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Source: Wildlife Biology, 19(1) : 94-101

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-037

Wildl. Biol. 19: 94-101 (2013)
DOI: 10.2981/12-037

Original article

Roaring counts are not suitable for the monitoring of red deer *Cervus elaphus* population abundance

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The successful management of large herbivores requires the monitoring of a set of indicators of ecological change (IEC) describing animal performance, herbivore impact on habitat and relative animal abundance. Roaring counts during the rut have often been used to assess the abundance of red deer *Cervus elaphus* populations, but a formal evaluation of this method is still lacking. In this paper, we examined the usefulness of the number of red deer recorded during roaring counts for managing red deer populations. Using standardised spotlight counts applied for the monitoring of red deer at La Petite Pierre, France, as a reference method, we found that roaring counts did not correlate with spotlight counts. Moreover, we did not find any evidence that roaring counts decreased with increasing number of male and female red deer harvested in the reserve during the previous hunting season. We thus conclude that managers should not rely on roaring counts for managing red deer populations.

Key words: abundance index, Cervus elaphus, count data, indicator of ecological change, red deer, roaring

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Received 5 April 2012, accepted 17 August 2012

Associate Editor: Klaus Hackländer

Deer populations have increased dramatically in size and distribution over recent decades both in Europe and North America (Andersen et al. 1998, Fuller & Gill 2001). As a result, in many areas, management goals are changing from protection to population control (Milner et al. 2006). Controlling deer populations is required to prevent damage to farming and forestry, deer-vehicle collisions or the spread of diseases (Rooney & Waller 2003, Côté et al. 2004, Gordon et al. 2004, Seiler 2004). In areas where large predators have been eliminated, deer populations are usually controlled through hunting (Langvatn & Loison 1999, Festa-Bianchet 2003, Milner et al. 2006). To define the hunting quotas, managers typically use estimates of population size obtained from counting methods (e.g. Williams et al. 2002).

Counting methods have repeatedly been shown to be neither accurate nor precise (CV > 30%; Andersen 1953, Gaillard et al. 2003) except when a high proportion of individuals are marked (Strandgaard 1967, Vincent et al. 1991). Andersen (1953) showed, for example, that counts in a population of roe deer *Capreolus capreolus* can lead to a threefold underestimation of the population size. Moreover, the absence of repeated counts within a year prevents the assessment of the precision of population estimates. Lastly, even the best estimate of population size does not provide the required information to set hunting plans because it does not provide information to managers about the state of the plant-herbivore system (Morellet et al. 2007).

In this context, researchers have developed new tools for managing ungulate populations, which are based on the monitoring of a set of indicators of ecological change (IEC; Cederlund et al. 1998, Morellet et al. 2007). An IEC is an easily measured parameter, sensitive to changes in the relationship between the population and its habitat (Cederlund et al. 1998). IEC are based on the concept of density-dependence (Bonenfant et al. 2009), from which wildlife managers should be able to monitor deer populations without population size estimates. Morellet et al. (2007) proposed to simultaneously monitor three categories of IEC describing 1) animal performance (Bonenfant et al. 2002, Zannèse et al. 2006, Garel et al. 2011), 2) habitat quality (Morellet et al. 2001, Chevrier et al. 2012) and 3) animal abundance (Vincent et al. 1991, Loison et al. 2006, Garel et al. 2010). It is important to note that only the complementarity of different IEC monitored over several years allows for the measurement of population-habitat relationships.

Among indices of red deer *Cervus elaphus* abundance, spotlight counts are commonly used by managers (e.g. Gunson 1979, McCullough 1982, Fafarman & DeYoung 1986). Recently, Garel et al. (2010) showed that, after controlling for observation conditions, spotlight counts can provide a reliable IEC of relative abundance for the monitoring and management of red deer populations living in forested areas. Spotlight counts are inexpensive and allow for rapid cover of large areas (McCullough 1982). However, this method is restricted to areas with good network of roads and tracks. An alternative option could be to carry out roaring counts from fixed spots (Albaret et al. 1989).

