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

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Abstract

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

Keywords

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

Introduction

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

In years of high oak fructification, acorns represent a high-quality and easily accessible resource (Kirkpatrick & Pekins, 2003) and are consumed by a wide variety of wildlife species, notably rodents, birds, and ungulates (den Ouden, Jansen, & Smit, 2005; Herrera, 1995; Steele, Knowles, Bridle, & Simms, 1993). Oak mast seeding has been shown to affect the demography (Bieber & Ruf, 2005), abundance (Schnurr, Ostfeld, & Canham, 2002), body condition (Harlow, Whelan, Crawford, & Skeen, 1975), movement (McShea & Schwede, 1993) and diet (den Ouden et al., 2005; Picard, Oleffe, & Boisaubert, 1991) of a wide variety of vertebrates via direct and indirect effects. The effects of mast seeding are strongly dependent on the type of consumer (Ostfeld & Keesing, 2000). For small species with a rapid increase rate – i.e. birds, rodents – mast seeding generally leads to a numerical response, with more individuals following mast years (Bogdziewicz, Zwolak, & Crone, 2016; Schnurr et al., 2002). As the home range of ungulates and birds may exceed the spatial scale of a mast seeding event, these species may also respond by moving towards areas where mast seeding occurs (Lindén, Lehikoinen, Hokkanen, & Väisänen, 2011; McShea & Schwede, 1993). Lastly, because pulsed resources are only available sporadically, the resource is mostly consumed by generalist species which are able to adapt their diet in the absence of the resource (Ostfeld & Keesing, 2000). Generalist consumers like black bear (*Ursus americanus*) (McDonald & Fuller, 2005) or wild boars (*Sus scrofa*) (Herrero, Irizar, Laskurain, García-Serrano, & García-González, 2005) have been shown to exhibit important dietary shifts in a context of oak mast seeding.

Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are amongst the most widespread ungulate species in Europe and often occur in sympatry in temperate forests. The coexistence of the two species is notably allowed by a segregation of their feeding niche (Storms et al., 2008). Red deer is classified as an “intermediate feeder”, able to adapt to fluctuations in resource availability and quality in its environment (Storms et al., 2008). Although the species avoids fibers as much as possible, it is able to consume grass when resources are scarce (Dumont et al., 2005). According to Hofmann’s classification of ruminant feeding types, roe deer has a “moose-type” digestive track (Hofmann, 1989), and is thus characterized by a strong selectivity and an inability to digest fiber-rich food items. This species has been identified as a typical "browser" and it mostly feeds on bramble, buds, forest fruits and cultivated seeds (Felton, Wam, Stolter, Mathisen, & Wallgren, 2018; Redjadj et al., 2014; Tixier & Duncan, 1996). Due to a more restricted feeding niche, roe deer is more dependent on the resource available in its habitat than red deer (Storms et al., 2008).

Since acorns are characterized by a high energetic content and digestibility, and are available in a period when other resources are scarce for red deer and roe deer (autumn and winter), we may expect these species to shift toward an acorn-enriched diet during years of mast seeding. However, acorns may also be considered as a nutritionally imbalanced food item – i.e. food that does not contain the same balance of nutrients as needed by the animal to reach the intake target (Simpson & Raubenheimer, 2011) – due to its low protein content (Kirkpatrick & Pekins, 2003). It has indeed been shown that species that consume a high proportion of acorns may exhibit a negative nitrogen balance (Harlow et al., 1975; Kirkpatrick & Pekins, 2003). The nutrient balancing hypothesis predicts that when sufficient food is available, the animal's goal is to reach a nutritionally balanced diet (Simpson & Raubenheimer, 2011). Under that perspective, deer would thus have to compensate acorn consumption with complementary food items that are rich in nitrogen. Acorns are also rich in tannins, secondary metabolites known to deter herbivores by lowering the digestibility and nutritional value of plant tissues (Iason, 2005). Cervids have been shown to be relatively tolerant to plant secondary metabolites such as tannins (Iason & Villalba, 2006), notably roe deer due to its salivary proteins that may bind with tannins (Tixier et al., 1997a). However, the ingestion of high levels of tannins comes with a cost (e.g. cost of detoxification) (Iason & Villalba, 2006) and whether this resource is sufficiently beneficial for red and roe deer to induce a dietary shift is still debated. Several studies have documented that acorns may dominate the diet of white-tailed deer (*Odocoileus virginianus*) (Harlow et al., 1975; McShea & Schwede, 1993), red deer (Picard et al., 1991) and roe deer (Abbas et al., 2011) in years of mast seeding. However, most of these studies were conducted over a period that did not exceed three years and were limited to a binary comparison of mast years vs. non-mast years, without any quantification of the magnitude of oak fructification. To our knowledge, an analysis of the relationship between the magnitude of oak fructification and deer diet is still lacking.

