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# Saving time and money by using diurnal vehicle counts to monitor roe deer abundance

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Despite being a widespread and important game species in Europe, scientifically reliable, easy applicable and cost effective methods for monitoring abundance of roe deer *Capreolus capreolus* populations do not yet exist. The currently recommended kilometric index (AI-p) captures temporal variation in the relative abundance of populations; however, because this index is carried out on foot, it is demanding in terms of sampling effort and difficult to apply at spatial scales of several hundred km<sup>2</sup> typical of deer management units. Here, we propose and test a modified version of the kilometric index by using a vehicle to carry out transects over large areas (AI-v). To validate this abundance index, we compared variation in population abundance estimated with AI-p and AI-v with capture–mark–recapture (CMR) estimates of population density in a roe deer population, Chizé (France), monitored for 24 years (including eight years when both indices were collected). We found no detectable effect of conditions of observation (temperature and precipitation) on either AI-p or AI-v. AI-p and AI-v were both positively and linearly related (on a log scale) to CMR estimates of population density, after accounting for uncertainty of CMR estimates by using a bootstrap procedure. AI-p was slightly better correlated to population density ( $r = 0.76$ ) than AI-v ( $r = 0.58$ ). The positive correlation of AI-p and AI-v with CMR density estimates as well as the reduced costs of conducting surveys by car instead on foot (–47%) suggest that diurnal vehicle counts of roe deer can provide a suitable abundance index to monitor temporal trends in roe deer populations at operational management scales. For reliable management of wildlife populations, diurnal vehicle counts of roe deer could be used in association with measures of animal performance and herbivore impacts on the habitat, within the framework of the indicators of ecological change.

Despite long-lasting methodological developments (reviewed by Seber 1982, 1986, Schwarz and Seber 1999), estimating the abundance of free-ranging populations of large herbivores is still particularly challenging (Gaillard et al. 2003b, Smart et al. 2004). The choice of a particular method should be made according to the aim of the study, the need for density estimates or for monitoring relative abundance over time, the required accuracy and precision, and the biology of the target species. Choosing one method over another will be a function of how much resources are available to conduct the data collection in terms of manpower or money. For large herbivores, spotlight (Progulske and Duerre 1964) or pellet (Putman 1984) counts, which are easier and less costly to implement than capture–mark–recapture methods or line-transects (Gill et al. 1997, Focardi et al. 2005), have

proven to be popular among biologists and wildlife managers to monitor population abundance (Harwell et al. 1979, McCullough 1982, Kie and Boroski 1995, McIntosh et al. 1995, Acevedo et al. 2010, Alves et al. 2013). The use of an index-based approach for management purposes has been criticized on the grounds that it lacks a rigorous sampling design and does not account for the detection probability of the index and so, cannot adequately reflect changes in animal abundance (Anderson 2001). Consequently, before any general implementation and recommendation to wildlife managers can be made, index-based methods should be validated using robust estimates of population size (or density) as obtained from distance sampling (Buckland et al. 2005) or capture–mark–recapture methods (Schwarz and Seber 1999). Such validation is especially required when counting animals in forested habitats where limited and spatially heterogeneous visibility leads to amplify the difficulty of getting reliable estimates of population size or density.

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A validation is a procedure aiming at showing that a proposed measure will effectively give the expected results (Rykiel 1996). Applied to abundance indices, the validation procedure compares the candidate index against temporal variation in the true population abundance (Rotella and Ratti 1986, Fuller 1991, Solberg and Sæther 1999, Garel et al. 2010) to test the ability of the abundance index to capture reliably changes (i.e. increase or decrease) of roe deer abundance. The validation of any abundance index is of paramount importance because previous studies already showed that abundance indices may or may not vary with population density (Garel et al. 2010). For instance, the number of red deer *Cervus elaphus* roars heard during the rut (Ciucci et al. 2009, Douhard et al. 2013) or the spotlight counts for white-tailed deer *Odocoileus virginianus* (Collier et al. 2013) and roe deer *Capreolus capreolus* (Gaillard et al. 2003b) failed to reflect variation in population abundance over time. Because the true population density of wild populations is generally unknown, the validation of abundance indices remains challenging, and is often overlooked in the current management practices (e.g. multi-specific aerial thermal-camera counts: Franke et al. 2012, pellet counts: Valente et al. 2014).

The European roe deer is the most abundant wild large herbivore in Europe and a key game species (Apollonio et al. 2010, Linnell and Zachos 2011). Many different management objectives (e.g. control of population density to prevent unacceptable levels of damage to crops and forests or to reduce vehicle collisions, selective shooting to increase quality of trophy animals,...) and count methods are currently in use for roe deer (Morellet et al. 2011). Management decisions most often rely specifically on the estimates of absolute population density (Putman et al. 2011) or on a joint monitoring of relative abundance, animal performance, and herbivore's pressure on its habitat (Morellet et al. 2007, Maublanc et al. 2016). Like for most forest dwelling species, the issue of monitoring the abundance of roe deer is even more acute than for species inhabiting more open habitats. Among others (Acevedo et al. 2010, Putman et al. 2011), the kilometric index (AI-p) has been used to track variation in roe deer abundance over time of a given management unit (Vincent et al. 1991). Based on a 10-year study in one roe deer population, AI-p has been shown to index reliably annual variation of the relative abundance of a forest roe deer population (Vincent et al. 1991). However, for economic reasons, managers seek the most cost-effective methods to monitor wildlife abundance (Garel et al. 2005) and the AI-p for roe deer is labour-intensive in that respect. To yield relevant results, the AI-p requires a sampling intensity of 3 km per 100 ha carried on foot (Vincent et al. 1991). These requirements have hampered the ability of wildlife managers and practitioners to monitor roe deer using AI-p at operational scales of management often covering several hundreds of km<sup>2</sup> (Zannèse et al. 2006). An obvious and appealing alternative would be a kilometric index based on vehicle counts (AI-v), which could save both time and manpower of managers when monitoring the abundance of roe deer populations over large areas.

Taking advantage from > 30 yearlong monitoring of the roe deer population at Chizé, France, we tested and compared the performance of two abundance indices derived from the number of animals seen per km on transects carried

out on foot (AI-p) and by car (AI-v). As this study site is fenced and includes a roe deer population with a high proportion of marked individuals, we could reliably estimate annual population densities by capture–mark–recapture (CMR; Strandgaard 1967, Gaillard et al. 1986) by dividing CMR estimates of population size by area in km<sup>2</sup>. We could then compare annual CMR estimates of population density with the two abundance indices among years. Our main goal was to validate the newly proposed kilometric index from diurnal vehicle counts by assessing its ability to capture trends over time in forest roe deer abundance. As generally observed for other counts (McCullough 1982, Fafarman and DeYoung 1986, Gerrodette 1987, Garel et al. 2010, Douhard et al. 2013), we expected 1) AI-p and AI-v to be affected by conditions of observation such as temperature and precipitation at the timing of counts and 2) both AI-p and AI-v to be positively and linearly associated with the CMR estimates of population density (Morellet et al. 2007). Secondly, we evaluated the relative costs-to-benefits ratio of AI-v compared to AI-p in terms of wildlife management by comparing the accuracy versus time and manpower requirement of each abundance index.

