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Original article

Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations?

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Management of large herbivores could be improved by investing less effort in estimating absolute abundance and more effort tracking variation over time of indicators of ecological change (IEC) describing animal performance, herbivore impact on habitat, and relative animal abundance. To describe relative changes in animal abundance, monitoring trends in numbers through indices may constitute a useful and low cost method, especially at large spatial scales. Reliability of indices to detect trends should be evaluated before they are used in wildlife management. We compared population trends estimated from spotlight counts, a standard census method for deer populations, with population size estimates of a red deer *Cervus elaphus* population monitored using Capture-Mark-Recapture (CMR) methodology. We found a strong negative effect of conditions of observation (e.g. rainfall) on both the number of animals (-24.4%) and the number of groups (-31.6%) seen per kilometre. After controlling for observation conditions, we found that these two abundance indices were linearly correlated with CMR estimates, with the group-based index being better correlated ($r = 0.75$) than the individual-based index ($r = 0.68$). These consistent trends between indices and CMR estimates provide support in using standardised spotlight counts as an IEC describing relative changes in abundance for the monitoring and management of red deer populations.

Key words: abundance index, Capture-Mark-Recapture, census method, Cervus elaphus, count data, indicators of ecological change, red deer

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Managers often consider estimates of population size essential to monitor wildlife populations (Williams et al. 2002). A plethora of survey methods have been proposed to estimate the abundance of animal populations (Seber 1982, Wilson et al. 1996, Schwarz & Seber 1999, Sutherland 2006). However, despite intensive research during the past century into the design and development of such methods, most available estimates of population size suffer from low accuracy and low precision, especially when considering large herbivores (Andersen 1953, Caughley 1977, Gonzales-Voyer et al. 2001, Gaillard et al. 2003, Collier et al. 2007). In addition, Capture-Mark-Recapture methods (CMR), which arguably provide the best approach to estimate reliably population size (Buckland et al. 2000), are also the most labour demanding, time-consuming and expensive when applied to large herbivores and may have difficulties meeting their underlying assumptions. Most of these methods are therefore of limited practicability in a management context where monitoring often takes place over large areas and requires low cost methods.

Recently, Morellet et al. (2007) challenged the usefulness of aiming at reliable population size estimates when managing large herbivores. Population size *per se* does not provide any functional information on the population-habitat system (e.g. density-dependence). Morellet et al. (2007) suggested tracking over time the variation of at least three categories of indicators of ecological changes (IEC): one describing animal performance (Zannèse et al. 2006), another describing herbivore impact on habitat (Morellet et al. 2001), and the last one describing relative animal abundance (Vincent et al. 1991). This approach should allow managers to achieve their specific objectives better than by counting populations (see also Strickland et al. 2008).

To describe relative changes in animal abundance, monitoring of abundance indices has been used (e.g. Vincent et al. 1991). This indirect approach offers an attractive, low-cost method to managers (Lancia et al. 1994, Williams et al. 2002, Engeman 2005). However, abundance indices should ideally first be validated against known standards, i.e. to find out whether variation in abundance index matches variation in population size (N), before using this index in wildlife management (e.g. Vincent et al. 1991, 1996, Gonzales-Voyer et al. 2001). As the true population size is seldom known for most wild populations, the validation of many abundance indices is still largely missing, and furthermore, their general use may be questionable (Anderson 2001, Thompson 2002, Anderson 2003).

Experimentation that repeatedly changes the target population size probably constitutes the most straightforward strategy to assess properly the reliability of abundance index, especially when a control area with no induced change is simultaneously monitored (Engeman 2005). Another alternative to validate abundance index is to perform comparison with other approaches estimating animal abundance, relative or absolute estimates, and check the consistency among methods in detecting trends in abundance (McKelvey & Pearson 2001, Garel et al. 2005, Loison et al. 2006).

