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ORIGINAL PAPER

The oak browsing index correlates linearly with roe deer density: a new indicator for deer management?

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Abstract Increasing populations of large herbivores during the last decades have had a major impact on vegetation. While several studies have looked for quantifying this impact in terms of plant biomass, plant survival or financial costs, the potential benefit of using the response of the vegetation to changes in browsing pressure by large herbivores to monitor their populations has been poorly investigated. As getting accurate estimates of density in populations of large herbivores is problematic, the use of indicators measuring the intensity of browsing might offer reliable alternative to managers. From the intensive monitoring of a roe deer population subject to an experimental manipulation of density, we looked for assessing the response of oak to changes of roe deer population size. Using a simple browsing index calculated from field data over 10 years, we found that this oak browsing index linearly increased with increasing population size of roe deer. This suggests that such an oak browsing index might be a reliable "indicator of ecological change" for monitoring roe deer populations in oak forests with natural regeneration.

Keywords Browsing · *Capreolus capreolus* · Capture–mark–recapture · Forestry · Monitoring · Natural regeneration · Oak regeneration · *Quercus petraea* · *Quercus robur*

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Introduction

Populations of large herbivores have increased their range and density substantially over recent decades, both in Europe (for roe deer: Gill 1990; Andersen et al. 1998) and North America (for white-tailed deer *Odocoileus virginianus*: Gill 1990; Warren 1997). Nowadays, roe deer populations occur at high densities throughout northwestern Europe and have increasing impacts on the forest ecosystems (Gill 1990; Kuiters et al. 1996).

The problems of deer browsing are well-known to foresters (Gill 1992). The browsing intensity caused by deer to vegetation cover depends on several factors such as game density and structure of food resources (Bergquist and Orlander 1998). Browsing by deer is now recognised as a principal factor limiting regeneration (Welch et al. 1995; Miller et al. 1998). However, studies of deer impacts along a large range of population densities remain scarce.

In the present paper, we proposed an index based on the intensity of roe deer browsing on oak (*Quercus petraea* Mattus. Liebl. and *Quercus robur* L.). Oak stands correspond to over a third of the French forests (Cazettes et al. 2003) and nearly represent a quarter of the standing volume of French forests (IFN 2006), placing France at the forefront of European oak products (Morel 2006) and second in the world after the USA (Bary Lenger and Nebout 1993). We used an experimental manipulation of population density of the intensively monitored roe deer population of Trois-Fontaines (e.g. Gaillard et al. 2003a) to assess how the intensity of oak browsing responded to changes of deer density. As roe deer populations are especially difficult to count (Strandgaard 1972; Gaillard et al. 2003b), an alternative to census based on indicators of ecological change has recently been proposed to monitor deer populations (Morellet et al. 2007). The principle of this approach relies on identifying the status of the relationship between the focal deer population and its habitat. Three types of indicators, each of them informing a specific compartment of the relationship (i.e. deer abundance, deer performance and deer impact on the vegetation), are measured to rank the focal population over its demographic trajectory going from colonization to saturation. All these indicators should thus be sensitive to changes of population size. In that context, we tested whether the intensity of oak browsing could be proposed as an indicator of ecological change informing about the compartment of the deer impact on vegetation.

Methods

The study was conducted in the *Territoire d'Etude et d'Expérimentation* of Trois-Fontaines, a 1,360-ha enclosed forest in northeastern France (48°43′ N, 4°56′ E). The climate is continental, characterized by cold winters (mean daily temperature in January is 2°C, data from Météo France) and hot, but not dry, summers (mean daily temperature in July is 19°C and total rainfall in July–August is 130 mm, data from Météo France). The study site is managed by the Office National des Forêts. The forest over-story is dominated by oak (*Quercus* spp.) and beech (*Fagus sylvatica*) while the coppice is dominated by hornbeam (*Carpinus betulus*; Dray et al. 2008). The soil is fertile and the forest is highly productive, with a long-term average of 5.9 m^3 of wood annually produced per hectare and high normalized difference vegetation index values during the growing season (Pettorelli et al. 2006). From a forestry viewpoint, the Trois-Fontaines forest is managed to produce oak stands with natural regeneration. Based on our current knowledge of food habits of roe deer (Duncan et al. 1998), the study site offers rich habitat for roe deer.