## Material and methods

### Study area

The study was carried out in a fenced population of roe deer located in the Réserve Biologique Intégrale of Chizé, a deciduous forest of 2614 ha in western France (46°05'N, 0°25'E) (Fig. 1). The climate is oceanic, under Mediterranean influence and is characterized by mild winters and hot, dry summers with frequent droughts (average temperatures of 6°C in January and 20°C in August). The Chizé forest includes three main habitats: an oak (*Quercus* spp.) forest with a hornbeam *Carpinus betulus* dominated by coppice in the north-east, an oak forest with Montpellier maple *Acer monspessulanum* coppice in the northwest, and a beech *Fagus sylvatica* forest in the south (see Pettorelli et al. 2003 for further details). Roe deer are free from hunting in the Chizé reserve. Some drive hunts with flushing dogs and hunting sessions from a hide are organized during the autumn (November–December) to remove wild boar *Sus scrofa*. In addition, because Chizé is a fenced reserve where the public is not allowed to enter, the frequency of humans' encounters and traffic are very low. Only forest managers and research biologists are authorized to drive or walk in the reserve throughout the year, and the hunters during the autumn.

### Data collection

#### Weather data

The French national weather agency (Météo-France) recorded and provided us with the average daily temperatures (in°C) and precipitations (in mm) for each 24-h period. The automatic weather station we used for Chizé was located at Beauvoir-sur-Niort (station no. 79031001), at a 5 km distance from the study site. Given the rather flat landscape and relatively short distance between the weather station and

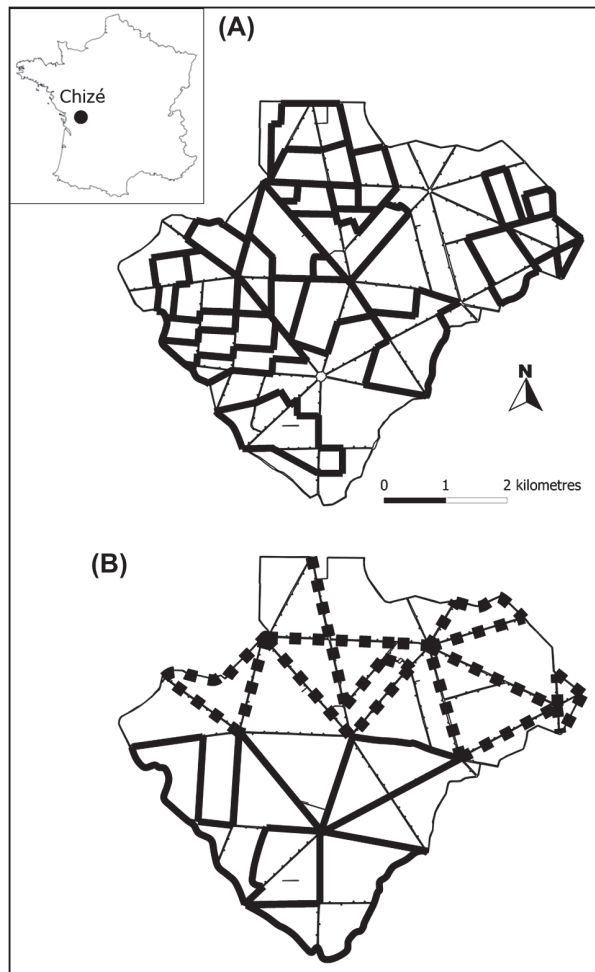


Figure 1. Inset: general location of the study site in France where roe deer population has been monitored for > 35 years. Maps of Chizé (2614 ha) with the spatial distribution of (A) transects sampled during pedestrian surveys (12 transects, thick black lines) and (B) the two transects sampled during vehicle surveys (transsect 1 = dashed black line, transsect 2 = solid black line).

our study site, the observed weather conditions reflected the local conditions of observation during the surveys.

#### **Pedestrian survey**

We estimated the annual relative abundance of roe deer from a kilometric index performed on foot, AI-p (Vincent et al. 1991) from 1989 to 2008 ( $n = 20$  years). The survey took place in March, i.e. after the hunting season to minimize human disturbance (Padié et al. 2015), and at the onset of herbaceous vegetation season and before budburst and leaf unfolding to maximize visibility. At this time of the year, the detection probability of deer is high and quite similar between the two sexes because males are not yet territorial (Bramley 1970). We walked 12 transects ranging between 5.8 and 6.8 km long, corresponding to a sampling effort of 2.9 km per 100 ha (Fig. 1A). We defined the length of transects based on the mean speed of pedestrians and on the period of maximal activity of roe deer, i.e. the 2–3 h after sunrise and the 2–3 h before sunset (Bubenik 1960, Maublanc et al. 1991). A mean speed of 3 km h<sup>-1</sup> and a period of maximal activity of roe deer of 2–3 h at dawn or dusk led to a transect

length ranging between 5 and 7 km. We then defined the number and location of transects so as to cover the whole study area. We walked transects along existing asphalted and forest service roads used for tree logging. One observer surveyed, on different days, each transect twice at dawn and at dusk (i.e. four repetitions in total for each transect) to match the period of maximal activity of roe deer. The number of repetitions per transect per year was based on previous studies and other sites (AI-p of roe deer in the Dourdan forest, Vincent et al. 1991; spotlight counts of red deer at La Petite Pierre Hunting Reserve, Garel et al. 2010) and is a tradeoff between the required precision and the amount of time and number of people available.

#### **Vehicle survey**

Surveys were carried out from a car between 2001 and 2012 ( $n = 12$  years), providing us with a vehicle kilometric index (AI-v). Observations were carried out in March for the same reasons than for the AI-p. Two people were consistently involved in the survey: one who did and recorded the observations, and a second who drove the car and also did observations. As for the AI-p, the length of transects was based on the mean speed of vehicles and on the period of maximal activity of roe deer. A mean speed of 10–15 km h<sup>-1</sup> (20 km h<sup>-1</sup> + stops for observation, as recommended for vehicle counts to maximize detection of deer in forest habitats, Garel et al. 2010) and a period of maximal activity of roe deer of 2–3 h at dawn or dusk led to a transect length ranging between 25 and 35 km. At Chizé, two cars drove two transects of 27.2 and 27.3 km long, corresponding to a sampling intensity of 2.1 km per 100 ha (Fig. 1B). Again, we set transects from existing asphalted roads so as to cover the whole study area. We surveyed each transect six times on different days (three times at dawn and three times at dusk) from 2001 to 2007, and 4 times from 2008 onwards (twice at dawn and dusk, respectively).