Spotlight surveys have been commonly used by managers as a census technique for monitoring the abundance of deer populations (e.g. Progulske & Duerre 1964, Gunson 1979, McCullough 1982, Fafarman & DeYoung 1986). For forest-dwelling deer, night counts are often preferred over direct observations during daylight hours partly because of their cryptic behaviour and partly because the eye reflection from *tapetum* makes deer detectable at night using a spotlight (e.g. McCullough 1982).

We aimed at assessing the reliability of spotlight counts to track trends in population size using long-term monitoring of a red deer *Cervus elaphus* population inhabiting highly forested areas in northeastern France. We considered both the number of animals and the number of groups seen during spotlight surveys (see also Acevedo et al. 2008) as potential candidate indices to monitor changes of red deer abundance. Some studies have suggested that conditions of observations encountered during surveys influence spotlight counts (e.g. Progulske & Duerre 1964). We therefore quantified and controlled for such effects before comparing our two indices against estimates of population size obtained from observations of individually marked animals (see Loison et al. 2006 for counts of chamois *Rupicapra rupicapra*).

Material and methods

Study area and population

We monitored the red deer population of the Petite Pierre National Reserve (PPNR; 2,674ha) located in the Vosges mountains, northeastern France (48.82°N, 7.34°E; 200-400 m a.s.l.). The climate is continental with oceanic influences characterised by mild winters and cool summers (mean January and mean July temperatures are 0.6°C and 18.4°C, respectively). Trees cover most of the PPNR (approximately 80%) and consist of a mosaic of silver fir *Abies alba*, douglas fir *Pseudotsuga douglasii*, Norway spruce *Picea abies* and European beech *Fagus sylvatica* stands. The red deer birth season spans May-June, and the rut takes place from mid-September to mid-October (Loe et al. 2005). The red deer population is hunted from 1 August to 1 February with, on average, 43 animals culled annually between 1977 and 2008.

Table 1. Population size ($\hat{N}$) estimated using Arnason et al.'s (1991) Capture-Mark-Resighting (CMR) method and abundance indices (AI-I: number of animals seen/km; AI-G: number of groups seen/km) obtained from spotlight counts of red deer, La Petite Pierre, France. Each year six censuses were performed on three routes. Within the period 1979-2008, CMR estimates were not available for all years because < 3 sighting classes (i.e. classes of sighting's frequencies of marked animals) were available some years ($n = 14$) to perform the goodness-of-fit tests (GOF; Arnason et al. 1991). The total number of animal seen (n), the number of sightings of marked animals (m) and the number of different marked individuals seen (mp) used to estimate $\hat{N}$ are reported. AIs were adjusted for 'good' conditions of observation during spotlight counts (see text for details).

Year	n	m	mp	GOF	$\hat{N}$	$SE_{\hat{N}}$	AI-I	AI-G
1985	331	25	15	0.42	279.34	80.48	0.552	0.149
1988	356	25	19	0.92	590.16	228.22	0.623	0.168
1989	389	22	12	0.86	267.99	76.59	0.677	0.160
1990	281	14	9	0.75	267.62	110.29	0.462	0.115
1993	272	22	10	0.55	136.67	34.76	0.436	0.108
1994	379	24	12	0.78	224.16	57.86	0.575	0.149
1996	365	27	15	0.47	263.63	68.69	0.573	0.159
1997	369	29	18	0.19	338.70	93.50	0.575	0.157
1998	367	27	12	0.45	180.56	41.14	0.637	0.139
1999	400	13	9	0.72	463.09	216.35	0.705	0.189
2001	314	16	10	0.46	282.43	105.92	0.571	0.143
2002	419	15	11	0.59	590.69	278.68	0.707	0.165
2003	384	27	13	0.09	214.60	51.01	0.626	0.156
2004	430	19	13	0.71	496.03	189.02	0.732	0.174
2005	375	16	10	0.76	337.29	126.73	0.626	0.159
2008	497	20	13	0.39	500.61	175.48	0.864	0.210