Counting red deer during the period of reproduction (rut) in autumn is often used in addition to spotlight counts, or when spotlight counts are difficult to apply (Bobek et al. 1986, Albaret et al. 1989), to assess trends in population abundance. Mature red deer males, like many other ungulates, commonly spend most of the year in areas separated from those occupied by the females except in the breeding season (Clutton-Brock & Albon 1979, Clutton-Brock et al. 1982). At this particular time of the year, stags use vocalisations (roars) to monopolise a number of hinds. With their highly conspicuous behaviour, red deer are easily detected during the rut based on acoustic and visual clues. Hence, roaring counts have two components: first, counting the number of roaring stags, and second, counting hinds and stags seen in rutting areas, both being used for the calculation of the abundance index. However, Ciucci et al. (2009) have suggested that roaring counts are poor indicators of red deer abundance because the timing of the survey is not consistently synchronous with the roaring peak. Overall, the roaring counts method has never been formally validated.

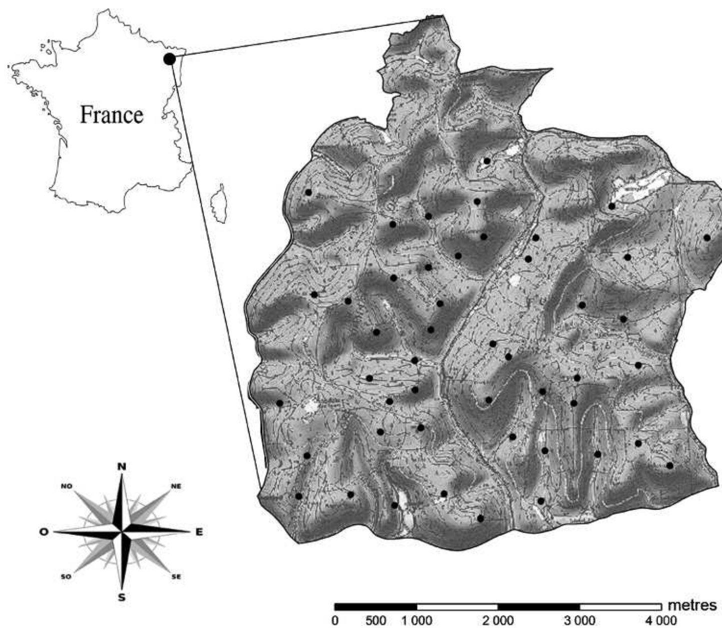
In our study conducted at La Petite Pierre, France, we examined the usefulness of roaring counts for the management of red deer populations. Managers of our study site have monitored red deer using both spotlight and roaring counts for 31 years. Providing that roaring counts allow for reliable assessment of the abundance of red deer resident populations, we expected a positive correlation between roaring and spotlight counts because spotlight counts provide a suitable measure of annual variation in abundance of the resident population (Garel et al. 2010). Second, as variation in hunting pressure accounted for most annual changes in population size in the studied population (Bonenfant et al. 2002, Richard et al. 2010; see also section Material and methods), the number of counted red deer during rut should decrease with the number of deer harvested during the previous hunting season (Garel et al. 2005b).

Material and methods

Study site and population

La Petite Pierre National Reserve (PPNR) is a 2,674 ha unfenced forest located in the Vosges mountain range, northeastern France (48.82°N, 7.34°E; Fig. 1). The PPNR is characterised by a succession of small hills and steep-sided valleys ranging between 200 and 400 m a.s.l. in elevation (see Fig. 1). The climate is continental with oceanic influences, leading to cold winters and cool summers (average January and July temperatures are 0.6 and 18.4°C, respectively). The PPNR consists of a balanced mix of broadleaved, mainly European beech *Fagus sylvatica*, and coniferous trees such as silver fir *Abies alba*, Norway spruce *Picea abies* and Douglas fir *Pseudotsuga douglasii*. The sandstone substrate produces acidic and poor soils, resulting in a vegetation of low

Figure 1. Location of the Petite Pierre National Reserve in northeastern France. The focused area details the landscape topography and the observation spots (•) during roaring counts.