#### **Reference method for annual estimates of population density**

The roe deer population has been intensively monitored by CMR since 1978. Each year, between ten and twelve days of capture (using drive netting) were organized, which allowed catching about half the roe deer present in this population (Gaillard et al. 2003a). The annual capture probability was close to 0.50 and did not show any trend throughout the study period (Gaillard et al. 2003a), suggesting that no change (e.g. behavioural change) occurred during our study. The high proportion of marked animals (> 70%) allowed getting reliable annual estimates of roe deer population densities (Strandgaard 1967, Gaillard et al. 2003a) using CMR methods (Lebreton et al. 1992, Gaillard et al. 1993). Mean estimated population density fluctuated between 6.4 (95% CI: 5.4–8.0) and 20.5 (17.1–25.7) roe deer > 1 year of age per square kilometre in March at Chizé (max in 1984 and 2006), in response to an experimental manipulation of population density by the removal of animals during annual catching for the purpose of roe deer translocation and population reinforcement programs (Supplementary material Appendix 1 Table A1). The sampling design for collecting data on abundance indices (AI-p and AI-v) and for estimating population size from CMR were then independent,

henceforth limiting greatly the risk of spurious correlation between abundance indices and CMR estimates of population density.

## Data analyses

### *Abundance indices and estimated population density*

Count data are usually modelled using a generalised linear model (GLM) with a Poisson distribution and a log link (known as a Poisson regression, Agresti 2002). Following Ver Hoef and Boveng (2007), we first checked the relationship between mean and variance in our data which is the main assumption of a Poisson distribution. As variance increased more than the mean, the negative binomial distribution fitted roe deer counts better than the Poisson distribution, so we used the former distribution for modelling both AI-p and AI-v in a GLM framework and for testing our hypotheses. We therefore modelled the number of deer observed using a GLM with a negative binomial distribution and a log link, entering the number of deer seen per transect as our response variable and the log-transformed (natural logarithm) effective length of transects (in km) as an offset variable (Zuur et al. 2009). The offset variable accounted for the variation in the distance walked or driven among transects and sometimes among years because of engine break or temporary inaccessibility of roads. We did not include transect as a random factor because it did not improve the model fit. We first investigated how observation conditions affected deer counts by testing the effect of the average temperature and precipitation during the day of survey and the effect of observation period (evening versus morning) on AI-p and AI-v (see Douhard et al. 2013 for a similar approach). We then investigated the relationships between AI-p or AI-v and population density at time  $t$  by entering the log-transformed population density ( $D_t$ ) estimated from CMR in late February as an explanatory variable of deer abundance (AI-p and AI-v) in March. The statistical model took the form:

$$\log(N_{i,k,t}) = \log(l_{i,k,t}) + \beta_0 + \beta_1 \times \log(D_t) + \beta_2 \times E$$

where,  $N_{i,k,t}$  is the number of counted deer on transect  $i$ , repetition  $k$  and year  $t$ . Transect length  $l_{i,k,t}$  is the offset variable, and  $\beta$ s are the estimated coefficients by the model.  $\beta_0$  is the model intercept,  $\beta_1$  is the effect of log-transformed CMR population density and  $\beta_2$  is the coefficient associated with the environmental effects (temperature or precipitation).

Population density being derived from CMR estimates of population size, it was known with some uncertainty (i.e. annual estimates came with a 95% CI) and, hence, violated one assumption of the linear model. We therefore accounted for the uncertainty in the CMR population density estimates by drawing the explanatory variable from a Gaussian distribution  $N(N_t, \sigma_t^2)$ , where  $N_t$  and  $\sigma_t^2$  are the expected mean and variance of the annual population size returned by the CMR modelling, which we divided by the study site area to yield roe deer population density  $D_t$  (Supplementary material Appendix 1 Table A1). We replicated the GLM fit 10 000 times and used the mean of coefficients and deviances as the estimated parameters of fitted models (Manly 1997). We performed an analysis of deviance (ANODEV) to test for the statistical significance of the effect of CMR

population density on AI-p and AI-v (Skalski et al. 1993). In addition to provide an estimate of the effect size, the ANODEV quantifies the proportion of the variation in the deer abundance (indices) across years that is accounted for by population density estimated by CMR (noted  $R^2_{dev}$ ).

Owing to the limited number of re-captured roe deer fawns, the population structure differed between CMR estimates of population density (only roe deer > 1 year of age in March) and the two abundance indices (all roe deer present in March–April). To account for the confounding effect of recruitment when analysing the relationships between AI-p or AI-v and CMR estimates of population density, we included juvenile survival, the key driver of recruitment at Chizé (Gaillard et al. 2013), as an explanatory variable of deer abundance in addition to CMR estimates in the GLM model. As juvenile survival only accounted for low proportion of the among-year variation in AI-p or AI-v, we chose not to include this marginal effect in the analyses.

We also performed a post hoc power analysis to detect a statistically significant change in abundance (+ 20% in 2 years) when using either AI-p or AI-v. To do so we simulated 10 000 datasets (Bolker 2008) according to the best fitted model, then estimated the slope of the population density effect by fitting the model that generated the data, and then extracted the corresponding p-values. The probability for the null hypothesis to be rejected knowing it is true (i.e.  $\beta$  error) is the proportion of p-values greater than the nominal  $\alpha = 0.05$ . We performed this power analysis by increasing the number of repetitions of transects within a year from 1 to 6 to test the effect of the number of repetitions on the statistical power to detect a change in abundance.

Comparing how AI-p and AI-v related to population density was not straightforward because the two abundance indices were measured on different density ranges (Supplementary material Appendix 1 Table A1). This difference, linked to the more recent implementation of AI-v compared to AI-p, could lead to spurious results when testing for the interaction between the count method and log-transformed population density. We therefore implemented a robust test using a bootstrap re-sampling procedure (Manly 1997) as follows: 1) we randomly drew data corresponding to a sequence of AI-p of the same length as the AI-v time series to balance the number of years for each count method; 2) count data from pedestrian and vehicle surveys were pooled; 3) we fitted a GLM model with a negative binomial distribution and a log link to model deer numbers as a function of transect length (log-transformed offset variable), a categorical binary variable describing the count method (taking values vehicle or pedestrian), population density estimated by CMR (log-transformed) and the first-order interaction term between count method and population density; 4) we extracted the coefficient value for the first-order interaction term. We replicated this procedure 10 000 times to build up an empirical distribution of the first-order interaction coefficients. We considered the first-order interaction coefficient to be significant at the 5%  $\alpha$ -level if none fell outside the 95% percentile range of the empirical distribution of the bootstrapped coefficients. We reported mean and standard error of parameter estimates.

We performed all analyses with the software R ver. 3.0.3 (<[www.r-project.org](http://www.r-project.org)>) and using the 'MASS' and 'ggplot2' statistical packages.

