

Acorns of introduced *Quercus rubra* are neglected by European Jay but spread by mice

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Abstract. Northern Red Oak (*Quercus rubra* L.; native in North America) is regarded as an invasive species in Central Europe, where it is the most common non-indigenous broad-leaved tree species in forestry. The species' impact on native ecosystems and thus its future management are discussed controversially. Because dispersal is an important step in an invasion process, we studied whether European Jays (*Garrulus glandarius* L.) and mice, both main dispersers of native oaks in Europe, mediate the dispersal of *Q. rubra* seeds. Morphological characteristics of *Q. rubra* and native *Q. robur* L. acorns were quantified according to their implications for dispersal. We tested experimentally whether and to what extent mice and jays collect acorns of both oak species and if their behavior depends on choice options (dual choice vs. no-choice). Acorns were offered on feeding platforms, controlled by scouting cameras. Results showed that *Q. rubra* acorns have a thicker pericarp, a rounder shape and a higher dry weight compared to acorns of *Q. robur*. In the behavioral assays jays avoided acorns of *Q. rubra* if they were offered together with those of *Q. robur* (dual choice) as well as when *Q. rubra* acorns were offered alone (no-choice). This selection behavior could be caused by the differences in morphological traits observed between the acorns of the two species. In contrast to jays, mice took acorns of both oak species likewise indicating that seed morphology does not affect the attractiveness of Red Oak acorns for rodents. In conclusion, *Quercus rubra* is collected by animals in Central Europe to a considerable amount but dispersal should be restricted to moderate distances mediated by mice, leading mainly to stabilizing and increasing existing populations rather than founding of new ones.

Keywords Northern Red Oak, invasive plant species, acorn morphology, seed dispersal, acorn selection experiment, European Jay, mice

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Introduction

Central European forests will be affected by climate change (Hemery 2008), resulting in substantial loss of silvicultural importance of some native tree species due to their susceptibility to summer drought (e.g. Kölling et al. 2009; Milad et al. 2013). Thus, the discussion on introduction and cultivation („assisted migration“) of exotic tree species re-emerges (e.g. Gray et al. 2011; Millar et al. 2007; Reif et al. 2011). Today a substantial part of commercial forestry is based on the cultivation of introduced non-native tree species (Sedjo 1999; Zobel et al. 1987) including Northern Red Oak (*Quercus rubra* L.). Introduced from North America in 1724, this species is currently the most common exotic broad-leafed tree species in Central European forestry (Schütt et al. 2011). However, nature conservation authorities consider *Q. rubra* an invasive species that causes a negative impact on the native bio-diversity (Kowarik 2010, Nehring et al. 2013, Woziwoda et al. 2014).

An important step in spreading of a plant species is the dispersal of its seeds, which is assisted by animals (Gosper et al. 2005). The majority of acorns of the oak species (*Quercus* spp.) are heavy and dispersed barochorously or by animals (Ducousso et al. 1993). Due to their high abundance and nutrient content they are attractive as food for many forest vertebrates (den Ouden et al. 2005). Hoarding of acorns in the soil by different animal species is essential in natural regeneration processes of almost all oak species because acorns not retrieved or eaten by other predators can germinate and thus seedlings can establish (Vander Wall 2001). Rodents and some jays are the most important hoarding dispersers. They transport acorns up to 100 m or in case of the jays even up to several kilometers (Ducousso et al. 1993; den Ouden et al. 2005; Vander Wall 1990, 2001). In its native range in North America, *Q. rubra* is mainly dispersed by the Blue Jay (*Cyanocitta cristata* L., Darley-Hill & Johnson 1981), and to minor extent by rodents

such as the Gray Squirrel (*Sciurus carolinensis* J.F.GMEL., Goheen & Swihart 2003), the American Fox Squirrel (*Sciurus niger* L., Short 1976) and the Eastern Chipmunk (*Tamias striatus* L., Pyare et al. 1993). In Europe, most effective dispersers of the native oaks (*Q. robur* L. and *Q. petraea* (MATT.) LIEBL.) are the Wood Mouse (*Apodemus sylvaticus* L.) and the European Jay (*Garrulus glandarius* L.) whereas pigeons, crows, squirrels and other mice are thought to be of minor importance (den Ouden et al. 2005). The question arises whether European Jays and mice could also disperse acorns of non-indigenous Red Oak in Central Europe. In this context, acorn morphology may play an important role as European Jays select acorns by morphological characteristics (Bossema 1979; Pons & Pausas 2007).

