df | *F* | *p* |
|---|---|---|---|
| Intercept | 975 | 388.1851 | <0.0001 |
| Rodent species | 975 | 279.2249 | <0.0001 |
| Category of consumption | 975 | 534.4558 | <0.0001 |
| Rodent * Consumption | 975 | 15.833 | <0.0001 |

# 4. Discussion

The results show that two species of rodent contribute to the mutualistic relationship with oak species with their embryo preserving behavioral, the wood mouse and the Algerian mouse. Preserving the embryo favors the plants because partially consumed attacked acorns can maintain germinative capacity [12, 22, 37]. This behavior is the contribution made by mutualistic rodents to their relationship with plants, in addition to transport [33, 3, 36]. However, this behavior also favors rodents. In the future, these acorns, from which resources have been obtained, may become new sources of food. They may become trees producing new acorns for future generations. This means having great capacity of foresight because these acorns can take about 100 years to become acorn-producing trees in some species, and by then, rodents will have produced more than 100 generations [18]. From the point of view of the human being this degree of foresight is incredible, but from the perspective of the evolution of the species, it could be to achieve the ultimate aim of perpetuating the species, the goal of any organism.

Two species of rodents that contribute this behavior to the relationship have long consumed acorns as a food source. This has allowed a mutual adaptation between plants and rodents in which both species benefit [10]. Until now it was considered that the relationship between both types of species was mutualistic because rodents simply provided transport for the acorns [34, 15]. However, preserving the embryo when partially consuming the acorn is proof that rodents also actively seek this mutualistic relationship [19]. They sacrifice the comfort of opening the acorns in the easiest way, from the distal, narrower part so that the embryo remains with a view to the future [7]. Partial consumption and preserving the embryo is innate behavior, it is not learned with experience because it does not change over time in mice that have not previously had contact with acorns [7]. Therefore, it must be built into their genes. It is the result of experiences of their ancestors during the consumption of acorns, food that has served as their sustenance since ancient times. The species that has not been in contact with acorns, that has not used them as food, does not exhibit this behavior (common vole).

Of the two species that show embryo preserving behavior the wood mouse is the one that practises it more intensely as it opened very few acorns from the apical end. Almost all of the acorns it attacks are opened from the basal part, far from the position of the embryo, even exceeding the number of those left intact [12, 22, 39]. The wood mouse has been consuming this type of food since ancestral times and its relationship with oak species has been adapting since then. However, the Algerian mouse arrived more recently in the Iberian Peninsula and although it has also fed on acorns for a long time, this collaborative behavior is not as established as in the wood mouse. It has been verified that the Algerian mouse, mostly prefers to open acorns from the basal part but attacks a greater number from the apical part than the wood mouse. The common vole, which does not use acorns as a food source does not show embryo preserving behavior. It attacks the acorns from the narrowest part, which allows it to open them more comfortably wasting less energy regardless of the position of the embryo or the preservation of this organ. They have never been in contact with this food, and it has not been possible to establish mutualistic relationships between plants and this specie of rodent. It is a simple predation relationship. Rodents of this species takes advantage of nutrients in acorns without worrying about the future. The common vole has recently arrived in this region. Its food source which is normal soft green herbaceous plants, may not be available due to drought and overpopulation. This can lead it to explore new sources and as we have seen here, acorns are good candidates because of their nutritional capacity. When this species attacks acorns, we know what their fate is, destruction, since they are totally depredated. This is the risk posed by the presence of common vole in areas dominated by oaks species. Their acorns are destroyed without the possibility of being disperse, thus contributing to their extinction. This species can therefore break the mutualistic relationship that the other two rodent species have with these plants [25].

The Algerian mouse ingests the least mass, possibly because it is the smallest species and therefore selects smaller acorns, as we have seen. The common vole, which is the largest species, ingests a greater mass of the acorns it attacks.

Therefore, the wood mouse and Algerian mouse are species that maintain a mutualistic relationship with oaks species. These relationships can be altered by the presence of a new species in an area. The common vole poses a risk to the expansion of oak species because it preys on the acorns, preventing their dispersion.

The mutualistic relationship between oaks species and the Algerian and wood mouse has been shown in this experiment. Both species contribute to the relationship with seed transport and although this behavior requires more energy, it maintains the relationship within the terms of mutualism, which, tfor both species of rodents, gives them a guarantee of the future. The contribution that the two rodent species make to the relationship with their embryo preserving behavior would be proof that both, plants and rodents, seek to make their relationship collaborative.

# 5. Conclusion

The behavior of the two rodent species that have been consuming acorns since ancient times aims to preserve the embryo so that acorns, although partially consumed, germinate and become more acorn-producing trees in the future.

This behavior is the contribution made by both species, which are used to eating acorns, to ensure that their relationship with oak species remains within the terms of mutualism.

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