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

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

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

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

Materials and methods

Study area

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

Diet analysis

We analyzed rumen samples taken from red deer and roe deer shot by hunters in LPP during the legal hunting season (from the beginning of October to the end of January). All samples came from animals tagged with annual hunting quotas delivered by the county prefect in compliance with the French Environmental Code (Art. R425-2 to 425-14113). The animals were not harvested following a protocol specific to this study. From 1986 to 2018, a total of 330 and 231 samples of red and roe deer rumen, respectively, had been collected. The number of rumen analyzed per year for each species is indicated Fig. 1.B. We noted the exact date of harvest for each culled animal. The inter-annual fluctuations in the number of rumen analyzed per year are the results of the management of deer populations in the NHWR that lead to fluctuations in the number of animals shot per year, a shortage of staff to collect and analyze the rumen before 2005, and occasional extreme climatic events (e.g. Lothar storm in December 1999) that could lead to an absence of harvest in some years.

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

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

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

Oak fruit production

Direct measurement

Sessile oak fructification was measured in LPP with the "ground-plot counting method" (Touzot et al. 2018), which consists in counting acorns on the ground under the tree crown in quadrats of known area and without protection against seed predators. For each monitored oak tree, 4 quadrats of 0.25 m^2 (0.5 m x 0.5 m) were placed at a distance of 1 m to 4 m from the trunk. Soon after the main acorn drop which generally occurs in the first two weeks of October, we gathered and counted the fruits collected in the four quadrats to obtain a number of acorns sampled per tree. From 2010 to 2017, 30 trees were monitored with this method in LPP. Selected trees were located at a sufficient distance from any other mature oak tree to avoid any potential contamination from any adjacent tree during the counting: they were selected randomly and no criteria on the characteristics of the trees (e.g. height, diameter, shape of the tree crown) were taken into account. The fructification f_i for a given year *i* was computed as the mean number of acorns sampled per tree:

$$f_i = \frac{\sum_{y=1}^{30} t_{y,i}}{30} \qquad \textbf{(Eq. 1)}$$

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

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

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

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

Modeling of oak mast seeding in LPP

The aim was to complete the eight years of fructification monitoring in LPP by modeling additional years. Schermer et al. (2018) identified April temperature and the previous year's fructification as the two main factors explaining oak mast seeding using a long-term monitoring of oak fructification in 30 sites of the European network RENECOFOR from 1993 to 2008 (Ulrich, 1995). Based on this result, we integrated the fructification data of LPP and of four of the RENECOFOR sites that were located within a 200 km radius in a predictive Bayesian model with April temperature and previous-year fructification as explanatory variables. Note that this model predicts a relative fructification, ranging between zero and 1. As the previous year's fructification was included in the model, the model is considered first order autoregressive – i.e. the precision of the prediction decreases for each additional year predicted. For this reason, we only kept for analysis the two first years (2008 and 2009). Finally, a total of 10 years (2 years with modeled fructification and 8 years with observed fructification) were available for the study. The predictive model is presented in detail in the Supplementary Material, Appendix C.

Data analysis

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

We analyzed the relationships between the relative fructification of oak and the mean annual acorn consumption of red deer and roe deer using a linear mixed-effect model (lme4 package) (Bates, Mächler, Bolker, & Walker, 2014) with two fixed effects (fructification and deer species) and one random effect (hunting season). We tested the significance of the effects using a type II Wald $\chi2$ test using the Anova function in the “car” package of R (Fox & Weisberg 2011). An interaction between the two fixed effects was included in the model. To fit the assumption of normality for the error distribution, the annual acorn consumption was arcsine square root transformed prior to analysis (Zar, 1984). For each species, we excluded from this analysis the years with less than 4 individuals. Oak fructification is characterized by significant temporal autocorrelations that we quantified in the Bayesian model (Supplementary material Appendix C, Fig. C.2). We checked that these temporal autocorrelations did not affect our linear model by examining the model residuals.

