ORIGINAL PAPER

Consequences of intraspecific variation in seed size: does the presence of small seeds reduce predation on large ones?

Paulina Celebias[1] · Michał Bogdziewicz[1,2]

Abstract

Seeds produced by individual plants often vary substantially in size. Typically, larger seeds produce seedlings that have higher chances of establishment and survival relative to seedlings produced by smaller seeds. However, larger seeds are also preferred by granivores due to larger caloric content. While choosing the patch to forage, granivores might avoid the ones with smaller, less preferred seeds. We tested a novel hypothesis that the production of different size seeds by a plant may be a strategy to decrease predation by granivores. We conducted a 3-year seed removal experiment. We presented *Quercus robur* acorns in forests in three configurations: large acorns alone, medium acorns alone, and large acorns mixed with small ones. The impact of seed size on seed survival was inconsistent: in the first year of the study, survival probability for seeds in the mixed treatment was significantly higher than survival probability of large seeds alone, supporting our hypothesis. However, in the following years, results were non-significant, probably because of reduced granivore selectivity in poor seed crop years. Our study demonstrated that the impact of neighbourhood of different size seeds seed survival varied over time in *Q. robur*. This provides limited evidence that intraspecific variation in seed size could evolve to shift the interaction between trees and scatter hoarders away from predation and towards mutualism.

Keywords Acorns · Granivores · Seed predation · Intraspecific variation in seed size · Sessile oak · Plant–animal interactions

Introduction

Seed dispersal is a key process influencing plant demography and recruitment (Herrera et al. 1994; Schupp and Fuentes 1995). Moving seeds away from parent plants can increase seed and seedling survival by decreasing distance- and density-dependent mortality (Schupp 1988; Comita et al. 2014; Schupp et al. 2019). By determining where seeds are deposited, dispersal impacts plant reproductive success (Wall 2002) and can impose selective pressures on seed morphology and phytochemistry (Herrera 2002). Many plant species, including major forest tree genera, rely on seed predators for dispersal of their seeds (Wall 1990; Gómez et al. 2019). Scatter-hoarding seed dispersers, such as rodents or corvids, consume seeds but also store them in shallow caches (Vander Wall 2010; Perea et al. 2011a; Pesendorfer et al. 2016). By storing seeds in a suitable environment, scatter-hoarding rodents increase the probability of seedling establishment (Steele et al. 2007; Zwolak and Crone 2012). Thus, scatter-hoarders act both as seed predators and seed dispersers, and the decision whether to store or consume a handled seed is important for structuring plant communities (Schupp and Fuentes 1995; Pesendorfer et al. 2018).

One major factor affecting the decision whether to store or predate seeds is seed traits (Lichti et al. 2017). A prominent trait affecting seed harvesting and fate is their size (Lichti et al. 2014). Larger seeds are a higher-quality resource (Theimer 2003) and thus have a higher removal chance (Wang and Ives 2017). In addition, larger and heavier seeds are more likely to be dispersed further (Moore et al.

✉ Paulina Celebias
  paulina.celebias@gmail.com

1   Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland

2   Laboratoire EcoSystèmes et Sociétés En Montagne, INRAE, Univ Grenoble Alpes, 2 rue de la Papeterie, BP 76, 38402 Saint-Martin-d'Hères Cedex, France

2007; Perea et al. 2011a; Wang and Ives 2017), while smaller seeds are more likely to be consumed (Wang and Ives 2017). Granivores foraging is driven by maximization of benefits. Larger seed represents higher nutritional reward but also increased cost caused by longer handling time. Since many plant species depend on animals for seed dispersal, animal seed-size or fruit-size preferences, in relation to the body size of the animal itself can shape the evolution of seed size (Muñoz and Bonal 2008; Sobral et al. 2013).

Besides affecting scatter-hoarding decisions, larger seed size often increases fitness through higher probability of seed persistence in the soil and higher seedling establishment (Seiwa 2000). Larger seeds have higher chances of establishment and survival as seedlings in the face of various hazards including competition from established vegetation (Leishman et al. 1995; Alcántara and Rey 2003). Large seeds are also able to survive predation even partial consumption (Perea et al. 2011b; Bartlow et al. 2018). Seedlings emerging from larger seeds tend to be better competitors (Landergott et al. 2012). Furthermore, plants originating from larger seeds can have higher fecundity (Larios et al. 2014).

Given these manifold consequences of seed size, it is not surprising that interspecific differences in seed size are widely studied (Westoby et al. 1992; Moles et al. 2007; Yi et al. 2019). However, variation in seed size can be large even within one individual (Sork et al. 1993; Herrera and Jovani 2010). Mechanisms driving the intraspecific variation in seed size are diverse. Plant modular construction can cause variability in the characteristics of copies of the same organ (leaves, flowers, fruits, seeds) produced in different modules of the same individual (Herrera 2017). For example, distribution of water within an individual depends on its height, where leaves on the lower position of a tree crown get more water than leaves located in the upper part of the crown (Menéndez and Concepción 1997). Similarly, photosynthetic performance varies depending on position and orientation of leaves in the crown (Escribano-Rocafort et al. 2016). Moreover, foliar damage can lead to failure in seed development (Strauss et al. 2015; Canelo et al. 2018). However, differences in seed size can originate not only from environmental factors, but can also be driven by natural selection if the variation in seed size maximizes seed survival and dispersal.

