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1 **How does oak mast seeding affect the feeding behavior of**
2 **sympatric red and roe deer?**

3

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17

18 **Abstract**

19 Oak reproduction is characterized by mast seeding with high inter-annual fluctuations in fruit
20 production. Such resource pulses can greatly affect ecosystem functioning and may cause seed
21 consumers to alter their mobility, demography, or diet. Consequences of mast seeding for seed
22 consumers remain poorly understood as their long timescale makes them difficult to study. We
23 investigated impacts of oak mast seeding on the feeding behavior of two sympatric European
24 deer species: red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). We analyzed their
25 rumen content over a 31-year period in tandem with 10 years of data on oak fructification (*i.e.*
26 8 years of field monitoring and two modelled years). Acorn production is strongly correlated
27 with consumption by both deer species. In years of high fructification, acorns represent more
28 than 50% and 35% of red and roe deer diet, respectively, confirming assumptions that deer
29 favor acorns when these are available. Red deer eat more acorns than roe deer both between
30 and within years. High acorn production in mast years appears to saturate the capacity of deer
31 to consume acorns. As the proportion of acorns increase in their diet, red deer eat more grasses
32 and less conifer browse. No dietary shift was found for roe deer. By inducing dietary shifts in
33 consumers, oak mast seeding can have cascading effects on ecosystem processes, notably on
34 the damages on conifers caused by red deer and the consequences for forest dynamics.

35 **Keywords**

36 Deer, diet, mast seeding, resource pulse, *Quercus*, acorn, *Cervus elaphus*, *Capreolus*
37 *capreolus*

38 **Introduction**

39 Resource pulses are events of increased resource availability characterized by low frequency,
40 large magnitude, and short duration relative to the lifespan of their consumers (Yang et al.,
41 2010). Pulsed resources occur in a wide range of ecosystems and have cascading effects at all
42 trophic levels. In terrestrial ecosystems, one of the most documented examples of pulsed
43 resources is the mast seeding of plants (Ostfeld & Keesing, 2000), which is defined as the
44 synchronous and highly variable production of seeds over the years by a population of plants
45 (Janzen, 1976). Initially, mast seeding was mainly interpreted as an evolutionary strategy that
46 aims at satiating seed and fruit predators (Ims, 1990; Janzen, 1971, 1976; Waller, 1993). The
47 predator satiation hypothesis is still supported by recent studies (Bogdziewicz, Espelta, Muñoz,
48 Aparicio, & Bonal, 2018; Moreira, Pérez-ramos, Abdala-roberts, & Mooney, 2017) and is
49 nowadays regarded as one of the main evolutionary causes of mast seeding, along with an
50 increased pollination efficiency during high flowering years (Lebourgeois et al., 2018; Pearse,
51 Koenig, & Kelly, 2016; Schermer et al., 2018). On a proximate level, recent studies tend to
52 converge on the idea that mast seeding likely results from the combination of internal resource
53 dynamics and weather cues (Bogdziewicz et al., 2019; Pearse et al., 2016). Although it is
54 practiced by some herbaceous species, the mast-seeding strategy has mainly been observed in
55 perennial species that can afford years without reproduction (Kelly, 1994; Waller, 1979). In
56 European temperate forests, this is notably the case of sessile (*Quercus petraea* (Matt.) Liebl.)
57 and pedunculate oak (*Quercus robur* L.) which exhibit a bimodal normal masting (Nussbaumer
58 et al., 2016), i.e. mast and non-mast years can be identified statistically but non-mast years are
59 generally associated with a minimal production of fruits (Kelly, 1994).

60 In years of high oak fructification, acorns represent a high-quality and easily accessible resource
61 (Kirkpatrick & Pekins, 2003) and are consumed by a wide variety of wildlife species, notably
62 rodents, birds, and ungulates (den Ouden, Jansen, & Smit, 2005; Herrera, 1995; Steele,

63 Knowles, Bridle, & Simms, 1993). Oak mast seeding has been shown to affect the demography
64 (Bieber & Ruf, 2005), abundance (Schnurr, Ostfeld, & Canham, 2002), body condition
65 (Harlow, Whelan, Crawford, & Skeen, 1975), movement (McShea & Schwede, 1993) and diet
66 (den Ouden et al., 2005; Picard, Oleffe, & Boisaubert, 1991) of a wide variety of vertebrates
67 via direct and indirect effects. The effects of mast seeding are strongly dependent on the type
68 of consumer (Ostfeld & Keesing, 2000). For small species with a rapid increase rate – i.e. birds,
69 rodents – mast seeding generally leads to a numerical response, with more individuals following
70 mast years (Bogdziewicz, Zwolak, & Crone, 2016; Schnurr et al., 2002). As the home range of
71 ungulates and birds may exceed the spatial scale of a mast seeding event, these species may
72 also respond by moving towards areas where mast seeding occurs (Lindén, Lehikoinen,
73 Hokkanen, & Väisänen, 2011; McShea & Schwede, 1993). Lastly, because pulsed resources
74 are only available sporadically, the resource is mostly consumed by generalist species which
75 are able to adapt their diet in the absence of the resource (Ostfeld & Keesing, 2000). Generalist
76 consumers like black bear (*Ursus americanus*) (McDonald & Fuller, 2005) or wild boars (*Sus*
77 *scrofa*) (Herrero, Irizar, Laskurain, García-Serrano, & García-González, 2005) have been
78 shown to exhibit important dietary shifts in a context of oak mast seeding.

