1 **Drivers of individual oak tree selection by acorn dispersing**

2 **animals inferred from a genotyped seedling cohort**

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1 **ABSTRACT:**

2 Seed-dispersing animals can strongly influence plant reproductive success and resulting
3 population structures. Few studies have disentangled different drivers of disperser foraging
4 behavior in natural settings and their actual relevance for plant fitness. Here we adopt a novel
5 approach to investigate the drivers of individual trees' dispersal success in a mixed
6 Pedunculate oak-Pyrenean oak (*Quercus robur* and *Q. pyrenaica*) forest stand. We genotyped
7 a seedling cohort ($n = 825$) upon emergence and performed Bayesian parentage analyses to
8 infer the acorn dispersal success of each oak tree in the stand. We then modeled this estimate
9 as a function of six tree characteristics. The absolute number of animal-dispersed seedlings
10 was exclusively predicted by crop size and the proportion of dispersed seedlings by the
11 number of fruiting oaks in the neighborhood. Neither the oak species nor tree height, acorn
12 size or shape played any role. Our findings contrast with results from experimental studies
13 and suggest that effective acorn dispersers, despite being scatter-hoarders, behaved much like
14 avian dispersers of fleshy-fruited species when selecting trees to forage on. Their behavior
15 should favor the dominance of large, prolific trees for the dynamics and genetic composition
16 of naturally regenerating oak stands.

17

18 **Keywords:** acorn dispersal, crop size, Eurasian jay, *Quercus robur*, *Quercus pyrenaica*,
19 reproductive success, rodents, scatter-hoarders.

20

1 INTRODUCTION

2 Seed dispersal by vertebrates is considered a key innovation in angiosperm evolution (Tiffney
3 2004). Effective seed dispersal is critical for the successful establishment of new individuals
4 and the resulting dynamics of plant populations and communities (Schupp et al. 2010). Seed-
5 dispersing animals hence can exert a direct and potentially strong influence on the fitness of
6 reproducing plants through their choice of the individuals they forage on. Their activity
7 leaves measurable imprints in the genetic structure and diversity of plant populations (García
8 and Grivet 2011, Hamrick and Trapnell 2011) and can drive rapid microevolutionary changes
9 (Galetti et al. 2013). A better understanding of the cues that guide foraging seed dispersers in
10 their choice of fruiting plants hence can provide valuable insights into the role of plant-
11 disperser interactions for the reproduction and resulting demo-genetic structure of plant
12 populations. Yet few studies have achieved to disentangle and compare different drivers of
13 seed disperser behavior under natural conditions. Moreover, short-term observations or
14 experiments tell little about the actual relevance of disperser behavior for plant reproductive
15 success.

16 Seed dispersers rely on a complex system of decision cues and spatial memory for selecting
17 the plants they forage on (Corlett 2011). Decision cues can be used hierarchically or
18 sequentially, and their role can vary depending on the animal's spatial scale of perception or
19 nutritional status. Scatter-hoarding species that collect and store seeds for later consumption
20 tend to behave differently than species that seek fleshy fruits to eat them immediately (Vander
21 Wall and Beck 2012). Most studies on disperser foraging decisions have focused on cues
22 related with either fruit abundance or fruit traits. Fruit crop size usually is a consistent
23 predictor for the amount of seeds removed from individual plants (Carlo and Morales 2008,
24 Prasad and Sukumar 2010). The abundance of fruits in the neighborhood (conspecific or
25 heterospecific) can also influence rates of seed removal, either positively through an

1 increased attraction of dispersers (Morales et al. 2012) or negatively owing to their satiation
2 (Saracco et al. 2005, Hampe 2008). On the other hand, diverse morphological, physical and
3 chemical fruit traits have experimentally been shown to influence fruit choice, highlighting
4 the capacity of frugivores to differentiate even subtle signals (Corlett 2011). Fruit traits can
5 also influence disperser foraging behavior under natural conditions, although their actual
6 relevance varies greatly across systems (Jordano 2000, Vander Wall 2010).