Here, we investigated how variation in sizes of seeds affects animal foraging decisions. Specifically, we asked whether the presence of smaller (less preferred) seeds can increase the persistence of larger ones in the environment through indirect interactions. Since variation in seed size can induce different decisions by shared predators, indirect interactions can arise between these seeds (Chase et al. 2002; Lichti et al. 2014; Bogdziewicz et al. 2019). Indirect interactions occur when the presence of one prey type alters the behaviour of shared a predator towards a second prey type (Strauss 1991). The presence of less attractive seeds may increase survival or abundance of both seed species (apparent mutualism). Alternatively, the presence of a favoured seed type may attract predators to the patch and increase predation upon less attractive seeds (apparent competition) (Holt and Lawton 1994).

We performed an experiment where we presented seeds of different sizes in three configurations: only large seeds, mix of small and large seeds, and only medium seeds. Small seeds are less attractive due to their lower per capita energetic value and thus can decrease visitation rates to the patch (Lichti et al. 2017; Wang and Ives 2017; Dylewski et al. 2020). Thus, we hypothesized that the production of seeds of different sizes by a plant is a strategy to decrease predation by granivores. Food resources are aggregated in patches of varying quality, so a key component of successful foraging is the selection of a favourable patch by consumers (Shimada et al. 2015). We hypothesized that granivores will preferentially forage in patches with larger seeds, relative to patches where large seeds are mixed with small seeds (H1). We also hypothesized that post-removal fate of large seeds in "large" treatment and in "mixed" treatment will vary. Specifically, we predict that large seeds from "mixed" treatment will be cached more frequently compared to seeds from "large" treatment (H2). In "mixed" treatment, granivores should choose small seeds for consumption first and then disperse large seeds, while in "large" treatment, some portion of large seeds will be eaten before dispersal.

Methods

Study site

We conducted experiments in two closely located forests: in Morasko Nature Reserve (52.4 N, 16.8 E) and in Puszcza Zielonka Landscape Park (52.6 N, 16.9 E), located in the Greater Poland Voivodeship in Poland. This region is characterized by cool, moist temperate climate. The average temperature in August is 21.7 °C and −2.6 °C in February. The average yearly precipitation is 373 mm with the highest precipitation in July (81 mm) and lowest in February (4 mm). We established 10 study plots: one in protected forest surrounding the Morasko Meteorite Reserve, and nine in managed forest of Puszcza Zielonka Landscape Park. Every plot was dominated by ∼70-year-old oaks. In the Morasko Meteorite Reserve, other species included black cherry (*Prunus serotina*), silver birch (*Betula pendula*) and the Scotch pine (*Pinus sylvestris*). In Puszcza Zielonka Landscape Park, oaks were mixed with European beech (*Fagus sylvatica*) and common hornbeam (*Carpinus betulus*). All the study sites had similar microsite with relatively low shrub cover. In our study plot, yellow-necked mouse was the main seed

disperser with population of 59 individuals/plot per month summer 2019 and 49 individuals/plot per month in summer 2020. Monitoring of dishes by camera traps indicated that only wood mice were responsive for seed removal.

Acorn preparation

Each year (2017, 2019, 2020) we bought common oak (*Quercus robur*) acorns from State Forests. We selected source locations that were possibly the closest to our study plots. We chose the common oak because it is widespread in Poland, is readily dispersed by scatter-hoarders (Jensen and Nielsen 1986; Smallwood et al. 2001; Bogdziewicz et al. 2017), and displays considerable variation in seed size (Landergott et al. 2012). We determined seed size by measuring seed length. Each year we measured all the seeds from the sample of 25 kg (c.a. 6000 acorns) and we picked seeds of the largest, the smallest and medium length, based on the distribution generated by measuring the sample of ~6000 acorns. In our study, the size of common oak acorns varied in length from 16.61 to 41.95 mm. The acorns were floated and then additionally examined to exclude non-viable seeds, i.e. mouldy, broken or infested by, e.g. *Curculio* sp. larvae. We divided acorns into three size categories: large and small in 2017 and large, medium, and small in 2019 and 2020 (Table 1).

Table 1 Length of acorns (mm) used for experiment in different treatments in 2017, 2019, and 2020

Seed size	2017	2019	2020
	Mean + SD	Mean + SD	Mean + SD
"Large"	31.06 ± 1.54	34.49 ± 3.00	33.5 ± 0.94
"Medium"	–	26.97 ± 0.49	27.38 ± 0.92
"Small"	22.50 ± 1.25	21.39 ± 1.41	22.45 ± 1.67

Removal experiment

Each year (2017, 2019, 2020) we performed a seed removal experiment using experimental acorns presented on Petri dishes. On each Petri dish, we presented 8 acorns in different configurations: only large acorns ("large" treatment), 4 large acorns with 4 small ones ("mixed" treatment), and only medium acorns ("medium" treatment). In 2020, we modified the experiment by displaying 6 large acorns in the "large" treatment instead of 8 acorns to equalize acorn mass between "large" and "mixed" treatment. In 2017, we monitored acorns for 30 days, and in 2019 and 2020 for 15 days (first 5 days, then on day 10 and 15) (Table 2). We shortened monitoring time in 2019 and 2020 due to much higher removal rates than in 2017 (see "Results" section).

