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# Indicators of ecological change: new tools for managing populations of large herbivores

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## Summary

**1.** High-density populations of large herbivores are now widespread. Wildlife managers commonly attempt to control large herbivores through hunting to meet specific management objectives, considering population density as the minimal key source of information. Here, we review the problems of censusing populations of large herbivores and describe an alternative approach, employing indicators of ecological change.
**2.** Estimating density of large herbivores with high precision and accuracy is difficult, especially over large areas, and requires considerable investment of time, people and money. Management decisions are often made on an annual basis, informed by population changes over the previous year. However, estimating year-to-year changes in density is not a realistic goal for most large herbivores. Furthermore, population density *per se* provides no information on the relationship between the population and its habitat.
**3.** For successful management of large herbivores, we need to consider not only the fate of the population, but rather changes in both population and habitat features, as well as their interaction. Managers require information on trends in both the animal population and habitat quality in order to interpret changes in the interaction between these two compartments.
**4.** We propose that a set of indicators of animal performance, population abundance, habitat quality and/or herbivore habitat impact provides relevant information on the population–habitat system. Monitoring temporal changes in these indicators provides a new basis for setting hunting quotas to achieve specific management objectives. This sort of adaptive management is employed widely in France for managing roe deer *Capreolus capreolus*.
**5.** *Synthesis and applications*. The management of large herbivores would be improved by investing fewer resources in trying to estimate the absolute abundance of ungulates, and more resources in collecting additional data to inform understanding of the ecological status of the ungulate–habitat system being managed. This paper presents a set of indicators of ecological change for monitoring the interaction between a population and its habitat as a basis for adaptive management to attain explicit goals and to improve knowledge of the system. This approach could improve management for a variety of large herbivores, by harmonizing actions at wide spatial scales.

*Key-words*: abundance estimates, ecological indicators, population monitoring, population size, population-habitat system, roe deer, ungulates, wildlife management

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The authors would like to dedicate this paper to Jean-Paul Vincent, who initiated this work in the early 1980s.

## Introduction

Populations of large herbivores have increased their range and density substantially over recent decades, both in Europe (for roe deer: Gill 1990; Andersen, Duncan & Linnell 1998) and North America (for white-tailed deer *Odocoileus virginianus*: Gill 1990; Warren 1997). This marked change in status has been accompanied by a concomitant increase in ungulate–human conflicts, primarily damage to farming and forestry (Gill 1992), ungulate–vehicle collisions (Groot Bruinderink & Hazebroek 1996) and the spread of disease (Simpson 2002). Large herbivores are usually controlled through hunting in order to meet specific management objectives (Sinclair 1997). Most populations are hunted on the basis of quotas, so reliable assessment of the demographic situation is necessary. As a general rule estimates of population density, or indices of density, provide the minimum information required for this (Williams, Nichols & Conroy 2002). Hence, counts of the whole population or sample plots using aerial censuses in open areas (e.g. Jachmann 2002) and drive censuses or other hunting-related methods in closed areas (e.g. Dzieciolowski *et al*. 1995) are used frequently to assess population size. Over the last 30 years, evidence has accumulated for problems of bias and imprecision in censusing large herbivores by all the widely used methods (e.g. Redfern *et al*. 2002 for aerial counts; Gaillard, Loison & Toïgo 2003 for ground counts). In this paper, we review these problems and subsequently propose indicators of ecological change as a promising alternative to estimates of population size. More specifically, we address the following questions:

**1.** Can the density of populations of large herbivores be estimated reliably, and do we really need absolute measures of population abundance to manage them successfully?

**2.** Is it possible to achieve management objectives for large herbivores by monitoring temporal fluctuations in a set of ecological indicators based on the responses of life history traits and/or habitat features to changes in population abundance, but which do not require direct estimates of population abundance?

In addition, we provide an overview of how a set of indices is used to monitor and manage roe deer throughout large parts of their range in France.