Spotlight counts

We conducted spotlight counts of red deer during February-April each year from 1979 to 2008. We used counts ($n = 288$) performed during 16 years only because CMR estimates could not be computed for every year (Table 1). During each survey, we simultaneously sampled three independent routes (median length of 33 km) within the entire PPNR and its periphery, and surveyed these routes twice a month using cars, except in 2005 (in which year, we performed only one survey in March and three surveys in April). Surveys started one hour after sunset and required approximately three hours to be completed at a driving speed of 20 km/hour. On each route, two observers searched for deer using 500,000 candle power spotlights, and a third passenger recorded the size and composition of all encountered deer groups.

We calculated for each survey and for each route sampled two abundance indices (AIs): one based on the number of deer seen (AI-I) and the other one based on the number of groups seen (AI-G; see Acevedo et al. 2008). We defined a group as one or more individual deer moving together and in the same direction. We considered individuals located > 50 m apart from others when first observed as belonging to different groups (Clutton-Brock et al. 1982). From the raw values of AI-I and AI-G, we performed the following steps to obtain annual adjusted estimates of AI-I and AI-G representing yearly averages of the number of deer or groups seen/km and corrected for observation conditions. We first used a generalised linear model (GLM) with a log-link and negative binomial distribution to analyse both group- and individual-based indices because counts are discrete data and most often overdispersed with respect to a Poisson distribution (Anscombe 1949, Bliss & Fisher 1953, White & Bennetts 1996). Data could also have been modelled using a quasi-Poisson distribution. We evaluated the estimated variance-to-mean relationship of our models (ver Hoef & Boveng 2007), which provided better support for the negative binomial distribution than a quasi-Poisson distribution. Our baseline model included year as a factor (16 modalities) and the logarithm of route length as an offset variable. We entered route length into our models because more deer were counted as route length increased (on log scale; number of deer: slope $= 0.038$, SE $=$ 0.009, $P < 0.001$; number of groups: slope $= 0.029$, SE $= 0.007$, $P < 0.001$) and because route length varied among years (from 8 to 48 km due to e.g. car breakdown). We then fitted models with a two-level factor describing the conditions of observation to test for the influence of weather conditions on the number of red deer counted (Progulske & Duerre

1964). We coded weather conditions as 'good' (i.e. clear sky) or 'not good' (i.e. occurrence of rainfall, snowfall and/or fog). Finally, we used back-transformed year-specific coefficients of the fitted model as yearly averages of the number of deer or groups seen/km, i.e. corrected values of annual AI-I and AI-G (see Table 1). We assessed the goodness-of-fit of our models using a Pearson χ^2 test (Agresti 2002).

Estimating population abundance using Capture-Mark-Recapture

We trapped and marked red deer annually from December to April using cage-traps baited with corn and sugar beetroot. During spotlight counts, we identified marked animals using 10 × 42 binoculars. Because the number of marked animals still alive at a given sampling occasion was unknown, we used the Capture-Mark-Resighting method developed by Arnason et al. (1991) to estimate population size ($\hat{N}$) based on the number of marked and unmarked deer observed during route surveys because the number of marked animals still alive at a given sampling occasion was unknown (Loison et al. 2006). We pooled group observations made during consecutive surveys (6/year) to obtain the three statistics required to compute $\hat{N}$: a) the number of individuals seen (both marked and unmarked; noted n), b) the total number of observations of marked individuals (noted m), and c) the total number of different marked individuals seen (noted mp; see Table 1). The application of this method requires the following assumptions to be fulfilled: 1) the population should be closed demographically (no emigration, no immigration, no death and no birth) over the period during which surveys are performed, 2) sightings of individuals should be independent from one survey to the next, 3) all individuals should have the same probability of being sighted, 4) marked and unmarked individuals should have the same probability of being seen, and 5) all marks should be identified and loss of marks should not occur (Arnason et al. 1991).