nutritive quality for herbivores. Roe deer and wild boar *Sus scrofa* are also present within the reserve. All three ungulates are managed through hunting, either with quotas (deer) or without quotas (wild boar). Since 1978, the red deer population has been hunted on an annual basis between 1 August and 1 February by both professional and sport hunters (more details on hunting practice in France can be found in Maillard et al. 2010). A temporal variation in hunting pressure controlled by the Office National de la Chasse et de la Faune Sauvage and the Office National des Forêts occurred throughout the study period (see Results), leading to marked variation in population size over the past 30 years (Richard et al. 2010). This management context provided us with a quasi-experimental manipulation of red deer density to assess the relevance of roaring counts as a management tool of red deer (Sinclair 1989). Every deer shot was sexed and aged. Our study area was free of predators that could have any influence on deer behaviour or habitat use.

Roaring counts

We analysed roaring counts of red deer performed during 31 consecutive years from 1978 to 2008. Each year, four surveys have been conducted ($N = 124$) at the time of the rut from mid-September to mid-October (Loe et al. 2005; mean date of counts was 25 September). Red deer were counted at 47 observation spots within the PPNR (see Fig. 1), with one or two observers at each spot. Counts were performed at dusk and the next morning at dawn, twice a year and required approximately three hours to be completed. Observations included both red deer seen and heard. The animals seen during counts were classified into three age-sex classes (calves, stags and hinds) according to antler and body size characteristics. For seen red deer, observers recorded the exact location, the direction and time of arrival and departure, the activity (roaring or silent) and the shape of antlers for males. For heard red deer, the approximate location, the start time and end of roar were recorded. Similarly to Ciucci et al. (2009), we used triangulation to locate red deer males more accurately using bearings taken by different observers. All this information was simultaneously analysed (by J-L. Hamann) to correct as far as possible for double counting and distinguish sighted stags from roaring stags. Hence, roaring males corresponded to stags that were not seen.

For each survey, we calculated an abundance index as the total number of red deer observed (AI-R). Poisson regression is often used to model count variables (Agresti 2002). However, overdispersion often occurs when a Poisson regression is used, resulting in an underestimated variance of the regression model parameters (Poortema 1999). Here, the overdispersion parameter Φ, calculated as a ratio of the deviance to degrees of freedom, was $>> 1$ for AI-R ($\Phi = 4.35$), providing evidence for overdispersion. Thus, similarly to Garel et al. (2010), we used generalised linear models (GLM) with a log-link and negative binomial distribution to obtain annual estimates of AI-R. The model included year as a factor (31 modalities) and both daily rainfall and daily mean temperature, which are likely to influence roaring counts (Ciucci et al. 2009). We coded the rainfall variable as a two-level factor (i.e. presence/absence of rainfall). Climate data were obtained from a Météo-France weather station at Danne-et-Quatre-Vents (48.7°N, 7.29°E) located < 5 km from our study area. To obtain corrected values of annual AI-R, we used back-transformed year-specific coefficients of the fitted model.

AI-R included both acoustic and visual components, which did not necessarily have the same detection probabilities, and these ones may be influenced by different factors. Consequently, we derived two other abundance indices following the procedure used for AI-R; one based on acoustic detection of stags (AI-Ra) and the other based on visually detected individuals (AI-Rv).

Estimates of population size and spotlight counts

Spotlight counts of red deer were conducted from February to April each year from 1979 to 2009 ($N = 495$). The method consisted of driving three independent routes (median length of 33 km) within the PPNR twice a month and counting every deer seen with a powerful spotlight. We used a generalised linear model with a log-link and negative binomial distribution to obtain the total number of red deer observed during annual spotlight counts (AI-I). The model included year as a factor (31 modalities), the route length (log-transformed) as an offset covariate and a two-level factor describing the conditions of observation ('good' (i.e. clear sky) vs 'bad' (i.e. occurrence of rainfall, snowfall and/or fog); see Garel et al. 2010 for details). As hunting occurred between roaring counts and spotlight counts five months later, we added the number of deer killed in the PPNR between the two counts as a variable. Indeed, the number of deer killed during the hunting season varied strongly among years and affected the number of red deer counted during spotlight counts negatively ($\beta = -0.028 \pm 0.010$, $P = 0.005$), supporting that hunting pressure accounted for most annual changes in population size (Bonenfant et al. 2002, Richard et al. 2010). More details about spotlight counts and its relationship with population size can be found in Garel et al. (2010). Here, we only used spotlight counts as a reference because spotlight counts were available for 31 years, whereas Capture-Mark-Recapture (CMR) estimates were available for only 16 years (Garel et al. 2010).