## The limits of abundance estimates

### THE LIMITS OF PRECISION AND ACCURACY

In their recent review, Williams *et al*. (2002) asserted that 'good estimates of population size are essential components of the data needed for evaluation of many conservation, wildlife, fisheries, and pest management programs'. However, estimating the size of large herbivore populations with high accuracy (i.e. low bias) and precision is difficult (see Andersen 1953 for a test which showed that counts of roe deer provided a value which was a third of the true population). Methods based on indirect estimation of animal density have been used, such as pellet groups (Putman 1984; Marques *et al*. 2001), animal vocalizations (Reby *et al*. 1998), DNA (Taberlet, Waits & Luikart 1999) and animal tracks (Stephens *et al*. 2006). Here, we focus on direct estimates of population size which are commonly assumed to provide the most accurate and precise measures of density for populations of large herbivores. Methods for estimating density directly have undergone major developments in the past century for application to wildlife populations, notably capture–mark–recapture (CMR), distance sampling and harvest models (Buckland, Goudie & Borchers 2000). These methods are based on direct animal surveys and must satisfy several assumptions in order to generate reliable estimates, which is rarely the case.

For species living in large open areas in Africa or North America, aerial counts are the rule (Jachmann 2002; Redfern *et al*. 2002). Unfortunately, aerial counts have been shown to be both imprecise and inaccurate because observers often miss a large proportion of animals in the field (Caughley 1974; Samuel *et al*. 1987; Redfern *et al*. 2002). The various sources of bias (e.g. spatial heterogeneities in visibility) can be taken into account using correction factors (see Pollock & Kendall 1987 for a review; Samuel *et al*. 1987 for detectability curves; and Mayer *et al*. 2002 for CMR methods based on re-sighting of known animals), but this will not necessarily improve precision (Mayer *et al*. 2002) for all conditions (Eberhardt *et al*. 1998). Year-to-year variation in density of large herbivores is typically low, so estimating this variation with sufficient precision and accuracy using aerial counts is commonly an exercise of questionable value.

In small holarctic forests with low visibility, ground counts of large herbivores, often based on hunting-related methods, are used frequently. However, there are major problems of accuracy and precision affecting such counts and Yoccoz, Nichols & Boulinier (2001) conclude that 'few survey methods permit the detection of all individual animals'. Among transect methods (Buckland *et al*. 1993), line transects are considered to be more efficient and less biased than strip transects (Burnham, Anderson & Laake 1985). However, their precision is largely unknown, as few studies have assessed performance of line transect methods using populations of known size (but see Gaillard, Boutin & Van Laere 1993) and density-dependent bias due to counting saturation is a problem (Southwell 1994).

CMR methods, embracing a large family of techniques (see Buckland *et al*. 2000 for a review), are among the most reliable to estimate population size of free-ranging large herbivores. Some studies have attempted to estimate the performance of these methods (McCullough & Hirth 1988 and Vincent *et al*. 1996 for the Petersen–Lincoln method), but the conclusions regarding estimated precision and accuracy are variable. When locating or counting individuals on plots, the ability to detect animals varies considerably between observers


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and some animals may not be detectable at all (Schwarz & Seber 1999). Indeed, in closed canopy habitats, zero detectability is a non-trivial issue for estimating the size of most populations of large mammals. Finally, to obtain reliable estimates of population size with the Petersen–Lincoln method, it may be necessary to capture and mark two-thirds of the population (Strandgaard 1967). Hence, estimating density of large herbivores with high precision and accuracy using ground counts is commonly as difficult as with aerial counts.

### THE COST AND USEFULNESS OF POPULATION SIZE

The cost of a method (i.e. salary and equipment) is an important issue, as resources available are generally limited, hence management programmes must often rely on less costly methods. Considering the cost and the problems of implementing them at a large scale, and the pitfalls associated with low accuracy and precision (reviewed above), in most cases censusing populations of large herbivores may not be a viable option for routine wildlife management. Even if we assume that counts are accurate and precise, population size in itself provides no information on the relationship between the population and its habitat (e.g. density-dependence) with respect to given management objectives. Similarly, population size provides no information on variation in the underlying demographic processes. A given change in population size may be due to a change in mortality alone, reproduction alone, or a combination of the two.

Wildlife biologists often use the concept of carrying capacity for management. However, carrying capacity is a difficult concept. Recently, del Monte-Luna *et al.* (2004) defined carrying capacity as 'a myriad of interrelated, ever-changing biotic and abiotic factors' that should not be assumed constant (see also Pastor, Moen & Cohen 1997; Georgiadis, Hack & Turpin 2003). While carrying capacity may be a useful concept when treated with caution, it is extremely difficult to quantify and information on the shape of the density-dependent function is rarely available, so the optimal sustainable population is very difficult to estimate.