7 Despite these advances, our understanding of disperser behavior and its consequences for
8 plant recruitment remains fragmentary. Studies on scatter-hoarders have largely focused on
9 fruit characteristics but rarely on the identity of the source plant (Vander Wall 2010,
10 Pesendorfer et al. 2016; but see Wästljung 1989, Morán-López et al. 2015), while studies of
11 other frugivores have focused much on fruit abundance and less on individual-level variation
12 in fruit traits (but see e.g. Sallabanks 1993, García et al. 2001). Most importantly, virtually no
13 studies have to date linked frugivore behavior with the fitness of the fruiting plant due to the
14 difficulty of tracking animal-mediated seed dispersal events and resulting plant establishment
15 (Schupp et al. 2010). Molecular ecological approaches can help overcome this limitation
16 (García and Grivet 2011). Parentage analyses based on genetic markers allow to infer the
17 source plants of dispersed seeds or seedlings and thus to quantify the reproductive success of
18 all adults in terms of the number of descendants they have achieved to disseminate and
19 establish across the population. This fitness measure can then be related with characteristics
20 of the fruiting plant and its environment.

21 Here, we combine field and molecular ecological research approaches to assess drivers of
22 individual oak tree selection by acorn-dispersing animals in a mixed Pedunculate oak-
23 Pyrenean oak (*Quercus robur* and *Q. pyrenaica*) forest stand. Effective acorn dispersal is
24 primarily performed by the Eurasian jay (*Garrulus glandarius*) in our study area (Gerzabek et
25 al. 2017). Jays are major dispersers of oak acorns across much of temperate Eurasia

1 (Pesendorfer et al. 2016). They are very efficient scatter-hoarders that can harvest, disperse
2 and store thousands of acorns within a single fruiting season (Kollmann and Schill 1996, den
3 Ouden et al. 2005). Their foraging behavior hence can have direct and significant
4 implications for the relative contribution of individual oak trees to plant recruitment at forest
5 stand level (Pesendorfer et al. 2018). Eurasian jays have been shown to favor large and slim
6 acorns and to differentiate among oak species in choice experiments (Bossema 1979, Pons
7 and Pausas 2007, Myczko et al. 2014). But it remains little known whether their foraging
8 decisions under natural conditions are primarily guided by acorn traits, local acorn
9 abundance, or other drivers (Pesendorfer et al. 2016, Morán-López et al. 2015).

10 We genotyped a cohort of recently germinated oak seedlings and performed parentage
11 analyses to quantify the effective dispersal success - estimated through the absolute number
12 or the proportion of seedlings emerging away from the mother tree - of each adult oak
13 growing within the forest stand. This estimate was then related with several tree features to
14 simultaneously test how these influenced the choice of individual oak trees by foraging jays.
15 Specifically, we addressed the following research questions: 1) How many seedlings does
16 each tree of the forest stand contribute to the genotyped cohort? 2) Can trees' dispersal
17 success be predicted from their species identity, height, crop size, acorn size or shape, or oak
18 abundance in their neighborhood? 3) What is the relative importance of these predictors for
19 explaining acorn dispersal success?

20

21 **MATERIALS AND METHODS**

22 **Study system**

23 The study was performed in the Forêt de Nezer (44°34' N, 1°00' W) ca. 50 km SW of
24 Bordeaux, SW France. The area is covered by extensive plantations of maritime pine (*Pinus*

1 *pinaster* Ait.) interspersed with small stands of broadleaf forests dominated by Pedunculate
2 oak (*Quercus robur* L.) and, to a lesser extent, Pyrenean oak (*Q.pyrenaica* Willd.). Such
3 stands are largely exempt from forest management. We selected a mixed oak forest stand with
4 ca. 280 adult Pedunculate and Pyrenean oaks (90% *Q. robur*, 10% *Q. pyrenaica*) for this
5 study. A detailed description of the stand can be found in Hampe et al. (2010). Acorn
6 dispersal in the area is performed by Eurasian jays as well as by rodents (primarily wood
7 mice, *Apodemus sylvaticus* L.) (Gerzabek 2016). Importantly, several jays were regularly
8 present in our study stand and different lines of evidence - field observations, the spatial
9 locations and microhabitats of sampled seedlings (Gerzabek 2016, Gerzabek et al. 2017) and
10 complementary experiments on acorn predation and dispersal on the ground (A. Hampe,
11 unpublished data) - suggest that only a limited proportion of the seedlings we sampled would
12 have been dispersed and cached by other animals than jays.