In 2019 and 2020, we additionally tracked the fates of removed seeds. We prepared seeds for tracking by tagging them with plastic labels before presenting on Petri dishes. We pierced a 1-mm diameter hole through the husk at the basal end of each acorn without damaging the cotyledon and the embryo. Then, we inserted and tied a steel wire (100-mm length, 0.2-mm diameter) to the acorn and attached a red plastic tag (20 × 40 mm) to the opposite end of the wire (Xiao et al. 2006; Yi et al. 2008). The set comprised of wire and tag weighed ~0.14 g. Each acorn was weighed (±0.01 g), and its tag was individually numbered. When monitoring acorns, we recorded their fate (IS—left in situ, EIS—eaten in situ, EAR—eaten after removal, RS—removed and left on surface, CAR—cached after removal, M—missing), and removal distance (for those that were carried away from the dishes). Recaching was not monitored. Since the proportion of cached seeds is a key variable that influences plant benefits in interactions with scatter-hoarders (Zwolak and Crone 2012), we focussed the analysis on the percentage of cached seeds.

Table 2 Summary of experimental design in 2017, 2019, and 2020

	2017	2019	2020
Location	Morasko Nature Reserve	Puszcza Zielonka Landscape Park	Puszcza Zielonka Landscape Park
	Removal experiment	Removal experiment + seed fate	Removal experiment + seed fate
Sample size	240 acorns	480 acorns	440 acorns
Stations	30	60	60
Treatments	Large (8 large acorns)	Large (8 large acorns)	Large (6 large acorns)
	Mixed (4 large + 4 small acorns)	Mixed (4 large + 4 small acorns)	Mixed (4 large + 4 small acorns)
		Medium (8 medium acorns)	Medium (8 medium acorns)
Plot	5 transects 250 m away from each other; stations spaced 30 m apart in each transect	One plot; stations spaced 30 m apart and arranged in 6 × 10 grid	Four plots; stations spaced 30 m apart and arranged in 4 × 4 grids on three plots and in 4 × 3 grid on one plot
Duration of acorn monitoring	30 days (8 days in a row, then every fourth day)	15 days (5 days in a row, then on 10th day and 15th day)	15 days (5 days in a row, then on 10th day and 15th day)

Statistical analysis

To test the effect of experimental treatments on the survival probability of seeds, we analysed the data with the mixed effects Cox models using 'survival' package (Therneau 2020) in R environment (R Development Core Team 2015). In the analysis, we defined survival probability as a probability of not being removed from the Petri dish. We tested the survival probability of different-sized seeds in three treatments, with station included as random intercept effect. To compare probability of survival of large seeds in "Large" and in "Mixed" treatment, we tested only large seeds in two treatments, with station included as random intercept effect.

To estimate whether the treatment had an impact on rodent seed choice, we analysed seed fate using generalized linear mixed models (GLMMs) implemented via 'glmmTMB' package (Brooks et al. 2017). To analyse the effects of treatment on seed dispersal, we constructed three binomial mixed models, each with treatment as fixed effect, and seed station included as random intercept. The responses were as follows: (1) seed was either removed or not; (2) when removed, seed was either eaten or not; and (3) when removed and not eaten, seed was either cached or left on the surface.

Finally, we analysed the distance of dispersal of acorns in different treatments. We used Gaussian-family generalized linear mixed models (GLMMs) implemented via 'glmmTMB' package (Brooks et al. 2017), with log-transformed dispersal distance as the response variable and station as the random intercept effect. We tested for statistical significance of fixed factors with Wald type II chi-square tests.

Results

Survival of seeds from different treatments

In 2017, the survival probability (i.e. probability of not being removed from the Petri dish) for seeds in the "mixed" treatment was significantly higher ($p < 0.001$) than the survival probability of seeds in the "large" treatment (Fig. 1). After 35 days, 43% of seeds in the "mixed" treatment survived, while only 6% survived in the "large" treatment. Moreover, the survival rate of large seeds was substantially higher in the "mixed" treatment compared to the "large" treatment ($p < 0.001$). This result supports our hypothesis that granivores prefer to forage in patches with large seeds, relative to patches with seeds of mixed sizes (H1). However, in 2019 and 2020, there was no significant difference in the probability of survival of seeds from different treatments. In 2019, after 15 days, 6.25% of acorns from the "mixed" treatment survived, 6.9% from the "large" treatment and no acorns survived from the "medium" treatment. Moreover, the survival

rates of large seeds in both "large" and "mixed" treatment were the same ($p = 0.18$ in 2019). In 2020, no acorns survived after 15 days.