## Indicators of ecological change

### THE CONCEPT OF ECOLOGICAL INDICATORS

Ecological indicators are used to assess and monitor the state of the environment over time (Cairns, McCormick & Niederlehner 1993). They can promote understanding of past ecological damage and provide early warning signs of impending ecological change, enhancing our ability to manage and solve these problems. Dale & Beyeler (2001) reviewed the criteria that an ecological indicator should meet: it should 'be easily measured, be sensitive to stresses on the system, respond to stress in a predictable manner, be anticipatory, predict changes that can be averted by management actions, be integrative, have a known response to disturbances, anthropogenic stresses, and changes over time, and have low variability in response'. As it is not possible to monitor every component of an ecological system or to find the 'ideal' indicator able to respect all these criteria, the challenge is to derive a manageable set of indicators that, together, meet these criteria and characterize some part of the system (Dale & Beyeler 2001). In the context of managing populations of large herbivores, we need indicators that provide information on the response of both the animals and their habitat to changes in population abundance.

### INDICATORS AND POPULATIONS OF LARGE HERBIVORES

In practice, for management to succeed, clear goals are required and the success of their application must be evaluated. Management objectives are rarely expressed as simple numbers, but commonly as trends in abundance. For Williams *et al.* (2002), 'managers typically wish to increase populations of species that are rare or are seen as beneficial, such as endangered species and many populations subject to sport hunting, and to decrease populations of nuisance or pest species'. The questions remain, however, of what are the 'ideal' population size and the 'right' number of individuals to harvest for a managed population? The best answer a deer manager can give to the question 'how many deer should there be?' is another question: 'how many do you want?' (Rutberg 1997).

In some cases, the goal is to preserve and protect 'natural resources and processes in a balanced, naturally functioning ecosystem' (Shafer-Nolan 1997). However, the goal will often be a compromise such as, for example, maximizing biodiversity and revenue from hunting and tourism, while minimizing damage to forestry/farming, road accidents and the risk of disease transmission (Williams *et al.* 2002; Seiler 2005; Mysterud 2006). This is a difficult exercise as it involves a variety of stakeholders who do not share a common currency and, hence, it is a complex issue to develop a quantitative function for identifying the best compromise (Skonhoft *et al.* 2002). However, several solutions do exist: an example of community-based wildlife management areas in Africa where monitoring is based on a set of indices is provided in du Toit (2002), and the approach used for roe deer management in France is described below. We propose that, for managing large herbivores, the way forward is to monitor a set of indicators which describe the interaction between the population and its habitat, providing a quantitative basis for management decisions to attain specific predefined goals. This approach, based on monitoring annual fluctuations of these indicators, allows decision-makers to quantify the changes that occur in the population–habitat system over time. The assumption is that, all things being equal, the temporal trends observed in the indicators reflect the demographic trajectory of the population.

The philosophy behind this idea, using indicators of ecological change to monitor populations of large herbivores, is rooted in the concept of density-dependence. Density-dependence is defined as the functional dependence of a vital rate on changes in population size (Williams *et al.* 2002) and provides a way to measure population–habitat relationships. Density-dependence is a commonly observed process in populations of large herbivores (Sæther 1997; Gaillard *et al.* 2000). One model used to describe the density-dependent dynamics of vertebrate populations is the generalized logistic model (or theta logistic model; Lande, Engen & Sæther 2003), where theta is an exponent determining the shape of the density-dependent response (with theta = 1 in the special case of the logistic model) (Fig. 1). At very low density, in the colonizing phase, population growth rate is close to $r_{max}$ (*sensu* Caughley 1977). Population productivity is, however, quite low at this stage because of the small population size. As population size increases, a small decrease in individual performance causes the population growth rate to decrease slowly, while population productivity increases. At a population size corresponding to a given proportion (e.g. 50% in the case of a logistic model) of the population size at which the population no longer grows, population productivity peaks (this is referred to as the point at which maximum sustainable yield can be realized; Caughley 1977). After this point, individual performance decreases markedly with increasing population size and also decreasing population productivity, until the population reaches saturation.