13

14 **Field sampling and laboratory analyses**

15 In early spring 2006, we delimited a study plot of 6 ha enclosing the oak forest stand and
16 surveyed all adult trees within this area and an adjacent belt of 100 m width. Trees were
17 identified as adults based on their size and on fruit set observations. Each tree was
18 individually tagged and mapped, its diameter at breast height (dbh) was measured, and
19 several buds were collected and stored at -80° C for later DNA isolation. We subsequently
20 measured six further variables for a subset of 79 arbitrarily chosen trees: (i) The oak species
21 (*Q. robur* or *Q. pyrenaica*) was determined in the field based on leaf morphology. (ii) Tree
22 height was measured with an ultrasound vortex. (iii) Acorn crop size during the 2005 fruiting
23 episode was quantified by counting the number of empty acorn cups in four 50x50 cm
24 squares randomly placed beneath the canopy in early 2006 and multiplying the census mean
25 with the dbh of the target tree (which served as a proxy for the canopy size). Moreover, we

1 collected 50 acorns from each tree in September 2006 to determine (iv) acorn size (by
2 measuring their weight to the nearest 0.1 mg) and (v) acorn shape (by measuring length and
3 width to the nearest 0.1 mm and calculating their ratio). (vi) We quantified the abundance of
4 adult oaks in the neighborhood by summing the number of trees within a radius of 10 meters
5 around the focal tree.

6 During late April and early May 2006, we performed a comprehensive survey of newly
7 emerged oak seedlings (i.e., those stemming from the 2005 fruiting episode) in our 6 ha study
8 plot. We sampled all seedlings emerging more than 2 m away from any adult oaks, searching
9 every part of the study plot at least twice and up to six times. Furthermore, we sampled 20%
10 of all seedlings emerging beneath adult oaks (i.e., up to 2 m beyond the canopy projection to
11 account for potential short-distance dispersal of acorns by wind or bouncing off of branches).
12 These 20% were sampled using a strict randomization protocol to ensure their representative
13 character (see Hampe et al. 2010 for details). We estimate that the resulting data set ($n = 825$
14 individuals) includes 25-30 % of the overall seedling cohort within the study plot. All
15 sampled seedlings were individually tagged and mapped, and one leaf was collected and
16 stored at -80°C until DNA isolation.

17 Trees and seedlings were genotyped using eight nuclear microsatellite (SSR) markers
18 (QrZAG11, QrZAG96, QrZAG112, QpZAG110, QrZAG5b, QrZAG7, QrZAG20, and
19 QrZAG87) as described in detail in Hampe et al. (2010). In addition, we genotyped all
20 individuals at 39 SNP loci as described in Gerzabek et al. (2017). We obtained readily usable
21 data for 33 SNPs that we merged with the SSR data to obtain individual multilocus
22 genotypes. Both the genotypic data and the field data underlying this study have been
23 deposited in Dryad (doi:10.5061/dryad.3j33t).

24

1 **Data analyses**

2 Our analysis proceeded in two steps. First, we quantified the fecundity and acorn dispersal
3 success of individual trees. Then we assessed how dispersal success was affected by a series
4 of tree-related parameters.