Testing roaring counts as an index of abundance

We first examined the relationship between AI-R estimated from the generalised model (see section Roaring counts) and AI-I, using a standard linear model. Then, we tested for the negative relationship between AI-R and the number of red deer shot within the PPNR during the previous hunting season using a standard linear model. We log-transformed all these variables to satisfy the homoscedasticity hypothesis of linear models (see also Loison et al. 2006, Garel et al. 2010). We tested the statistical significance of correlation coefficients (r) by examining whether zero was included within coefficient confidence interval at 95%.

Results

Roaring counts (inter-annual $CV = 22\%$) led to an average of 69.0 ± 1.9 animals during the study period. Visual and acoustic detections accounted for 70% and 30% of the total number of observed red deer, respectively. Temperature ranged from 7.3 to 20.6°C (averaging 13.3°C across study years) and was negatively correlated with AI-R ($\beta = -0.024 \pm 0.010$, $P = 0.016$). AI-R tended to decrease with the occurrence of rainfall ($\beta = -0.083 \pm 0.049$, $P = 0.095$). Once the conditions of observation were accounted for, AI-R was highly variable from year to year ($\chi^2 = 121.8$, $df = 30$, $P < 0.001$) ranging from 46.0 ± 5.6 animals in 1991 to 108.4 ± 12.1 animals in 1997 (Fig. 2). Since the value of deviance divided by the number of degrees of freedom was close to 1 ($\Phi = 1.41$), the model fitted the data satisfactorily.

In contradiction with our first prediction, the log-transformed AI-R was not correlated to log-transformed AI-I ($r = -0.01$, $CI = -0.36 - 0.34$, $N = 31$ years; Fig. 3). We also assessed the relationship between the two components of AI-R (AI-Ra and AI-Rv) and AI-I, but our results remained unchanged with or without distinguishing between visual and acoustic detection of deer (see Appendix I).

On average, 43 red deer were shot each year between 1978 and 2007 in the PPNR, but the hunting effort varied considerably among years, with 78 deer shot during the 1979 hunting season and 24 during the 1996 hunting season. Contrary to our second prediction, log-transformed AI-R was not influenced by the log number of male and female red deer killed

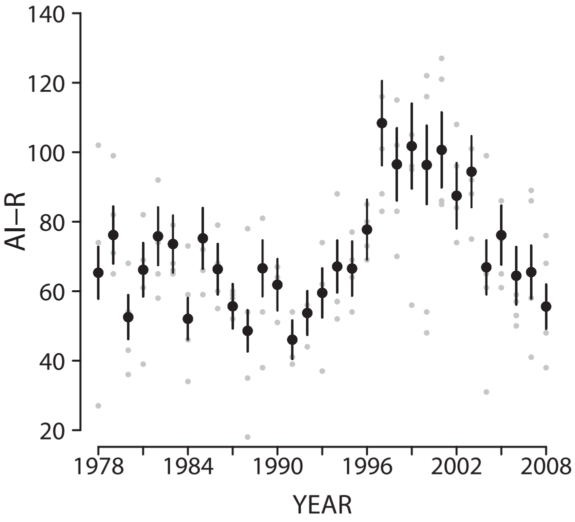


Figure 2. Yearly variations in the total number of red deer observed during roaring counts (AI-R) from 1978 to 2008 in the red deer population of the La Petite Pierre, France. Estimates (± SE) account for climatic conditions and were obtained from a negative binomial model (see Material and methods), and the grey points correspond to raw data.

