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Influence of hurricane Lothar on red and roe deer winter diets in the Northern Vosges, France

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Abstract

Extreme climatic events, such as hurricanes, may profoundly affect herbivore population dynamics and habitat use by returning tracts of mature forest to early seral stages where food and cover resources rapidly develop. Modifications of habitat use by roe deer (*Capreolus capreolus*) following hurricane Lothar have been demonstrated in a French forest, and it has been suggested that the combination of a reduction in hunting due to hunters' inability to access the areas and an improvement in habitat characteristics in clearings resulted in Lothar having a positive effect on roe deer population dynamics. Here, we studied the winter diet of red deer (*Cervus elaphus*) and roe deer before and after hurricane Lothar in a heavily damaged forest, assuming that the hurricane, by creating numerous clearings in which food availability for herbivores increased rapidly, allowed deer to specialize on preferred plant species that benefited from habitat modifications, particularly bramble and grasses. According to their feeding types and ecology, we expected that the increase in the availability of grasses and bramble after the hurricane would result in an increase in the proportions of these plants in the diet of red deer and an increase in the proportion of bramble in the diet of roe deer. Analysis of stomach contents revealed that consumption of grasses by red deer almost doubled following the hurricane, but no effect on bramble consumption by either deer species could be detected. Our study also revealed a significant annual variation in bramble consumption, which suggests that its availability as a food resource for deer varies from year to year, and this may have masked the hurricane effect. We then discuss the role of disturbances in improving habitat for forest ungulates, and the role of key alternative food resource in helping forest managers to find solutions for mitigating ungulate impact on tree regeneration.

Keywords: *Capreolus capreolus*; *Cervus elaphus*; Deer browsing; Diet; Forest regeneration; Hurricane Lothar

1. Introduction

Forest succession, whether natural or anthropogenic, plays a major role in structuring habitat and resource distribution for wild herbivores. In managed forests, regimes of clearance and subsequent regeneration provoke an increase in the availability of browse and cover in early seral stages, which declines when the tree canopy closes over (Halls and Alcaniz, 1968; Irwin and Peek, 1983; Gill et al., 1996; Partl et al., 2002). Succession from early regeneration stages to mature forest has been shown, in an English coniferous woodland, to result in a decline in roe deer (*Capreolus capreolus* L.) numbers after a decline in browse supply (Gill et al., 1996). Extreme climatic events returning mature forests to early seral stages may equally influence ungulate populations.

In December 1999, hurricane Lothar struck France, Switzerland and Germany, and caused widespread destruction to forests (see http://www.notre-planete.info/geographie/risques_naturels/tempetes_0.php for further details). Studies carried out in French forests suggest that roe deer may have benefited from the creation of hurricane-related clearings, at least in the short term (Gaillard et al., 2003; Widmer et al., 2004; Said and Servanty, 2005). Roe deer responded to habitat modifications caused by the hurricane by reducing their home range size and concentrating in timber stands, where most of the damage had occurred (Widmer et al., 2004). No negative effect on roe deer population dynamics parameters (i.e. survival and pregnancy rates, litter size) could be detected and it is suggested that the combination of a reduction in

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hunting due to hunters' inability to access the areas and an improvement of habitat characteristics in clearings, particularly food availability, resulted in Lothar having a positive effect on roe deer population dynamics (Gaillard et al., 2003). Knowing the influence that such an extreme climatic event can have on ungulate habitat selection and population dynamics, one might reasonably assume that hurricane Lothar will also have had an influence on ungulate diets, although this has not been demonstrated yet.

Variations in the botanical composition of the diets of roe and red (*Cervus elaphus* L.) deer have been reviewed by Tixier and Duncan (1996) and Gebert and Verheyden-Tixier (2001). From their work (see also Cornelis et al., 1999), the main cause of variation in diet for both species appears to be the habitat used by the deer, implying that food availability in selected habitat is a key determinant of the diet (Duncan et al., 1998). We assume that hurricane Lothar, by creating numerous clearings in which grasses, forbs and shrub species developed rapidly (Degen et al., 2005), caused an increase in food availability for wild herbivores. Among plants which benefited most from the hurricane were bramble, which is considered a very palatable plant for deer, and grasses, which are not very palatable for roe deer but very important as a constituent of red deer diet (Gonzalez-Hernandez and Silva-Pando, 1999). Optimal foraging theory applied to diet composition predicts that an increased density of preferred food items will increase specialization on those items (Emlen, 1966; Schoener, 1971; Pulliam, 1974; Pyke et al., 1977). We studied the diets of red and roe deer hunted in winters preceding and following 1999 in a heavily damaged forest of northeastern France and we expected that the increase in the availability of grasses and bramble after the hurricane would result in an increase in the proportion of these plants in the diet of red deer (an intermediate feeder, Hofmann, 1989) and an increase in the proportion of bramble in the diet of roe deer (''the type example of a concentrate selector'', Hofmann, 1989).