### Indirect interactions between seed of different sizes

In 2019, the distance of dispersal was marginally different across treatments ($p = 0.053$, $df = 2$, $X^2 = 5.86$). Seeds from the "large" treatment were dispersed on average 3.7 m further compared to the "mixed" treatment ($p = 0.03$, $\beta = 5.9$, $SE = 2.64$) and on average 1.4 m further compared to the "medium" treatment ($p = 0.08$, $\beta = 4.61$, $SE = 2.59$; Table 3), supporting our hypothesis stating that apparent mutualism would occur between large and small acorns in mixed treatment H2. Distance of dispersal was also associated with the final fate of the seeds ($p < 0.001$, $df = 2$, $X^2 = 44.03$). Cached seeds ($p < 0.001$, $\beta = 16.74$, $SE = 2.53$) and eaten seeds ($p < 0.001$, $\beta = 14.55$, $SE = 3.16$) were transported further than seeds left on the ground surface. Moreover, treatment affected the final seed fate ($p = 0.02$, $df = 2$, $X^2 = 8.22$). In contrast to our prediction, seeds from the "medium" treatment had a higher probability of being cached compared to the "large" (95% vs. 74%; $p = 0.02$, $\beta = 2.07$, $SE = 0.88$) and the "mixed" treatment (60%: $p = 0.004$, $\beta = 2.62$, $SE = 0.92$). In 2019, 26% of all presented seeds were cached.

Moreover, to investigate whether there were any indirect interactions between different size seeds, we analysed the fate of large acorns in both the "large" and the "mixed" treatment. The distance of dispersal for large seeds in both "large" and "mixed" treatment was similar (Table 3; $p = 0.12$, $df = 1$, $X^2 = 2.36$). Also, large seeds in both treatments were eaten (4.6% in the "Large" and 4.6% in the "Mixed treatment; $p = 0.37$, $df = 1$, $X^2 = 0.8$) and cached (17% in the "Large" and 7.5% in the "Mixed" treatment; $p = 0.56$, $df = 1$, $X^2 = 0.35$) at a similar rate. This result suggests a lack of apparent mutualism between large and small acorns in the "mixed" treatment.

In contrast to 2019, in 2020, treatment did not impact the distance of dispersal ($p = 0.53$, $df = 2$, $X^2 = 1.48$) (Table 3). However, the distance of dispersal was associated with the final fate of seeds ($p < 0.001$, $df = 2$, $X^2 = 27.99$) with cached seeds dispersed further than eaten seeds ($p = 0.001$, $\beta = 10.34$, $SE = 2.71$) or seeds that were left on the surface ($p < 0.001$, $\beta = 16.44$, $SE = 3.42$). Treatment did not affect scatter-hoarders' decision whether to eat or to cache encountered seeds, so our hypothesis H1 and H2 were not supported at this stage. In 2020, 9% of all dispersed acorns were cached.

When we analysed the fate of large seeds in "large" and "mixed" treatment, we found that the treatment had a significant influence on the distance of dispersal ($p = 0.04$, $df = 1$, $X^2 = 4.10$). Large seeds from "large" treatment were carried over greater distances than large seeds from "mixed"

Fig. 1 Survival probability of acorns, for different treatments in 2017 (total of 240 acorns), 2019 (total of 480 acorns) and 2020 (total of 460 acorns). Treatment with large-size acorns is represented by blue line, treatment with medium-size acorns by green line and treatment with mixed-size acorns by red line. Shaded area indicates 95% confidence intervals
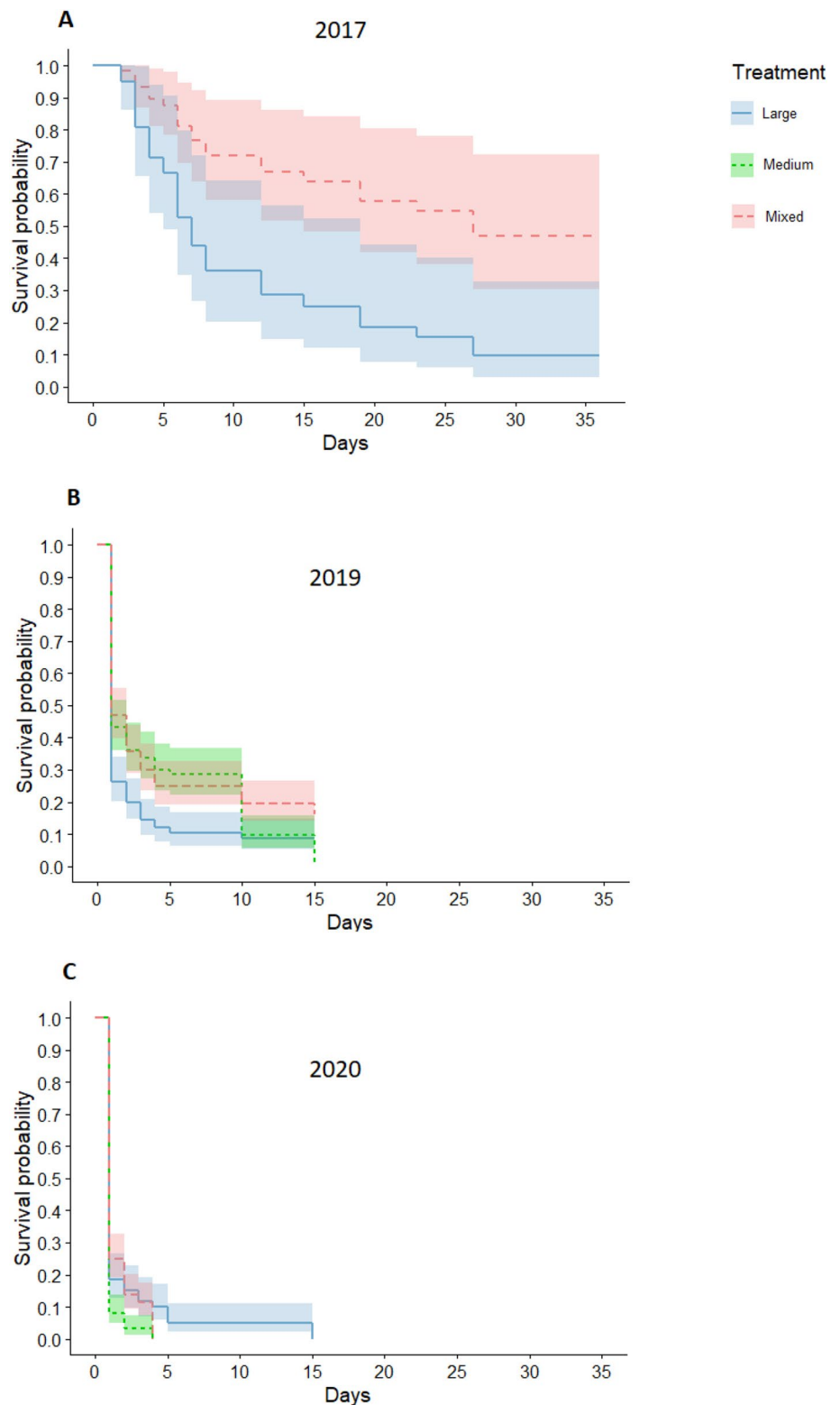
treatment (8.6 m vs. 7.2 m; $p = 0.04$, $\beta = 10.47$, SE = 5.20). However, similarly to the results from 2019, the treatment had no impact on the foragers decision whether to consume or to cache a seed.

