The browsing index: new tool uses browsing pressure to monitor deer populations

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Abstract Usual counts of deer populations generally show low reliability, especially at the high-density levels deer have recently reached in most parts of Europe. Since 1990, researchers and managers have looked for index methods to replace counts. Monitoring vegetation changes over time in response to deer browsing could be useful for managers to index deer abundance. We assessed the feasibility of using Aldous-derived vegetation surveys to monitor the population-habitat interaction over time. We first developed an original statistical procedure to define a reliable measure of deer browsing. Then we applied our browsing index to a case study involving a roe deer (*Capreolus capreolus*) population that was monitored intensively over 18 years and increased 5-fold in size. Our browsing index closely tracked the roe deer population size, the species-specific browsing rates differed widely, and bramble (*Rubus* sp.) could be reliably used to assess total browsing pressure of roe deer. Because it is an easy tool to use and involves much lower costs than traditional counts, our browsing index can be viewed as an efficient and reliable indicator of ecological change according to deer population status.

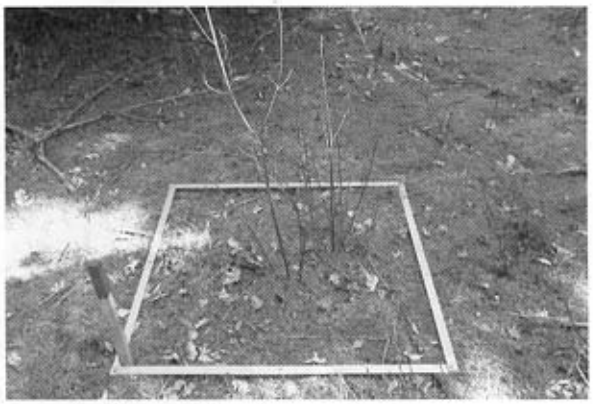
Key words Bayesian statistics, browse-deer interaction, browsing pressure, browsing index, *Capreolus capreolus*, France, monitoring population, roe deer, winter feeding

Roe deer (*Capreolus capreolus*) populations have increased in Europe since 1980 (Gill 1990, Andersen et al. 1998). High-density populations are now widespread, and managers require new tools to monitor them (McShea et al. 1997, Warren 1997). Most deer populations are hunted according to quotas that require a reliable assessment of population status. In the past, deer populations have been monitored using census methods (Caughley 1977, Seber 1982). Total counts of individuals in the entire area occupied by the population or on sampling plots using drives or hunting-related methods have been the most popular way to assess population size of deer (Cederlund et al. 1998). However, tests of reliability of counts have highlighted 3 main problems that limit the usefulness of census as a monitoring tool for deer populations (Andersen 1953, Gaillard et al. 1992, Gaillard and Boisaubert 1995). First, interpretation of changes in population size is ambiguous because density-dependent and density-independent factors may cause variation in population size. Second, accuracy of counts is low, especially at high density, when counts are often underestimations (Van Laere et al. 1999). Third, precision of counts is low (a coefficient of variation <20% is almost impossible to reach, Caughley 1977). Because of these problems, new tools to manage abundant deer populations are

Address for Nicolas Morellet, Philippe Ballon, and Yves Boscardin: Cemagref, Ecosystèmes Forestiers et Paysages, Domaine des Barres 45290 Nogent-sur-Vernisson, France. Address for Stéphane Champely: Département des Sports, University of Lyon, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France. Address for Jean-Michel Gaillard: Unité Mixte de Recherche 5558, University of Lyon, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France; e-mail: gaillard@biomserv.univ-lyon1.fr.

essential (Waller and Alverson 1997).

Roe deer is the most abundant deer species in Europe (Andersen et al. 1998) and is one of the most difficult to count (Cederlund et al. 1998). Thus, since 1990, researchers and managers have looked for index methods to replace counts as the basis for long-term population monitoring. Among these indices, a kilometric index of number of deer observed/km of transect sampled on foot (Vincent et al. 1991); the females' reproductive success, measured as number of fawns/female (Vincent et al. 1995) or as number of fawns/successful female (i.e., females with fawns at heel; Boutin et al. 1987); winter body mass of fawns (Maillard et al. 1989, Vincent et al. 1995, Gaillard et al. 1996); adult cohort jaw length (Hewison et al. 1996); and group size in winter (Bideau et al. 1983, Vincent et al. 1995) all provide reliable information on the status of roe deer populations (from colonization to saturation). All these indices are based on direct field observations of animals. When a population increases from colonization to saturation, the habitat is expected to change with the deer population. Indeed, managers aim to find an equilibrium between the deer population and its habitat that corresponds to the objectives fixed by society (Sinclair 1997). An indirect approach of monitoring this equilibrium based on vegetation surveys could therefore be useful for managers. This concept has led Guibert (1997) to propose a measure of the consumption of woody plants by deer in winter as a new monitoring tool. In fact, Aldous (1944) was the first to propose the consumption of woody plants to monitor deer populations, and several studies have been conducted on this topic in the last few years (Eiberle and Wenger 1983, Ballon et al. 1992, Picard et al. 1993, Guthorl 1994, Odermatt 1996). However, a central problem remains unsolved: how to measure among-year changes in woody plant consumption by deer in a given area. To answer this question, one needs to consider the entire population–habitat system rather than either the vegetation component or the deer component separately. Some authors have worked on the dynamics of plant use by deer during winter and have established relevant but time-consuming approaches to deer impact surveys of only limited value for managers (Brown and Doucet 1991, Doenier et al. 1997). Here, we propose a new method to measure browsing pressure on woody plants during winter (following Aldous 1944) and report a field application that suggests our method may allow managers to monitor deer populations reliably over a large range of ecological situations.