79 Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are amongst the most
80 widespread ungulate species in Europe and often occur in sympatry in temperate forests. The
81 coexistence of the two species is notably allowed by a segregation of their feeding niche
82 (Storms et al., 2008). Red deer is classified as an “intermediate feeder”, able to adapt to
83 fluctuations in resource availability and quality in its environment (Storms et al., 2008).
84 Although the species avoids fibers as much as possible, it is able to consume grass when
85 resources are scarce (Dumont et al., 2005). According to Hofmann’s classification of ruminant
86 feeding types, roe deer has a “moose-type” digestive track (Hofmann, 1989), and is thus
87 characterized by a strong selectivity and an inability to digest fiber-rich food items. This species

88 has been identified as a typical “browser” and it mostly feeds on bramble, buds, forest fruits
89 and cultivated seeds (Felton, Wam, Stolter, Mathisen, & Wallgren, 2018; Redjadj et al., 2014;
90 Tixier & Duncan, 1996). Due to a more restricted feeding niche, roe deer is more dependent on
91 the resource available in its habitat than red deer (Storms et al., 2008).

92 Since acorns are characterized by a high energetic content and digestibility, and are available
93 in a period when other resources are scarce for red deer and roe deer (autumn and winter), we
94 may expect these species to shift toward an acorn-enriched diet during years of mast seeding.
95 However, acorns may also be considered as a nutritionally imbalanced food item – i.e. food that
96 does not contain the same balance of nutrients as needed by the animal to reach the intake target
97 (Simpson & Raubenheimer, 2011) – due to its low protein content (Kirkpatrick & Pekins,
98 2003). It has indeed been shown that species that consume a high proportion of acorns may
99 exhibit a negative nitrogen balance (Harlow et al., 1975; Kirkpatrick & Pekins, 2003). The
100 nutrient balancing hypothesis predicts that when sufficient food is available, the animal’s goal
101 is to reach a nutritionally balanced diet (Simpson & Raubenheimer, 2011). Under that
102 perspective, deer would thus have to compensate acorn consumption with complementary food
103 items that are rich in nitrogen. Acorns are also rich in tannins, secondary metabolites known to
104 deter herbivores by lowering the digestibility and nutritional value of plant tissues (Iason,
105 2005). Cervids have been shown to be relatively tolerant to plant secondary metabolites such
106 as tannins (Iason & Villalba, 2006), notably roe deer due to its salivary proteins that may bind
107 with tannins (Tixier et al., 1997a). However, the ingestion of high levels of tannins comes with
108 a cost (e.g. cost of detoxification) (Iason & Villalba, 2006) and whether this resource is
109 sufficiently beneficial for red and roe deer to induce a dietary shift is still debated. Several
110 studies have documented that acorns may dominate the diet of white-tailed deer (*Odocoileus*
111 *virginianus*) (Harlow et al., 1975; McShea & Schwede, 1993), red deer (Picard et al., 1991) and
112 roe deer (Abbas et al., 2011) in years of mast seeding. However, most of these studies were

113 conducted over a period that did not exceed three years and were limited to a binary comparison
114 of mast years vs. non-mast years, without any quantification of the magnitude of oak
115 fructification. To our knowledge, an analysis of the relationship between the magnitude of oak
116 fructification and deer diet is still lacking.

117 The recent increase of deer populations in most northern hemisphere countries, and especially
118 the damage that they cause on young forest stands is a major issue for sustainable forest
119 management (Bégin, Tremblay, Thiffault, Pothier, & Côté, 2016; Côté, Rooney, Tremblay,
120 Dussault, & Waller, 2004). A modification of red and roe deer diets in years of mast seeding is
121 likely to change their consumption of forest vegetation, both in composition and intensity.
122 Understanding how oak mast seeding shapes red and roe deer diet is thus critical to assess the
123 consequences of this phenomenon on the forest damage caused by the two species. The issue is
124 all the more important as several studies have reported that oak fructification is determined by
125 spring weather conditions: mast-seeding frequency is thus likely to be sensitive to changes in
126 climate conditions (Koenig, Knops, Carmen, Stanback, & Mumme, 1996; Schermer et al.,
127 2018). In the context of a long-term monitoring of red and roe deer rumen content and oak
128 fructification in La Petite Pierre National Hunting and Wildlife Reserve (NHWR), we will
129 examine the following hypotheses:

130 H1: Because of their high energetic content and digestibility, acorns are highly consumed by
131 both deer species during years of mast seeding, especially in October, at the peak of acorn
132 availability.

133 H2: Red deer consumes a higher proportion of acorns than roe deer during mast years, due to
134 its better ability to adapt to fluctuating resources.

135 H3: To compensate for the acorn's low protein content, acorn consumption affects red and roe
136 deer diet in favor of the more nutritious items in autumn and winter – i.e. mainly bramble for
137 roe deer and bramble and grass for red deer (Dumont et al., 2005).