5 *Quantifying individual dispersal success* - We performed a parentage analysis using a
6 Bayesian approach as implemented in the software MEMMseedlings (Gerzabek et al. 2017).
7 Unlike many other parentage assignment procedures (but see Moran and Clark 2011), our
8 approach jointly considers genotypes, spatial locations and tree mating parameters to infer
9 parentage and allowed us to distinguish between the mother and the father tree of a given
10 seedling - a highly relevant information for our study purpose. We adapted MEMMseedlings
11 to use a two-step procedure (explained in detail in Gerzabek et al. 2017) where the first step
12 consisted in the estimation of all fecundity and dispersal parameters. The second step
13 consisted in computing the posterior probability of each tree within the stand to be the mother
14 of a given sampled seedling and the posterior probability that this seedling originates from
15 seed migration. Based on these probabilities, we then assigned each sampled seedling
16 categorically to its most likely mother tree (that is, either the tree with the highest posterior
17 probability or a non-sampled mother-tree from outside the stand if the posterior probability of
18 immigration exceeded those of the local mother trees).

19 Our parentage analysis served two purposes: First, it enabled us to identify the mother trees
20 of our seedlings and to estimate the maternal reproductive success of each tree within the
21 stand by summing up the number of seedlings assigned to this individual. Second, it allowed
22 us to infer categorically whether a given seedling had been dispersed away from its source
23 tree or not (we consider that an animal is always the vector in the former case). We
24 considered that any seedling growing beneath its assigned mother tree stemmed from an
25 acorn that had directly fallen from the mother tree to the ground without being handled by an

1 animal seed disperser. These acorns were classified as “non-dispersed” and the remaining
2 acorns (i.e., those growing either away from any adult oak or beneath an oak that was not
3 assigned as their mother tree) as “dispersed”. The sum of dispersed acorns was used as a
4 proxy for individual trees’ “absolute” dispersal success and the proportion between the
5 dispersed acorns and the overall number of acorns mothered by a given tree was used as an
6 estimate of its “relative” dispersal success.

7 *Predictors of individual dispersal success* - We constructed generalized linear models to
8 assess the relative effect of different tree features on the absolute and the relative dispersal
9 success of individual trees. Models included the following predictor variables: tree species,
10 tree height, crop size, acorn size, acorn shape, and adult oak abundance in the neighborhood.
11 Crop size and adult oak abundance were log transformed to reach a better fit. We considered
12 no interaction terms in the final model after conducting preliminary tests. Our models
13 assumed quasi-Poisson (absolute dispersal success) and binomial (relative dispersal success)
14 errors.
15 Finally, we assessed direct relationships between tree crop size and absolute dispersal success
16 using an analysis of density dependence. For this purpose, we performed a linear regression
17 with our crop size index as predictor and the number of successfully dispersed seedlings as
18 response variable (both log-transformed). All but the parentage analysis were performed in R
19 version 3.3.0 (R Development Core Team 2016).

20

21 **RESULTS**

22 We could assign a total of 678 seedlings (82% of the overall sample) to a local mother tree
23 and classify 307 of them as non-dispersed and 371 as dispersed. A total of 115 trees (39% of
24 the local adult population) mothered at least one seedling and 87 (30%) at least one

1 successfully dispersed seedling. The distribution of seedling production was highly skewed
 2 (Fig. 1), although the trend was weaker among the dispersed seedlings (Kolmogorov-
 3 Smirnov: $D = 0.24$, $P = 0.002$).

4 The subset of 79 trees that we had characterized in the field produced 468 seedlings, of which
 5 237 had been dispersed. A total of 47 trees mothered at least one seedling and 38 at least one
 6 successfully dispersed seedling.

7 *Predictors of individual seed dispersal success* – Most tree-related variables showed large
 8 variation (Table S1 in the Online Appendix). The generalized linear model on absolute
 9 dispersal success revealed a marked positive effect of crop size (slope = 0.78), whereas
 10 relative dispersal success was exclusively predicted by, and negatively related (slope = -1.26)
 11 with, the number of fruiting oak trees within the neighborhood of the focal tree (Table 1;
 12 Figures S1a and S1b in the Online Appendix show the underlying relationships between
 13 absolute and relative dispersal success with the different predictor variables). Figure 2 shows
 14 the observed values and model predictions for the two significant variables (while Figure S2
 15 in the Online Appendix shows predictions for the same model with intervals estimated by
 16 10,000 permutations). Neither the oak species nor tree height or the acorn traits size and
 17 shape exerted any noteworthy effect on dispersal success (either absolute or relative). Finally,
 18 the regression between our crop size index and absolute dispersal success generated a slope
 19 of 0.30 ($F = 29.7$, $P < 0.001$, $R^2 = 0.28$), significantly smaller than 1 ($t = -12.52$, $df = 77$, $P <$
 20 0.001).