### Implementation costs

The annual global costs, including staff and car costs for AI-p, AI-v and the CMR method were calculated for a 1000 ha-survey based on the experience for the roe deer long-term monitoring at Chizé. We calculated the number of hours spent per observer (i.e. man-hours), the number of observers involved in each survey, and the number of kilometres covered in car for the vehicle survey. We then estimated the cost of manpower per hour according to the French standard cost for technical staff and the car cost per kilometre from the French national fee charge, which includes gas consumption, car maintenance and depreciation.

## Results

### Preliminary analyses

Since we surveyed the same transects multiple times within a year, we initially used generalised linear mixed models (GLMM; Bolker et al. 2009) with transect identity as a random factor to avoid pseudo-replication problems (Hurlbert 1984). In all cases, fitting a GLMM with a random intercept did not improve the model fit compared to a GLM (likelihood-ratio-test:  $\chi^2 = 1.16$ ,  $p = 0.282$  for AI-p and  $\chi^2 \approx 0$ ,  $p \approx 1.000$  for AI-v). The high variability of counts for a given transect in a given year (coefficient of variation = 69% for AI-p and 37% for AI-v) likely accounted for this lack of

transect effect. We thus considered counts within a transect as being independent observations and used simple GLMs to analyse variation in AI-p and AI-v.

### Validating abundance indices

AI-p was slightly higher than AI-v but the difference was not significant (AI-p =  $0.64 \pm 0.39$  roe deer per km and AI-v =  $0.59 \pm 0.30$ ;  $\beta = -0.094 \pm 0.069$ ,  $z$ -value =  $-1.360$ ,  $p = 0.174$ , Fig. 2; Supplementary material Appendix 1 Table A1). Both AI-p and AI-v were highly and positively correlated (Pearson's correlation:  $t = 10.041$ ,  $DF = 6$ ,  $R = 0.972$ ,  $p < 0.001$ ; for years with complete cases ( $n = 8$ ); Supplementary material Appendix 1 Fig. A2). Although the number of repetitions for AI-v was  $> 4$  (6) during the first years of survey, this number stabilized to four in recent years (Fig. 2). Variation in the repetition number over time did not affect the coefficient of variation of counts, which remained similar when considering all the repetitions or when retaining only four (32% versus 33%).

The goodness-of-fit of the negative binomial model to the count data was satisfactory for AI-v ( $\chi^2 = 125.8$ ,  $DF = 112$ ,  $p = 0.176$ ) and borderline for AI-p ( $\chi^2 = 982.3$ ,  $DF = 908$ ,  $p = 0.043$ ). However, the coefficient of over-dispersion ( $\hat{c}$ ) for AI-p was only 1.08, suggesting no over-dispersion in the count data. Contrary to our first expectation, we found only a weak effect of observation conditions (temperature and precipitation) on both AI-p and AI-v and detected a slight negative effect of average daily temperature on AI-p ( $\beta = -0.017 \pm 0.007$ ,  $z$ -value =  $-2.384$ ,  $p = 0.017$ ). We also tested for the effect of observation period (morning vs. evening) and found no statistically detectable effect, although the number of roe deer seen per km tended to be higher in the morning for AI-p (mean =  $0.66 \pm 0.53$  (SD) in the morning versus  $0.63 \pm 0.59$  in the evening;  $\beta = 0.091 \pm 0.047$ ,  $z$ -value =  $1.940$ ,  $p = 0.052$ ) and in the evening for AI-v ( $0.54 \pm 0.30$  in the morning versus  $0.63 \pm 0.37$  in the evening;  $\beta = 0.135 \pm 0.074$ ,  $z$ -value =  $1.833$ ,  $p = 0.067$ ).

As expected for a reliable abundance index, AI-p and AI-v were linearly (on the log-scale) and positively related

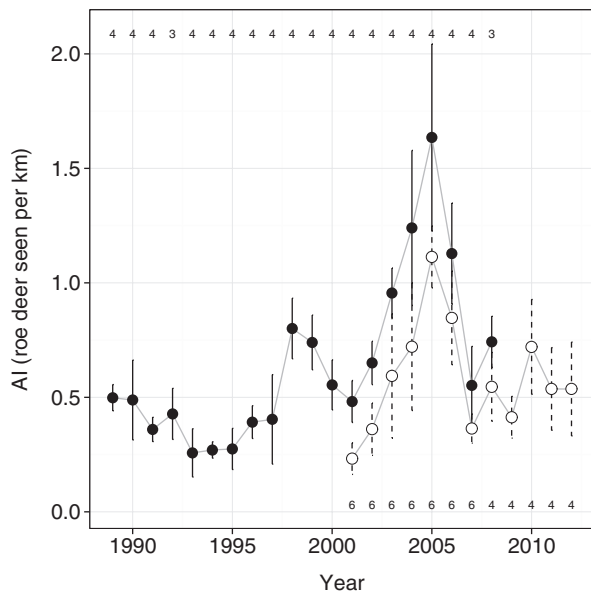


Figure 2. Annual variation (with 95% confidence interval) in the kilometric index (AI: number of roe deer seen per km) at Chizé, France: dark and white points for pedestrian and vehicle index, respectively. The number of repetitions per year is given at the top of the plot for pedestrian surveys and at the bottom for vehicle surveys.

Table 1. Output of the negative binomial models fitted to model the relationship between kilometric index (pedestrian (AI-p) or vehicle (AI-v)) and population density of roe deer in Chizé, France ( $D_{CMR}$  is the estimated population density (roe deer  $> 1$  year of age only, per  $km^2$ ) using capture-mark-recapture method), and results of the post hoc power analyses performed for the models (10 000 simulations and four repetitions of transects within a year).  $\theta$  is the estimated inflation factor of the negative binomial distribution. Power measures the risk to reject the null hypothesis when it is true for a change in population density of 10% between two consecutive years and thereby quantifies the statistical power of our models ( $\alpha = 0.05$ ).