138

139

140

141 **Materials and methods**

142

143 *Study area*

144 La Petite Pierre National Hunting and Wildlife Reserve (hereinafter referred to as “LPP”) is a
145 2.674 ha unfenced forest located in the Vosges mountain range, in northeast France (48.5°N,
146 7.0°E). The climate is continental with oceanic influences, involving cool summers and mild
147 winters: mean January and July temperatures since 1986 at the Phalsbourg weather station,
148 located 10 km from LPP, are respectively 1.35 °C and 19.0 °C (data from Météo France). Snow
149 accumulation is rare. The mean elevation is 300 m and the topography is characterized by a
150 succession of small hills and steep-sided valleys. The sandstone substrate produces poor acidic
151 soils; the vegetation is thus characterized by a low diversity and low nutritional quality for
152 herbivores. The forest is structured in even-aged clusters of trees, and includes roughly an equal
153 proportion of broadleaved (mainly common beech *Fagus sylvatica* and sessile oak) and
154 coniferous (mainly silver fir *Abies alba*, Norway spruce *Picea abies* and Scots pine *Pinus*
155 *sylvestris*) tree species. Free-ranging populations of red deer, roe deer and wild boar are present
156 in LPP. The reserve is free of big game predators and ungulate populations are managed through
157 hunting, with an average of 48 (min: 24, max: 102) red deer and 43 (min: 19, max: 88) roe deer
158 harvested per year since 1986. The annual population dynamics of red deer in LPP estimated
159 using the capture-mark-recapture method from 1986 to 2018 are presented in Supplementary
160 material Appendix B, Fig. B.1.

161 *Diet analysis*

162 We analyzed rumen samples taken from red deer and roe deer shot by hunters in LPP during
163 the legal hunting season (from the beginning of October to the end of January). All samples
164 came from animals tagged with annual hunting quotas delivered by the county prefect in

165 compliance with the French Environmental Code (Art. R425-2 to 425-14113). The animals
166 were not harvested following a protocol specific to this study. From 1986 to 2018, a total of
167 330 and 231 samples of red and roe deer rumen, respectively, had been collected. The number
168 of rumen analyzed per year for each species is indicated Fig. 1.B. We noted the exact date of
169 harvest for each culled animal. The inter-annual fluctuations in the number of rumen analyzed
170 per year are the results of the management of deer populations in the NHWR that lead to
171 fluctuations in the number of animals shot per year, a shortage of staff to collect and analyze
172 the rumen before 2005, and occasional extreme climatic events (e.g. Lothar storm in December
173 1999) that could lead to an absence of harvest in some years.

174 For each culled individual, 500 g of rumen were frozen until analysis. Once defrosted, the
175 samples were washed and sieved through a 5-mm mesh. The material is sieved to avoid an
176 overrepresentation of the larger particles (Chamrad & Box, 1964), that are harder to digest and
177 that occupy more space (note that sieving could however lead to a slight under-estimation of
178 certain food items such as lignified fragments). The rumen content was also carefully mixed to
179 ensure that all items were randomly distributed. The material was then sorted macroscopically
180 using a method derived from the point-frame technique developed by Chamrad & Box (1964):
181 a portion of the sieved items was mixed with water and placed in a rectangular tray. A grid with
182 100 intersection points at the bottom of the tray allowed the selection of 100 items
183 (Supplementary material, Appendix E, Fig. E.1), which were identified to the lowest possible
184 taxon using a binocular loupe and a reference collection of the local flora. This process was
185 repeated 3 times so that 300 items could be identified per rumen. The proportion of a given
186 taxon in a rumen was computed as a percentage of occurrence of the taxon in the rumen. It has
187 been shown by Dubois (1992) that this percentage of occurrence was not significantly different
188 from the percentage obtained when the whole rumen sample was analyzed, nor from the
189 weighted percentage obtained after drying and weighing the 300 items.

190 For the purpose of the analysis, we grouped all the taxa in 15 food categories: acorns, shrub
191 leaves, conifer needles, grasses, dry fruits, fern, deciduous leaves, crops, fungi, dicotyledonous
192 herbaceous species, buds, bryophytes, animal fragments, unidentified and others. For each
193 rumen analyzed, the proportion of a given food category in the diet was computed as the sum
194 of the proportions of all the taxa that belonged to the food category. The main taxa of each food
195 category are listed in Supplementary material Appendix D, Table D.1.

196 As the acorns were partly digested, genetic analyses would have been necessary to identify the
197 oak species (sessile or pedunculate). Although sessile oak is far more abundant than
198 pedunculate oak in the studied forest, the category ‘acorns’ thus includes the fruits of both oak
199 species.

200

201 *Oak fruit production*

202 Direct measurement

203 Sessile oak fructification was measured in LPP with the “ground-plot counting method”
204 (Touzot et al. 2018), which consists in counting acorns on the ground under the tree crown in
205 quadrats of known area and without protection against seed predators. For each monitored oak
206 tree, 4 quadrats of 0.25 m² (0.5 m x 0.5 m) were placed at a distance of 1 m to 4 m from the
207 trunk. Soon after the main acorn drop which generally occurs in the first two weeks of October,
208 we gathered and counted the fruits collected in the four quadrats to obtain a number of acorns
209 sampled per tree. From 2010 to 2017, 30 trees were monitored with this method in LPP.
210 Selected trees were located at a sufficient distance from any other mature oak tree to avoid any
211 potential contamination from any adjacent tree during the counting: they were selected
212 randomly and no criteria on the characteristics of the trees (e.g. height, diameter, shape of the

213 tree crown) were taken into account. The fructification f_i for a given year i was computed as the
214 mean number of acorns sampled per tree:

$$215 \quad f_i = \frac{\sum_{y=1}^{30} t_{y,i}}{30} \quad (\text{Eq. 1})$$

216 Where $t_{y,i}$ represents the number of acorns sampled for tree y in year i .

217 This value was divided by the maximum fructification observed at LPP during the study period
218 to obtain a relative fructification F_i , ranging between zero and 1.

$$219 \quad F_i = \frac{f_i}{\max(f_{2010}, \dots, f_{2017})} \quad \text{with } i \in [2010; 2017] \quad (\text{Eq. 2})$$

220 In addition, a categorical variable reflecting relative fructification was created, with three
221 classes corresponding to increasing F_i values: low ($F_i < 0.15$), partial ($F_i \in [0.15, 0.6]$) and
222 high ($F_i > 0.6$) relative fructification.