## THE USE OF ECOLOGICAL INDICATORS TO MONITOR POPULATIONS OF LARGE HERBIVORES

Based on the concept of density-dependence (Fig. 1), it is possible to build a set of indicators to monitor populations of large herbivores. All parameters that respond to changes in relative density (i.e. changes in population size for a given habitat quality) can be viewed as candidate ecological indicators. To assess accurately the state of the relationship between a population and its habitat along the colonization–saturation continuum, we propose monitoring indicators of relative animal abundance, individual performance (reproduction, mortality, phenotypic quality), habitat quality and the impact of the population on that habitat.

The use of indices purporting to measure 'relative abundance' has been debated widely (Anderson 2001 vs. Engeman 2003). For Anderson (2001), the problem concerns the difficulty of dealing with confounding effects between the parameter of interest, population size and the (unknown) detection probability of animals. Indeed, the index of abundance ($c$) is the product of the abundance ($N$) and a detection or encounter probability ($p$): such that $c = pN$. When using an index, we assume implicitly a constant detection probability across habitat types, observers and many other factors.

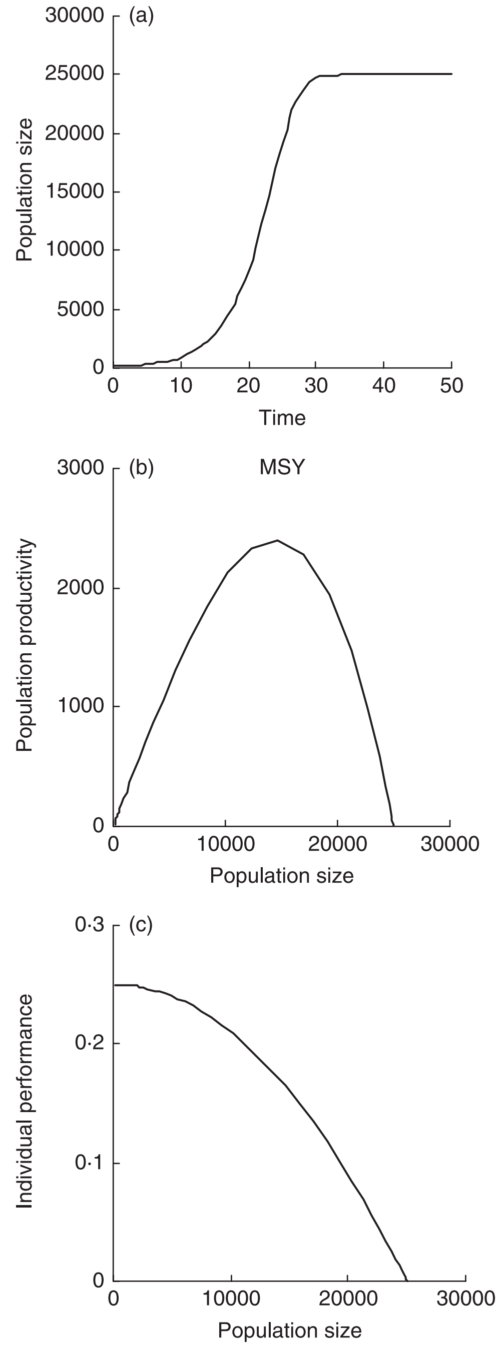


**Fig. 1.** Growth of a theoretical population following a theta logistic model, with an initial number of animals $N = 100$, growth rate $r = 0{\cdot}25$, carrying capacity K = 25 000 and theta = 2·0. (a) Changes of the population size over time; (b) variation in population productivity in relation to population size, with maximum population productivity (MSY) occurring at around 60% of carrying capacity; and (c) variation in individual performance in relation to population size.

Indices must therefore have been validated against known standards, and must be used in a consistent way. For example, the kilometric index (the number of animals seen per km of standardized winter transect sampled on foot; Vincent, Gaillard & Bideau 1991) is used widely to measure the relative abundance of roe deer populations in France and was shown to be correlated closely with CMR estimates of population