Myczko et al. (2014) recently showed that European Jays prefer acorns of *Q. robur* (Pedunculate Oak) to *Q. rubra* ones if they are offered together in a dual choice experiment and tend to pick more Red Oak acorns in late autumn compared to early autumn. They concluded that under limited supply of Pedunculate Oak acorns jays might take more Red Oak ones and thus contribute substantially to long distance seed dispersal. However, it is still ambiguous to what extent jays will collect Red Oak acorns if they are available exclusively and moreover to what extent native rodents contribute to dispersing *Q. rubra* acorns.

Therefore our study aims at (1) quantifying the morphological differences between acorns of *Q. rubra* and *Q. robur*; (2) in a field experiment, analyzing whether European Jays and mice disperse acorns of *Q. rubra*, and (3) whether this dispersal depends on choice options for European Jays and mice.

Materials and methods

Acorn material

Quercus robur and *Q. rubra* acorns were collected in October 2012 at 2 sites each species

and in October 2013 at 10 (*Q. robur*) and 5 sites (*Q. rubra*) in forest stands and parks within the city limits of Bayreuth. At each site, a minimum of three trees was sampled. All collected acorns were subjected to a flotation test and only sinking (well developed) ones were randomly chosen for investigations. Acorns collected in October 2012 were stored at 12–18 °C in open plastic bags until gathering dry weight in March 2013. Acorns collected in October 2013 were kept up to four weeks in cloth bags in a refrigerator (-2 to +8 °C) before they were used for morphological measurements and selection experiments.

Acorn morphology

Length (without acorns' foremost tip) and maximum width of 1340 *Quercus rubra* and 1340 *Q. robur* acorns were measured with a calliper rule and the acorns were stored again in a refrigerator until they were used for selection experiments. The pericarp thickness was measured in additional 30 acorns per species with the same calliper rule at the acorn's widest point. In addition, 60 acorns of each species were dried at 80 °C to a constant weight (compartment dryer: Memmert, UL 50) and dry weight was gathered (Lab weighing scale: Mettler Toledo, AE 240).

Acorn selection experiment

Study site. Field experiments were carried out at the Ecological-Botanical Gardens,

University of Bayreuth, Germany (EBG, 49° 55' 45" N; 11° 35' 10" E, 355 to 370 m a.s.l.) which is 16 ha in size comprising rather passively managed woodland and grasslands to a large extent. Experiments were conducted from October 18th to November 13th 2013. Acorn yield of native oak species in the Botanical Gardens during that autumn was low. During the experiments there was some precipitation on 6 days (overall sum 9.3 mm, maximum 1.0 mm / 10 min). Mean day and night temperature was 10 °C and 8 °C, respectively. Lowest temperature was -3 °C and highest 21 °C (data from meteorological station at the EBG).

Experimental set up. Acorns of *Quercus robur* and *Q. rubra* were offered to birds and mice using two types of platforms (see table 1, figure 1). In a first design, acorns of *Q. rubra* and *Q. robur* were offered together (= dual choice experiment). In a second experiment, acorns of either *Q. robur* or *Q. rubra* were offered (= no-choice experiment). We selected randomly which of the two oak species was offered on each day. In each set up, 30 randomly chosen acorns per oak species were offered randomly spread on the feeding platforms (80 x 80 cm, figure 1). Each experiment was carried out separately at daytime and at night. Twice a day, at sunset and sunrise, the remaining acorns were removed, counted, and the platforms were loaded again. According to decreasing day length in autumn, exposition time was 10 - 11.5 h day and 12.5 - 13 h night, respectively.