223

224 Modeling of oak mast seeding in LPP

225 The aim was to complete the eight years of fructification monitoring in LPP by modeling
226 additional years. Schermer et al. (2018) identified April temperature and the previous year's
227 fructification as the two main factors explaining oak mast seeding using a long-term monitoring
228 of oak fructification in 30 sites of the European network RENECOFOR from 1993 to 2008
229 (Ulrich, 1995). Based on this result, we integrated the fructification data of LPP and of four of
230 the RENECOFOR sites that were located within a 200 km radius in a predictive Bayesian model
231 with April temperature and previous-year fructification as explanatory variables. Note that this
232 model predicts a relative fructification, ranging between zero and 1. As the previous year's
233 fructification was included in the model, the model is considered first order autoregressive –
234 i.e. the precision of the prediction decreases for each additional year predicted. For this reason,

235 we only kept for analysis the two first years (2008 and 2009). Finally, a total of 10 years (2
236 years with modeled fructification and 8 years with observed fructification) were available for
237 the study. The predictive model is presented in detail in the Supplementary Material, Appendix
238 C.

239

240 *Data analysis*

241 Effect of oak fructification on the mean acorn proportion in red and roe deer diet

242 We analyzed the relationships between the relative fructification of oak and the mean annual
243 acorn consumption of red deer and roe deer using a linear mixed-effect model (lme4 package)
244 (Bates, Mächler, Bolker, & Walker, 2014) with two fixed effects (fructification and deer
245 species) and one random effect (hunting season). We tested the significance of the effects using
246 a type II Wald χ^2 test using the Anova function in the “car” package of R (Fox & Weisberg
247 2011). An interaction between the two fixed effects was included in the model. To fit the
248 assumption of normality for the error distribution, the annual acorn consumption was arcsine
249 square root transformed prior to analysis (Zar, 1984). For each species, we excluded from this
250 analysis the years with less than 4 individuals. Oak fructification is characterized by significant
251 temporal autocorrelations that we quantified in the Bayesian model (Supplementary material
252 Appendix C, Fig. C.2). We checked that these temporal autocorrelations did not affect our linear
253 model by examining the model residuals.

254 Intra-annual variations in the proportion of acorns in the diet were analyzed and compared for
255 the two deer species on the month scale. Intra-annual variations were assumed to depend on the
256 total annual amount of available resources, the analyses were thus performed separately for
257 years with low ($n = 6$), partial ($n = 3$) and high ($n = 1$) relative fructification. For each of the
258 three categories of relative fructification, we conducted a two-way ANOVA to test the effect of

259 species (factor with two levels: “red deer” and “roe deer”), month (ordered factor with four
 260 levels: “October”, “November”, “December” and “January”) on the proportion of acorns in the
 261 diet. For each class of relative fructification, an interaction between the two factors was
 262 included. In the case of a significant effect of the month, we tested the differences between the
 263 four levels of this factor with Tukey’s HSD test.

264

265 Effect of acorn consumption on red deer and roe deer feeding behavior

266 The aim was to investigate whether the main resources consumed by red and roe deer were
 267 favored or discriminated against when the proportion of acorns increased in the diet. In a first
 268 step, we determined which of the 15 food categories were the most consumed by each deer
 269 species. We defined $\gamma_{[\text{red}]i,k}$ and $\gamma_{[\text{roe}]i,k}$ as the proportion of the food category i ($i \in [1; \dots; 15]$) in
 270 the rumen k for red deer and roe deer, respectively. We computed the total proportion of each
 271 food category i in the diet of red deer ($\Gamma_{[\text{red}]i}$) and roe deer ($\Gamma_{[\text{roe}]i}$) as:

$$\left\{ \begin{array}{l} \Gamma_{[\text{red}]i} = \frac{\sum_{k=1}^{n_{[\text{red}]}=330} \gamma_{[\text{red}]i,k}}{\sum_{j=1}^{15} \sum_{k=1}^{n_{[\text{red}]}=330} \gamma_{[\text{red}]j,k}} = \frac{\sum_{k=1}^{n_{[\text{red}]}=330} \gamma_{[\text{red}]i,k}}{330} \\ \Gamma_{[\text{roe}]i} = \frac{\sum_{k=1}^{n_{[\text{roe}]}=231} \gamma_{[\text{roe}]i,k}}{\sum_{j=1}^{15} \sum_{k=1}^{n_{[\text{roe}]}=231} \gamma_{[\text{roe}]j,k}} = \frac{\sum_{k=1}^{n_{[\text{roe}]}=231} \gamma_{[\text{roe}]i,k}}{231} \end{array} \right. \quad (\text{Eq. 3})$$