Example of the sampling plot, a quadrat.

Study area

The study occurred in the state forest of Dourdan, located near Paris, France. The elevation of the study area, an 830-ha forest, varied from 100 to 169 m. The climate was typical of mild temperate areas, with quite hot summers (i.e., mean temperature in July >20° C) and cool winters (mean temperature in January around 5° C). The forest was composed of oak (*Quercus sessiliflora*, 90%) and Norway pine (*Pinus silvestris*, 10%). The study area was delineated by a highway (A 10) to the west and by the Orge Valley to the east, which limited exchanges with other roe deer populations.

The size of the roe deer population of this forest has been monitored intensively by capture–mark–recapture methods (with ca 10 marked deer between 1980 and 1982, 30 between 1982 and 1985, and 65 between 1986 and 1989) for 10 years (1980–1989) and by a kilometric index for 18 years (1980–1997, ≈120 km of trails covering the whole forest were sampled between 2 and 6 times within a year [Vincent et al. 1991]). Prior to 1979, the roe deer population was hunted intensively, but total cessation of hunting between 1979 and 1990 allowed the population to increase steadily. Subsequently, between 1990 and 1994 the population decreased due to intensive hunting and since 1995 the population increased (based on the kilometric index) to the high-density level observed during 1986–1989. A few red deer (*Cervus elaphus*) have been occasionally observed in the forest since 1990, but no precise data are available on their status in this forest.

Methods

Sampling procedures

We used the method developed by Guibert (1997) to sample vegetation. We based sampling on a systematic procedure applied on a 200-m grid network. We defined the grid network in 1991 and marked it permanently in the field using wooden stakes. We performed sampling yearly from 15 to 31 March, just prior to vegetation growth, from 1991 to 1997 to obtain a measure of consumption over the entire winter. At each corner of a grid cell, we sampled woody plants on a 40-m^2 plot (radius of 3.57 m). We sampled 200 plots annually. For each woody species occurring on the plot and reachable by deer (less than 1.2 m and having some live parts that could be eaten by deer), we noted occurrence of consumption by looking for presence of scars (i. e., particular cut plane left by the deer teeth) on twigs. We ignored nonwoody plants because the herbivore species that ate those plants could include roe deer, hares (*Lepus europaeus*), or rodents. In contrast, for woody species, the cut plane allows easy differentiation between deer and small mammals. We considered all woody species found on plots except ivy (*Hedera helix*) because consumption is often difficult to determine on this species. We considered a woody plant species as consumed when >5% of the twigs available to deer were cut by deer. The same well-trained person conducted sampling each year except 1991. We then calculated an index of feeding pressure for the entire forest to monitor the browse–deer interaction. We calculated the browsing index as number of sampling units (i. e., the 40 m^2 plots) with ≥1 browsed/number of units with ≥1 woody plant species present. To understand trends better, we also calculated the species-specific browsing index for individual species that were present on ≥10% of sampling units.

Browsing index

A systematic sampling scheme with n plots was used. Number of plots with ≥1 species available was counted and denoted n_a. Number of plots with ≥1 species browsed was denoted n_b.

Number of plots with ≥1 species available is a random variable N_a and is such that

$$N_a \sim \mathrm{B}(n,\pi_a)$$

from a binomial distribution of index n and parameter $\pi_a \times \pi_a$ is the probability that we observed ≥1 species in a given plot. We can note that this specific distribution is not really important for the following developments and we could use, for example, a more dispersed one.

We use also a (conditional) binomial distribution with index n_a to model number of browsed plots n_b:

$$N_b \mid N_a = n_a \sim \mathrm{B}(n_a,\pi_b) \qquad (1)$$

where π_b is the parameter of interest that hereafter will be called the browsing index. π_b is the probability that a plot will be considered to be browsed provided a species was available on that plot.

A Bayesian approach

The basic idea of Bayesian statistics is to use an *a priori* probability distribution for the parameters of interest (here π_b and incidentally π_a). By means of Bayes formula, we can use the likelihood function (and the data) to improve our knowledge of the parameters. The result gives a posterior probability distribution for the parameters.

To represent our prior information about the browsing index, we assumed that it has an uniform distribution. We had indeed no reason to prefer any one value over any other. This kind of distribution is called a non-informative prior. We also assumed that the prior of π_a is independent from that of π_b.

Another name for the uniform distribution is the beta(1,1) distribution. The beta is a versatile family of distributions on [0,1] driven by 2 parameters (Figure 1):

$$\pi_b \sim \mathrm{beta}(1,1). \qquad (2)$$

In our context the Bayes formula becomes

$$p(\pi_b \mid n_a,n_b) = \frac{p(n_b \mid n_a,\pi_b) \times p(\pi_b)}{p(n_b \mid n_a)}, \qquad (3)$$

with $p(\pi_b|n_a,n_b)$ the posterior density of the browsing index, $p(\pi_b)$ the prior density (Eq. 2), $p(n_b|n_a,\pi_b)$ the likelihood corresponding to the conditional distribution of N_b (Eq. 1), and $p(n_b|n_a)$ is here to ensure that the area under the posterior density is 1.