Platforms used for birds were constructed as

Table 1 Experimental design for the field experiments

Disperser	Jays (table)				Mice (tunnel)	
	Dual choice	No-choice (either <i>Q. robur</i> or <i>Q. rubra</i> offered)		Dual choice	No-choice (either <i>Q. robur</i> or <i>Q. rubra</i> offered)	
Number of acorns per replicate	30 <i>Q. robur</i> + 30 <i>Q. rubra</i>	30 <i>Q. robur</i>	30 <i>Q. rubra</i>	30 <i>Q. robur</i> + 30 <i>Q. rubra</i>	30 <i>Q. robur</i>	30 <i>Q. rubra</i>
Number of replicates	day n = 9 + 9 night n = 9 + 9	n = 9	n = 9	n = 9 + 9 n = 9 + 9	n = 9	n = 9
Date (year 2013)	Oct 28-31	Oct 18-26		Oct 28-31	Oct 18-26 and Nov 8-13	



Figure 1 Feeding platforms used for the experiments and installed scouting cameras. Platforms used for mice (left) were constructed as tunnels, platforms used for birds (right) as tables

tables (figure 1), placed one meter above the ground with three posts in the center of the table preventing mice and other mammals to climb or jump it. The tables were placed on a meadow, freestanding but with woodland in the background. Platforms used for mice were formed as a tunnel (figure 1) placed on the ground in shrubs or woodlands, having a height of ten centimeter and a removable lid for putting acorns into it. Two opposite sides of the tunnel were closed by a plank, the other two by a broad-meshed chicken wire to allow only mice to enter. There were three platforms of each kind, and each platform was used for three replicates. Each day all platforms were placed at another of three preselected sites at the Botanical Gardens. Distance between platforms at each site was in the minimum 55 m. Scouting cameras were installed at two platforms of each kind, one camera working with a white flash (Cuddeback Capture, Model 1125) and one with an infrared flash (Cuddeback Attack IR, Model 1156). Photographed animals were identified as exactly as possible according to Corbet & Ovenden (1982).

Data analysis

With the help of a linear model we tested whether the number of removed acorns depends on oak species, disperser, daytime, their pairwise interactions, the choice option (no-choice and dual choice respectively), and the

interaction of choice option with the disperser group (birds and mice). Furthermore, for each disperser group, oak species (*Q. rubra* and *Q. robur*) and daytime (day or night) it was tested by Mann-Whitney-U-test whether there were differences regarding the number of removed acorns between no-choice and dual choice experiment. Because there were no differences between them and the linear model showed no significant effect of choice option (see table 2, 3 in results), data of both experiments were pooled for the analysis, whether there are differences in the acorn removal between oak species, disperser and daytime (Kruskal-Wallis- and posthoc pairwise Mann-Whitney-U-test with Bonferroni correction). Differences in morphological parameters between *Quercus rubra* and *Q. robur* were analyzed by a Mann-Whitney-U-test.

Data analysis was done with the software package R (R Core Team, 2013), RStudio version 0.97.551 and additionally the package *sciplot* (Morales 2012). For creating figures, the graphic programs Inkscape 0.48 and gimp 2.8 were used.

Results

Acorn morphology

Acorns of *Quercus robur* and *Q. rubra* were significantly different in all morphological pa-

rameters measured (figure 2). *Q. rubra* acorns were 2.3 cm long and 1.9 cm wide (figure 2 a, b), therefore clearly shorter and wider than those of *Q. robur* and thus of a rounder shape (figure 2 c). 4.9 % of the Red Oak acorns were even wider than long (shape < 1), which never was the case in *Q. robur*. On the other hand 14 % of *Q. robur* acorns are more than twice as long as wide, which never was found in *Q. rubra*. The pericarp of *Q. rubra* acorns was 3.5 times thicker than that of *Q. robur* (figure 2 d). Further acorns of *Q. rubra* were heavier (dry weight 3.4 g) than *Q. robur* ones (figure 2 e). The appearance of acorns was also different for both species. Fresh *Q. rubra* acorns were more or less dark reddish brown and covered with a thin furry coating, which came off by and by. In contrast the surface of *Q. robur* acorns was glabrous, rather pale and ochre with typical dark longitudinal stripes.