	Model parameters	Kilometric index	
		Pedestrian	Vehicle
Estimation from the data	$\log(D_{CMR})$ estimate	1.352	1.675
	(SE)	(0.089)	(0.291)
	$R^2$ (deviance)	0.757	0.575
Post hoc power analyses (simulations)	$\theta$	4.064	7.512
	$\log(D_{CMR})$ estimate	1.334	1.665
	power	0.382	0.269

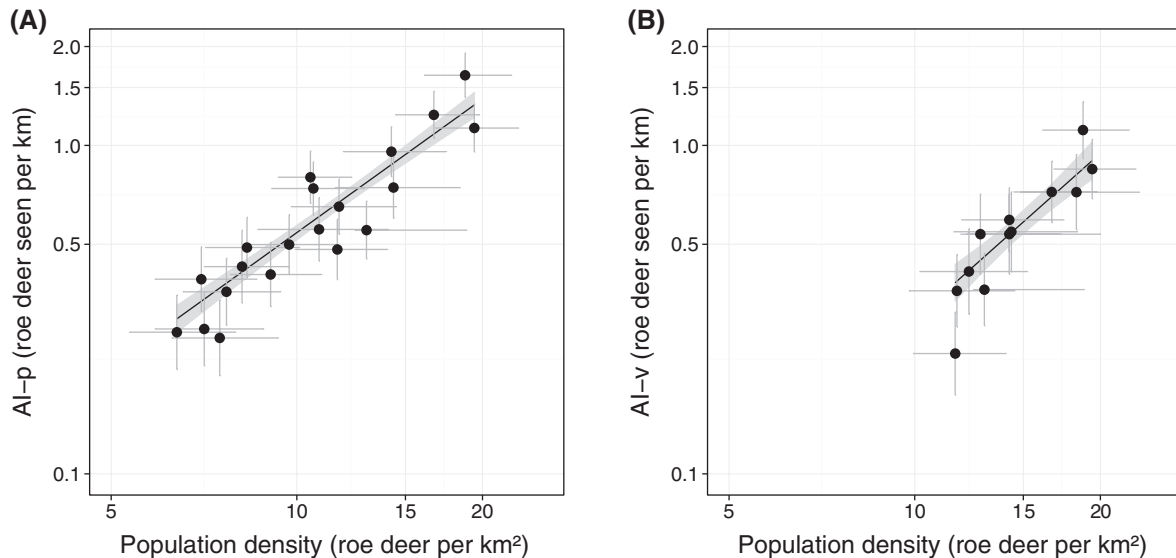


Figure 3. Relationships (log-log plots, with 95% confidence interval) between kilometric indices (AIs) and CMR estimates of population density (per km<sup>2</sup>) at Chizé, France. AI-p corresponds to the number of roe deer seen per km during pedestrian surveys (A) and AI-v during vehicle surveys (B).

with population density estimated by CMR (Table 1, Fig. 3). About 76% and 58% of the average yearly variation in AI-p and AI-v, respectively, was accounted for by variation in population density. When accounting for recruitment in the models, we found a statistically significant effect of juvenile survival in addition to the effect of CMR population density estimates on the yearly variation in AI-p ( $\beta = 0.525 \pm 0.100$ ,  $z = 5.243$ ,  $p < 0.001$ ) but not in AI-v ( $\beta = 0.195 \pm 0.133$ ,  $z = 1.469$ ,  $p = 0.142$ ). However, as juvenile survival only accounted for 6% of the among-year variation in AI-p, while CMR population density accounted for 76% (3% and 58% in AI-v), we chose to keep the simplest model including only CMR estimates for further comparisons. The estimated slopes of the relationship between abundance indices and CMR estimates of population density differed between AI-p and AI-v (bootstrap test; interaction between AI type and  $\log(\text{CMR})$ :  $\beta = 0.688 \pm 0.132$ ,  $p < 0.001$ ; steeper slope for AI-v than for AI-p; Fig. 3). Overall, because population density accounted for more of time variation in AI-p than in AI-v and because the explanatory power of AI-p (0.38 with four repetitions; Table 1, Fig. 4) was slightly better than that of AI-v (0.27), despite its lower slope, the ability to detect a given change in population abundance was slightly greater using AI-p than AI-v. We also found that the power to detect a 10% change in roe deer abundance was similar for AI-p and AI-v for a low number of transect repetitions but was higher for AI-p than AI-v when the number of repetition was  $> 2$  (Fig. 4).

### Implementation costs

Conducting survey by car (AI-v) instead of on foot (AI-p) reduced running costs substantially (by 47%; Table 2). Both abundance indices were far less expensive than the running costs of the CMR sampling design (by 93% and 96% for AI-p and AI-v, respectively; Table 2).

### Discussion

The comparison between the average number of roe deer observed per kilometre and the CMR estimates of population density suggests that variation in roe deer abundance among years is reliably captured by variation in both AI-p and AI-v (Fig. 3). The positive correlation between

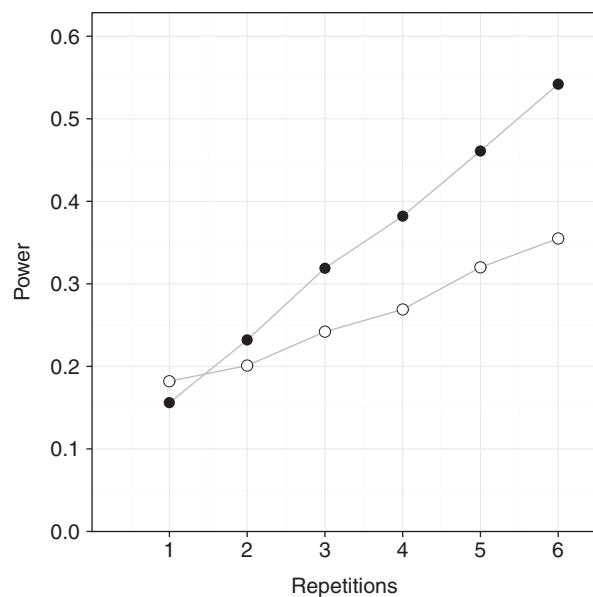


Figure 4. Results of the post hoc power analysis performed for the generalized linear models fitted to roe deer count data (AI-p and AI-v) using a negative binomial distribution (10 000 simulations) according to the number of repetitions per transect per year. Power measures the risk to reject the null hypothesis when it is true for a change in population density of 10% between two consecutive years and thereby quantifies the statistical power of our models ( $\alpha = 0.05$ ). Dark and white points for pedestrian and vehicle index, respectively.

Table 2. Annual costs of pedestrian/vehicle kilometric index and capture–mark–recapture method for a 1000 ha-survey area based on Chizé experiment on roe deer, France.

Cost type	Kilometric index		Capture–mark–recapture method
	Pedestrian	Vehicle	
No. of man-hours	33	8	122
No. of observers	1	2	4
Man cost	35€/man/hour	35€/man/hour	35€/man/hour
No. of kilometres (car)	–	83	–
Car cost	–	0.587€/km	–
Total cost	1151€	609€	17080€

abundance indices and population density of roe deer is linear over a threefold variation in mean estimated population density, which ranged between 6.4 and 20.5 deer per km<sup>2</sup> at Chizé. For AI-p, as shown by Vincent et al. (1991) who first validated the AI-p at Dourdan, a deciduous mixed forest (900 ha) in France where roe deer density increased from about 5 to 15 deer per km<sup>2</sup> over ten years, our 20 years of monitoring provide an additional independent replication of a consistent positive and linear relationship with population density and hence, lend further empirical support for the general applicability of this method to monitor forest-dwelling roe deer populations.