This framework is appropriate because one wants to estimate the binomial parameter using a beta distribution for prior. The beta prior is called the natural conjugate of the binomial likelihood. That is, the posterior distribution remains in the family of beta distributions (Lee 1997:77).

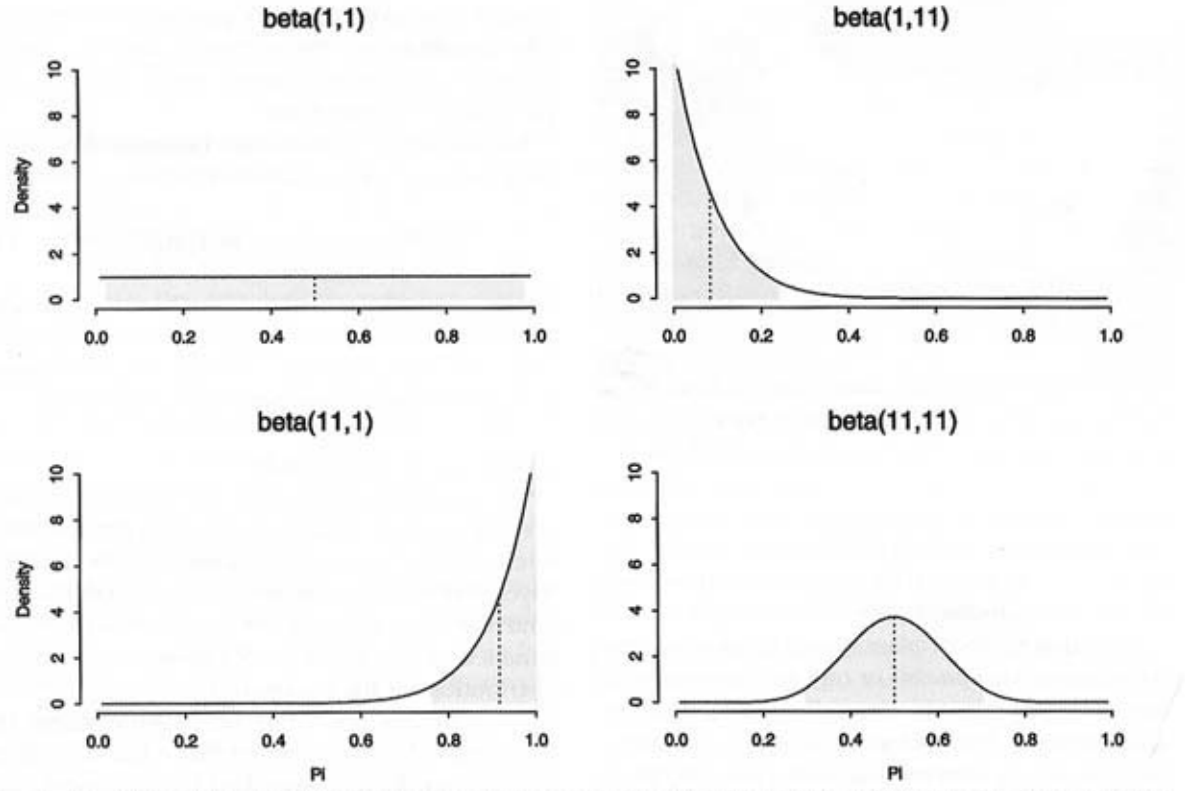


Figure 1. Four shapes of beta (continuous line) representing the possible results for the posterior distribution of the browsing index. The point estimation is given by the dotted line, and the shaded area is the 95% high-density interval.

The parameters of the resulting posterior beta distribution are

$$\pi_b | n_a, n_b \sim \text{beta}(1 + n_b, 1 + n_a - n_b). \quad (4)$$

A point estimator for the browsing index

The usual estimator in Bayesian inference is the posterior mean. For the beta distribution it reduces to the simple analytical expression:

$$\pi_b = \frac{1+n_b}{2+n_a}. \quad (5)$$

The behavior of the estimator of the browsing index is interesting, especially in extreme results of sampling:

1. $n_a = 0$ (no species observed), here $\hat{\pi}_b = 1/2$. The data provide no additional knowledge about the browsing index. We use a safe estimation.
2. $n_a \neq 0$ and $n_b = 0$ (no observed browsing on the set of plots): here $\hat{\pi}_b = 1/(2+n_a)$. This quantity can become very low, but it will never be zero. It is not realistic to consider that the probability of observing a browsed plot is zero. With other plots, a different plot size, or more plots, we would probably obtain a different result.
3. $n_a \neq 0$ and $n_b = n_a$ (all plots are browsed): here,

$$\hat{\pi}_b = \frac{1+n_b}{2+n_a} = 1 - \frac{1}{2+n_a}.$$

This quantity can converge to 1. This is the reverse situation of the previous one.

4. $0 < n_a < n_b$: here,

$$\hat{\pi}_b = \frac{1+n_b}{2+n_a}.$$

is similar to the naive estimator n_b/n_a which presents problems in the 3 previous cases. The usual confidence limits for a proportion are not suitable to this estimator. This is because the denominator n_a is a random quantity.

A statistical interval for the browsing index

Several definitions of a Bayesian confidence interval exist in the literature. We use the very classical approach of the high-density interval. At a given

$(1-\alpha)$ probability level, we look for an interval such that the density of the posterior distribution of the parameter π_b at any point inside it is greater than the density at any point outside it. One advantage of the Bayesian approach is the clear probabilistic interpretation of the resulting confidence interval. The selected values of the parameters are *stricto sensu* the most probable values.