273 Where $n_{[\text{red}]}$ and $n_{[\text{roe}]}$ are the respective numbers of red and roe deer rumens collected. The
 274 computed proportions of each category are presented in Supplementary material Appendix D,
 275 Table D.1. We only selected for this analysis the categories that represented on average more
 276 than 5% of the diet of a given deer species ($\Gamma_{[\text{red}]} > 5\%$ or $\Gamma_{[\text{roe}]} > 5\%$). The categories “others”
 277 and “unidentified” were not included, nor was the “acorns” category. $N_{[\text{red}]}$ and $N_{[\text{roe}]}$ food
 278 categories represented more than 5% of red and roe deer diet, respectively. To restrict the
 279 analysis to these categories, we computed the relative proportions of each selected category i

280 in the rumen k ($\gamma'_{[red]i,k}$ and $\gamma'_{[roe]i,k}$) so that for each rumen, the relative proportions of the N
 281 selected categories add up to 1:

$$\left\{ \begin{array}{l} \gamma'_{[red]i,k} = \frac{\gamma_{[red]i,k}}{\sum_{j=1}^{N_{[red]}} \gamma_{[red]j,k}} \\ \gamma'_{[roe]i,k} = \frac{\gamma_{[roe]i,k}}{\sum_{j=1}^{N_{[roe]}} \gamma_{[roe]j,k}} \end{array} \right. \quad \text{(Eq. 4)}$$

283 Since for each rumen, the relative proportions of the selected food categories add up to 1, we
 284 studied the effect of acorn proportion in the diet (γ_{acorn}) on these proportions with a
 285 multinomial Dirichlet regression. We fitted for each deer species the following Dirichlet
 286 multinomial regression model on a system with N equations :

$$\left\{ \begin{array}{l} \ln(\gamma'_1) = \alpha_1 + \beta_1 * \ln(\gamma_{acorn}) \\ \dots \\ \ln(\gamma'_i) = \alpha_i + \beta_i * \ln(\gamma_{acorn}) \\ \dots \\ \ln(\gamma'_N) = \alpha_N + \beta_N * \ln(\gamma_{acorn}) \end{array} \right. \quad \text{(Eq. 5)}$$

288

289 We used the R package “DirichletReg” (Maier, 2014) to run the Dirichlet multinomial
 290 regression models. All the analyses were performed with the R statistical framework (R Core
 291 Team 2019).

292

293 **Results**

294

295 *Inter-annual variations of acorn consumption and oak fructification*

296 From 2008 to 2017, oak fructification in LPP exhibited high inter-annual fluctuations (Fig. 1A).
297 The maximum fructification in the study site occurred during the hunting season 2011/2012
298 (109 acorns/m², relative fructification = 1). The following year, oak fructification reached a
299 minimum of 0 acorns/m² (relative fructification = 0). From 1986 to 2017, acorns represented
300 on average 9.4% and 4.2% of the red and roe deer diet, respectively. The peak of oak
301 fructification (hunting season 2011/2012) in LPP matched the peak of acorn consumption for
302 both deer species (Fig. 1). In that season, acorns represented on average 52% and 34% of red
303 and roe deer diet, respectively. At the inter-annual scale, the proportion of acorns in the diet
304 was 15% higher on average ($p < 0.001$) in red deer than in roe deer. Mean acorn proportion in
305 the diet significantly increased with oak fructification ($p < 0.001$), with a higher slope for red
306 deer ($p = 0.027$) (Supplementary material: Appendix A, Fig. A.1; Appendix F, Table. F.1).

307

308 *Intra-annual variations in acorn consumption*

309 On the intra-annual scale, the proportion of acorns in the red deer diet was also higher than in
310 the roe deer diet in a context of low ($p = 0.005$), partial ($p = 0.018$) and high ($p = 0.034$) relative
311 fructification (Fig. 2; Supplementary material Appendix F, Table. F.2). The interaction between
312 deer species and month was not significant in years of low ($p = 0.58$), partial ($p = 0.49$) or high
313 ($p = 0.16$) fructification (Supplementary material Appendix F, Table. F.2), which means that
314 for the three classes of relative fructification, red deer consumed a higher proportion of acorns
315 than did roe deer throughout the hunting season. In years of low relative fructification, acorns

316 represented an average of 4% and 1% of red and roe deer diet, respectively, and remained stable
317 from October to January ($p = 0.43$) for both deer species. In years of partial relative
318 fructification, the proportion of acorns in the diet of both deer species was lower in December
319 and January than in October and November ($p < 0.001$). Red and roe deer respectively
320 consumed 47% and 34% of acorns in October, while these proportions decreased to respectively
321 14% and 15% in January (Fig. 2). In the context of high relative fructification, acorn proportion
322 remained stable throughout the hunting season in red and roe deer diet ($p = 0.13$), with an
323 average proportion of 52% and 34%, respectively.

324

325 *Effect of acorn consumption on red and roe deer feeding behavior*

326 For red deer, 4 out of the 14 food categories represented more than 5% of the species' diet, and
327 were therefore selected for the analysis: shrub leaves, conifer needles, grasses, and ferns
328 (Supplementary material Appendix D, Table D.1). Fig. 3 shows the relationship between the
329 relative proportion (γ') of these four food categories and the proportion of acorn in the diet, and
330 the fitted Dirichlet regressions. The multinomial Dirichlet regression conducted for red deer
331 indicates that the relative proportion of conifer needles significantly decreased when the
332 proportion of acorns in the diet increased, while the relative proportion of grasses significantly
333 increased (Table 1). The fitted model indicated that when acorns were marginal in the diet
334 (acorn proportion $\leq 1\%$), red deer mainly consumed shrub leaves ($\gamma' = 43\%$) and conifer needles
335 ($\gamma' = 29\%$), while ferns ($\gamma' = 12\%$) and grasses ($\gamma' = 16\%$) only represented a minor part of the
336 diet. In contrast, acorn-enriched rumens of red deer contained almost as much grasses ($\gamma' =$
337 34%) as shrub leaves ($\gamma' = 47\%$) while conifer needles ($\gamma' = 5\%$) were almost absent from the
338 diet (Fig. 3).