Some of the assumptions were unlikely to be completely fulfilled because natural mortality probably occurred during the survey period (assumption 1), roads were fixed and females have well defined home range (assumption 2; Hamann et al. 1997), and observers sometimes recorded marked deer without being able to identify them (assumption 5). The proportion of non-identified marked animals was low (7%) and these animals were included in n only. As we were interested in yearly variation of population size, bias in population estimate would not make up a major problem as long as we can assume that this bias was constant. Moreover, assumption 3 can be evaluated using the goodness-of-fit test (GOF) developed by Arnason et al. (1991). We also performed this test to check whether surveys were not independent and some deer were repeatedly sighted (assumption 2).

The fourth assumption is the most critical one and the most difficult to test because no statistics can be derived from unmarked animals' behaviour (Arnason et al. 1991). However, we are not aware of any published study reporting difference in behaviour or conspicuousness between marked and unmarked animals. We therefore confidently assumed that marked and unmarked animals had the same sightability. We implemented Arnason et al.'s (1991) approach in the software R (R Development Core Team 2007) to perform the analysis (R codes available on request from M. Garel).

Abundance indices as proxies of population size

We assessed the relationships between the yearly averages of the abundance indices (individual based/AI-I and group based/AI-G) estimated from generalised linear models (see section Spotlight counts) and annual population size estimates ($\hat{N}$; see Table 1). Similarly to Loison et al. (2006), we log-transformed these values because log-transformed data provided better fit models than untransformed data. For the three time-series (i.e. spotlight counts and CMR estimates), we did not find any evidence of auto-correlation (lag of one year: $\rho_{AI\text{-}I} = 0.17$, $P = 0.45$; $\rho_{AI\text{-}G} = 0.13$, $P = 0.58$; $\rho_{\hat{N}} = -0.24$, $P = 0.30$; Ljung & Box 1978) so we used standard linear models to model ln(AI-I) and ln(AI-G) as a function of ln($\hat{N}$). We also explicitly tested for a potential saturation of spotlight counts as estimates of population size increased (e.g. Ericsson & Wallin 1999). We would expect saturation to lead to non-linear relationships between ln($\hat{N}$) and ln(AIs) so a second order polynomial term of ln($\hat{N}$) was tested.

Results

Spotlight counts (raw data) led to an average of 0.60 animals/km ($\sigma^2_{AI-I} = 0.14$; range: 0.00-1.97) and 0.15 groups/km ($\sigma^2_{AI-G} = 0.006$; range: 0.00-0.41). For both the number of deer and groups seen, we found a strong negative effect of suboptimal condition of observations (AI-I: slope = -24.4%, SE = 12.3%, P = 0.047; AI-G: -31.6%, SE = 9.9%, P = 0.001). Corrected values of annual AI-I and AI-G obtained from these models were highly and positively correlated (see Table 1; r = 0.92, $P < 0.001$). Models fitted the data satisfactorily (AI-I: $\chi^2 = 262.4$, df = 271, P = 0.64; AI-G: $\chi^2 = 287.8$, df = 271, P = 0.23).

When applying Arnason et al.'s (1991) method, we did not find any evidence of a deviation of the number of resightings per marked animal from a truncated Poisson distribution (see Table 1) suggesting that the annual population estimates can be computed. The estimate of the median population size over the study period was 281 animals. Note that some annual estimates were associated with a relatively large uncertainty (e.g. in 2002).

The log-transformed indices correlated well with the log-transformed CMR estimates (Fig. 1). The correlation improved when considering groups (r = 0.75, $P < 0.001$) instead of individuals (r = 0.68, P = 0.004). For both indices, the slopes were much lower than 1 (ln(AI-I): slope = 0.266, SE = 0.078, $P < 0.001$; ln(AI-G): slope = 0.285, SE = 0.067, $P < 0.001$), indicating that changes in AIs were not proportional to changes in CMR estimates. We did not find any evidence of non-linear relationships between the log-transfomed indices and the log-transformed CMR estimates (ln(AI-I): $CMR^2 = -0.04$, SE = 0.18, P = 0.84; ln(AI-G): $\ln(\hat{N})^2 = -0.15$, SE = 0.15, P = 0.34), providing little support for a saturation of counts within the observed range of variation in estimates of population size.