Statistical intervals are computed using S-Plus® routines available from the authors. The most current situation is that the beta distribution is unimodal ($0<n_b<n_a$). In this case, the algorithm is a search in the family of intervals $[L,U]$ corresponding to the given confidence level. One selects the one with $p(U)=p(L)$ where p is the probability density function of beta.

In the continuous monitoring situations (e.g., Dourdan), it seems advisable to use the results of the preceding years to improve the ongoing estimation. This can easily be done in a Bayesian framework. The important point is to determine an informative prior:

$$\text{beta}(a^{(k-1)},b^{(k-1)})$$

that summarizes the information from the preceding year $(k-1)$.

To clarify the meaning of such prior information, it is important to consider that first, the mean of the distribution $a^{(k-1)}/(a^{(k-1)}+b^{(k-1)})$ is the estimated value of the browsing index obtained in the previous year and second that the quantity $(a^{(k-1)}-1)+(b^{(k-1)}-1)$ is in a sense the number of observations.

Then using the Bayes formula (Eq. 3), one can update this prior information by the likelihood corresponding to the current year k (where $n_a^{(k)}$ is the number of plots with at least 1 species available and $n_b^{(k)}$ is the number of browsed plots both in year k) to obtain a posterior distribution

$$\text{beta}(a^{(k)}+n_b^{(k)};b^{(k-1)}+n_a^{(k)}-n_b^{(k)}) \qquad (6)$$

The new estimator of choice will be again the posterior mean

$$\hat{\pi}_b^{(k)}=\frac{a^{(k-1)}+n_b^{(k)}}{a^{(k-1)}+b^{(k-1)}+n_a^{(k)}}. \qquad (7)$$

Several methods can be imagined to provide adequate values for $a^{(k-1)}$ and $b^{(k-1)}$. We propose to compute these values from 2 easily perceived quantities:

1. The estimation of the browsing index from the preceding year $\hat{\pi}_b^{(k-1)}$. This value is defined automatically.
2. A credibility $\alpha(0\leq\alpha\leq1)$ of the value of this index in terms of percentage of equivalent available plots in the current year. For instance, if number of available plots in the current year k is $n_a^{(k)}=200$ and credibility is $\alpha=25\%$, the information of the year $(k-1)$ worth $\alpha n_a^{(k)}=50$ available plots.

A little algebra shows that

$$a^{(k-1)}=(\alpha n_a^{(k)}+2)\hat{\pi}_b^{(k-1)} \qquad (8a)$$

and

$$b^{(k-1)}=(\alpha n_a^{(k)}+2)(1-\hat{\pi}_b^{(k-1)}). \qquad (8b)$$

The choice of this credibility is indeed a subjective one. We decide to choose α to improve our estimator (Eq. 7) from 2 points of view. The first criterion is to maximize the correlation between the reliable kilometric index and the new estimator of the browsing index computed from $\alpha=0$ (a very flat prior) to $\alpha=1$ (the prior information is equivalent to the current year information). This correlation is maximum around 30–40% (Figure 2*a*). The second criterion is to reduce the confidence limits of the browsing index. We consider the average length (for the 6 years observed in Dourdan) of the confidence limits of the new estimator from again $\alpha=0$ to $\alpha=1$. The more information, the narrower the limits (Fig. 2*b*). By using $\alpha=1/3$, this average length is reduced by 8%. Figure 3 is the direct comparison of the estimator with $\alpha=0$ and the one with $\alpha=1/3$. Clearly, the main effect is a smoothing of the evolution coupling with a small reduction of the confidence limits.

Results

The browsing index changed markedly over the study (Figure 3). The level of the browsing pressure tended to decrease slightly between 1992 and 1995, whereas it increased significantly between 1995 and 1997 (0.63 [95% HDI: 0.57–0.68] in 1995 versus 0.86 [95% HDI: 0.82–0.90] in 1997). Yearly variation in the browsing index was related linearly to the kilometric index ($r=0.93$ and see Figure 4). Because it has been assessed previously that kilometric index closely fit yearly variation in population size (Vincent et al. 1991), we can conclude that