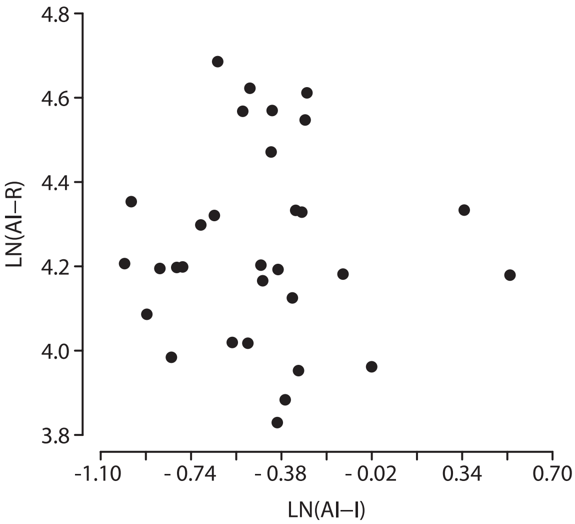


Figure 3. Relationship between roaring count index (AI-R) and the spotlight counts (AI-I) on a log scale ($r = -0.01$, $P = 0.96$) in the red deer population of the La Petite Pierre, France.

during the previous hunting season ($r = -0.27$, CI = -0.58 - 0.09, N = 30 years).

Discussion

Roaring counts are commonly used in addition to spotlight counts by managers in European countries to monitor red deer populations (Ciucci et al. 2009). For instance, the method has been systematically used since the 1970s to monitor the endangered Corsican red deer *C. e. corsicanus* in Sardinia (Lovari et al. 2007). Indeed, at the time of the mating season, red deer gather and are easily detected, particularly roaring stags, due to movements and sounds. Although roaring counts might be a useful alternative to counting methods such as spotlight counts in mountainous areas (Bobek et al. 1986, Albaret et al. 1989), a formal evaluation of its reliability has been lacking. In our study, we found no relationship between the total number of red deer observed during roaring counts (AI-R) and spotlight counts, suggesting that roaring counts do not capture the variation of abundance of the resident deer population.

Bias can occur in analysis of counts when data contain sources of variation other than the changes in the size of the population. Potential sources of variation include weather, habitat or differences between observers in their ability to detect animals (Garel et al. 2005a). These effects should be taken into account to get reliable measures of population change (for an example in red deer, see Garel et al. 2010). Here, we reported a negative relationship between temperature and AI-R, which can be explained by a reduction of animal activity when temperature increases. Garel et al. (2005b) found similar results on ground and aerial counts during summer in mouflon *Ovis gmelini musimon*. Roars can usually be heard from a long distance in good weather conditions, and therefore, sampling points in the field are generally separated by several hundred metres. Heavy rainfall decreases the vocal activity of stags (Pépin et al. 2001). However, the negative effect of rainfall on AI-R we reported here reflected the difficulty for observers to see animals under rainy conditions rather than a difficulty to hear roars (see Appendix I).

In addition to weather conditions, the proportion of roaring stags in a population depends on several factors such as condition of the stags, age structure, population density, quality and spatial distribution of the resources (Clutton-Brock & Albon 1979, Carranza 1995, Pépin et al. 2001, Yoccoz et al. 2002). Moreover, differential visibility of the various age and sex classes introduces additional sources of uncertainty in the population abundance estimates (Ciucci et al. 2009). Deer activity during the rut is fundamentally different between sexes, with stags roaring and moving a lot, whereas females remain rather elusive during this period. The detection probability is thus higher and less variable in males than in females which explains that 62% of the red deer recorded during the rut in the PPNR were males.