Discussion

We found that both the number of animals and the number of groups seen per kilometre during standardised spotlight counts provided reliable indices of relative abundance of red deer. Our study indicates that spotlight counts should enable managers to track annual changes of population size. As reported for the kilometric index used to monitor roe deer *Capreolus capreolus* populations (Vincent et al. 1991), AIs based on spotlight counts can thus be interpreted as a relevant indicator of abundance (*sensu* Morellet et al. 2007) and provide suitable tools for the monitoring and management of red deer populations living in similar habitats.

We found that the group-based measure (AI-G) correlated better relative to population size ($\hat{N}$) than the individual-based measure (AI-I). This result is consistent with recent findings on red deer (Acevedo et al. 2008), though in a different ecological context (Mediterranean habitats) and unfortunately based on across-site comparisons instead of required longitudinal analysis of a given population (see

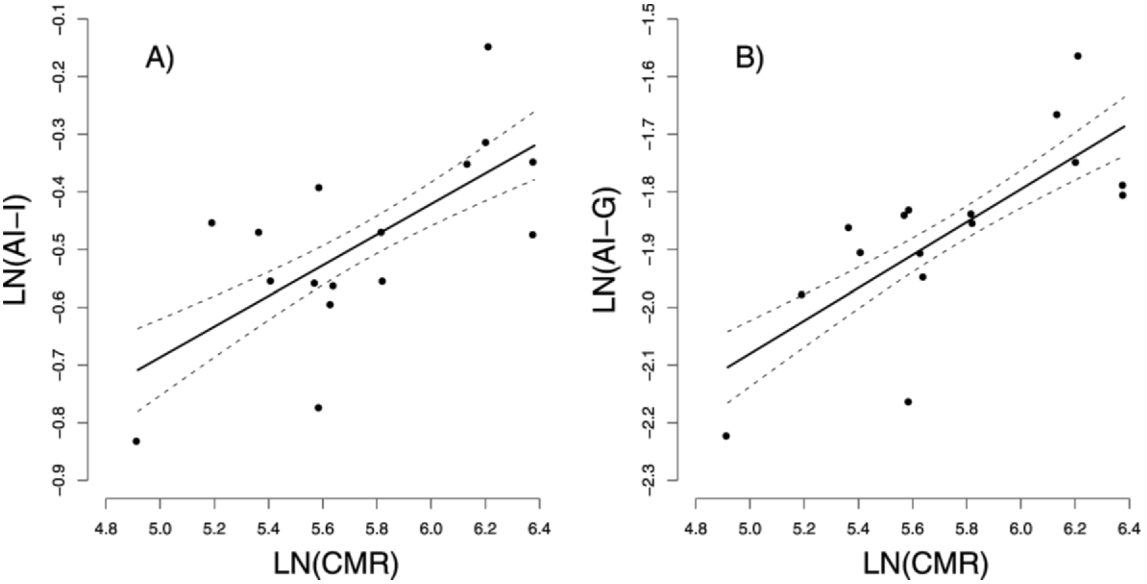

Figure 1. Relationships (± SE) between abundance indices (AIs; after log-transformation) obtained during annual spotlight counts and CMR estimates (after log-transformation) of population size (Arnason et al. 1991) computed from observations of marked animals seen during these censuses (see Table 1). A) shows the number of animals seen/km (AI-I), and B) shows the number of groups seen/km (AI-G).