**Table 1.** Indicators of ecological change developed and validated by the French Roe Deer Group

| Indicators dealing with variation of | Indicator name | Description | Validation |
|---|---|---|---|
| Population abundance | Kilometric index | Number of deer observed per kilometre of transect sampled on foot, from standardized transects, at dawn and dusk | Vincent *et al.* (1991) |
| | Group size | Number of deer per group in winter | Vincent *et al.* (1995) |
| Quality and performance of individuals in the population | Female reproductive success | Number of fawns per female during winter<br>Number of fawns per reproducing female (i.e. females with fawns at heel) during summer | Vincent *et al.* (1995)<br>Boutin *et al.* (1987) |
| | Body mass of fawns | Total measured body mass or carcass mass of fawns during winter (hunting period) | Maillard, Boisaubert & Gaillard (1989); Gaillard *et al.* (1996) |
| | Cohort jaw length | Total jaw length, considering different age classes determined by jugular tooth wear during winter (hunting period) | Hewison *et al.* (1996) |
| | Hind foot length of fawns | Length from the top of the calcaneum to the tip of the hoof on fawns during winter (hunting period) | Toïgo *et al.* 2006 |
| Habitat impact and habitat use | Browsing index | Measure of browsing pressure of deer on woody plants just prior to vegetation growth in a series of 1 $m^2$ sampling plots | Morellet *et al.* (2001) |

density in an intensively studied population (Vincent *et al.* 1991; see Table 1). The kilometric index accounted for 86% of the variance ($P < 0{\cdot}001$) in the number of roe deer, that varied threefold, in the Chizé reserve (another intensively studied population) over a period of 18 years (D. Maillard, J. M. Gaillard, D. Delorme & G. Van Laere unpublished data).

To illustrate monitoring based on indicators of ecological change, we explore different scenarios of temporal changes in a given set of indicators (Fig. 2). The most straightforward case would be constant values for all indicators (Fig. 2a), suggesting that the relationship between the managed population and its habitat has not changed over time. Alternatively, consider a population increasing in size in a habitat of constant quality (i.e. no habitat impact of the herbivore, Fig. 2b), which occurs commonly during the colonization phase. A third scenario describes a constant population with an increasing impact on its habitat over time (Fig. 2c; i.e. habitat quality decreases, as does individual performance). Another scenario, currently common for populations of large herbivores, is where numbers increase over time leading to a decline in habitat quality and, hence, individual performance, as in a classical density-dependent response (Fig. 2d).

Using this system to monitor and manage populations of large herbivores the first step is to set explicit goals, for example, in terms of animal performance, population productivity and/or habitat quality. Managers then monitor the population–habitat system to evaluate whether the goals have been achieved using various indicators of ecological change to describe each component of the system (e.g. performance, productivity, habitat quality, herbivore impact, etc.). By measuring these indicators annually using standardized protocols (to minimize measurement error), temporal variation can be quantified and compared to expectations. Within a given year, measurement of each indicator is replicated a certain number of times in order to generate confidence limits using standard statistical procedures and to assess the statistical significance of annual change. In the present context of indicators of ecological change, it is inappropriate to compare absolute index values across study areas because indices are not equivalent in different habitats or consistent when applied over large geographical areas. The final step is then to set new hunting quotas with the aim of provoking an adjustment in the population–habitat system in order to approach the predefined goals. At least during the first years of monitoring, this is equivalent to a trial-and-error process. As information is accumulated over the years the evaluation of temporal trends improves, so that managers can adjust more accurately the observed status of the population–habitat system to the desired goals. Clearly, the aim is to achieve the stated goal, rather than to simply witness changes in the designated indicators. As it is conceivable that a given indicator may cease to indicate the state of the system component for which it was designed, indicators should not become integral components of the goals themselves. In this context of information accumulation, Bayesian statistics are pertinent for modelling temporal variation in the indicators (see Morellet *et al.* 2001 for an example). Thus, as soon as data are available for a single sampling year, this provides information for building an informative distribution on which to base the prior, directing future sampling effort.

The use of indicators of ecological change to monitor populations of large herbivores contributes therefore to adaptive management, which deals with scientific uncertainty by incorporating a set of models representing competing hypotheses about system responses to