In mountainous areas, the altitudinal movements of red deer from a low-elevation winter range to a high-elevation summer range is a common pattern of migration (Mysterud et al. 2001). In the PPNR, due to a very low range in elevation (see section Material and methods), such an altitudinal migration to benefit from high quality food did not occur. However, a marked sex-specific seasonal migration occurred in relation to mating opportunities. While females tend to occupy the same particular area during the whole year, in autumn, males move to rutting areas that are up to 30 km from the area occupied during the rest of the year (Bonenfant 2004:226). This form of partial migration (*sensu* Dingle & Drake 2007) has also been reported in a red deer population in Sweden where an average distance of 14 km and a maximum distance of 47 km were recorded between rut and summer/winter observations (Jarnemo 2008). Consequently, a high proportion of the stags that are observed during roaring counts are not resident of PPNR. On the contrary, red deer counted and monitored during spotlight counts that occurred from February to April were resident deer of PPNR. A combination of seasonal migration and unreliability of roaring counts are likely to explain the lack of a positive relationship between AI-R and spotlight counts found in our study. Although we can not prove that roaring counts were unreliable because the population size in autumn was unknown, the observed effects of hunting provided further support to our interpretation. Indeed, we found an absence of a relationship between AI-R and the number of red deer harvested in the reserve during the previous hunting season, whereas hunting quotas led to a decrease in the number of red deer counted during spotlight counts.

Successful management of large herbivores requires the monitoring of IEC describing animal performance, herbivore impact on habitat and animal abundance (Morellet et al. 2007). Monitoring temporal changes in these indicators provides a basis for setting hunting quotas to achieve specific management objectives. In this sense, spotlight counts provide a reliable index of the abundance of resident populations in a given area for red deer (Garel et al. 2010). On the other hand, roaring counts cannot be interpreted as a reliable IEC because they do not track abundance of the resident population of red deer despite a much larger sampling effort compared to spotlight counts (average annual number of 184 observers for roaring counts vs 72 for spotlight counts). Based on a least-cost approach for achieving management objectives, roaring counts should not be used for managing resident red deer populations.

Acknowledgements - we are grateful to the Office National des Forêts and to all volunteers for their participation during roaring counts. We would also like to thank Météo-France for the climatic data and Aurélie Barboiron for Figure 1. We also thank Stefano Focardi and an anonymous reviewer for insightful comments on a previous draft of the manuscript.

References

Agresti, A. 2002: Categorical Data Analysis. 2nd edition. - John Wiley & Sons, New York, New York, USA, 710 pp.

Albaret, M., Lartiges, A. & Peroux, R. 1989: Recensements des cerfs au brame. Essais réalisés sur la Pinatelle d'Allanche (Cantal). - Bulletin Mensuel de l'Office National de la Chasse 132: 21-26. (In French).

Andersen, J. 1953: Analysis of a Danish roe-deer population (*Capreolus capreolus* (L)) based upon the extermination of the total stock. - Danish Review of Game Biology 2: 127-155.

Andersen, R., Duncan, P. & Linnell, J.D.C. 1998: The European Roe Deer: The biology of Success. - Scandinavian University Press, Oslo, Norway, 376 pp.

Bobek, B.K., Perzanowski, K. & Zielinski, J. 1986: Red deer population census in mountains: testing of an alternative method. - Acta Theriologica 31: 423-431.

Bonenfant, C. 2004: Rôle des contraintes évolutives dépendantes du sexe en biologie des populations: l'exemple du Cerf Élaphe (*Cervus elaphus*). - PhD thesis, University Claude Bernard Lyon 1, Lyon, France, 344 pp.

Bonenfant, C., Gaillard, J-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. 2009: Empirical evidence of density-dependence in populations of large herbivores. - Advances in Ecological Research 41: 313-357.

Bonenfant, C., Gaillard, J-M., Klein, F. & Loison, A. 2002: Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. - Ecography 25: 446-458.

Carranza, J. 1995: Female attraction by males versus sites in territorial rutting red deer. - Animal Behaviour 50: 445-453.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J-M., Boiseaubert, B., Ballon, P. & Duncan, P. 1998: Managing roe deer and their impact on the environment: maximising the net benefits to society. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European roe deer: the biology of success, Scandinavian University Press, Oslo, Norway, pp. 337-372.

Chevrier, T., Saïd, S., Widmer, O., Hamard, J.P., Saint-

Andrieux, C. & Gaillard, J-M. 2012: The oak browsing index correlates linearly with roe deer density: a new indicator for deer management? - European Journal of Wildlife Research 58: 17-22.

Ciucci, P., Catullo, G. & Boitani, L. 2009: Pitfalls in using counts of roaring stags to index red deer (*Cervus elaphus*) population size. - Wildlife Research 36: 126-133.