Direct effects of seed size

In 2019, we investigated the impact of acorn size (regardless of treatment) on the fate of acorns. We found that acorn size

Table 3 Mean distance of dispersal of seeds from different treatments, of seeds of different sizes and of different fates of seeds in 2019 and 2020

	2019 Mean ± SD	2020 Mean + SD
Treatment (m)		
"Large"	10.5 ± 7.6	10.6 ± 10.3
"Mixed"	6.7 ± 6.6	7.7 ± 9.6
"Medium"	9.1 ± 7.5	9.4 ± 11.6
Seed size (m)		
Large	9.9 ± 7.4	8.6 ± 8.5
Small	4.9 ± 5.9	8.5 ± 11.4
Medium	9.1 ± 7.5	9.4 ± 11.6
Seed fate		
Eaten	5.9 ± 7.8	6.4 ± 10.2
Cached	9.4 ± 6.6	12.8 ± 10.8
Left on ground surface	2.6 ± 3.5	2.9 ± 30.3

had substantial impact on distance of dispersal ($p = 0.01$, $df = 2$, $X^2 = 9.05$). Small seeds were dispersed closer to the station than large ($p = 0.004$, $\beta = 8.9$, SE = 3.04) and closer than medium seeds ($p = 0.02$, $\beta = 8.99$, SE = 3.76) (see Table 3). Moreover, while the size of an acorn had no impact on the decision whether to consume the seed ($p = 0.06$, $df = 2$, $X^2 = 5.52$), it did have an impact on the decision to cache ($p = 0.008$, $df = 2$, $X^2 = 9.748$). Medium-size acorns were cached more frequently than both large ($p = 0.01$, $\beta = -2.10$, SE = 0.86) and small acorns ($p = 0.002$, $\beta = -3.24$, SE = 1.04).

In 2020, seed size had no impact on the distance of dispersal. However, we detected a significant effect of seed size on foragers decision whether to consume encountered seeds ($p = 0.04$, $df = 2$, $X^2 = 6.59$). Small seeds were eaten more frequently than large seeds ($p = 0.02$, $\beta = 1.22$, SE = 0.53) and more frequently than medium seeds ($p = 0.03$, $\beta = 1.32$, SE = 0.60). The impact of seed size on caching decision was not significant.

Discussion

Indirect interactions among seeds of different sizes appeared context-dependent, as evidenced by inconsistent results obtained in different years of our investigation. Small acorns protected large acorns from removal by granivores only in the first year of study. Similarly, treatment had varying effects on the distance of dispersal and on acorn fate over the years. Thus, while our results remain inconclusive, production of different size seeds might be the mechanism to decrease predation by granivores.

The outcomes of many interactions between species are not static and are influenced by biotic and abiotic factors (Bronstein 1998). While interactions like obligate mutualism remain relatively constant, other interactions are prone to substantial increase or decrease in the magnitude of the effect due to context dependency (Chamberlein et al. 2014). For example, benefits may increase as mutualist populations grow, but then may shift downwards at very large population size (Bronstein 1994). Studies of longer duration tend to show greater variation in observed phenomena (Chamberlein et al. 2014). Single-year studies can overestimate effects, or miss detection at all (Nosek et al. 2012). Therefore, long-term observations are required to understand many studied phenomena. Our study lasted 3 years and showed varying impact of offering together seeds of different sizes on their dispersal. The reason for this inconsistency might be the varying conditions across study years caused by the two mast events, and following changes in mice population size.