339 In the case of roe deer, three food categories represented more than 5% of the diet and were
340 selected for the analysis: shrub leaves, conifer needles and ferns (Supplementary material
341 Appendix D, Table D.1). The multinomial Dirichlet regression indicated that for roe deer, the
342 relative proportions of these 3 food categories remained unchanged when the acorn proportion
343 increased in the diet (Table 1, Fig. 3).

344

345 **Discussion**

346

347 *Oak fructification as a major determinant of deer diet*

348 Oak mast seeding is a characteristic example of resource pulse that may lead to a significant
349 dietary shift for several generalist consumers (Herrero et al., 2005; McDonald & Fuller, 2005;
350 Sato & Endo, 2006). Although deer are known for consuming mainly plant tissues (Dumont et
351 al., 2005; Storms et al., 2008; Tixier et al., 1997b), our study confirmed that both red and roe
352 deer shifted their diet to an acorn-enriched one in a context of oak mast seeding, consistently
353 with our hypothesis (H1). When the peak of fructification occurred, acorns represented more
354 than half of the red deer diet (52%), which is consistent with the proportions found in the study
355 of Picard et al. (1991) in a context of oak mast seeding (50.8%). In addition, it is likely that in
356 both cases, these proportions were underestimated as they were obtained with rumen content
357 analyses, a technique which is known for overestimating poorly digestible items (e.g. grasses,
358 woody shoots or dead leaves) and for underestimating the most digestible portions of the diet
359 (e.g. forbs, acorns) (McInnis, Vavra, & Krueger, 1983). Our study also provides evidence that
360 in a context of partial fructification, acorns still represent a large part of the red and roe deer
361 diet. This result suggests that this resource is particularly palatable for both deer species.
362 Considering the daily quantity of food ingested by both deer species (Brown, 1992), the
363 proportions of acorn found in deer diet also indicates that at high densities, red and roe deer
364 may strongly contribute to acorn predation in temperate forests, along with boars, rodents and
365 birds (den Ouden et al., 2005). Several authors have discussed the potential benefits of an acorn-
366 enriched diet for their consumers. Pekins and Mautz (1988) and Harlow et al. (1975) showed
367 that the consumption of acorns by white-tailed deer instead of wintergreen leads to a strong
368 increase in metabolizable energy per gram, resulting in a reduced foraging time and the meeting

369 of energy requirements in winter. McDonald and Fuller (2005) also reported a positive effect
370 of acorn consumption on milk quality for black bear females. In the case of red and roe deer,
371 the consequences of acorn consumption are still poorly documented and deserve further
372 investigation as it could have positive effects on the population dynamics of these species, as
373 reported for wild boar (Bieber & Ruf, 2005).

374 In the case of partial fructifications, we observed an intra-annual variability in acorn
375 consumption for both deer species: consistently with our initial hypothesis (H1), acorn
376 proportion in the diet was higher in October and in November, the month of the main acorn
377 drop and the following. The main assumption to explain this pattern is a depletion of the acorn
378 stock from October to January due to predation by deer (Harlow et al., 1975; Tixier & Duncan,
379 1996) but also by the other seed consumers such as wild boars (Herrera, 1995), rodents or jays
380 (den Ouden et al., 2005; Steele et al., 1993). Under this assumption, this result suggests that a
381 partial fructification is not sufficient to induce a satiation of the seed predators (Kelly, 1994)
382 and therefore that a large proportion of all acorns available is consumed. Consequently, the low
383 remaining quantity of acorns might not be sufficient to ensure the regeneration success of oak
384 stands. An alternative hypothesis is that the palatability and/or the nutritional value of acorns
385 decreased from October to January due to a fast degradation of acorn tissues when lying on the
386 soil. Tejerina et al. (2011) showed that in the case of holm oak (*Quercus ilex*) the content in
387 several phenolic compounds increased throughout autumn and winter, probably due to the
388 process of ripening and germination. Acorns are also more likely to be rotten or damaged by
389 pathogens at a more advanced stage of the acorn crop season. Despite this potential decrease in
390 acorn palatability, it is noteworthy that in the case of high fructification, acorn consumption
391 remained stable until January for both species (Fig. 2). This observation provides strong support
392 for the resource depletion hypothesis as an explanation for the decrease in the proportion of
393 acorns in the diet observed after November in years of partial fructification. This phenomenon

394 could also be interpreted as a factual argument supporting the predator satiation hypothesis as
395 a possible evolutionary explanation for mast seeding (Ims, 1990; Kelly, 1994). Indeed, the
396 predator satiation hypothesis assumes that seed predators exhibit a type II or type III functional
397 response, i.e. at high seed densities, the proportion of attacked seeds should decrease with
398 increasing seed densities (Bogdziewicz et al., 2018; Moreira et al., 2017). In our study, as the
399 main acorn drop occurs in October, the acorn density necessarily decreases from October to
400 January because of predation. Under the assumption that acorn proportion in deer diet reflects
401 the quantity of acorns consumed, a constant acorn consumption throughout this period – as
402 observed in a context of high fructification – would indicate that the proportion of predated
403 acorns decreases with acorn density. Our results therefore seem to confirm that the red and roe
404 deer's diet modification in response to mast seeding is compatible with the predator satiation
405 hypothesis.