Acorn selection by mice and jays

Installed scouting cameras documented only European Jays (*Garrulus glandarius*, see figure 3) at the tables (38 shots) and only mice at the tunnels (661 shots). Finally it is evident that the tunnel platforms were specific to mice and the tables to jays as potential acorn dispersers. About half of the visiting mice were identified

either as *Apodemus sylvaticus* (Wood Mouse) or as *Apodemus flavicollis* MELCHIOR (Yellow-Necked Mouse, see figure 3). The photos taken did not allow to distinguish between these two taxa. Only 12 photographs pictured mice with small ears and shorter tail being characteristic of *Clethrionomys glareolus* SCHREBER (Bank Vole), *Microtus arvalis* PALLAS (Common Vole) and *Pitymys subterraneus* DE SÉLYS LONGCHAMPS (European Pine Vole). On the remaining photos it was not possible to detect species specific traits.

Removal of acorns depended on daytime, disperser, oak species and their pairwise interactions (table 2). Mice and jays differed in their activity regarding daytime (interaction disperser * daytime) and in their preferences

Table 2 Results of a linear model: Influence of the tested parameters on the number of removed acorns

Parameter	Estimate	p-value
disperser	104.5	< 0.001
daytime	28.9	< 0.001
oak species	24.8	< 0.001
choice option	-1.1	0.839
daytime * disperser	-118.1	< 0.001
oak species * daytime	45.9	< 0.001
oak species * disperser	-32.8	< 0.001
choice option * disperser	6.1	0.431

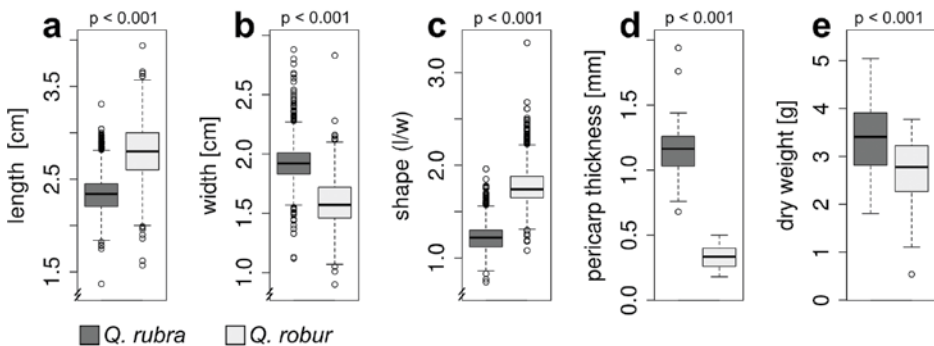


Figure 2 Morphological characteristics of acorns of *Quercus rubra* and *Q. robur*: Length (a, n = 1430), width (b, n = 1430), shape (length/width, c, n = 1430), pericarp thickness (d, n = 30) and dry weight (e, n = 60). Median and quartiles are given, open dots represent outliers. Significant differences were determined by a Mann-Whitney-U-test.



Figure 3 European Jay (left, on a table platform) and a mouse (right, possibly *Apodemus sylvaticus* or *A. flavicollis*, in a tunnel platform). Photo on the left was taken by hand, the other at night by a scouting camera

for the acorns of the two oak species (interaction disperser * oak species). Jays took acorns only by day, removing nearly all acorns of *Quercus robur*, but hardly ever picking *Q. rubra* acorns (about 4 %, figure 4). Mice took almost all acorns at night, and about 25 % by day. They did not distinguish between acorns of the two oak species (figure 4). In total, mice carried off more acorns than jays.

The choice option, whether fruits of both oak species were offered together (dual choice) or separately (no-choice), had no significant effect on amount of acorns per oak species removed, neither for jays nor for mice (table 3), and there was no interaction of the choice option and the disperser (table 2). However, for jays there was a slight but insignificant tendency for taking more *Q. rubra* acorns in the dual choice than in the no-choice option (table 3).

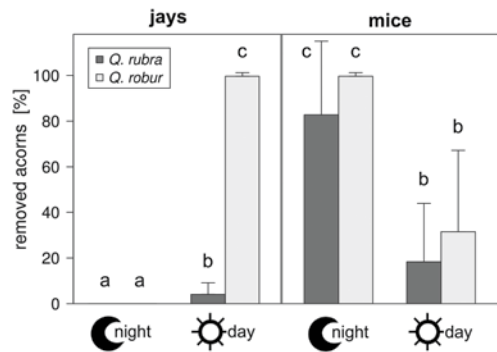


Figure 4 Percentage of removed acorns depending on disperser (jays vs. mice), daytime (night vs. day) and oak species (*Quercus rubra* vs. *Q. robur*). Each time 30 acorns per species were offered. Data of no-choice and dual choice experiment were pooled. Mean and standard deviation are given (n = 18). Significant differences are indicated by different lower case letters (pairwise Mann-Whitney-U-test with Bonferroni correction)