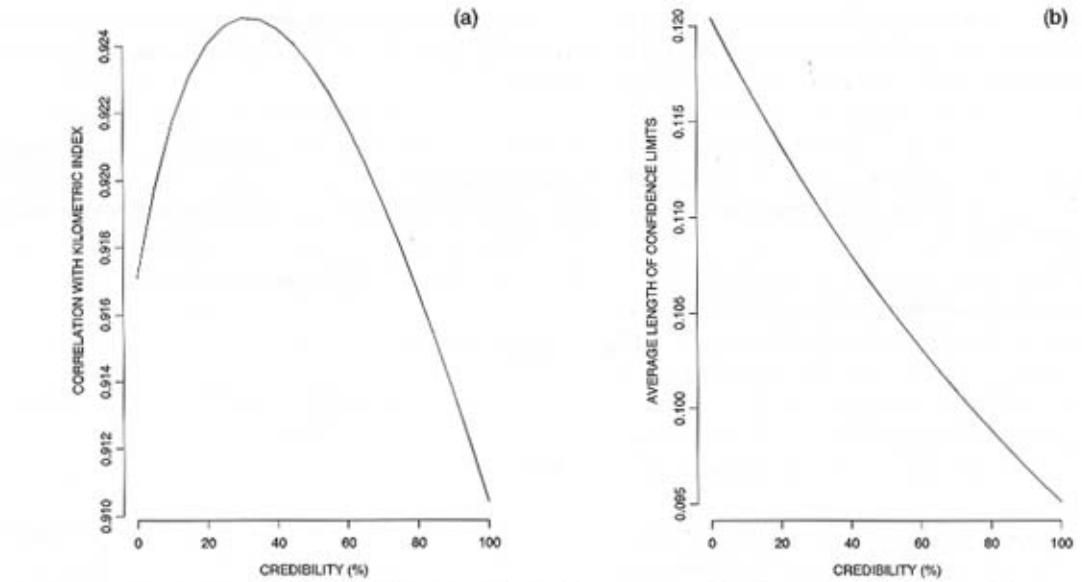


Figure 2. (*a*) Correlation between the kilometric index and the estimation of the browsing index computed from $\alpha = 0$ to $\alpha = 1$; (*b*) Average length (for the 6 years) of the confidence limits of the same estimation also from $\alpha = 0$ to $\alpha = 1$.

browsing pressure tracked the roe deer population size.

We identified 35 browse species during the study. Variations of the species-specific browsing index differed widely (Figure 5). Some species (e.g., oak) were consumed little by roe deer and did not react to the increase of population size after 1995 (browsing index of 0.03 [95% HDI: 0.01–0.06] in 1995 and 1997). On the other hand, hornbeam (*Carpinus betulus*, browsing index of 0.06 [95% HDI: 0.02–0.11] in 1995 versus 0.33 [95% HDI: 0.25–0.42] in 1997), common honeysuckle (*Lonicera peryclimenu*, browsing index of 0.48 [95% HDI: 0.41–0.55] in 1995 versus 0.81 [95% HDI: 0.76–0.87] in 1997), and bramble (browsing index of 0.57 [95% HDI: 0.0.50–0.63] in 1995 versus 0.84 [95% HDI: 0.79–0.89] in 1997) had variable consumption in close relation to the size of the roe deer population (correlation between species-specific browsing index and total browsing index of 0.97, 0.95, and 0.98 for hornbeam, common honeysuckle, and bramble, respectively).

Honeysuckle and bramble were the most intensively browsed species. Moreover, bramble and honeysuckle are important items of roe deer diet during winter (see Tixier and Duncan 1996 for a review). Thus, monitoring the bramble browsing index provided a reliable way to assess total browsing pressure at Dourdan.

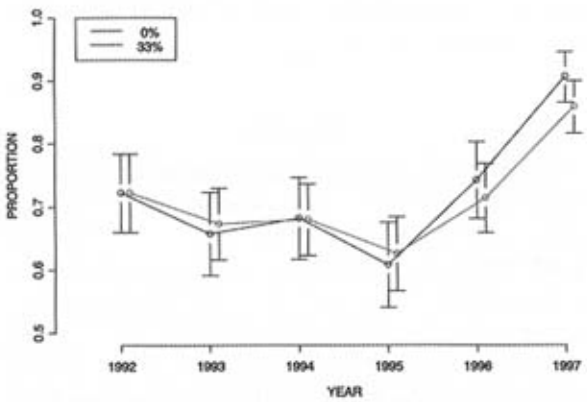


Figure 3. Comparison of 2 estimations of the browsing index computed with $\alpha = 0$ (solid line) and $\alpha = 1/3$ (dotted line) for 6 years (1992–1997) in Dourdan forest, France. Bars indicate 95% high-density intervals.

Discussion

The browsing index appears to be a very useful tool to monitor the browse-deer interaction. This index closely tracked the fluctuations of a roe deer population over time, so that the changes in browsing pressure were partly accounted for by changes in roe deer population size in the Dourdan forest. However, browsing pressure reflects changes in herbivore population size and availability of resources. Monitoring a species-specific browsing index also may provide a means to better understand temporal trends of browsing pressure. For instance, we found a close relationship between the bramble browsing index and the overall