2. Study area

The study was conducted in la Petite-Pierre National Hunting and Wildlife Reserve (NHWR), a 2700 ha unfenced forest area located in the Vosges mountain range, northeastern France (48.5°N, 7°E), at a mean elevation of 300 m (Fig. 1). The climate is continental with oceanic influence, leading to mild winters and cool summers (mean January and mean July temperatures are 0.6 and 18.4 °C, respectively, data from Météo France station in Phalsbourg) (Bonenfant et al., 2002). Snow accumulation is rare. La Petite-Pierre NHWR is characterized by a succession of small hills and steep-sided valleys. The sandstone substrate produces acidic and poor soils, resulting in the vegetation being of little diversity and low nutritive quality (*sensu* Gonzalez-Hernandez and Silva-Pando, 1999) for herbivores. The forest is structured in even-aged clusters of trees, and comprises roughly equal proportions of broadleaved trees, mainly beech (*Fagus sylvatica* L.), and coniferous, mainly Silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* Karst.) and Scots pine (*Pinus sylvestris* L.) (Hamann et al., 1997; Klein and Hamann, 1999). Red deer, roe deer and wild boar (*Sus scrofa* L.) are present within the Reserve. The area is free of big game predators and ungulate populations are managed through hunting, either with quotas (deer) or without (wild boar). Red and roe deer population densities have been maintained at relatively constant levels since 1984, at around three to five red deer and six to seven roe deer per square kilometer (Hamann, personal communication). On 26 December 1999, hurricane Lothar blew down 480 ha of mature forest in la Petite-Pierre NHWR, creating clearings of up to 50 ha apiece (ONF, personal communication).

3. Materials and methods

Rumen contents were taken from red and roe deer shot in winter by *Office National de la Chasse et de la Faune Sauvage* (ONCFS) and *Office National des Forêts* (ONF) staff in la Petite-Pierre NHWR between 1993 and 1997 (27 and 38 samples, respectively), and between 2002 and 2004 (28 and 35 samples, respectively) (Table 1).

3.1. Stomach contents analysis

Samples of about 500 g of rumen contents were frozen and later washed over a sieve with a 5.0 mm mesh. The retained material was sampled and sorted macroscopically using a method adapted from the point-frame technique developed by Chamrad and Box (1964). Sieved items were mixed with water and spread over a rectangular tank on the bottom of which a grid formed 100 intersection points, allowing the selection of 100 items. This process was repeated three times in order to obtain a sample of 300 items per rumen contents, from which the percentage occurrence of each item could be calculated. Percentage occurrence estimated from a sample of 300 items was not significantly different from percentage occurrence measured from the entirety of the sieved items, neither was it different from the weight percentage obtained after drying and weighing the 300 items (Dubois, 1992). Each plant fragment found was separated and identified to the lowest possible taxon using reference collections. For the purpose of the analysis, items were grouped into seven food categories: grasses (*Carex* sp., *Deschampsia* sp., *Festuca* sp., *Luzula* sp., *Poa* sp.), forbs (herbaceous plants other than grasses) and deciduous browse and shrubs, bramble (*Rubus* sp.), ligneous material (mainly tree branches), conifers (Norway spruce, Scots pine and Silver fir), ferns (*Athyrium filix-femina* (L.) Roth, *Dryopteris* sp.), and others (unidentified items and occasional field crops and mushrooms).

3.2. Statistical analyses

We first performed a multivariate analysis to check for a possible effect of sampling year on diet composition inside each group of samples collected before and after the hurricane. Each food category in the diet is presented as a proportion, the sum of which is equal to one, so food categories could not be considered statistically independent (Baubet et al., 2004).