Discussion

Table 3 Results of selection experiments (dual choice vs. no-choice option)

			Percentage of removed acorns (mean ± sd)		p-value
			Dual choice	No-choice	
Jay	Night	<i>Q. rubra</i>	0.0 ± 0.0	0.0 ± 0.0	--
		<i>Q. robur</i>	0.0 ± 0.0	0.0 ± 0.0	--
	Day	<i>Q. rubra</i>	5.9 ± 5.7	2.2 ± 3.7	0.142
		<i>Q. robur</i>	100.0 ± 0.0	99.3 ± 2.2	0.374
Mice	Night	<i>Q. rubra</i>	84.8 ± 30.4	80.7 ± 35.6	0.737
		<i>Q. robur</i>	99.3 ± 2.2	100.0 ± 0.0	0.374
	Day	<i>Q. rubra</i>	10.4 ± 16.0	26.3 ± 31.4	0.636
		<i>Q. robur</i>	27.8 ± 30.8	35.2 ± 41.6	0.644

European Jays avoid acorns of introduced *Quercus rubra*

Our results confirm that jays prefer acorns of *Quercus robur*, when they are allowed to choose between the acorns of native *Q. robur* and North American *Q. rubra*, as already shown by Bossema (1979) and Myczko (2014). In addition we demonstrated that Red Oak acorns are generally largely unattractive for jays as they even were mostly ignored when they were offered alone. It is known that European Jays swallow up to five acorns in their esophagus and carry one in the bill and therefore they prefer long and slim ones (Bossema 1979). As we measured, acorns of *Q. rubra* were clearly shorter, wider and heavier than those of *Q. robur*, which may cause problems for transport and may explain why jays avoid these exotic acorns. Because of throat limitation the upper width for swallowing an acorn is stated as 1.9 cm (Pons & Pausas 2007), being exactly the median of *Q. rubra* acorns' width we measured. Thus half of all Red Oak acorns are likely to wide to be swallowed by jays. Furthermore jays may select acorns visually by color and shell texture (Bossema 1979; Pons & Pausas 2007). Acorns of *Q. rubra* are darker, more pubescent and less shiny than the ones of *Q. robur* and therefore both species may be distinguished easily by jays. Considering that jays seem to be able to identify damaged acorns by their consistency (Bossema 1979; Pons & Pausas 2007), we assume that they are also able to discriminate between acorns of *Q. rubra* and *Q. robur* cause of their different shell thickness. Additionally the thick shell of *Q. rubra* acorns makes them difficult to husk (Bossema 1979). Even the Blue Jay (*Cyanocitta cristata*), an important disperser of *Q. rubra* in North America (Darley-Hill & Johnson 1981), favors acorns of *Quercus* species with thinner walls and of smaller size compared to *Q. rubra* acorns, which are only taken when other acorns are scarce (Moore & Swihart 2006). Hence it is important whether European Jays would be-

have similar and take more acorns of *Q. rubra* when alternative food is scarce, e.g. during winter or if fruit set of the native oaks is low. Myczko et al. (2014) found that more *Q. rubra* acorns were removed by European Jays in late than in early autumn and explained this observation with decreasing acorn availability over the autumn. But this conclusion seems untenable considering our results. Even if only *Q. rubra* fruits were supplied, jays tended to take even less of these acorns compared to the dual choice experiment, which indicates the low attractiveness of Red Oak acorns for jays even without an offered alternative. However, we assume that jays cannot distinguish perfectly between acorns of both species and take *Q. rubra* acorns accidentally when collecting those of *Q. robur*. Given that European Jays hardly take acorns of introduced *Q. rubra*, long distance dispersal of this species should be low because jays are by far the most important long distance dispersers (up to several kilometers) of acorns in Central Europe (Gomez 2003; den Ouden et al. 2005). Nevertheless, since they take *Q. rubra* acorns in rare cases, they may contribute to some long distance dispersal resulting in founding of new populations as well.