Roe deer are generalist herbivores that feed selectively (Duncan et al. 1998). In western Europe, the principal food plants of this browsing ungulate in summer are oak, hornbeam, maple, hawthorn and dogwood (Duncan et al. 1998) and ivy (*Hedera helix*) in autumn and winter. In deciduous forests, roe deer consume ligneous species throughout the whole year (Picard et al. 1993). The availability of ligneous and semi-ligneous plants, which are preferentially eaten by roe deer (Duncan et al. 1998), increased after the hurricane Lothar that impacted the study area in December 1999 (Widmer et al. 2004).

Roe deer at Trois-Fontaines have been intensively monitored since 1975 using capture–mark–recapture (CMR) methods (e.g. Gaillard et al. 1993, 2003a). Annual removals allowed managers to keep the size of the roe deer population at about 200–250 individuals >1 year of age in March between 1977 and 2000 (Gaillard et al. 2003a). Between 2001 and 2003, removals were stopped as part of an experimental manipulation of density, leading the number of roe deer to increase markedly. Before the density manipulation, the population was highly productive with almost all 2-year-old females giving birth to an average of 1.80 fawns (Gaillard et al. 1998) and high annual survival (0.82 and 0.93 for adult males and females, respectively; Gaillard et al. 1993), leading to high population growth rate (λ of 1.37) when we accounted for the annual removal of deer, which is close to the maximum population growth rate for roe deer (Nilsen et al. 2009). After the experimental increase of population density, some density-dependent responses occurred in fawn body mass and fawn summer survival (Nilsen et al. 2009).

Oak surveys were conducted annually between 1996 and 2005, excluding 1999 and 2000 as a consequence of the hurricane Lothar. The observation period usually ran between October 15 and November 15. We only took measurements in common stands of oak (*Q. petraea* Mattus. Liebl. and *Q. robur* L.), either from natural regeneration, from regenerations regularly treated by foresters or from "mixed regeneration regimes" (i.e. a mixture of natural regeneration and plantation). We used the protocol "natural regeneration and stands not aligned" (see Saint-Andrieux 1994 for further details). Each year, we sampled all the homogenous forest plots in which planting of oak was accessible to deer (i.e. less than 120 cm; Table 1). The low number of such zones allowed us an almost exhaustive sampling. In each plot and whatever its area, we used a systematic random design to record oak in 50 sampling units (Fig. 1). On each sampled unit, the four planting of oak closest to the centre were checked to assess evidence of browsing on the terminal shoot (0—seedling not consumed, 1—seedling consumed) that occurred after the starting of the last vegetation flush. The oak browsing index was defined as the proportion of seedlings consumed in the unit (number of seedlings consumed/number of seedlings examined).

We fitted generalized linear mixed models (with a binomial link function) with random intercept to assess the relationship between the oak browsing index (OBI) and population density. We used OBI as the dependent variable,

Table 1 Sampling intensity for each year of the study of the oak browsing in the Trois-Fontaines forest, France

Year	Number of stands sampled	Total number of forest plots sampled	Studied area (ha)
1996	19	950	121
1997	14	700	79
1998	14	700	80
2001	10	500	45
2002	16	800	44
2003	13	650	36
2004	16	800	57
2005	15	750	53

the year (1996 to 2005) or the CMR estimate of roe deer population size as the independent variable, and we controlled for possible confounding effects of the type of regeneration (natural vs. treated (either partially or fully planted), added as a fixed factor) and of the forest plots (to avoid pseudo-replication problems sensu Hurlbert (1984), added as a random factor). As OBI was measured as a number of events relative to a number of trials, we used a logit link with errors binomially distributed. We tested the significance of the model terms for the fixed effects using Wald tests. To select the best model, we used the Akaike information criterion (AIC) as recommended by Burnham and Anderson (2002). We retained the model with the lowest AIC value (i.e. the best compromise between accuracy and precision). When the difference between two competing models was less than 2, we retained the simplest model according to the parsimony rules (Burnham and Anderson 2002). We also calculated AIC weights to measure the likelihood that a given model would be the best among the set of models fitted (Burnham and Anderson 2002). We performed all the analyses using the R 2.6.1 statistical package (R Development Core Team 2007).