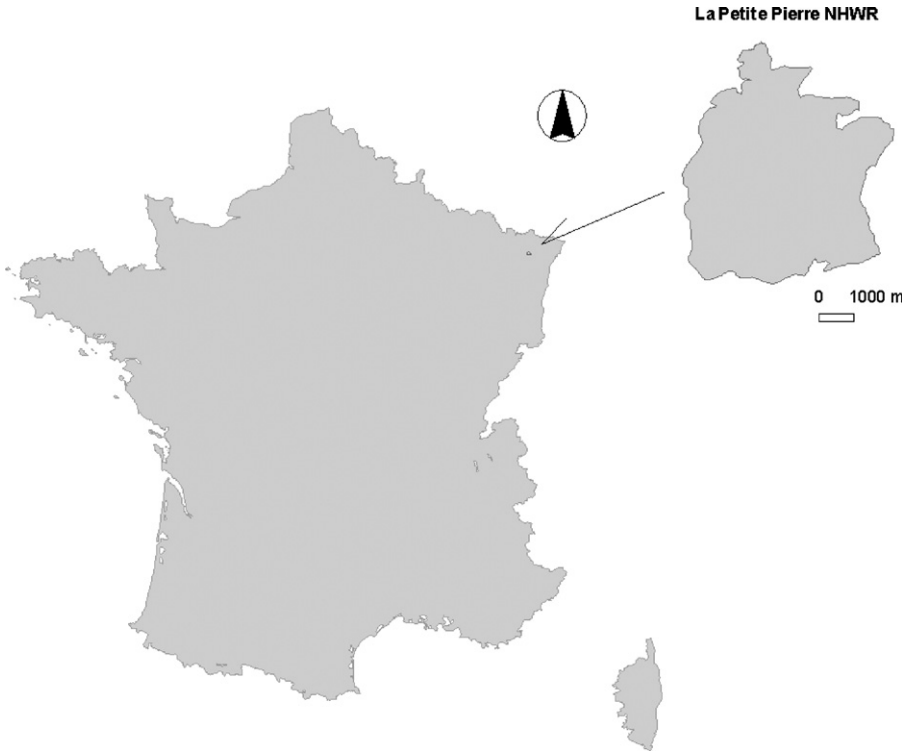

Fig. 1. Location of la Petite-Pierre National Hunting and Wildlife Reserve in France.

Aitchison (1986) proposed a general methodology, mainly used in habitat selection studies (Aebischer et al., 1993), which uses a log-ratio transformation to obtain n-1 linearly independent variables. After applying the log-transformation in which zero proportions were allowed a value smaller than the smallest positive value in the data set, i.e. 0.0001 (Aebischer et al., 1993), the data were divided into two groups corresponding to years before and after Lothar. The possible effect of sampling year on diet composition in each data set was tested through a MANOVA procedure, in which the n-1 independent variables are the response and the year of sampling is the factor.

Differences in food category proportions before and after Lothar were further investigated through two-factor nested ANOVA procedures performed on the original data set, which allowed us to test for a hurricane effect after taking annual variations in diet composition into account. Residuals were checked for normality using diagnostic graphs in S-PLUS (Venables and Ripley, 1994). Statistical significance was declared at $\alpha < 0.05$.

Table 1
Stomach contents sampling distribution (n) among years before and after hurricane Lothar

	Red deer	Roe deer
Pre-Lothar		
1993	5	–
1994	–	11
1995	6	10
1996	9	9
1997	7	8
Post-Lothar		
2002	6	4
2003	22	18
2004	–	13

4. Results

4.1. Annual variation in diet

Multivariate analysis of diet composition revealed that the only significant effect of sampling year was for roe deer samples collected before hurricane Lothar (red deer: before Lothar Wilk's $\lambda = 0.2891$, $P = 0.1036$, after Lothar Wilk's $\lambda = 0.7954$, $P = 0.5131$; roe deer: before Lothar Wilk's $\lambda = 0.3525$, $P = 0.0157$, after Lothar Wilk's $\lambda = 0.6434$, $P = 0.3714$). However, possible effects of sampling year may have been overlooked because of the number of years sampled after the hurricane being too few.

4.2. Red and roe deer diet composition

Examination of mean proportions of food categories composing diets showed that red deer winter diet is composed mainly of grasses and conifers, along with a substantial proportion of bramble, while roe deer winter diet is composed mainly of bramble and conifers (Figs. 2 and 3).

4.3. Impact of hurricane Lothar on diet composition

Among the three main food categories composing red deer winter diet, only the proportion of grasses was significantly different before (mean ± S.E.: 0.1766 ± 0.0282) and after the