Intra-annual variations in the proportion of acorns in the diet were analyzed and compared for the two deer species on the month scale. Intra-annual variations were assumed to depend on the total annual amount of available resources, the analyses were thus performed separately for years with low (n = 6), partial (n = 3) and high (n = 1) relative fructification. For each of the three categories of relative fructification, we conducted a two-way ANOVA to test the effect of species (factor with two levels: "red deer" and "roe deer"), month (ordered factor with four levels: "October", "November", "December" and "January") on the proportion of acorns in the diet. For each class of relative fructification, an interaction between the two factors was included. In the case of a significant effect of the month, we tested the differences between the four levels of this factor with Tukey's HSD test.

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

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

$$\begin{cases} \Gamma_{[red]i} = \dfrac{\sum_{k=1}^{n_{[red]}=330} \gamma_{[red]_{i,k}}}{\sum_{j=1}^{15}\sum_{k=1}^{n_{[red]}=330} \gamma_{[red]_{j,k}}} = \dfrac{\sum_{k=1}^{n_{[red]}=330} \gamma_{[red]_{i,k}}}{330} \\ \\ \Gamma_{[roe]i} = \dfrac{\sum_{k=1}^{n_{[roe]}=231} \gamma_{[roe]_{i,k}}}{\sum_{j=1}^{15}\sum_{k=1}^{n_{[roe]}=231} \gamma_{[roe]_{j,k}}} = \dfrac{\sum_{k=1}^{n_{[roe]}=231} \gamma_{[roe]_{i,k}}}{231} \end{cases} \qquad \textbf{(Eq. 3)}$$

Where $n_{[red]}$ and $n_{[roe]}$ are the respective numbers of red and roe deer rumens collected. The computed proportions of each category are presented in Supplementary material Appendix D, Table D.1. We only selected for this analysis the categories that represented on average more than 5% of the diet of a given deer species ($\Gamma_{[red]} > 5\%$ or $\Gamma_{[roe]} > 5\%$). The categories "others" and "unidentified" were not included, nor was the "acorns" category. $N_{[red]}$ and $N_{[roe]}$ food categories represented more than 5% of red and roe deer diet, respectively. To restrict the analysis to these categories, we computed the relative proportions of each selected category i in the rumen k ($\gamma'_{[red]i,k}$ and $\gamma'_{[roe]i,k}$) so that for each rumen, the relative proportions of the *N* selected categories add up to 1:

$$\begin{cases} \gamma'_{[red]_{i,k}} = \frac{\gamma_{[red]_{i,k}}}{\sum_{j=1}^{N[red]} \gamma_{[red]_{j,k}}} \\ \\ \gamma'_{[roe]_{i,k}} = \frac{\gamma_{[roe]_{i,k}}}{\sum_{j=1}^{N[roe]} \gamma_{[roe]_{j,k}}} \end{cases} \qquad \textbf{(Eq. 4)}$$

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

$$\begin{cases} \ln(\gamma'_1) = \alpha_1 + \beta_1 * \ln(\gamma_{acorn}) \\ \dots \\ \ln(\gamma'_i) = \alpha_i + \beta_i * \ln(\gamma_{acorn}) \\ \dots \\ \ln(\gamma'_N) = \alpha_N + \beta_N * \ln(\gamma_{acorn}) \end{cases} \qquad \textbf{(Eq. 5)}$$

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

Results

Inter-annual variations of acorn consumption and oak fructification

From 2008 to 2017, oak fructification in LPP exhibited high inter-annual fluctuations (Fig. 1A). The maximum fructification in the study site occurred during the hunting season 2011/2012 (109 acorns/m^2, relative fructification = 1). The following year, oak fructification reached a minimum of 0 acorns/m^2 (relative fructification = 0). From 1986 to 2017, acorns represented on average 9.4% and 4.2% of the red and roe deer diet, respectively. The peak of oak fructification (hunting season 2011/2012) in LPP matched the peak of acorn consumption for both deer species (Fig. 1). In that season, acorns represented on average 52% and 34% of red and roe deer diet, respectively. At the inter-annual scale, the proportion of acorns in the diet was 15% higher on average ($p < 0.001$) in red deer than in roe deer. Mean acorn proportion in the diet significantly increased with oak fructification ($p < 0.001$), with a higher slope for red deer ($p = 0.027$) (Supplementary material: Appendix A, Fig. A.1; Appendix F, Table. F.1).