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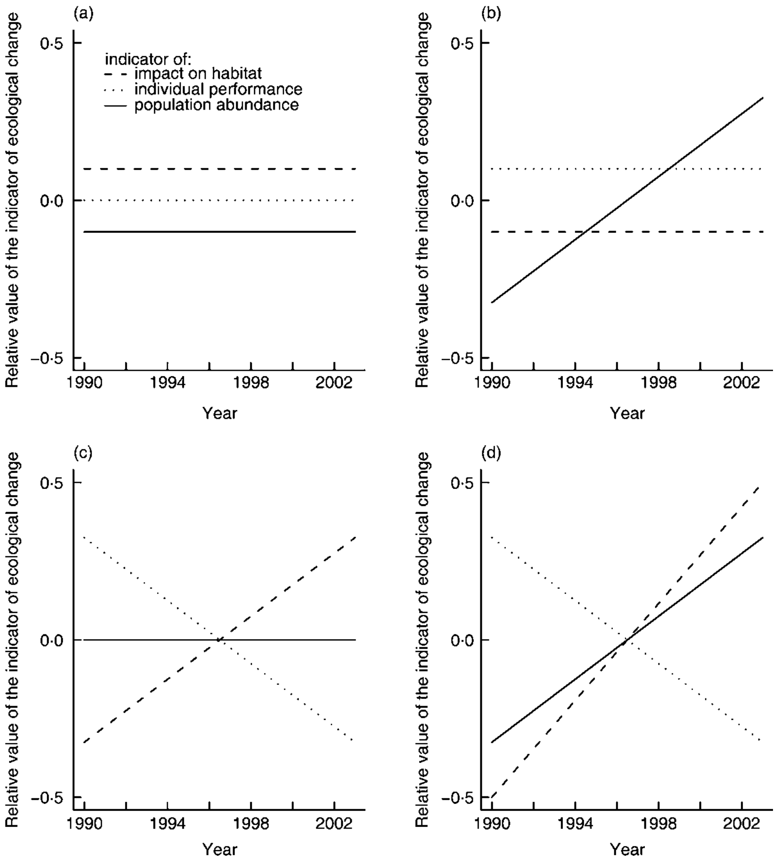


**Fig. 2.** Theoretical temporal changes of a set of indicators describing population abundance, individual performance and habitat impact in a population–habitat system. To simplify the representation of the four (of an infinite number of possible) different scenarios, we have assumed linear relationships over time and an arbitrary scale for the variation of the indicator centred around zero, with marked temporal patterns: (a) a stable situation without any variation of the population–habitat system; (b) a colonizing population; (c) a situation of declining habitat resources; and (d) a classic case of density-dependence with impact on both compartments of the population–habitat system.

management (Runge & Johnson 2002). Information on the response of the system to management is gathered continuously and is used to improve biological understanding and inform future decision-making (Nichols, Johnson & Williams 1995; Shea *et al.* 1998; Williams *et al.* 2002). The term 'adaptive' refers to managers learning about systems as they attempt to manage them (Lancia *et al.* 1996). The learning process may be enhanced by performing large-scale experiments/manipulations (Walters 1986), but in most western European countries (with complex ownership rights and large numbers of pressure groups with contrasting objectives) this is seldom feasible when managing large areas.

## THE MONITORING AND MANAGEMENT OF ROE DEER AS A CASE STUDY

Population monitoring based on indicators of ecological change was first developed to manage roe deer populations in France (Cederlund *et al.* 1998). In the context of increasing roe deer numbers and associated problems managers have clear management objectives, in terms of optimal population size in relation to variable costs and benefits at the scale of management units. Decisions are made by committees at the 'Département' level (scale of several thousand km$^2$), including representatives of the forestry, hunting, farming and conservation lobbies. They first set the management goal for each unit (scale of approximately 100 km$^2$), for example, to reduce the roe deer population, and then set the hunting quota accordingly. The ecological indicators are used therefore as a technical basis for a social and political process, including all the interest groups involved, which sets common goals and adjusts management of the deer to achieve them via the quotas allocated to each management unit. Currently these procedures do not involve quantitative models of the relationships between deer abundance and damage to forestry, probabilities of collisions, etc., but are based on expert opinion and Bayesian adjustments on the basis of experience (see also du Toit 2002). For roe deer, indicators describing animal performance, population abundance, habitat quality and the interaction between the population and its habitat have been developed and validated by the French roe deer group (Table 1). Here, we describe only those indicators that have been tested and validated in intensively monitored roe deer populations. Currently, the indicators of ecological change describe the performance of the herbivore population and its impact on woody vegetation. In the future, we expect that further work will provide tools for monitoring other sociological and ecological problems such as car collisions, ecosystem biodiversity, overgrazing and predator abundance in relation to the status of ungulate populations. In France, a review in 1996 showed that roe deer monitoring occurred over 8·4 million ha (56% of its geographical range); over the majority (65%) of this area, ecological indicators were used (Maillard, Gaultier & Boisaubert 1999), principally the kilometric and body mass indices (Table 2).