406

407 *Interspecific differences in acorn consumption*

408 At both the intra-annual (Fig. 2) and inter-annual scale (Fig. 1, Supplementary material
409 Appendix A, Fig. A.1), we found a higher acorn proportion in the red deer diet than in the roe
410 deer diet, in agreement with our initial hypothesis (H2). This pattern is most likely related to
411 the digestive morphology of the two studied species. As an intermediate feeder, red deer has
412 been shown to be highly adapted to fluctuations in resource availability (Storms et al., 2008).
413 In winter, in a context of scarce resources, this species switches to a grass-based diet, despite
414 the high fiber content of this resource (Dumont et al., 2005; Redjadj et al., 2014). In contrast,
415 as a browser, roe deer is far more selective and has a more restricted feeding niche (Tixier et
416 al., 1998). The higher flexibility of red deer may partly explain why it exploits the sudden
417 increase of resource availability to a greater extent than roe deer. In addition, while although
418 acorn pulp has been shown to be highly digestible, the shell, also ingested by deer, is poorly

419 digestible and rich in fibers (Kirkpatrick & Pekins, 2003). Since roe deer is unable to feed on
420 poorly digestible items, we may assume that the acorn shell's nutritional characteristics prevent
421 roe deer from consuming a high proportion of acorns, while red deer is not limited thanks to its
422 more flexible stomach structure. This result could also be interpreted under the framework of
423 the nutrient balancing hypothesis (Simpson & Raubenheimer, 2011): red deer's consumption
424 of significant portions of grass tissues with a very low secondary metabolites content might
425 balance for acorn high tannin content. On the other hand, due to the high secondary metabolite
426 content in the food items preferred by roe deer (i.e. deciduous leaves, dicot herbs), this species
427 would not be able to compensate for the high input of tannins by acorns. Interspecific
428 differences in acorn consumption may also be explained by the nutritional requirements of the
429 two studied species. Indeed, red deer are classified as capital breeders as they rely on fat stored
430 during summer and autumn to face winter; while roe deer are income breeders and are unable
431 to store fat reserves (Brown, 1992). The main nutritional property of acorns is their high
432 energetic content (Kirkpatrick & Pekins, 2003) and this resource is mainly available in autumn.
433 We may therefore assume that consuming acorns may be more beneficial for red deer by
434 providing extra fat reserves for winter.

435

436 *Consequences of acorn consumption on deer feeding behavior*

437 Our analyses of the composition of red and roe deer diets were consistent with their respective
438 feeding types. Red deer has a diverse diet that included fiber-rich items such as grasses while,
439 as reported in other studies (Storms et al., 2008; Tixier et al., 1997b), roe deer has a poorly
440 diversified bramble-based diet (Supplementary material Appendix D, Table D.1), one of the
441 most digestible species available in winter (Dumont et al., 2005). The proportions of all the
442 items consumed are likely to decrease with an increasing proportion of acorns in the diet.
443 Nevertheless, it is critical to understand whether acorns, due to their nutritional characteristics,

444 change the relative proportions of these resources in deer diet in order to assess whether some
445 plant species will be more affected than others by increased acorn availability.

446 Our results showed that increased acorn consumption strongly reduced the proportion of conifer
447 shoots in the red deer diet, as they were partly replaced by grasses, in agreement with our
448 hypothesis (H3). Indeed, although the energetic content of acorns is higher than that of most
449 items available in autumn and winter, their protein content is relatively low and animals that
450 consume acorns may exhibit a negative nitrogen balance (Abbas et al., 2011; Kirkpatrick &
451 Pekins, 2003). In winter, grasses have been shown to be more nutritious than the conifer species
452 present in the study area (*i.e.* silver fir, Norway spruce and Scots pine) (Dumont et al., 2005).
453 In the framework of the nutrient balancing hypothesis, grasses and acorns could be seen as
454 nutritionally complementary food items – *i.e.* combination of nutritionally imbalanced foods
455 that jointly enable animals to reach their nutrient intake target (Simpson & Raubenheimer,
456 2011). Switching from conifer shoots to grasses would allow red deer to benefit from the
457 energetic content of acorns while maintaining a positive nitrogen balance. This result could thus
458 be interpreted as an argument supporting the nutrient balancing hypothesis, along with similar
459 dietary shifts that have been observed in moose when provided with supplementary feeding
460 (Felton, Felton, Cromsigt, et al., 2016; Felton, Felton, Raubenheimer, et al., 2016).

461 Surprisingly, roe deer's diet composition was not affected by acorn consumption. This may be
462 explained by the fact that unlike red deer, acorn proportion rarely exceeded 50% in the roe deer
463 diet, which lowered the risk of a nitrogen imbalance for this species. In addition, the main items
464 consumed by roe deer – *i.e.* bramble, conifer shoots and ferns – have a relatively similar protein
465 content (Gonzalez-Hernandez & Silva-Pando, 2007), and mostly differ in their digestibility
466 (Dumont et al., 2005). Previous studies have shown that red deer has a more diversified diet
467 and is better able to adapt its feeding behavior in a context of resource scarcity than roe deer
468 due to different digestive physiologies (Richard, Gaillard, Saïd, Hamann, & Klein, 2010;

469 Storms et al., 2008). Our results therefore support the idea that in the context of a resource
470 pulse, although both species adapt their feeding behavior, red deer shows more flexibility to
471 benefit from the increased resource availability.