Mice take acorns of exotic and native oak likewise

In contrast to jays mice did not select between acorns of both *Quercus* species. Obviously different acorn morphology of the two oak species is no selection criterion for mice. Mice should be able to carry both clenching them between their teeth, and obviously the higher dry weight of *Q. rubra* acorns is not hindering. Furthermore, considering that mice can even crack the hard shell of hazelnuts, their nimble handling and opening of the thick pericarp of Red Oak acorns would not come as a surprise. Nevertheless, the number of exotic acorns transported by mice is notable. In their study on Mediterranean oaks Pons & Pausas (2007b) found some acorn selection

by mice regarding the oak species whereby they tended to prefer heavier acorns. This is consistent with our finding that the mice did not avoid the heavier acorns of *Q. rubra*. It is known that rodents select seeds olfactorily and by chemical compounds (Steele et al. 2001). Acorns of the red oak section (*Lobatae*) have a high tannin and lipid contents in contrast to the white oak section ones (*Quercus*), including the Central European oak species (Nixon 1993; Smallwood et al. 2001). Tannins cause a bitter taste, affect digestion and are a chemical defense against predators (Vander Wall 2001). Studies on North American squirrels and chipmunks found preference for acorns of the white oak section over acorns of the red oak section (incl. *Q. rubra*) due to their lower tannin content (Pyare et al. 1993; Short 1976). On the other hand, high tannins prevent insect infestation (Smallwood et al. 2001) and the high nutritive lipid content can reduce the negative effect of tannins on acorn preference (Smallwood & Peters) and can make seeds more attractive for rodents (Ivan & Swihart 2000), which may lead to preferential caching and even a better dispersal of acorns of the red oak section (Smallwood et al. 2001). Beside the controversial discussion how those tannins and lipids affect the selection behavior of rodents, our results gave no indication that mice select between native *Q. robur* and introduced *Q. rubra*.

Rodents are generally considered to be less effective in dispersing seeds than jays, because of relative low dispersal distances (Ducousso et al. 1993; Gomez et al. 2008; Jensen & Nielsen 1986) and because they are important acorn predators (Ducousso et al. 1993; Gomez et al. 2008). Sork (1984) found North American rodents dispersing acorns of *Q. rubra* up to 20 m, but with a predation rate of 99 %. Similar patterns were revealed for two *Apodemus* and two oak species in Japan (Iida 1996). In Central Europe however, the Wood Mouse (*Apodemus sylvaticus*) is considered to be a quite effective acorn disperser (den Ouden et al. 2005). Although it hoards the seeds at a mean distance

of only 7.5 m, several relocating events can finally lead to much higher dispersal distances (den Ouden et al. 2005). In Danish heathlands *Apodemus sylvaticus*, *A. flavicollis* and other mice mediated a rapid colonization with native oaks (Jensen & Nielsen 1986). These two mice species were the most frequent ones observed in our study, which, as we have shown, took the same amount of acorns of *Q. rubra* and *Q. robur*. Additionally and in contrast to the European Jay, Wood Mice store the acorns in habitats with closer vegetation which provide better protection against herbivores but lower light availability for the seedlings (den Ouden et al. 2005). For *Q. rubra*, which is regarded as an intermediate shade tolerant species (Sander 1990), this would even be an advantage compared to the shade intolerant *Q. robur* (Schütt et al. 2011). Overall, mice are quite effective dispersers of the Red Oak acorns.

Conclusion

Quercus rubra, regarded as an invasive species in Central Europe (Kowarik 2010; Nehring et al. 2013), regenerates naturally in its new environment. We tested whether Central European animals are effective seed dispersers of this introduced species. Regarding the acorn collecting behavior of mice and jays observed in our study we conclude that *Q. rubra* is dispersed quite well. The results indicate minor dispersal of *Q. rubra* over long distances by European Jays but an intense dispersal over moderate distances mediated by mice. In general this promotes local regeneration and increases population size and stability rather than advancing colonization of new sites as long distance transport do (Gomez 2003; Vander Wall 2001). We suggest that the spread of the introduced *Q. rubra* is also favored by other additional factors as dispersal e.g. low mildew infection of the leaves or low insect damage of the acorns (Goßner & Gruppe 2004; Goßner & Simon 2005).

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