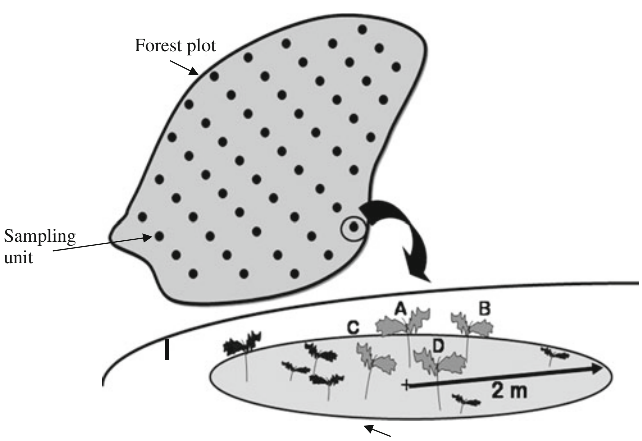

Fig. 1 Sampling design of roe deer browsing on oak. In each of the 50 sampling units within a given forest plot, the browsing occurrence was recorded from the four (*A*, *B*, *C*, *D*) oak seedlings closest to the centre of the sampling unit

Results

Only one of the seven candidate models received some statistical support (Table 2). This best model included a marked influence of the type of regeneration, of the year, of interactions between the type of regeneration (with increased damage from natural to tree nursery stands) and the year and of roe deer population size (Tables 2 and 3). According to the selected model, the OBI steadily increased with increasing population size as illustrated (Fig. 2) when regressing the best annual estimates of OBI against roe deer population size estimated using CMR (slope of 0.076± 0.009 [slope±SE]), corresponding to an increase of density from about 13 to 28 roe deer/km^2.

Discussion

The OBI as defined here provides a simple metric of roe deer browsing that responded strongly to changes of roe deer population size and appears thereby as a reliable candidate to become an indicator of "ecological change" (sensu Morellet et al. 2007) that are increasingly used to assess and monitor populations of ungulates (Cairns et al. 1993). Up to now, indicators measuring changes of population abundance (e.g. kilometric index, Vincent et al. 1991), of quality and performance of individuals (e.g. fawn

Table 2 Models fitted to predict variation in the OBI in relation to changes of roe deer population size (CMR), year (1996–2005) and type of regeneration at Trois-Fontaines, France

Response variable	Random effect	Fixed effect	AIC	ΔAIC	w_i
OBI	Forest plot	CMR+type+year+year×type	372.2	0.00	0.99
		CMR+type+year	380.9	8.70	0.01
		CMR+type	392.4	20.20	0
		CMR	417.4	45.20	0
		Year+type	441.9	69.70	0
		Year+type+year×type	442.5	70.30	0
		Year	481.4	109.20	0

The forest plot was included as a random factor. The AIC, the ΔAIC between a given model and the best model and the w_i are provided

OBI oak browsing index, *CMR* capture–mark–recapture, *AIC* Akaike information criterion, *ΔAIC* change in AIC, w_i AIC weight

Table 3 Estimates, SE and statistical significance (*z* test and *P* value) of parameters influencing the OBI from the selected model (model 1, see Table 1)

Response variable	Parameter	Estimate	SE	*z* test	*P* value
OBI	(Intercept)	−45.10	42.62	−1.06	0.29
	CMR	0.0064	0.00075	8.48	0.000
	Type	−198.34	61.05	−3.25	0.0012
	Year	0.021	0.021	0.96	0.34
	Year× type	0.099	0.031	3.26	0.0011

This model includes the effects of roe deer population size (CMR), the type of regeneration (type, with mixed plantation as a reference), the year and the interaction between year (1996–2005) and type of regeneration on the oak browsing index at Trois-Fontaines, France