From a slight modification of the kilometric index (AI-p, Vincent et al. 1991) with the use of a vehicle during the day, we show that the number of roe deer seen per kilometre on transects carried out by car (AI-v) reflects the relative abundance of roe deer populations. AI-v is indeed positively related with CMR estimates of population density (Fig. 3B). The small but not statistically significant difference in the average number of deer sighted per kilometre between AI-v and AI-p (0.59 versus 0.64) is likely related to the use of a car that makes noise and moves at a higher speed than pedestrians, leading the detection probability of roe deer to be slightly lower from a car than on foot. Because indicators of relative abundance like AI-p or AI-v do not estimate the detection probability, observation conditions should be kept as constant as possible across years (by using the same set of transects) to obtain a reliable relationship with CMR estimates of population density. These two conditions were fulfilled in our study for AI-p and AI-v. As the correlation between AI-v and population density (58%) was slightly lower than that obtained when using AI-p (76%; Table 1), the performance of AI-v appears to be slightly lower than that of AI-p for indexing population density in roe deer. Finally, although the slope of the relationship between abundance index and population density was higher for AI-v than for AI-p, AI-v was also slightly less precise leading to a lower explanatory power to detect a variation in population density for AI-v (0.27 with four repetitions; Table 1, Fig. 4) than that for AI-p (0.38). Consequently, one would need more repetitions or more years using AI-v than AI-p for detecting a given change in population density. For both indices, our results about the statistical power to detect a given change in abundance highlighted the importance to repeat transects within a year (Fig. 4). Indeed, the probability to detect a 10% variation in roe deer abundance between two years is 3.50 times greater when using six than when using one repetition for AI-p. The corresponding ratio is 1.75 for AI-v.

Finally, we showed that the conditions of observation did not markedly influence any of the abundance indices of roe deer population. We only found a weak effect of average daily temperature on pedestrian index, reflecting a decrease of 1.7% in AI-p with an increase of 1°C in temperature. The limited effect of weather conditions we report here contrasts with other count-based studies of deer that showed strong effects of precipitation or temperature (Progulske and Duerre 1964, McCullough 1982, Garel et al. 2005). In red deer for instance, spotlight counts decreased by ca 25% when done in sub-optimal conditions of observation (Garel et al. 2010). We suggest that the relatively mild weather conditions at Chizé could account for the absence of detectable effects of weather conditions as compared to the harsher conditions faced by the red deer in more mountainous habitats (Garel et al. 2010).

The AI-v has two main advantages over AI-p. First, the logistic costs of AI-v are substantially lower than those of AI-p, thanks to the much shorter time needed to drive than to walk along the transects (Table 2). Both abundance indices remain far less expensive than the annual running costs of the CMR sampling design, which amounts to approximately 17 000€ a year for a 1000 ha-survey area. Overall the time saved by driving instead of walking transects partly compensates for the gas costs and for the additional operator required to perform observations from vehicles. Second, driving transects allows a coverage of larger areas for comparable effort (in man hours), which is closer to the operational scales of wildlife management, which generally involve areas covering several thousands of ha. For instance at Chizé, switching from AI-p to AI-v reduced the number of transects from 12 (6 km long, one observer) to 2 (27 km long, two observers). Holding manpower constant, the number of transects sampled would be three times greater for AI-v than for AI-p. Consequently, an area three times larger can be sampled using AI-v compared to AI-p (i.e. 3 × 2600 ha). Overall, although slightly less powerful to detect trends over time in roe deer abundance, the use of AI-v is economically advantageous over AI-p (Table 2) and allows managers to survey larger areas.

### Implementation of the diurnal vehicle counts

When implementing AI-v in new areas, we advise managers to follow the following recommendations:

- *Period.* Survey should take place in March, i.e. after the hunting season to minimize human disturbance (Padié et al. 2015), at the onset of herbaceous vegetation season and before budburst and leaf unfolding to maximize visibility.



- *Periodicity*. Monitoring should be performed on an annual basis because roe deer have an annual life cycle and at the same period to obtain similar conditions of observation and thereby the possibility to compare reliably indices across years (Morellet et al. 2007). Moreover, managers have to update monitoring data on managed populations every year to assess changes in abundance over years and fix hunting quotas. A yearly monitoring is thus required to allow managers to assess as quickly as possible the population trend.

- *Repetitions*. To account for the high variability of counts from an individual transect in a given year, each transect should be repeated 4 times at least to minimize confidence intervals (at Chizé, the coefficient of variation of counts was similar with 4 or more repetitions and the statistical power to detect a given change in abundance was satisfactory with four repetitions). Repetitions should be done within a period less than four weeks, to avoid changes of detection probability due to local disturbance including recreational activity, woodland management, vegetation growth or weather conditions.

- *Duration*. A given survey should last less than three hours, depending on the transect length, within the 2–3 h after sunrise and the 2–3 h before sunset to match the period of maximal activity of roe deer (Bubenik 1960, Maublanc et al. 1991). Dawn and dusk also correspond to periods of minimal recreational activities (i.e. minimal human disturbance).

- *Transect length*. Each transect should be 25–35 km long, based on the mean speed of vehicles (10–15 km h<sup>-1</sup>) and on the period of maximal activity of roe deer (2–3 h at dawn or dusk). As AI-v is carried out by car this method obviously requires the availability of a road network, which may limit the use of AI-v in some management areas. Based on our results, a road density of approximately 2 km per 100 ha is enough to get reliable results. We recommend to drive only secondary roads with low traffic to count roe deer, mainly for security reasons because the vehicle has to drive at a very low speed (10–15 km h<sup>-1</sup>) when using the AI-v method.

- *Spatial distribution of transects*. AI-v should be applied on a study area that corresponds to a roe deer population management unit, free of the administrative limits. Transects should sample all types of habitats within the landscape. The proportions of the different habitat types crossed by transects should be representative of the relative proportions of the different habitats present in the study area (i.e. the population unit). The number of transects is then defined in relation to the tradeoff between the length of transects and an appropriate coverage of the study area. Once defined, it is important to sample the same set of transects over years to minimize the inter-annual variation in detection probability and to assess inter-annual variation in relative abundance.

- *Observers*. For each transect and repetition two persons need to take place in a vehicle, driving at a mean speed of 10–15 km h<sup>-1</sup>. Observers should be selected for their observation skills (bird watchers, hunters) and trained by teaming up for a while with experienced observers. An important point also is to try having the same observers every year to limit the variation in detection rate as much as possible.

If needed, managers may reduce the costs of monitoring, for example in the case of very large study areas or limited financial/human resources, by decreasing the number of transects, always keeping a good representativeness of the different habitat types, rather than by reducing the frequency of monitoring (for the reactivity of managers to abundance changes) or the number of repetitions per transect per year (for the precision of abundance index).

Note that AI-v has only been validated in forested areas and it should be cautiously used and interpreted when performed in other habitat types such as agricultural environments because changes in deer behaviour may occur in different habitats which, in turns, might affect the detection probability of deer. For instance, in open landscape roe deer form much larger groups (Hewison et al. 2001) that the observer may or may not detect, hence increasing the variability of counts among repetitions. In open landscape, deer may be also more prone to disturbance or initiate a flight at a much longer distance than in forested areas (De Boer et al. 2004), again with a risk of observers to miss present deer.