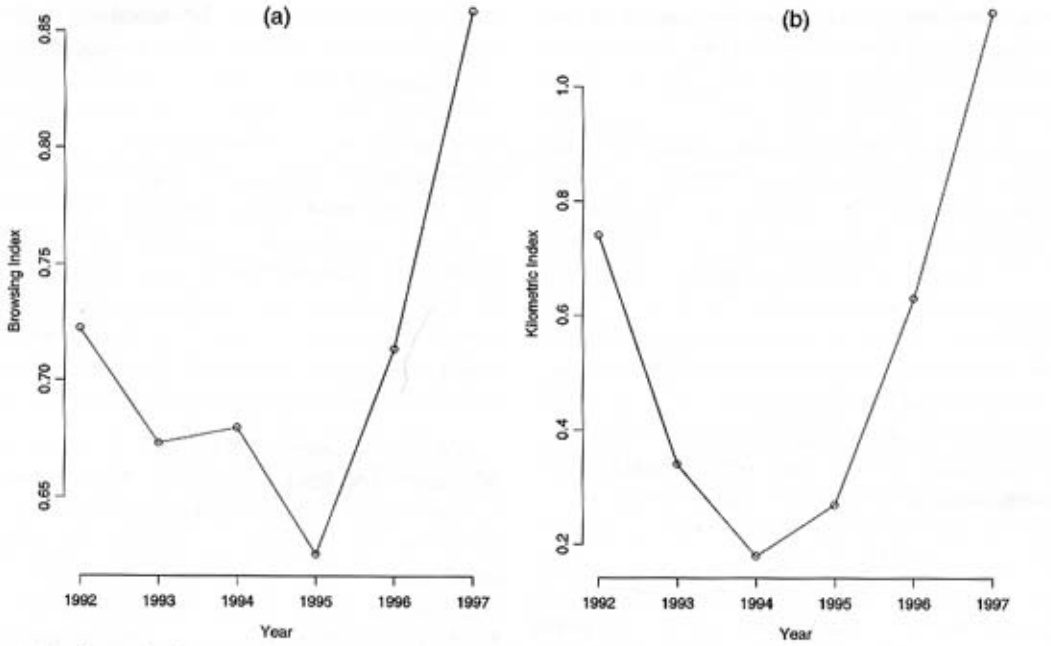


Figure 4. (*a*) Relationship between the browsing index with credibility $\alpha = 1/3$ and the kilometric index from 1992 to 1997 in Dourdan. (*b*) Kilometric index monitored during the same period.

browsing index. Therefore our approach provides a means to track the variation of deer impact on woody plants over time and to assess the magnitude of browsing pressure on the most available species during winter. The idea of using individual browse species to track deer population is not a

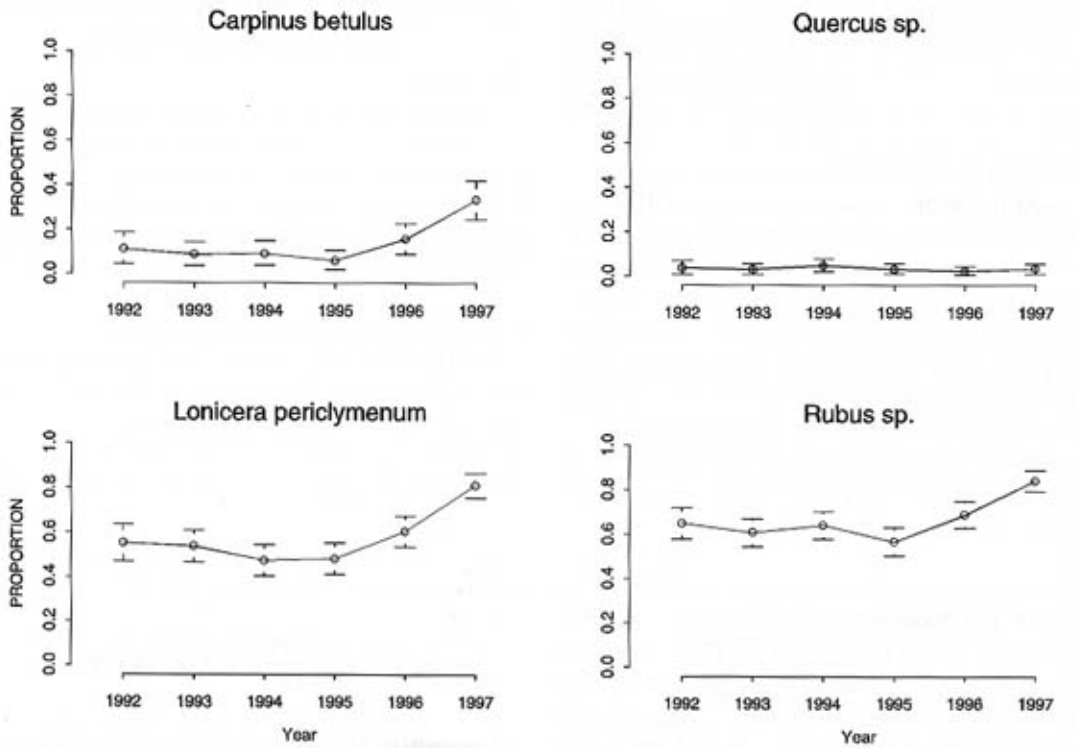


Figure 5. Changes in the browsing index ($\alpha = 1/3$) of the 4 most available browse species (hornbeam, oak, honeysuckle, and bramble) over 6 years (1992–1997) in the Dourdan forest, France. Bars indicate 95% high-density intervals.

new one but parallels the range management concept of using key species in making stocking-rate determination (Bonham 1989). As a tool for monitoring deer pressure on vegetation, our browsing index corresponds exactly to that which Waller and Anderson (1997:223) define as "efficient and reliable indicators capable of serving as 'early warning signs' of impeding ecological change." This index could therefore be a decision-making tool for the deer manager. A browsing index can thus be added to the preliminary list of indicators of ecological changes that reflect roe deer–forest relationships, such as the kilometric index (Vincent et al. 1991) and juvenile body mass (Gaillard et al. 1996).

Because plant species may vary in palatability depending on the plant community, using individual species such as brambles may not be recommended as a general tool to monitor roe deer over its entire geographic range. However, brambles are widespread in western Europe and have been shown to markedly affect roe deer population dynamics under a large range of ecological contexts. For example, Gill (1994) reported that a marked decrease in bramble cover was associated with a decrease in body weight and recruitment rate in a roe deer population of southern England. Therefore, although further work is required to assess the suitability of the browsing index method as a tool to monitor roe deer populations in Fennoscandian or Mediterranean ecosystems where brambles are not widespread, we are confident that our technique can be adopted by managers in most roe deer habitat of western Europe.