Clutton-Brock, T.H. & Albon, S.D. 1979: The roaring of red deer and the evolution of honest advertisement. - Behaviour 69: 145-170.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: behavior and ecology of two sexes. - University of Chicago Press, Chicago, Illinois, USA, 400 pp.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. 2004: Ecological impacts of deer overabundance. - Annual Review of Ecology and Systematics 35: 113-147.

Dingle, H. & Drake, V.A. 2007: What is migration? - Bioscience 57: 113-121.

Fafarman, K.R. & DeYoung, C.A. 1986: Evaluation of spotlight counts of deer in South Texas. - Wildlife Society Bulletin 14: 180-185.

Festa-Bianchet, M. 2003: Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. - In: Festa-Bianchet, M. & Apollonio, M. (Eds.); Animal behavior and wildlife conservation, Island Press, Washington D.C., USA, pp. 191-207.

Fuller, R.J. & Gill, R.M.A. 2001: Ecological impacts of increasing numbers of deer in British woodland. - Forestry 74: 193-199.

Gaillard, J-M., Loison, A. & Toïgo, C. 2003: Variation in life history traits and realistic population models for wildlife: the case of ungulates. - In: Festa-Bianchet, M. & Appolonio, M. (Eds.); Animal behavior and wildlife conservation, Island Press, Washington D.C., USA, pp. 115-132.

Garel, M., Bonenfant, C., Hamann, J-L., Klein, F. & Gaillard, J-M. 2010: Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? - Wildlife Biology 16(1): 77-84.

Garel, M., Cugnasse, J-M., Gaillard, J-M., Loison, A., Santosa, Y. & Maublanc, M-L. 2005a: Effect of observer experience on the monitoring of a mouflon population. - Acta Theriologica 50: 109-114.

Garel, M., Cugnasse, J-M., Loison, A., Gaillard, J-M., Vuiton, C. & Maillard, D. 2005b: Monitoring the abundance of mouflon in South France. - European Journal of Wildlife Research 51: 69-76.

Garel, M., Gaillard, J-M., Jullien, J-M., Dubray, D., Maillard, D. & Loison, A. 2011: Population abundance and early spring conditions determine variation in body mass of juvenile chamois. - Journal of Mammalogy 92: 1112-1117.

Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. 2004: The management of wild large herbivores to meet economic, conservation and environmental objectives. - Journal of Applied Ecology 41: 1021-1031.

Gunson, J.R. 1979: Use of night-lighted census in management of deer in Alberta and Saskatchewan. - Wildlife Society Bulletin 7: 259-267.

Jarnemo, A. 2008: Seasonal migration of male red deer (*Cervus elaphus*) in southern Sweden and consequences for management. - European Journal of Wildlife Research 54: 327-333.

Langvatn, R. & Loison, A. 1999: Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in Central Norway. - Wildlife Biology 5(4): 213-223.

Loe, L.E., Bonenfant, C., Mysterud, A., Gaillard, J-M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N. & Stenseth, N.C. 2005: Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. - Journal of Animal Ecology 74: 579-588.

Loison, A., Appolinaire, J., Jullien, J-M. & Dubray, D. 2006: How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*? - Wildlife Biology 12(1): 77-88.

Lovari, S., Cuccus, P., Murgia, A., Murgia, C., Soi, F. & Plantamura, G. 2007: Space use, habitat selection and browsing effects of red deer in Sardinia. - The Italian Journal of Zoology 74: 179-189.

Maillard, D., Gaillard, J-M., Hewison, M., Ballon, P., Duncan, P., Loison, A., Toïgo, C., Baubet, E., Bonenfant, C., Garel, M. & Saint-Andrieux, C. 2010: Ungulate status and management in France. - In: Apollonio, M., Andersen, R. & Putman, R. (Eds.); European Ungulates and their Management in the 21st Century, Cambridge University Press, New York, New York, USA, pp. 441-475.

McCullough, D.R. 1982: Evaluation of night spotlighting as a deer study technique. - Journal of Wildlife Management 46: 963-973.