21

22 **DISCUSSION**

23 **Dispersal success of individual trees**

24 A large part of the seedling cohort stemmed from only a handful of mother trees while many

1 trees did not at all contribute to the seedling pool. Strong inequality in individual fecundity is
2 a widespread phenomenon in tree populations (Moran and Clark 2012) and can persist into
3 the stage of dispersed and established recruits (Schnabel et al. 1998, Sezen et al. 2007,
4 Hampe et al. 2013). Our systematic distinction of dispersed and non-dispersed offspring
5 enabled us however to detect that the skew in tree fecundity was weaker among the dispersed
6 descendants than among the overall cohort. The most likely explanation for this difference is
7 that trees with large crop sizes have a lower proportion of their acorns dispersed as a
8 consequence of disperser satiation (Hampe 2008). The existence of such an effect is
9 confirmed by the analysis of density dependence, and it is little surprising: Even highly
10 efficient scatter-hoarders such as Eurasian jays (Bossema 1979, Kollmann and Schill 1996,
11 Pesendorfer et al. 2016) should be overwhelmed by a stand-scale crop that is likely to sum
12 hundreds of thousands of acorns. Our result is at odds with the hypothesis proposed by
13 Vander Wall & Beck (2012) that scatter-hoarding seed dispersers should rarely be satiated
14 when foraging (but rather when recovering the cached seeds). The rather marked satiation
15 effect that we observed (regression slope between crop size and dispersal success = 0.30)
16 implies that acorn dispersers are a limited resource in our system for which fruiting trees have
17 to compete. Under such circumstances, tree features that influence disperser behavior can
18 directly affect dispersal success and resulting mother tree fitness (Gerzabek et al. 2017).

19

20 **Tree-related predictors of dispersal success**

21 Both absolute and relative dispersal success were exclusively driven by patterns of acorn
22 abundance, although in different ways. The most fecund trees achieved to effectively disperse
23 the greatest absolute amount of descendants. This finding fully supports the predator
24 dispersal hypothesis (Vander Wall 2010, Pesendorfer et al. 2016), which poses that larger
25 seed crops result in fitness benefits from increased seed dispersal by seed-hoarding animals.

1 When we accounted for the effect of tree fecundity by calculating relative instead of absolute
2 dispersal success, we found that this measure was negatively related with the abundance of
3 adult oaks in the neighborhood of the target tree. Although we could not quantify the crop
4 sizes of all these trees, the number of adult oaks is likely to represent a reasonably suitable
5 proxy for the local abundance of acorns. In line with our detection of a satiation effect, this
6 finding indicates that trees are competing for dispersers with their direct neighbors
7 (corresponding to the spatial scale addressed by our 10-m radius).

8 On the contrary, neither the oak species nor acorn size or shape had any measurable influence
9 on dispersal success (although the first result must be interpreted with some caution given the
10 absence of highly fecund *Q. pyrenaica* individuals; see Figs. S1a and b in the Online
11 Appendix). Our finding is noteworthy because to date most quantitative studies of drivers
12 assumed to influence the behavior of acorn dispersers have primarily focused on the oak
13 species as well as morphological or chemical traits of the acorns (e.g. Bossema 1979, Scarlett
14 and Smith 1991, Pons and Pausas 2007, Wang and Chen 2009, Shimada et al. 2015). These
15 traits have often been shown to influence the choice of scatter-hoarders under experimental
16 conditions. However, their actual relevance for effective acorn dispersal success in natural
17 settings is questioned by the results of our multi-factor study, which confirm instead the role
18 of more rarely investigated drivers such as the crop size or the spatial distribution of fruiting
19 trees (Morán-López et al. 2015, Pesendorfer and Koenig 2016; see also Pesendorfer et al.
20 2016).