We used the same *a priori* non-informative uniform distribution to describe the browsing index. However, as soon as 1 sampling year had been collected, it would have been possible to use the previous year's data to build informative distributions for the prior. One consequence of this idea is the possibility of keeping the amount of final information constant while reducing sampling effort by using annually renewed informative priors. The equilibrium between the prior information and the complementary sampling necessary requires investigation.

In this study we considered measurements from 1 observer. For broader applications, some modifications can be easily incorporated. First, reducing the area of the sampling unit to 1.0 m^2 would offer a better sampling design by allowing a larger range of people to collect field data. Second, by using such a small area, the 5% threshold of consumption used to categorize the browsed or unbrowsed classes can be removed. Thus, a species would be classed as browsed when ≥1 sign of browsing is noted and as unbrowsed when no sign of consumption by deer can be detected. Using this modification would ensure a simple binary coding. In association with other wildlife indicators, our method could be used to monitor deer population trends and their impact on vegetation during winter. Our methodology provides an easy to use tool, from a statistical and practical viewpoint, and its much lower costs compared to traditional counting techniques enhances its feasibility.

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Appendix: an example of computing the Browsing index

The data

Let's say that data are available for years 1 and 2. The number of available plots is (respectively for year 1 and year 2) $n_a^{(1)}=196$ and $n_a^{(2)}=195$ and the corresponding number of browsed plots is $n_b^{(1)}=142$ and $n_b^{(2)}=128$ (these are data from Dourdan in 1992 and 1993).

Using a non-informative prior

For the first year, there is no previous information, so the *a priori* distribution for the browsing index is beta(1,1). Then, combining with the data $n_a^{(1)}=196$ and $n_b^{(1)}=142$, one obtains a posterior beta(1+142,1+196−142) [see Eq. 4], that is to say beta(143,55).

The mean of this distribution, which is our point estimator of the browsing index, is

$$\hat{\pi}_b^{(1)} = \frac{1+142}{2+196} \approx 0.722 \quad \text{[See Eq. 5]}.$$

Computing the 95% high-density interval is more difficult because one needs to consider the density

function $p()$ of the beta(143,55) and to determine two values L and U with $p(L)=p(U)$, and include 95% of the density. Our S-Plus® function gives $L=0.659$ and $U=0.783$ with $p(L)=p(U)=1.861$. The probability of the beta(143,55) to the left of L is 0.0278 and to the right of U is 0.222, which sums to 5% outside our high-density interval.

Using an informative prior

For the second year, we use the information from the preceding year—that is to say, $\hat{\pi}_b^{(1)} \approx 0.722$. With a credibility $\alpha = 1/3$ and a number of available plots $n_a^{(2)} = 195$ for the current year, one obtains a corresponding information of $\alpha n_a^{(2)} = 195/3 = 65$ available plots for the previous year. Using the given formula [See Eqs. 8a and 8b], one computes

$$a^{(1)} = (65 + 2) \times 0.722 \approx 48.4$$

and

$$b^{(1)} = (65 + 2) \times (1 - 0.722) \approx 18.6.$$

So the informative *a priori* distribution for the browsing index is beta(48.4,18.6), and, combining with $n_a^{(2)} = 195$ and $n_b^{(2)} = 128$, one obtains a posterior beta(48.4+128,18.6+195−138) distribution [See Eq. 6], that is to say beta(176.4,85.6).

The resulting point estimator is

$$\hat{\pi}_b^{(2)} = \frac{48.4 + 128}{48.4 + 18.6 + 195} \approx 0.673 \quad \text{[See Eq. 7]}.$$

The 95% high-density interval [$L = 0.616$, $U = 0.729$] computed using the S-Plus® routine is such that $p(L)=p(U)=2.03$ where $p()$ is the density function of the beta(176.4,85.6) giving 0.026 to the left of L and 0.024 to the right of U, summing to 5%.

Literature cited

Aldous, S. E. 1944. A deer browse method. Journal of Mammalogy 25: 130–136.

Andersen, J. 1953. Analysis of the Danish roe deer population based on the extermination of the total stock. Danish Review of Game Biology 2:127–155.

Andersen, R., P. Duncan, and J. D. C. Linnell. 1998. The European roe deer: the biology of success. Scandinavian University, Oslo. Norway.

Ballon, P., B. Guibert, JP. Hamard, and Y. Boscardin. 1992. Evolution of roe deer browsing pressure in the forest of Dourdan. Pages 513–518 *in* F. Spitz, G. Janeau, G. Gonzalez and S. Aulagnier, editors. Proceedings of the International Symposium "Ongulés/Ungulates 91". Société française pour l'étude et la protection des mammifères and Institut de recherche sur les grands mammifères, Paris-Toulouse, France.

Bideau, E., J. P. Vincent, and F. Maire. 1983. Evolution saisonnière de la taille des groupes chez le chevreuil en milieu forestier. Revue d'Ecologie (Terre et Vie) 37: 161–169.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. Wiley and Sons, New York, New York, USA.

Boutin, J. M., J. M. Gaillard, D. Delorme, and G. Van Laere. 1987. Suivi de l'évolution de la fécondité chez le chevreuil (*Capreolus capreolus*) par l'observation des groupes familiaux. Gibier Faune Sauvage 4: 255–265.

Brown, D. T., and G. J. Doucet. 1991. Temporal changes in winter diet selection by white-tailed deer in a northern deer yard. Journal of Wildlife Management 55: 361–376.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley and Sons, Chichester, New York, USA.