We suggest possible explanations for the reported variation in results among years. The higher survival rate of the "mixed" versus "large" treatment in 2017 could be a false positive result. However, the environmental conditions in each year of study differed significantly. The populations of rodents were low in 2017, rendering per capita food availability for rodents relatively high. In contrast, the two mast years that occurred in the fall of 2018, (of European beech, *F. sylvatica*) and in 2019 (of common oak, *Quercus robur*) (personal observation), likely allowed mice population to grow substantially (Wolff 1996; Selva et al. 2012; Zwolak et al. 2016). The increase in population size likely resulted in higher competition for resources between individuals (Eva et al. 2016). Consequently, rodents can become less selective (Soininen et al. 2013), choosing also less preferred food. Thus, selection of different size seeds might occur only in years with low granivore population size relative to acorn abundance, when granivore population is satiated (Vander Wall 2010; Greenberg and Zarnoch 2018). This speculation is supported by dramatically different survival rates of acorns among years. In 2017, when we detected the treatment effects, 42.1% of all acorns survived after two weeks of study compared to 4.8% in 2019 and 0% survival in 2020.

Moreover, contrary to our prediction, the post-removal fate of large seeds in "Large" and "Mixed" treatment was not significantly different. Also, medium-sized seeds were cached more frequently across all treatments. The reason for preferences for medium-sized seeds may be that for a small granivore the largest acorns might be inconvenient to handle or simply too large to carry due to gape limitation (Muñoz and Bonal 2008; Rehling et al. 2021). Moreover, granivores face a trade-off between energetic benefits and handling time that rises with seed size (Muñoz and Bonal 2008; Stephens and Krebs 2019), which may lead to preference for harvesting and caching of medium-sized seeds

Table 4 Summary of tested predictions and results

Prediction	Result
Granivores prefer patches with larger acorns relative to patches with mixed large and small acorns (H1)	Partially supported. Acorns from "Large" treatment had lower survival rate compared to acorns from "Mixed" treatment in one year of study
Large acorns from "Mixed" treatment will be cached more frequently compared to large acorns from "Large" treatment (H2)	Unsupported. Fate of large acorns in both treatments was the same

rather than large and small ones (Wang et al. 2013). On the other hand, large seeds that require longer handling time but contain more energy are carried away over greater distances to reduce probability of pilferage (Jansen et al. 2004; Wang et al. 2013). Small, less valuable seeds are usually eaten in situ more frequently (Vander Wall 2003). Thus, when foraging, decisions of granivores strongly depend on seed size, and the choice granivores make may decrease foraging on large seeds in the presence of small seeds through apparent predation (Lichti et al. 2014). However, the choice whether to harvest a seed also depends on environmental conditions and per capita food availability, which affects selectivity of rodents, and may decrease the magnitude of indirect interaction between different size seeds.

In summary (Table 4), our study demonstrated that the impact of neighbourhoods of different size seeds of common oak on seed survival varied over time. Since granivores display preferences towards different size seeds and towards higher-quality patches for foraging, we proposed a hypothesis that the production of different-sized seeds by a plant may be a strategy to decrease predation by granivores. During the first year of our study, the result supported our hypothesis, but in the following years, we did not detect an impact of seed mixing on seed survival. The lack of clear patterns in rodent seed preferences may result from varying environmental conditions and fluctuations in population density of small mammals. It suggests that the selection is intermittent, occurring only in years of low rodent abundance relative to acorn abundance. That could be important given that most of the population-level oak recruitment occurs in years when the rodents are satiated (Crawley and Long 1995). Our study provides evidence that intraspecific variation in seed size may have evolved to shift the interaction between trees and scatter hoarders away from predation and towards mutualism.

Declarations

References

Alcántara JM, Rey PJ (2003) Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. J Evol Biol 16:1168–1176. https://doi.org/10.1046/j.1420-9101.2003.00618.x

Bartlow AW, Agosta SJ, Curtis R et al (2018) Acorn size and tolerance to seed predators: the multiple roles of acorns as food for seed predators, fruit for dispersal and fuel for growth. Integr Zool 13:251–266. https://doi.org/10.1111/1749-4877.12287

Bogdziewicz M, Crone EE, Steele MA, Zwolak R (2017) Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. J Ecol 105:310–320. https://doi.org/10.1111/1365-2745.12673

Bogdziewicz M, Lichti NI, Zwolak R (2019) Consumer-mediated indirect interaction with a native plant lowers the fitness of an invasive competitor. J Ecol 107:12–22. https://doi.org/10.1111/1365-2745.13023

Bronstein JL (1994) Conditional outcomes in mutualistic interactions. Trends Ecol Evol 9:214–217. https://doi.org/10.1016/0169-5347(94)90246-1

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) "glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling." R J 9(2):378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

Bronstein JL (1998) The contribution of ant-plant protection studies to our understanding of mutualism. Biotropica 30:150–161. https://doi.org/10.1111/j.1744-7429.1998.tb00050.x

Canelo T, Gaytán Á, González-Bornay G, Bonal R (2018) Seed loss before seed predation: experimental evidence of the negative effects of leaf feeding insects on acorn production. Integr Zool 13:238–250. https://doi.org/10.1111/1749-4877.12292