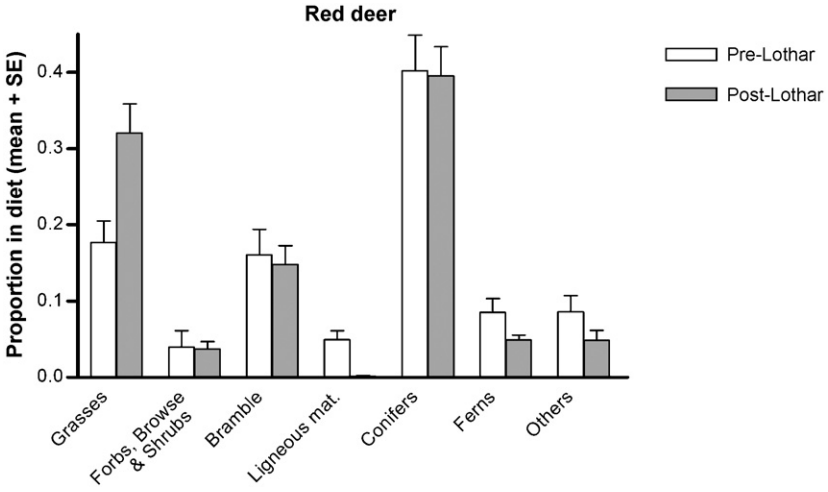

Fig. 2. Mean + S.E. proportions of food categories in red deer winter diet before (Pre-Lothar) and after (Post-Lothar).

hurricane (mean ± S.E.: 0.3204 ± 0.0382). The proportion of bramble in red and roe deer winter diets was not significantly different before and after the hurricane, whereas the consumption of categories of low palatability (i.e. ligneous material) showed a significant change for both species (red deer: mean ± S.E.: 0.0494 ± 0.0122 before and 0.0017 ± 0.0017 after Lothar; roe deer: mean ± S.E.: 0.0145 ± 0.0058 before and 0.0013 ± 0.0009 after Lothar). The analysis revealed significant annual variations in the proportion of bramble in the diet of roe deer, and conifers and ligneous material in the diet of both species (Table 2).

5. Discussion

Hurricane Lothar has been shown to influence both habitat use and population dynamics of roe deer (Gaillard et al., 2003; Widmer et al., 2004), and it has been suggested that these changes were the result of modifications of the spatial distribution and availability of food and shelter resources. Here, we assumed that the rapid development of grasses and bramble in clearings after the hurricane would have allowed red and roe deer to be more selective regarding food items included in their diets. However, as we had no information on food availability before and after the hurricane, we could not evaluate changes in diet selectivity directly. We therefore investigated changes in diet composition and expected an increase in the proportion of grasses and bramble in red deer diet and of bramble in that of roe deer.

Grasses and bramble were amongst the plants that benefited most from habitat modifications following the hurricane (Degen et al., 2005) and both are available in winter when most other food sources are depleted. Grasses make up an important part of red deer diet across all habitats and seasons in Europe (Gebert and Verheyden-Tixier, 2001) and bramble, when available, is frequently eaten by deer (Jackson, 1980; Hosey, 1981; Hearney and Jennings, 1983; Birkenstock and Maillard, 1989; Picard and Gégout, 1992). The results of our study partially support our predictions, as the proportion of grasses in red deer diet almost doubled after the hurricane. Consumption of bramble by both species, however, did not show any significant change due to the hurricane.

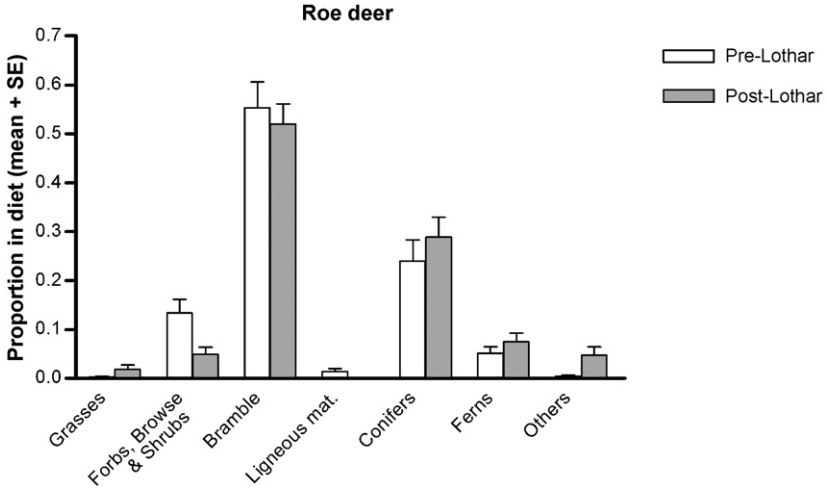

Fig. 3. Mean + S.E. proportions of food categories in roe deer winter diet before (Pre-Lothar) and after (Post-Lothar).