Cederlund, G., J. Bergqvist, P. Kjellander, R. Gill, J-M. Gaillard, B. Boisaubert, P. Ballon, and P. Duncan. 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. Pages 337–372 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. The European roe deer: the biology of success. Scandinavian University, Oslo, Norway.

Doenier, P. B., G. D. DelGiudice, and M. R. Riggs. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin 25: 235–243.

Eiberle, K., and C. Wenger. 1983. Zur Bedeutung der Forstlichen Betiebsart für das Reh. Schweizerische Zeitschrift für Forstwesen 134: 191–206.

Gaillard, J. M., and B. Boisaubert. 1995. Mieux connaître les populations de cervidés. Des comptages aux bioindicateurs. Arborescence 56: 3–6.

Gaillard, J. M., D. Delorme, J. M. Boutin, G. Van Laere, and B. Boisaubert. 1996. Body mass of roe deer fawns during winter in 2 contrasting populations. Journal of Wildlife Management 60: 29–36.

Gaillard, J. M., A. J. S. Sempéré, J. M. Boutin, G. Van Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Canadian Journal of Zoology 70: 1541–1545.

Gill, R. 1990. Monitoring the status of European and North American cervids. GEMS Information Series global environment monitoring system. United Nations Environment Programme, Nairobi, Kenya.

Gill, R. 1994. The population dynamics of roe deer (*Capreolus capreolus* L.) in relation to forest habitat succession. Dissertation, The Open University, Milton Keynes, United Kingdom.

Guibert, B. 1997. Une nouvelle approche des populations de chevreuils en forêt: "l'indice de pression sur la flore." Bulletin Technique de l'Office National des Forêts 32: 5–13.

Guthori, V. 1994. Zusammenhänge zwischen des Populationsdichte des Rehwildes (*Capreolus capreolus*, Linné 1758) und dem Verbissdrack auf die Waldvegetation. Z. Jagdwiss, 40: 122–136.

Hewison, A. J. M., JP. Vincent, E. Bideau, J-M. Angibault, and R. J. Putman. 1996. Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. Journal of Zoology 239: 573–581.

Lee, P. M. 1997. Bayesian statistics—an introduction. Arnold, London, United Kingdom.

Maillard, D., B. Boisaubert, and J-M. Gaillard. 1989. La masse corporelle: un bio-indicateur possible pour le suivi des populations de chevreuils. Gibier Faune Sauvage 6: 57–68.

McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. The science of overabundance: Deer ecology and population management. Smithsonian Institution, Washington, D.C., USA.

Odermatt, O. 1996. Zur Bewertung von wildverbiss die "method Eiberle". Schweiz. Z. Forstwes 147:177–199.

Picard, J. F., B. Boisaubert, D. Maillard, and M. H. Maire. 1993. Dynamique de l'abroutissement dû au chevreuil (*Capreolus capreolus* L.) dans une hêtraie-chênaie calcicole (forêt de Haye, Meurthe et Moselle). Revue Forestière Française 45: 525–538.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Griffin, London, United Kingdom.

Sinclair, A. R. E. 1997. Carrying capacity and the overabundance of deer. A framework for management. Pages 380–394 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance. Deer ecology and population management. Smithsonian Institution, Washington, D.C., USA.

Tixier, H., and P. Duncan. 1996. Are European roe deer browsers? A review of variations in the composition of their diets. Revue d'Ecologie. (Terre Vie) 51:3–17.

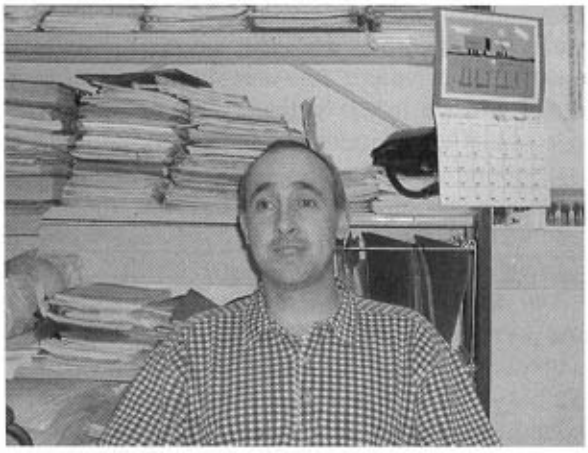
Van Laere, G., D. Maillard, J. M. Boutin, and D. Delorme. 1999. Le suivi des populations de chevreuils: des méthodes traditionnelles d'estimation aux indicateurs population-environnement. Bulletin Mensuel de l'Office National de la Chasse 244:46–53.

Vincent, J-P., J-M. Gaillard, and E. Bideau. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. Acta Theriologica 36:315–328.

Vincent, J. P., E. Bideau, A. J. M. Hewison, and J. M. Angibault. 1995. The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). Journal of Zoology 236:371–382.

Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217–226.

Warren, R. J. 1997. The challenge of deer overabundance in the 21st century. Wildlife Society Bulletin 25:213–214.



Stéphane Champley (right) is a biometrician, has a Ph.D., and has a permanent position as assistant professor. His main interests involve data analysis. ***Jean-Michael Gaillard*** (top right) has a Ph.D. and is director of research at CNRS. His main interest is population dynamics of large herbivores. ***Philippe Ballon*** (at left in bottom right photo) is a forestry engineer and ***Yves Boscardin*** (at right in bottom right photo) is a forestry technician, both with CEMAGREF. Both are heavily involved in the assessment and quantification of deer damage on forests.

Associate editor: *Krausman*