**Table 2.** Proportion of French 'Départements' using different methods to monitor roe deer populations, from a survey performed in 2005. These results came from 73 Départements (of 83) involved in roe deer management

| Method | Proportion |
|---|---|
| Indicators of ecological change | |
| Kilometric index | 46·6% |
| Body mass | 32·9% |
| Index of habitat impact/use | 13·7% |
| Female reproductive success | 6·8% |
| Jaw length of fawns | 5·5% |
| Hind foot length of fawns | 5·5% |
| Group size | 2·7% |
| Other methods | |
| Spotlight census | 42·5% |
| Hunting information | 32·9% |
| Total counts | 26·0% |
| Number of vehicle collisions | 21·9% |
| Density obtained by interview | 16·4% |
| Car counts | 11·0% |

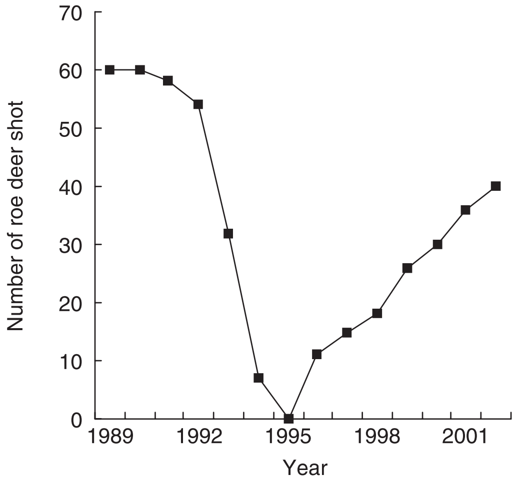


**Fig. 3.** Number of roe deer shot in the 830-ha forest of Dourdan from 1989 to 2002.

The roe deer population of the Dourdan forest provides a useful example of how this monitoring system works. In this 830-ha forest, between 1986 and 1989 the management objective was to increase population size in order to document the density-dependent responses of the deer, hence hunting was stopped and the resultant density was relatively high (approximately 25 deer km$^2$, Vincent *et al.* 1991). From 1989 to 1995, the objective was to reduce the deer population to favour timber production, so hunting was restored at high levels until 1992 with intermediate levels in 1993–4 (Fig. 3). Thereafter, the management objective was to promote the roe deer population for commercial hunting and recreation without diminishing timber production. Hunting was absent in 1995, but increased progressively until 2002 (Fig. 3). Certain indicators of ecological change were measured from 1992 (Fig. 4). The kilometric index indicated that the roe deer population was stable or decreased slightly from 1992 to 1995, increased from 1995 to 1997, and then stabilized until 2002 (Fig. 4a). A similar pattern was observed for the browsing index (Fig. 4b) and, to some extent, an inverse pattern for hind foot length (Fig. 4c) and body mass (Fig. 4d), although data were not available for all years for these latter indicators due to the absence of culling. We interpret these patterns to indicate a rapid increase in population density from 1995 to 1997 or 1998 accompanied by an increase in the impact on the habitat and a consequent density-dependent decrease in individual performance (condition) of successive cohorts. The quality of the information provided by these ecological indicators depends clearly on sample sizes. To ensure that the indicators of population performance are informative during periods of low cull quotas, hunting should focus on fawns which are particularly sensitive to density-dependence (Gaillard *et al.* 2000). In the current situation, with abundant ungulate populations, small sample sizes are rarely a problem.