OBI oak browsing index, *CMR* capture–mark–recapture, *SE* standard error

body mass: Gaillard et al. 1996, hind foot length of fawns: Toïgo et al. 2006 or cohort-specific jaw length: Hewison et al. 1996) and of population impact on the habitat (e.g. browsing index, Morellet et al. 2001) have been shown to provide reliable tools for managers to assess the relationship between a deer population and its habitat. The marked linear relationship we obtained at Trois-Fontaines between oak browsing and roe deer population size (corresponding to a twofold increase of density from about 13 to 28 roe deer/km^2) suggests that the OBI is likely to detect changes in roe deer habitat relationships in most deciduous forests of western Europe with natural regeneration of oak stands. By quantifying the response of a common forest tree with high economical value to changes of deer density, the OBI might offer a useful complement to other indicators such as

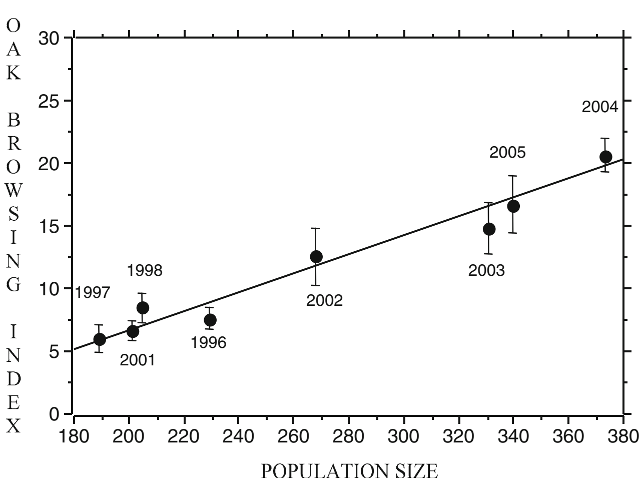

Fig. 2 Relationship between density (measured by population size estimated by capture–recapture methods) and the oak browsing index between 1996 and 2005 at Trois-Fontaines, France

the browsing index (measured from the sampling of all woody plants on 40 m^2 plots; Morellet et al. 2001). However, it likely that the strong linear relationship we reported here between the oak browsing index and roe deer density should not occur in the whole range of deer densities. At higher density than the density range monitored here (i.e. with a maximum of about 28 roe deer/km^2), we can expect that the rate of increase of the oak browsing index with density should decline until becoming null at some density threshold for which all the oaks would have been browsed. However, the degree of utilization of oak by roe deer at a given density is likely to be ecosystem-dependent (Mysterud 2006). Therefore, the prediction of the density at which the oak browsing index will not be useful anymore is far from an easy task.

Browsers like roe deer usually prefer plants with high nitrogen and low fibre content (Hobbs et al. 1983; Danell et al. 1994) and have therefore differential impacts according to the plant species (Gill 1992; Chevallier-Redor et al. 2001). Oaks have high nitrogen contents and are thus selected for by roe deer (Pellerin et al. 2010) and are widespread in Europe. As the response of highly preferred plant species in terms of increased browsing pressure depends on their abundance (Mysterud et al. 2010), the combination of high abundance and high appetence of oak for roe deer explains why the consumption of this tree species responds so quickly to changes of roe deer density (Barancekova et al. 2007). The benefit of using the OBI to monitor roe deer populations over large spatial scales is thus potentially high. However, roe deer co-occur with other ungulate species in most European forests (Apollonio et al. 2010) that also feed on oak and leave similar signature on the stem, so that it is currently not possible to tease apart the relative contribution of the different species to deer browsing. In particular, roe deer is sympatric with red deer *Cervus elaphus* in more than 50% of forests in France nowadays (Maillard et al. 2010) so that getting a measure of the relative contribution of roe deer on the oak browsing index is impossible in those places in the absence of a method allowing disentangling roe deer from red deer browsing signatures.

While roe deer is the only large wild herbivore for which a monitoring based on a complete set of indicators of ecological change (i.e. including measures of population abundance, measures of animal performance and measures of impact on plants; Morellet et al. 2007) has been calibrated, some indicators have been used to monitor populations of white-tailed deer (Strickland and Demarais 2000), mule deer *Odocoileus hemionus* (Keyser et al. 2006) and red deer (Garel et al. 2010). We encourage the development of this approach for abundant populations of large herbivores that are especially difficult to count (Gaillard et al. 2003b) to improve their management.

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