## Management implications

At the landscape scale, different factors such as the availability of food resources, changes in the habitat (e.g. massive clearcut like observed after the Lothar hurricane in December 1999, woodland management,...), or the presence of other ungulate species may cause AI-v to vary independently from roe deer abundance. Monitoring animal abundance only is not sufficient to provide the required information on the full range of the interactions between the population and its habitat to manage an ungulate population. Indicators of ecological change (IECs; Dale and Beyeler 2001, Morellet et al. 2007, Strickland et al. 2008) are efficient tools to monitor simultaneously these three information types in time: population abundance, animal performance and impact of herbivores on plants. Wildlife managers increasingly make use of IECs to monitor deer populations and implement management policies in Europe (Morellet et al. 2007, Acevedo et al. 2008, Meriggi et al. 2008, Apollonio et al. 2010, Michallet et al. 2015, Pierson and deCalesta 2015, Maublanc et al. 2016) and in the USA (Strickland et al. 2008).

For roe deer, the annual monitoring of the pedestrian kilometric index AI-p (Vincent et al. 1991), of winter body mass or hind foot length of fawns (Gaillard et al. 1996, Toïgo et al. 2006), and of browsing indices (Morellet et al. 2001, Chevrier et al. 2012) provide relevant information on the changes that occur in the population–habitat system over time. The trends of these indicators over time inform managers on the demographic trajectory of the population and thereby facilitate the achievement of predefined management goals. The proposed diurnal vehicle kilometric index (AI-v) may also be carried out to monitor relative abundance (Michallet et al. 2015), given that road density is not a limiting factor. Being densely forested (with 94% of forest cover), Chizé is representative of the original roe deer habitat (Andersen et al. 1998). Roe deer being a selective feeder highly attracted by ecotones, they intensively use road edges because this habitat provides animals with abundant and high quality food (Saïd et al. 2005,

McLoughlin et al. 2007). Consequently, we do not expect roe deer to avoid roads because of human or vehicle disturbance so that AI-v should reliably perform in areas where the frequency of humans or vehicles is much higher than at Chizé. The successful validation of AI-v based on CMR estimates of population density should encourage wildlife managers to use the diurnal vehicle counts (AI-v) to monitor changes of roe deer relative abundance over time within a forested management unit. As abundance indices do not account for imperfect detection, they cannot be used to estimate absolute population densities and cannot be compared among different populations. Instead, AI-v and AI-p have to be monitored over the years and how it responds to variation in harvest bags.

The use of a common abundance index for several species of large herbivores is tempting because wildlife managers deal more and more with sympatric populations of roe deer, red deer and wild boar (see Saint-Andrieux et al. 2012 in France). For instance, both red and roe deer are frequently recorded during spotlight counts despite this method is valid for red deer only (Gaillard et al. 2003b, Garel et al. 2010). We strongly advice against this practice and recommend wildlife managers to use the appropriate and validated methods for each species of interest.

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## References

- Acevedo, P. et al. 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. – *J. Zool.* 276: 37–47.
- Acevedo, P. et al. 2010. Estimating roe deer abundance from pellet group counts in Spain: an assessment of methods suitable for Mediterranean woodlands. – *Ecol. Indic.* 10: 1226–1230.
- Agresti, A. 2002. *Categorical data analysis*, 2nd edn. – Wiley.
- Alves, J. et al. 2013. Pellet group count methods to estimate red deer densities: precision, potential accuracy and efficiency. – *Mamm. Biol.* 78: 134–141.
- Andersen, R. et al. 1998. *The European roe deer: the biology of a success*. – Scandinavian Univ. Press.
- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. – *Wildl. Soc. Bull.* 29: 1294–1297.
- Apollonio, M. et al. 2010. *European ungulates and their management in the 21st century*. – Cambridge Univ. Press.
- Bolker, B. M. 2008. *Ecological models and data in R*. – Princeton Univ. Press.
- Bolker, B. M. et al. 2009. *Generalized linear mixed models: a practical guide for ecology and evolution*. – Trends Ecol. Evol. 23: 127–135.
- Bramley, P. S. 1970. Territoriality and reproductive behaviour of roe deer. – *J. Reprod. Fertil.* 11(Suppl.): 43–70.
- Bubenik, A. B. 1960. Rythme nyctéméral et le régime journalier des ongulés sauvages, problèmes théoriques, rythme d'activité du chevreuil. – *Mammalia* 24: 1–59.
- Buckland, S. T. et al. 2005. *Distance sampling*. Encyclopedia of biostatistics. – Wiley.
- Chevrier, T. et al. 2012. The oak browsing index correlates linearly with roe deer density: a new indicator for deer management? – *Eur. J. Wildl. Res.* 58: 17–22.
- Ciucci, P. et al. 2009. Pitfalls in using counts of roaring stags to index red deer (*Cervus elaphus*) population size. – *Wildl. Res.* 36: 126–133.
- Collier, B. A. et al. 2013. Spotlight surveys for white-tailed deer: monitoring panacea or exercise in futility? – *J. Wildl. Manage.* 77: 165–171.
- Dale, V. and Beyeler, S. C. 2001. Challenges in the development and use of ecological indicators. – *Ecol. Indic.* 1: 3–10.
- De Boer, H. Y. et al. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. – *Wildl. Biol.* 10: 35–41.
- Douhard, M. et al. 2013. Roaring counts are not suitable for the monitoring of red deer *Cervus elaphus* population abundance. – *Wildl. Biol.* 19: 94–101.
- Fafarman, K. R. and DeYoung, C. A. 1986. Evaluation of spotlight counts of deer in south Texas. – *Wildl. Soc. Bull.* 14: 180–185.
- Focardi, S. et al. 2005. Distance sampling effectively monitored a declining population of Italian roe deer *Capreolus capreolus italicus*. – *Oryx* 39: 421–428.
- Franke, U. et al. 2012. Aerial ungulate surveys with a combination of infrared and high-resolution natural colour images. – *Anim. Biodivers. Conserv.* 35: 285–293.
- Fuller, T. K. 1991. Do pellet counts index white-tailed deer numbers and population change? – *J. Wildl. Manage.* 55: 393–396.
- Gaillard, J.-M. et al. 1986. L'estimation d'effectifs à partir de capture-marquage-recapture: application au chevreuil (*Capreolus capreolus*). – *Gibier Faune Sauvage* 3: 143–158.
- Gaillard, J.-M. et al. 1993. Roe deer survival patterns – a comparative analysis of contrasting populations. – *J. Anim. Ecol.* 62: 778–791.
- Gaillard, J.-M. et al. 1996. Body mass of roe deer fawns during winter in two contrasting populations. – *J. Wildl. Manage.* 60: 29–36.
- Gaillard, J.-M. et al. 2003a. Effects of hurricane Lothar on the population dynamics of European roe deer. – *J. Wildl. Manage.* 67: 767–773.
- Gaillard, J.-M. et al. 2003b. Variation in life history traits and realistic population models for wildlife management: the case of ungulates. – In: Festa-Bianchet, M. and Apollonio, A. (eds), *Animal behavior and wildlife conservation*. Island Press, pp. 115–132.
- Gaillard, J.-M. et al. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. – *Ecol. Lett.* 16(S1): 48–57.
- Garel, M. et al. 2005. Monitoring the abundance of mouflon in South France. – *Eur. J. Wildl. Res.* 51: 69–76.
- Garel, M. et al. 2010. Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? – *Wildl. Biol.* 16: 77–84.
- Gerrodette, T. 1987. A power analysis for detecting trends. – *Ecology* 68: 1364–1372.
- Gill, R. M. A. et al. 1997. The use of portable thermal imaging for estimating deer population density in forest habitats. – *J. Appl. Ecol.* 34: 1273–1286.
- Harwell, F. et al. 1979. The spotlight count method for surveying white-tailed deer in Texas. – *Texas Parks and Wildlife Dept.*