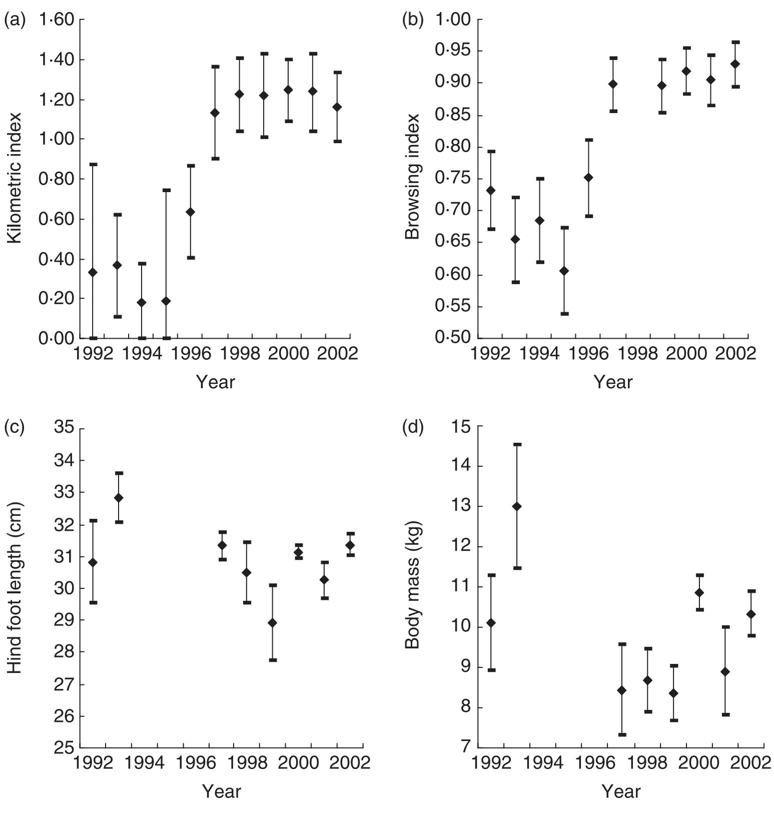


**Fig. 4.** The set of indicators of ecological change for monitoring the roe deer population of Dourdan forest between 1992 and 2002: (a) the kilometric index; (b) the browsing index; (c) the hind foot length of roe deer fawns; and (d) the eviscerated body mass of roe deer fawns. Bars indicate 95% confidence intervals for a, c and d and 95% high-density intervals (Morellet *et al.* 2001) for b.

## SPATIAL SCALE – THE USE OF ECOLOGICAL INDICATORS OVER LARGE AREAS

The indicators of ecological change described above were designed to monitor roe deer population trends over time at local scales and have indeed been validated within single forests (10–50 km$^2$). However, roe deer are often managed at much wider spatial scales (several thousand km$^2$). Of the ecological indicators validated for roe deer, some are more easily transposable to larger areas than others. For example, morphological measures such as fawn body mass, adult jaw length or hind foot length can be measured on all hunted individuals (Zannèse *et al.* 2006), as is performed routinely on Forestry Commission land in the United Kingdom (roe deer jaw length: Hewison *et al.* 1996) and in Norwegian municipalities (red deer body mass: Yoccoz *et al.* 2002; ovulation rate: Langvatn *et al.* 2004; moose *Alces alces* body mass: Solberg *et al.* 2004). While at this scale it is easier to monitor indices of body condition than indices of population abundance or habitat impact, it is possible to use indices of abundance at wide spatial scales: for instance, the abundance of birds in France is monitored routinely using indices (Julliard, Jiguet & Couvet 2004). Finally, satellite measures [Normalized Difference Vegetation Index (NDVI); Pettorelli *et al.* 2005] are a promising avenue of investigation for monitoring habitat quality at a landscape scale.

When it is necessary to take management decisions for larger areas, costs will often prohibit the monitoring of a full set of indicators across an entire region with the same intensity recommended for smaller areas. A solution could involve subsampling, stratifying management units into relatively homogeneous blocks and subsampling blocks to provide a representative picture for the region. By combining information across the region, it may be possible to monitor the population–habitat system efficiently at the landscape scale, although the validity of these indicators at this scale remains largely unknown (but see Zannèse *et al*. 2006).

### THE STANDARDIZATION AND DEVELOPMENT OF ECOLOGICAL INDICATORS

As the management of large herbivores occurs over large areas, many observers are generally required and hence protocols need to be simple to minimize observer bias. In addition, there are many sources of uncertainty that must be dealt with, including environmental variation, structural uncertainty, partial observability and partial controllability (Nichols *et al*. 1995). Consequently, the use of rigorous methods and standardized protocols is essential and observers must be trained thoroughly. As data accumulate over time, it becomes easier to separate real changes from variations due to noise (e.g. between-year differences in conditions, sampling techniques, observers, etc.).

To our knowledge, the roe deer is the only large wild herbivore where monitoring is based on a set of indicators indexing abundance, animal performance and habitat quality. We believe that the development of similar tools for other large herbivores would improve their management.

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