Table 2
F and *P* values for two factors (Lothar and year) nested ANOVAs

	Red deer		Roe deer	
	F	*P*	*F*	*P*
Grasses				
Lothar	8.7314	0.0048	3.1873	0.0788
Year	0.5048	0.7324	1.4660	0.2129
Forbs, browse and shrubs				
Lothar	0.0111	0.9167	7.1486	0.0094
Year	0.9844	0.4248	1.9942	0.0909
Bramble				
Lothar	0.1176	0.7331	0.2911	0.5913
Year	2.3321	0.0688	3.8283	0.0042
Ligneous material				
Lothar	21.5981	<0.0001	5.0066	0.0286
Year	5.6725	0.0005	2.3998	0.0463
Conifers				
Lothar	0.0128	0.9104	0.8177	0.3691
Year	2.9982	0.0272	4.3606	0.0017
Ferns				
Lothar	3.7543	0.0584	1.2279	0.2718
Year	1.9079	0.1240	1.4300	0.2251
Others				
Lothar	2.2621	0.1390	7.1931	0.0092
Year	0.8597	0.4948	1.7734	0.1305

Grasses are generally available to deer all the year round, provided that they are not over-grazed or covered in deep snow for long periods, which is not the case in our study area. Red deer could therefore take advantage of the expansion of grasses in the numerous clearings caused by Lothar, and reduced their consumption of less palatable food items such as ligneous materials. Bramble retains its leaves in winter and therefore represents an important resource for herbivores when other food sources become depleted. However, in case of a sudden drop in temperature, bramble leaves can be nipped by the frost and their palatability is then greatly reduced. Bramble growing in clearings are particularly subject to frost damage, as they do not benefit from the protection of the forest canopy against sudden changes in temperature (Wehrlen, personal communication). The significant yearly variation observed in bramble consumption, both by red and roe deer, suggests that its availability as a food source varies annually, and we expect this variation to be dependent on temperature conditions in winter. This means that deer might benefit from the rapid growth of bramble in clearings resulting from habitat modifications, but this would be conditional upon climatic conditions which cause annual variation in the availability of bramble as winter food source.

Natural disturbances such as hurricanes may benefit wild herbivores by creating clearings where food and shelter resources develop rapidly. This increase in the quality of habitats for herbivores could be considered a natural deterrent as regards damage to young trees, as the presence of additional forage with high palatability can reduce browsing on regenerating forest (Partl et al., 2002). However, this is mitigated by the fact that natural habitat modifications can have a positive effect on herbivore population dynamics (Gaillard et al., 2003) and that animals are attracted to clearings (Widmer et al., 2004), precisely the forest patches where future regeneration will take place.

6. Management implications

The results of our study shed light on the potential impact of deer on forest regeneration in clearings, whether natural or anthropogenic. The predisposition of forest to herbivore damage is a result of both attractiveness of the habitat and available food resources, and the relationship between them (Reimoser and Gossow, 1996). The rapid growth of vegetation in clearings after hurricane Lothar provided red and roe deer with forest patches in which they could find both food and cover resources. This is particularly true for bramble, which constitutes good hiding cover and represents a substantial component of the diet of both species. However, the ratio of settling stimulus to available food in clearings can change rapidly if bramble leaves are nipped by the frost, and damage to seedlings of commercial species could therefore increase. In patches where the forest regenerates naturally, the high density of seedlings and their dispersal represent a good natural diversion against browsing (Reimoser and Gossow, 1996). In addition, bramble, even if nipped by the frost, may still represent a physical barrier protecting seedlings. In patches where the forest is regenerated artificially, either because natural regeneration is hampered by a lack of seed trees or because foresters want to favour different tree species, plantations are often made on bare ground after mowing. Then, the fact that a few seedlings are concentrated in spots with easy access by animals can greatly increase the risk of damage to regenerating forest, particularly if the availability of alternative food sources is reduced by harsh climatic conditions.

In forests of the Vosges mountain range, the presence of understory vegetation in regeneration patches reduces herbivore browsing intensity on silver fir saplings, an important commercial species (Heuzé et al., 2005a,b). The expansion of alternate food sources in clearings caused by hurricane Lothar may reduce the pressure herbivores put on the regeneration of commercial trees. However, our study suggests that annual variation in the availability of alternate foods, particularly bramble, might result in annual variation in the predisposition of regeneration patches to damage by red and roe deer. Furthermore, because of the annual variation in winter food availability, in some years the difference between seasonal food availability may be very high and while there may be good conditions for an increase in deer populations in the summer, the shortage of food in winter will lead to an increase in damage (Reimoser and Gossow, 1996). The risk of damage to seedlings of commercial species by red and roe deer is therefore very difficult to predict from year to year, but the predisposition of regeneration patches to damage could probably be reduced by forestry practices inspired by natural regeneration processes in clearings following disturbances.

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