- Hewison, A. J. M. et al. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. – *Can. J. Zool.* 79: 679–689.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. – *Ecol. Monogr.* 54: 187–211.
- Kie, J. G. and Boroski, B. B. 1995. Using spotlight counts to estimate mule deer population size and Trends. – *Calif. Fish Game* 81: 55–70.
- Lebreton, J. D. et al. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – *Ecol. Monogr.* 62: 67–118.
- Linnell, J. D. C. and Zachos, F. E. 2011. Status and distribution patterns of European ungulates: genetics, population history and conservation. – In: Putman, R. et al. (eds) *Ungulate management in Europe: problems and practices*. Cambridge Univ. Press, pp. 12–53.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. – Chapman and Hall.
- Maublanc, M. L. et al. 1991. Le chevreuil. – *Rev. d'Écol. Suppl.* 6: 155–183.
- Maublanc, M. L. et al. 2016. Indicators of ecological change (IEC) as efficient tools for managing roe deer populations: a case study. – *Eur. J. Wildl. Res* 62: 189–197.
- McCullough, D. R. 1982. Evaluation of night spotlighting as a deer study technique. – *J. Wildl. Manage.* 46: 963–973.
- McIntosh, R. et al. 1995. Monitoring the density of a roe deer *Capreolus capreolus* population subjected to heavy hunting pressure. – *For. Ecol. Manage.* 79: 99–106.
- McLoughlin, P. D. et al. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. – *Ecology* 88: 3192–3201.
- Meriggi, A. et al. 2008. A review of the methods for monitoring roe deer European populations with particular reference to Italy. – *Hystrix-Ital. J. Mammal.* 19: 23–40.
- Michallet, J. et al. 2015. Les ICE, des outils largement utilisés au niveau national. – In: Proc. of the Indicator of Ecological Change Conference, France.
- Morellet, N. et al. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. – *Wildl. Soc. Bull.* 29: 1243–1252.
- Morellet, N. et al. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. – *J. Appl. Ecol.* 44: 634–643.
- Morellet, N. et al. 2011. The census and management of populations of ungulates in Europe. – In: Putman, R. J. et al. (eds), *Ungulate management in Europe: problems and practices*. Cambridge Univ. Press, pp. 106–143.
- Padié, S. et al. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. – *Oikos* 124: 1536–1546.
- Pettorelli, N. et al. 2003. Age and density modify the effects of habitat quality on survival and movements of roe deer. – *Ecology* 84: 3307–3316.
- Pierson, T. G. and deCalesta, D. S. 2015. Methodology for estimating deer browsing impact. – *Hum. Wildl. Interact.* 9: 67–77.
- Progulske, D. R. and Duerre, D. C. 1964. Factors influencing spotlighting counts of deer. – *J. Wildl. Manage.* 28: 27–34.
- Putman, R. J. 1984. Facts from feces. – *Mammal Rev.* 14: 79–97.
- Putman, R. J. et al. 2011. Assessing deer densities and impacts at the appropriate level for management: a review of methodologies for use beyond the site scale. – *Mamm. Rev.* 41: 197–219.
- Rotella, J. J. and Ratti, J. T. 1986. Test of a critical density index assumption: a case study with gray partridge. – *J. Wildl. Manage.* 50: 532–539.
- Rykiel, E. J., Jr. 1996. Testing ecological models: the meaning of validation. – *Ecol. Modell.* 90: 229–244.
- Säid, S. et al. 2005. Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. – *J. Zool.* 267: 301–308.
- Saint-Andrieux, C. et al. 2012. La progression récente des grands ongulés sauvages en France. – *Faune Sauvage* 294: 10–17.
- Schwarz, C. J. and Seber, G. A. F. 1999. Estimating animal abundance: review III. – *Stat. Sci.* 14: 427–456.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edn. – Griffin, London, UK.
- Seber, G. A. F. 1986. A review of estimating animal abundance. – *Biometrics* 42: 267–292.
- Skalski, J. R. et al. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. – In: Lebreton, J. D. and North, P. M. (eds), *Marked individuals in the study of bird populations*. Birkhäuser Verlag, pp. 9–28.
- Smart, J. C. R. et al. 2004. Monitoring woodland deer populations in the UK: an imprecise science. – *Mamm. Rev.* 34: 99–114.
- Solberg, E. J. and Sæther, B. E. 1999. Hunter observations of moose *Alces alces* as a management tool. – *Wildl. Biol.* 5: 107–117.
- Strandgaard, H. 1967. Reliability of Peterson method tested on a roe deer population. – *J. Wildl. Manage.* 31: 643–651.
- Strickland, B. K. et al. 2008. Variation in mass and lactation among cohorts of white-tailed deer *Odocoileus virginianus*. – *Wildl. Biol.* 14: 263–271.
- Toïgo, C. et al. 2006. How does environmental variation influence body mass, body size and body condition? Roe deer as a case study. – *Ecography* 29: 301–308.
- Valente, A. M. et al. 2014. Living on the edge: roe deer (*Capreolus capreolus*) density in the margins of its geographical range. – *PLoS ONE* 9(2): e88459.
- Ver Hoef, J. M. and Boveng, P. 2007. Quasi-poisson vs negative binomial regression: how should we model overdispersed count data? – *Ecology* 88: 2766–2772.
- Vincent, J. P. et al. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. – *Acta Theriol.* 36: 315–328.
- Zannèse, A. et al. 2006. Spatial structure of roe deer populations: towards defining management units at a landscape scale. – *J. Appl. Ecol.* 43: 1087–1097.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (available online as Appendix wlb-00274 at <[www.wildlifebiology.org/appendix/wlb-00274](http://www.wildlifebiology.org/appendix/wlb-00274)>). Appendix 1.