21 Taken together, our results suggest that the selection of trees by acorn dispersers relies
22 primarily on visual choice based on acorn abundance and not on features that can only be
23 properly perceived from within the tree (such as acorn traits) and would have to be
24 memorized until subsequent foraging visits. In this sense, acorn dispersers in our system
25 behaved much like many avian frugivores of fleshy-fruited species (Saracco et al. 2005,

1 Hampe 2008, Carlo and Morales 2008, Prasad and Sukumar 2010, Vander Wall and Beck
2 2012). Our research approach prevented us from assessing whether acorn dispersers, once
3 settled within or beneath a given tree, tended to select certain acorn phenotypes over others.
4 Such hierarchical selection behavior is also known from frugivores of fleshy-fruited species
5 (Sallabanks 1993, Corlett 2011). However, acorn choice within the same tree should be of
6 relatively minor relevance for its dispersal success and resulting fitness.

7

8 **Consequences for oak regeneration**

9 Foraging decisions of seed dispersers are particularly important for plant species that depend
10 on a small suite of vectors for their dispersal. This is the case with the European oaks, for
11 which the Eurasian jay is widely acknowledged to be the major effective seed disperser
12 (Bossema 1979, Gómez 2003, Pesendorfer et al. 2016). The species' relevance stems not only
13 from the quantity of acorns it can mobilize and the average distance of dispersal events but
14 also from its tendency to increase the survival chances of dispersed acorns by hiding them
15 within the ground, often in microhabitats that are favorable for seedling establishment
16 (Bossema 1979, Kollmann and Schill 1996, Gómez 2003, den Ouden et al. 2005). Different
17 lines of evidence suggest that jays are likely to be responsible for much of the effective acorn
18 dispersal in our study stand (Gerzabek et al. 2017). Our findings that they (i) base their
19 foraging decisions on tree crop size and (ii) are satiated by the stand-scale acorn crop implies
20 that the foraging behavior of jays tends to favor the dominance of large, prolific trees in the
21 recruitment and resulting genetic composition of naturally regenerating oak forests. A
22 previous study performed in our oak stand revealed that the spatial genetic structure of the
23 adult tree population strikingly resembles that of the dispersed seedling cohort (Hampe et al.
24 2010). This similarity was explained by the fact that most younger adults and most dispersed
25 seedlings probably stem from the same few large founder trees. If true, it would represent an

1 empirical evidence that the foraging behavior of acorn dispersers such as jays may indeed
2 have a measurable long-term impact on the population structure of naturally regenerating oak
3 forests.

4

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11 G.G., E.K.K. and A.H. analyzed the data. All three co-authors contributed to the final text and
12 approved its final version.

13

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Table 1. Effects of the oak species, tree height, crop size, acorn size and shape, and the number of adult oaks in a radius of 10 meters around the target tree on the absolute number (= absolute dispersal success) and the proportion (= relative dispersal success) of effectively dispersed offspring according to generalized linear models (type II ANOVA, Wald χ^2 test).

Variable	Absolute dispersal success			Relative dispersal success		
	<i>F</i>	d.f.	<i>P</i>	χ^2	d.f.	<i>P</i>
Species	1.43	1	0.23	1.24	1	0.27
Tree height	0.21	1	0.64	0.38	1	0.54
Crop Size	25.87	1	<<0.001	0.23	1	0.63
Acorn size	1.27	1	0.26	0.77	1	0.38
Acorn shape	0.66	1	0.42	0.95	1	0.33
Number of adult oaks	1.13	1	0.29	48.72	1	<<0.001

- 1 **Figure 1.** Seedling production by individual *Quercus robur* mother trees. Each column
- 2 corresponds to a reproducing tree. Dark blue bars indicate those seedlings that were actually
- 3 dispersed away from the mother tree and light blue bars those that failed to be dispersed.
- 4 Black circles beneath columns indicate trees for which individual trait data were gathered.
- 5

6

Figure 2. Observed values and model predictions for each of the two single significant predictors that we identified in our regression analyses of absolute (a) and relative (b) acorn dispersal success. Shaded areas indicate the 95% confidence intervals.