472

473 **Conclusion**

474 Resource pulse events such as oak mast seeding are known to have a major influence on
475 ecosystem functioning but these events are inherently difficult to study due to their rare
476 occurrence. Based on oak-deer interactions, we showed that oak mast seeding, by providing a
477 significant alternative forage in a period of low resource availability, induced a dietary shift for
478 both red and roe deer. These two species included large proportions of acorns in their diet
479 whenever this resource was available. We also provided evidence that red deer, owing to its
480 broader feeding niche, showed more flexibility than roe deer in its diet to exploit the resource
481 pulse by including a larger proportion of acorns and by adapting the relative proportion of other
482 resources consumed. Red deer dietary shift from conifer – economically valuable trees – to
483 grass suggests that mast seeding could lead to a short-term reduction of the forest damages
484 caused by deer, which would have significant implications for forest management.
485 Nevertheless, further studies should test whether red deer dietary shift is sufficient to affect the
486 browsing damages caused by this species. In addition, if acorn consumption were to benefit
487 deer reproductive success as it has been shown for wild boar (Bieber & Ruf, 2005), in years
488 following mast seeding, higher damages could be expected to occur due to a combination of
489 resource scarcity and increased deer population. Further studies should thus be carried out to
490 better understand how mast seeding may affect deer populations. More generally, as resource
491 pulses like mast seeding are likely to be sensitive to climate change, there is an increasing need

492 for long-term studies on the consequences of these events for temperate forest ecosystem
493 functioning.

494

495

496

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498

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509

510 **Appendix A. Supplementary data**

511 Supplementary material related to this article can be found, in the online version, at XXXXX.

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692

693

694 **Figure captions**

695

696 Fig. 1. Inter-annual variations in (A) oak relative fructification and (B) the proportion of acorn
697 in red deer and roe deer diet. Fructifications values are given as the proportion of acorns counted
698 for a given year with the ground-plot method (Touzot et al., 2018) relative to the maximum
699 ever counted at that site (mean \pm standard error). Years are presented as hunting seasons to
700 allow comparison between the two graphs.

701

702 Fig. 2. Intra-annual variation in the proportion of acorns in red deer and roe deer diet (mean \pm
703 standard error) for different fructification levels. Months with $n < 2$ were removed from the
704 dataset.

705

706 Fig. 3. Relative proportions of the main food categories consumed, in relationship with the
707 proportion of acorn in the diets of (a) red deer and (b) roe deer. The lines represents the fitted
708 Dirichlet regression model (Eq. 5). Red lines indicate significant relationships ($p < 0.05$). Model
709 results for each food category are presented in Table 1.

710

711 **Table 1:** α_2 coefficient statistics from Dirichlet regression of the model referring to Eq. 5 for
 712 estimating the relative proportion of the main resources consumed by red deer and roe deer
 713 with the proportion of acorns in the diet.

714

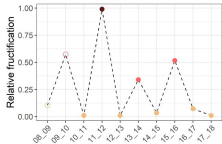
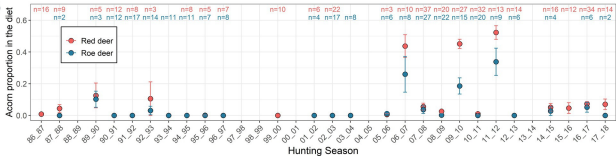
	Red deer			Roe deer		
	Estimate	SE	p-value	Estimate	SE	p-value
Shrub leaves	0.3772	0.4946	0.45	0.5907	0.8868	0.51
Conifer needles	-2.0336	0.4788	< 0.001*	0.8428	0.8405	0.316
Fern	0.5215	0.4604	0.26	0.9886	0.7215	0.171
Grasses	1.2168	0.4456	0.006*			

715

716

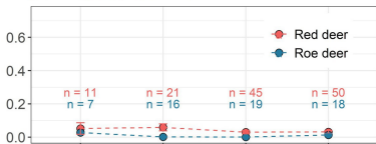
(A)

- Field data
 - Modelled
-
- Low
 - Partial
 - High Fructification

**(B)**

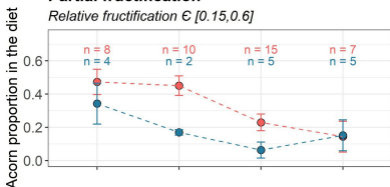
Low fructification

Relative fructification < 0.15



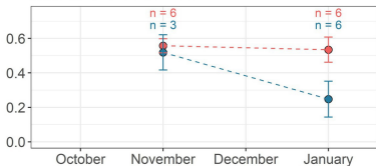
Partial fructification

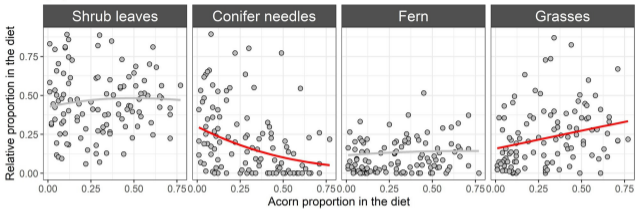
Relative fructification $\in [0.15, 0.6]$



High fructification

Relative fructification > 0.6



(A)**(B)**