Intra-annual variations in acorn consumption

On the intra-annual scale, the proportion of acorns in the red deer diet was also higher than in the roe deer diet in a context of low ($p = 0.005$), partial ($p = 0.018$) and high ($p = 0.034$) relative fructification (Fig. 2; Supplementary material Appendix F, Table. F.2). The interaction between deer species and month was not significant in years of low ($p = 0.58$), partial ($p = 0.49$) or high ($p = 0.16$) fructification (Supplementary material Appendix F, Table. F.2), which means that for the three classes of relative fructification, red deer consumed a higher proportion of acorns than did roe deer throughout the hunting season. In years of low relative fructification, acorns represented an average of 4% and 1% of red and roe deer diet, respectively, and remained stable from October to January ($p = 0.43$) for both deer species. In years of partial relative fructification, the proportion of acorns in the diet of both deer species was lower in December and January than in October and November ($p < 0.001$). Red and roe deer respectively consumed 47% and 34% of acorns in October, while these proportions decreased to respectively 14% and 15% in January (Fig. 2). In the context of high relative fructification, acorn proportion remained stable throughout the hunting season in red and roe deer diet ($p = 0.13$), with an average proportion of 52% and 34%, respectively.

Effect of acorn consumption on red and roe deer feeding behavior

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

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

Discussion

Oak fructification as a major determinant of deer diet

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

In the case of partial fructifications, we observed an intra-annual variability in acorn consumption for both deer species: consistently with our initial hypothesis (H1), acorn proportion in the diet was higher in October and in November, the month of the main acorn drop and the following. The main assumption to explain this pattern is a depletion of the acorn stock from October to January due to predation by deer (Harlow et al., 1975; Tixier & Duncan, 1996) but also by the other seed consumers such as wild boars (Herrera, 1995), rodents or jays (den Ouden et al., 2005; Steele et al., 1993). Under this assumption, this result suggests that a partial fructification is not sufficient to induce a satiation of the seed predators (Kelly, 1994) and therefore that a large proportion of all acorns available is consumed. Consequently, the low remaining quantity of acorns might not be sufficient to ensure the regeneration success of oak stands. An alternative hypothesis is that the palatability and/or the nutritional value of acorns decreased from October to January due to a fast degradation of acorn tissues when lying on the soil. Tejerina et al. (2011) showed that in the case of holm oak (*Quercus ilex*) the content in several phenolic compounds increased throughout autumn and winter, probably due to the process of ripening and germination. Acorns are also more likely to be rotten or damaged by pathogens at a more advanced stage of the acorn crop season. Despite this potential decrease in acorn palatability, it is noteworthy that in the case of high fructification, acorn consumption remained stable until January for both species (Fig. 2). This observation provides strong support for the resource depletion hypothesis as an explanation for the decrease in the proportion of acorns in the diet observed after November in years of partial fructification. This phenomenon could also be interpreted as a factual argument supporting the predator satiation hypothesis as a possible evolutionary explanation for mast seeding (Ims, 1990; Kelly, 1994). Indeed, the predator satiation hypothesis assumes that seed predators exhibit a type II or type III functional response, i.e. at high seed densities, the proportion of attacked seeds should decrease with increasing seed densities (Bogdziewicz et al., 2018; Moreira et al., 2017). In our study, as the main acorn drop occurs in October, the acorn density necessarily decreases from October to January because of predation. Under the assumption that acorn proportion in deer diet reflects the quantity of acorns consumed, a constant acorn consumption throughout this period – as observed in a context of high fructification – would indicate that the proportion of predated acorns decreases with acorn density. Our results therefore seem to confirm that the red and roe deer's diet modification in response to mast seeding is compatible with the predator satiation hypothesis.