Chamberlein SA, Bronstein JL, Rudges JA (2014) How context dependent are species interactions? Ecol Lett 17(7):881–890. https://doi.org/10.1111/ele.12279

Chase JM, Abrams PA, Grover JP et al (2002) The interaction between predation and competition: a review and synthesis. Ecol Lett 5:302–315. https://doi.org/10.1046/j.1461-0248.2002.00315.x

Comita LS, Queenborough SA, Murphy SJ et al (2014) Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J Ecol 102:845–856. https://doi.org/10.1111/1365-2745.12232

Crawley MJ, Long CR (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. J Ecol 83:683–696. https://doi.org/10.2307/2261636

Dylewski Ł, Ortega YK, Bogdziewicz M, Pearson DE (2020) Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecol Lett 23:1024–1033. https://doi.org/10.1111/ele.13499

Escribano-Rocafort AG, Ventre-Lespiaucq AB, Granado-Yela C et al (2016) The expression of light-related leaf functional traits depends on the location of individual leaves within the crown of isolated *Olea europaea* trees. Ann Bot 117:643–651. https://doi.org/10.1093/aob/mcw004

Eva J, Marta H, Ladislav C (2016) Rodent food quality and its relation to crops and other environmental and population parameters in an agricultural landscape. Sci Total Environ 562:164–169. https://doi.org/10.1016/j.scitotenv.2016.03.165

Gómez JM, Schupp EW, Jordano P (2019) Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biol Rev 94:874–902. https://doi.org/10.1111/brv.12481

Greenberg CH, Zarnoch SJ (2018) A test of the predator satiation hypothesis, acorn predator size, and acorn preference. Can J For Res 48:237–245. https://doi.org/10.1139/cjfr-2017-0381

Herrera CM (2002) Plant animal interactions: an evolutionary approach. Wiley

Herrera CM (2017) The ecology of subindividual variability in plants: patterns, processes, and prospects. Web Ecol 17:51–64. https://doi.org/10.5194/we-17-51-2017

Herrera CM, Jovani R (2010) Lognormal distribution of individual lifetime fecundity: insights from a 23-year study. Ecology 91:422–430

Herrera CM, Jordano P, Lopez-Soria L, Amat JA (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecol Monogr 64:315–344. https://doi.org/10.2307/2937165

Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. Annu Rev Ecol Syst 25:495–520. https://doi.org/10.1146/annurev.es.25.110194.002431

Jansen PA, Bongers F, Hemerik L (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecol Monogr 74:569–589. https://doi.org/10.1890/03-4042

Jensen TS, Nielsen OF (1986) Rodents as seed dispersers in a heath—oak wood succession. Oecologia 70:214–221. https://doi.org/10.1007/BF00379242

Landergott U, Gugerli F, Hoebee SE et al (2012) Effects of seed mass on seedling height and competition in European white oaks. Flora Morphol Distrib Funct Ecol Plants 207:721–725. https://doi.org/10.1016/j.flora.2012.09.001

Larios E, Búrquez A, Becerra JX, Venable DL (2014) Natural selection on seed size through the life cycle of a desert annual plant. Ecology 95:3213–3220. https://doi.org/10.1890/13-1965.1

Leishman MR, Westoby M, Jurado E (1995) Correlates of seed size variation: a comparison among five temperate floras. J Ecol 83:517–529. https://doi.org/10.2307/2261604

Lichti NI, Steele MA, Zhang H, Swihart RK (2014) Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758. https://doi.org/10.1890/13-1657.1

Lichti NI, Steele MA, Swihart RK (2017) Seed fate and decision-making processes in scatter-hoarding rodents. Biol Rev 92:474–504. https://doi.org/10.1111/brv.12240

Menéndez A, Concepción M (1997) Variaciones en las relaciones planta-insectos fitófagos: efectos de factores bióticos y abióticos.

Moles AT, Ackerly DD, Tweddle JC et al (2007) Global patterns in seed size. Glob Ecol Biogeogr 16:109–116. https://doi.org/10.1111/j.1466-8238.2006.00259.x

Moore JE, McEuen AB, Swihart RK et al (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88:2529–2540. https://doi.org/10.1890/07-0247.1

Muñoz A, Bonal R (2008) Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. Anim Behav 76:709–715. https://doi.org/10.1016/j.anbehav.2008.03.017

Nosek BA, Spies JR, Motyl M (2012) Scientific Utopia: II. Restructuring incentives and practices to promote truth over publishability. Perspect Psychol Sci 7:615–631. https://doi.org/10.1177/1745691612459058

Perea R, Miguel AS, Gil L (2011a) Acorn dispersal by rodents: the importance of re-dispersal and distance to shelter. Basic Appl Ecol 12:432–439. https://doi.org/10.1016/j.baae.2011.05.002

Perea R, San Miguel A, Gil L (2011b) Leftovers in seed dispersal: ecological implications of partial seed consumption for oak regeneration. J Ecol 99:194–201. https://doi.org/10.1111/j.1365-2745.2010.01749.x

Pesendorfer MB, Sillett TS, Koenig WD, Morrison SA (2016) Scatter-hoarding corvids as seed dispersers for oaks and pines: a review of a widely distributed mutualism and its utility to habitat restoration. Condor 118:215–237. https://doi.org/10.1650/CONDOR-15-125.1