Milner, J., Bonenfant, C., Mysterud, A., Gaillard, J-M., Csányi, S. & Stenseth, N.C. 2006: Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. - Journal of Applied Ecology 43: 721-734.

Morellet, N., Champely, S., Gaillard, J-M., Ballon, P. & Boscardin, Y. 2001: The browsing index: new tool uses browsing pressure to monitor deer populations. - Wildlife Society Bulletin 29: 1243-1252.

Morellet, N., Gaillard, J-M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F. & Maillard, D. 2007: Indicators of ecological change: new tools for managing populations of large herbivores. - Journal of Applied Ecology 44: 634-643.

Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. 2001: Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. - Journal of Animal Ecology 70: 915-923.

Pépin, D., Cargnelutti, B., Gonzales, G., Joachim, J. & Reby, D. 2001: Diurnal and seasonal variations of roaring ac-

tivity of farmed red deer stags. - Applied Animal Behaviour Science 74: 233-239.
Poortema, K. 1999: On modelling overdispersion of counts. - Statistica Neerlandica 53: 5-20.
Richard, E., Gaillard, J-M., Saïd, S., Hamann, J-L. & Klein, F. 2010: High red deer density depresses body mass of roe deer fawns. - Oecologia 163: 91-97.
Rooney, T.P. & Waller, D.M. 2003: Direct and indirect effects of white-tailed deer in forest ecosystems. - Forest Ecology and Management 181: 165-176.
Seiler, A. 2004: Trends and spatial patterns in ungulate-vehicle collisions in Sweden. - Wildlife Biology 10(4): 301-313.
Sinclair, A.R.E. 1989: Population regulation in animals. - In: Cherrett, J.M. & Bradshaw, A.D. (Eds.); Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications, Oxford, UK, pp. 197-241.
Strandgaard, H. 1967: Reliability of the Petersen method tested on a roe deer population. - Journal of Wildlife Management 31: 643-651.
Vincent, J-P., Gaillard, J-M. & Bideau, E. 1991: Kilometric index as biological indicator for monitoring forest roe deer populations. - Acta Theriologica 36: 315-328.
Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002: Analysis and management of animal populations: modeling, estimation, and decision making. - Academic Press, New York, New York, USA, 817 pp.
Yoccoz, N.G., Mysterud, A., Langvatn, R. & Stenseth, N.C. 2002: Age- and density-dependent reproductive effort in male red deer. - Proceedings of the Royal Society, Series B 269: 1523-1528.
Zannèse, A., Baïsse, A., Gaillard, J-M., Hewison, A.J.M., Saint-Hilaire, K., Toïgo, C., Van Laere, G. & Morellet, N. 2006: Hind foot length: An indicator for monitoring roe deer populations at a landscape scale. - Wildlife Society Bulletin 34: 351-358.

Appendix I. Relationship between spotlight counts (AI-I) and the acoustic (AI-Ra) and visual (AI-Rv) components of roaring counts

Methods

We used generalised linear models (GLM) with a log-link and negative binomial distribution to obtain annual standardised estimates of AI-Ra and AI-Rv. The models included year as a factor (31 modalities), and the daily rainfall and daily mean temperature which were likely to influence the results of roaring counts. We coded the rainfall variable as a two-level factor (i.e. presence/absence of rainfall). We examined the relationship between AI-Ra and AI-Rv estimated from the generalised model and AI-I, using a standard linear model. We tested the significance of correlation coefficients (r) by examining whether zero was included within coefficient confidence interval at 95%.

Results

We found no evidence of any influence of climate on AI-Ra (all P-values > 0.40) while AI-Rv decreased with increasing temperature ($\beta = -0.030 \pm 0.013$, P = 0.02) and rainfall ($\beta = -0.130 \pm 0.060$, P = 0.04). Neither the log-transformed AI-Ra nor the log-transformed AI-Rv was correlated with the log-transformed AI-I (LN AI-Ra: r = -0.35, CI = -0.69 - 0.11, N = 31 years; LN AI-Rv: r = 0.14, CI = -0.33 - 0.55, N = 31 years).