Interspecific differences in acorn consumption

At both the intra-annual (Fig. 2) and inter-annual scale (Fig. 1, Supplementary material Appendix A, Fig. A.1), we found a higher acorn proportion in the red deer diet than in the roe deer diet, in agreement with our initial hypothesis (H2). This pattern is most likely related to the digestive morphology of the two studied species. As an intermediate feeder, red deer has been shown to be highly adapted to fluctuations in resource availability (Storms et al., 2008). In winter, in a context of scarce resources, this species switches to a grass-based diet, despite the high fiber content of this resource (Dumont et al., 2005; Redjadj et al., 2014). In contrast, as a browser, roe deer is far more selective and has a more restricted feeding niche (Tixier et al., 1998). The higher flexibility of red deer may partly explain why it exploits the sudden increase of resource availability to a greater extent than roe deer. In addition, while although acorn pulp has been shown to be highly digestible, the shell, also ingested by deer, is poorly digestible and rich in fibers (Kirkpatrick & Pekins, 2003). Since roe deer is unable to feed on poorly digestible items, we may assume that the acorn shell's nutritional characteristics prevent roe deer from consuming a high proportion of acorns, while red deer is not limited thanks to its more flexible stomach structure. This result could also be interpreted under the framework of the nutrient balancing hypothesis (Simpson & Raubenheimer, 2011): red deer's consumption of significant portions of grass tissues with a very low secondary metabolites content might balance for acorn high tannin content. On the other hand, due to the high secondary metabolite content in the food items preferred by roe deer (i.e. deciduous leaves, dicot herbs), this species would not be able to compensate for the high input of tannins by acorns. Interspecific differences in acorn consumption may also be explained by the nutritional requirements of the two studied species. Indeed, red deer are classified as capital breeders as they rely on fat stored during summer and autumn to face winter; while roe deer are income breeders and are unable to store fat reserves (Brown, 1992). The main nutritional property of acorns is their high energetic content (Kirkpatrick & Pekins, 2003) and this resource is mainly available in autumn. We may therefore assume that consuming acorns may be more beneficial for red deer by providing extra fat reserves for winter.

Consequences of acorn consumption on deer feeding behavior

Our analyses of the composition of red and roe deer diets were consistent with their respective feeding types. Red deer has a diverse diet that included fiber-rich items such as grasses while, as reported in other studies (Storms et al., 2008; Tixier et al., 1997b), roe deer has a poorly diversified bramble-based diet (Supplementary material Appendix D, Table D.1), one of the most digestible species available in winter (Dumont et al., 2005). The proportions of all the items consumed are likely to decrease with an increasing proportion of acorns in the diet. Nevertheless, it is critical to understand whether acorns, due to their nutritional characteristics, change the relative proportions of these resources in deer diet in order to assess whether some plant species will be more affected than others by increased acorn availability.

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

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

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

Conclusion

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

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Appendix A. Supplementary data

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

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Figure captions

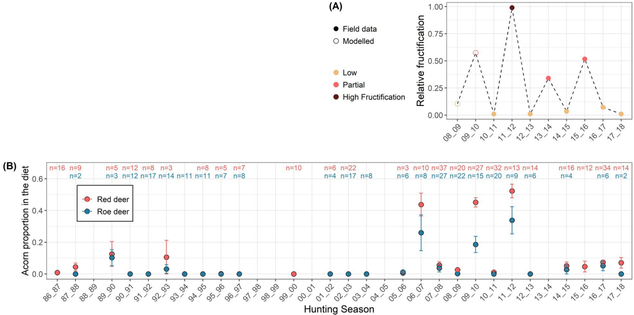
Fig. 1. Inter-annual variations in (A) oak relative fructification and (B) the proportion of acorn in red deer and roe deer diet. Fructifications values are given as the proportion of acorns counted for a given year with the ground-plot method (Touzot et al., 2018) relative to the maximum ever counted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