Pesendorfer MB, Baker CM, Stringer M et al (2018) Oak habitat recovery on California's largest islands: scenarios for the role of corvid seed dispersal. J Appl Ecol 55:1185–1194. https://doi.org/10.1111/1365-2664.13041

Rehling F, Jaroszewicz B, Braasch LV et al (2021) Within-species trait variation can lead to size limitations in seed dispersal of small-fruited plants. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.698885

Schupp EW (1988) Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51:71–78. https://doi.org/10.2307/3565808

Schupp EW, Fuentes M (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. Écoscience 2:267–275. https://doi.org/10.1080/11956860.1995.11682293

Schupp EW, Zwolak R, Jones LR et al (2019) Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and pervasive. AoB PLANTS. https://doi.org/10.1093/aobpla/plz067

Seiwa K (2000) Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. Oecologia 123:208–215

Selva N, Hobson KA, Cortés-Avizanda A et al (2012) Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PLoS ONE 7:e51267. https://doi.org/10.1371/journal.pone.0051267

Shimada T, Takahashi A, Shibata M, Yagihashi T (2015) Effects of within-plant variability in seed weight and tannin content on foraging behaviour of seed consumers. Funct Ecol 29:1513–1521. https://doi.org/10.1111/1365-2435.12464

Smallwood PD, Steele MA, Faeth SH (2001) The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: tannins, insects, and seed germination. Am Zool 41:840–851. https://doi.org/10.1093/icb/41.4.840

Sobral M, Guitián J, Guitián P, Larrinaga AR (2013) Selective pressure along a latitudinal gradient affects subindividual variation in plants. PLoS ONE 8:e74356. https://doi.org/10.1371/journal.pone.0074356

Soininen EM, Ravolainen VT, Bråthen KA et al (2013) Arctic small rodents have diverse diets and flexible food selection. PLoS ONE 8:e68128. https://doi.org/10.1371/journal.pone.0068128

Sork VL, Bramble J, Sexton O (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528–541. https://doi.org/10.2307/1939313

Steele MA, Carlson JE, Smallwood PD et al (2007) 14 Linking seed and seedling shadows a case study in the Oaks (quercus). Seed dispersal 322

Stephens DW, Krebs JR (2019) Foraging theory. Princeton University Press

Strauss SY (1991) Indirect effects in community ecology: their definition, study and importance. Trends Ecol Evol 6:206–210. https://doi.org/10.1016/0169-5347(91)90023-Q

Strauss SY, Conner JK, Lehtilä KP (2015) Effects of foliar herbivory by insects on the fitness of *Raphanus raphanistrum*: damage can increase male fitness. Am Nat. https://doi.org/10.1086/323116

Theimer TC (2003) Intraspecific variation in seed size affects scatter-hoarding behaviour of an Australian tropical rain-forest rodent. J Trop Ecol 19:95–98

Therneau T (2020). A Package for Survival Analysis in R. R package version 3.2-7

Vander Wall SB (2003) Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34. https://doi.org/10.1034/j.1600-0706.2003.11973.x

Vander Wall SB (2010) How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. Philos Trans R Soc B Biol Sci 365:989–997. https://doi.org/10.1098/rstb.2009.0205

Wall SBV (1990) Food hoarding in animals. University of Chicago Press

Wall SBV (2002) Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83:3508–3516. https://doi.org/10.2307/3072099

Wang B, Ives AR (2017) Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. Oecologia 183:751–762. https://doi.org/10.1007/s00442-016-3793-0

Wang B, Ye C-X, Cannon CH, Chen J (2013) Dissecting the decision making process of scatter-hoarding rodents. Oikos 122:1027–1034. https://doi.org/10.1111/j.1600-0706.2012.20823.x

Westoby M, Jurado E, Leishman M (1992) Comparative evolutionary ecology of seed size. Trends Ecol Evol 7:368–372. https://doi.org/10.1016/0169-5347(92)90006-W

Wolff JO (1996) Population fluctuations of mast-eating rodents are correlated with production of acorns. J Mammal 77:850–856. https://doi.org/10.2307/1382690

Xiao Z, Jansen PA, Zhang Z (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. For Ecol Manag 223:18–23. https://doi.org/10.1016/j.foreco.2005.10.054

Yi X, Xiao Z, Zhang Z (2008) Seed dispersal of Korean pine Pinus koraiensis labeled by two different tags in a northern temperate forest, northeast China. Ecol Res 23:379–384. https://doi.org/10.1007/s11284-007-0392-x

Yi F, Wang Z, Baskin CC et al (2019) Seed germination responses to seasonal temperature and drought stress are species-specific but not related to seed size in a desert steppe: implications for effect of climate change on community structure. Ecol Evol 9:2149–2159. https://doi.org/10.1002/ece3.4909

Zwolak R, Crone EE (2012) Quantifying the outcome of plant–granivore interactions. Oikos 121:20–27. https://doi.org/10.1111/j.1600-0706.2011.19849.x

Zwolak R, Bogdziewicz M, Rychlik L (2016) Beech masting modifies the response of rodents to forest management. For Ecol Manag 359:268–276. https://doi.org/10.1016/j.foreco.2015.10.017