Morellet et al. 2007). Two mechanisms could be involved to account for a better performance of AI-G compared to AI-I. First, it is probably easier to count groups than to count the number of deer within a group (Collier et al. 2007) so that group counts may be more accurate than individual deer counts. Second, it is well established that large herbivore group size increases with habitat openness (e.g. Jarman 1974, Pays et al. 2007). One proximal cause explaining this relationship may involve a higher probability of visually detecting congeners in open than in closed habitats. The red deer population we monitored inhabits a highly forested area (approximately 80%) where the ability of deer to form large groups, which are often seen in meadows, may be strongly constrained. Therefore, when population size increases, the number of groups rather than the size of the groups would be expected to increase. Accordingly, group size (measured as AI-I/AI-G; see Table 1) poorly correlated with CMR estimates ($r = -0.13$, $P = 0.62$). As proposed, this outcome would likely have been different in more open areas, as reported for Alpine ibex *Capra ibex* in which group size of males provided a relevant indicator of abundance (Toïgo et al. 1996).

The partial fulfilment of the assumptions required to estimate population size based on the Arnason-Schwarz-Gerrard's model (see section Methods) and a low number of marked animals relative to population size might have contributed to blur the relationships between AIs and the CMR estimates of population size. In addition, high variances in population size estimates associated with the highest population sizes (see Table 1) probably originates from the non-isometric (slope < 1; see Fig. 1) relationship between the number of animal seen and population size, so that the proportion of animal counted (n) decreased as population size ($\hat{N}$) increased. Years with high population size were thus expected to be associated with higher uncertainty in population size estimates, because Arnason et al. (1991) recommended that n should be at least twice as large as $\hat{N}$ to achieve an acceptable precision of $\hat{N}$.

The usefulness of indices to monitor trends in population abundance has been widely debated (Anderson 2001, 2003, Engeman 2003). Indeed, such methods assume that the relationship between population size (N) and indices (C) is linear and that indices represent a constant proportion (P) of N across observers, habitat types and years (Tracey et al. 2005), i.e. $C = N \times P$. As constant detection probability is seldom checked and probably rarely occurs (see e.g. Gonzales-Voyer et al. 2001, Gould et al. 2005), different approaches have been proposed to deal with failure of this assumption (Pollock et al. 2002, Thompson 2002). Among these approaches, using a standardised protocol to keep detectability as constant as possible and including covariates that may influence detectability in the analysis appear to be especially important. We showed that visual conditions during spotlight surveys had a large effect on both AIs and have to be controlled for. Previous studies have suggested that weather conditions may have limited effects on spotlight counts (Gunson 1979, McCullough 1982, Fafarman & DeYoung 1986), except during summer when temperature has been reported to influence the number of animals observed (Progulske & Duerre 1964, see also Garel et al. 2005 based on ground and aerial counts of mouflon *Ovis gmelini musimon*).

As not all influential covariates can be measured, modelled or even identified, the ideal approach would be to estimate explicitly the detection probability as part of the monitoring design (Anderson 2001, Pollock et al. 2002, Williams et al. 2002, MacKenzie et al. 2005). However, this procedure (e.g. the double observer approach; Nichols et al. 2000) would result in higher costs to estimate P that might not be counterbalanced by marked improvements of the reliability of the AIs. Tracey et al. (2005) have shown for different medium-sized mammals that despite quite large variation in P, rough indices still proved useful to detect large variation in population size. Accordingly, AI-I has been successfully used to account for density dependence in life-history traits in our red deer population (Bonenfant et al. 2002). In addition, the primary concern of deer managers is often to prevent overabundance of herbivore populations (Mysterud 2006) rather than predicting accurately how many animals may be harvested or not. From our perspective (see also Engeman 2005), AIs can adequately fulfill these goals.

Finally, we also found that AI-I increased at a lower rate than CMR estimates (slopes < 1). The population growth rate estimated from spotlight counts would therefore be increasingly underestimated as population size increases, assuming that CMR estimates were not increasingly overestimated, which suggests that spotlight counts should not be used as an absolute estimate of animal abundance when modelling population dynamics. This result has thus strong biological implications for studies relying on AI-I to estimate population growth rate of populations living in similar habitats (e.g. McCullough 1983).

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