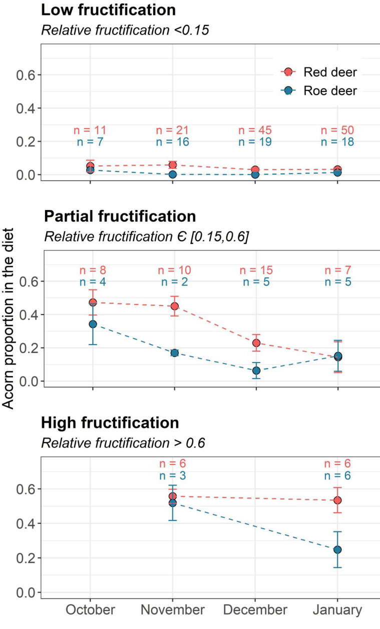
Fig. 2. Intra-annual variation in the proportion of acorns in red deer and roe deer diet (mean ± standard error) for different fructification levels. Months with $n < 2$ were removed from the dataset.

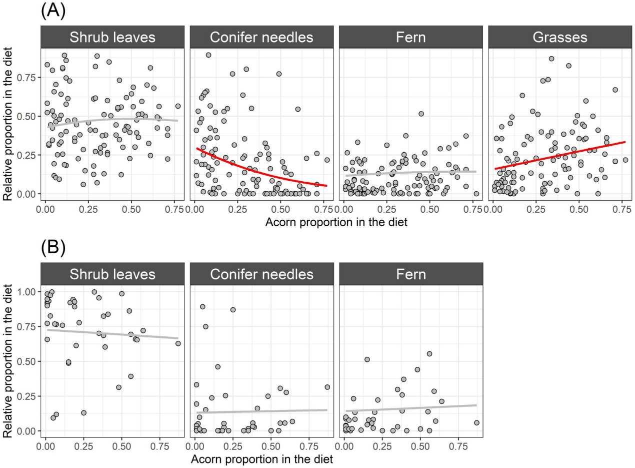
Fig. 3. Relative proportions of the main food categories consumed, in relationship with the proportion of acorn in the diets of (a) red deer and (b) roe deer. The lines represents the fitted Dirichlet regression model (Eq. 5). Red lines indicate significant relationships ($p < 0.05$). Model results for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

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

	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***			


(A)
● Field data
○ Modelled
● Low
● Partial
● High Fructification
Relative fructification
1.00
0.75
0.50
0.25
0.00
08_09
09_10
10_11
11_12
12_13
13_14
14_15
15_16
16_17
17_18
(B)
Acorn proportion in the diet
0.6
0.4
0.2
0.0
Red deer
Roe deer
n=16
n=9
n=2
n=5
n=3
n=12
n=12
n=8
n=17
n=3
n=14
n=11
n=8
n=11
n=5
n=7
n=7
n=8
n=10
n=6
n=4
n=22
n=17
n=8
n=3
n=6
n=10
n=8
n=37
n=27
n=20
n=22
n=27
n=15
n=32
n=20
n=13
n=9
n=14
n=6
n=16
n=4
n=12
n=34
n=6
n=14
n=2
86_87
87_88
88_89
89_90
90_91
91_92
92_93
93_94
94_95
95_96
96_97
97_98
98_99
99_00
00_01
01_02
02_03
03_04
04_05
05_06
06_07
07_08
08_09
09_10
10_11
11_12
12_13
13_14
14_15
15_16
16_17
17_18
Hunting Season


Low fructification
Relative fructification <0.15
Red deer
Roe deer
n = 11
n = 7
n = 21
n = 16
n = 45
n = 19
n = 50
n = 18
0.0
0.2
0.4
0.6
Partial fructification
Relative fructification Є [0.15,0.6]
n = 8
n = 4
n = 10
n = 2
n = 15
n = 5
n = 7
n = 5
0.0
0.2
0.4
0.6
Acorn proportion in the diet
High fructification
Relative fructification > 0.6
n = 6
n = 3
n = 6
n = 6
0.0
0.2
0.4
0.6
October
November
December
January


(A)
Shrub leaves
Conifer needles
Fern
Grasses
Relative proportion in the diet
0.00
0.25
0.50
0.75
Acorn proportion in the diet
0.00
0.25
0.50
0.75
(B)
Shrub leaves
Conifer needles
Fern
Relative proportion in the diet
0.00
0.25
0.50
0.75
1.00
Acorn proportion in the diet
0.00
0.25
0.50
0.75