

Can we use the young : female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model

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Summary

1. Management decisions for exploited species often rely on count ratios, such as the young to adult female ratio as a proxy of birth rate, and the decrease in the ratio between yearling and females in year $t + 1$ and the young : female ratio in year t to obtain juvenile survival. However, the reliability of such estimates has yet to be demonstrated.
2. We investigated the consistency of the young to female ratio method by using observations on individually marked female red deer. These females were known to have raised their calves to weaning successfully. We compared temporal variation in the proportion of females with a calf at heel from count ratios with the probability of observing a calf with its mother from marked animals.
3. The proportion of females observed with a calf at heel decreased over time (from 0.43 early May to 0.15 early March). This measure was influenced by individual variation and by interactive effects of year and habitat type, although there was no direct relationship with the density of vegetation cover.
4. The proportion of females seen with a calf at heel assessed from counts did not correspond with the probability of observing a female with a calf at heel, given that she successfully weaned a calf in autumn (estimated from direct observation). The probability of observing a female with a calf was highest in September (0.4) prior to the rut and lowest just after the birth season (0.08) and during the rut (0.18).
5. The temporal pattern in the probability of observing a calf with its mother, given that she successfully weaned a calf, reflected changes in the mother–calf bond from birth to weaning, rather than changes in offspring mortality or changes in pregnancy rates. These variations in the probability of observing the mother–calf pair in the field may lead to strong biases in count ratio-based methodologies.
6. *Synthesis and applications.* This study has important implications for the management of ungulate populations when decisions are based on count ratios. Our results indicate that count-based estimates of vital rates are misleading, especially in closed habitats. Pregnancy rate and juvenile survival rate are both key parameters in detecting density-dependence responses. Reliable estimates of survival and pregnancy rates obtained from marked animals and foetus sampling are more accurate. Alternatively, yearly monitoring of young body mass or bone length coupled with an index of grazing pressure would improve the assessment of population dynamics.

Key-words: calf detectability, count ratios, individual based data, methodology, mother–calf bond, population management, vital rates

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Introduction

Reliable estimates of vital rates such as survival and reproduction are required for both management and scientific studies of ungulate population dynamics. Estimating the size of ungulate populations is a particularly difficult task (Caughley 1977; Gaillard, Loison & Toïgo 2003). Although any change in population size involves changes in vital rates (Odum 1971; Lebreton & Clobert 1991; Eberhardt 2002), obtaining reliable estimates of vital rates usually requires the capture and marking of a large number of individuals, followed by a monitoring of marked animals over several years (Lebreton *et al.* 1992).

Capture–mark–recapture methodology can provide accurate and unbiased estimates of survival rates but this is costly and often problematic (Lebreton *et al.* 1992; Schwarz & Seber 1999; Lebreton & Pradel 2002). An alternative approach is to use count ratios from distinct segments of a population to assess survival and reproductive patterns (Caughley & Sinclair 1994). For example, the proportion of females seen with a calf at heel at the end of the birth season has often been used as a proxy of birth rate (elk *Cervus canadensis* L., Eberhardt *et al.* 1996; white-eared kob *Kobus kob leucotis* A. Smith., Fryxell 1987; moose *Alces alces* L., Laurian *et al.* 2000). Likewise, the decrease in female to young ratio over time and the ratio between the yearling : female ratio in year $t + 1$ and calf : female ratio in year t are commonly used to obtain juvenile survival rates (Sarno *et al.* 1999; Byrom 2002; Crampe, Gaillard & Loison 2002). However, such methods can be misleading because they do not account for temporal changes or variation in the probability of detection among different age and sex classes (Nichols 1992). Moreover, using young : female ratios confounds birth rate and juvenile survival within a single parameter. It has been shown that juvenile survival is much more sensitive to environmental perturbations, such as changes in density and climatic conditions, than birth rates of adult females (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Eberhardt 2002). Therefore, managers relying on such information to formulate management policies may wrongly assess population dynamics (Eberhardt 1977).

Problems in vital rate assessment when using measures based on count ratios have been reported, yet very few studies have measured differences in detectability according to age and sex classes (Caughley 1974; Downing, Mickael & Poux 1977; Gasaway & Dubois 1987; McCullough *et al.* 1994). Direct comparisons between figures obtained from count ratios and those obtained from more intensive population monitoring involving marked animals are rare (but see Noyes *et al.*

2000; McCorquodale 2001). In this study, we compared temporal variation in the probability of observing a female with her calf at heel from simple calf : hind ratios with that obtained from a reference method derived from monitoring marked deer. The results were interpreted in terms of management implications and reliability of ratio methods for assessing ungulate population dynamics.

Material and methods

STUDY AREA

La Petite Pierre National Reserve (PPNR) is a 2800-ha forest located in north-east France (48°5'N, 7°E) in the Vosges mountains at a mean elevation of 300 m. The climate is continental, with oceanic influences characterized by mild winters and cool summers (mean January and mean July temperatures are 0.6 °C and 18.4 °C, respectively). The red deer *Cervus elaphus* L. population inhabits a temperate forest of silver fir *Abies alba* Miller, douglas-fir *Pseudotsuga douglasii* Mirbel, Norway spruce *Picea abies* Karsten and European beech *Fagus sylvatica* L. The area is free of mammalian predators that could have any influence on juvenile and adult survival of red deer (Guinness, Clutton-Brock & Albon 1978).

METHODS

In PPNR, the managers of the Office National de la Chasse et de la Faune Sauvage (ONCFS, Gerstheim, France) have, over 20 years (1980–99), recorded 1917 observations of red deer, both in groups and as single animals, at all times of year. In any given group, all observed deer were sexed (male, female, unidentified) and aged (unsexed calf, adult, unidentified). These data were used to assess the change in female to young ratios over time. Moreover, every winter (November–March) since 1975, some deer have been caught, tranquilized with a xylazyn–ketamin mix, marked with plastic eartags, and fitted with leather collars or radio-collars. Overall, between 15% and 20% of females have been individually marked in PPNR.

Subsequent analyses were restricted to groups with marked females so that the reproductive status of a female could be monitored from one sighting occasion to another. Reproductive status was recorded as: (i) without a calf at heel; (ii) with a calf at heel; (iii) unknown, when the maternal relationship was not obvious or observation time was too short to obtain reliable identification. The average distance between a mother and her calf was usually less than 10 m (Clutton-Brock, Guinness & Albon 1982), thus maternal status could be assessed accurately from visual observations (> 89% accurate; Vankova *et al.* 2001). We are confident that assignment of an alien calf to a given female was very unlikely to have occurred in our study. For each deer location, the type of vegetation cover in which the deer was seen was categorized as follows: (1) agricultural land with corn

and sugar beet fields; (2) roads and buildings adjacent to private gardens or orchards; (3) unfenced meadows of forage grass species; (4) regenerated mixed forest containing medium-sized trees of hazel *Corylus avellana* L., birch *Betula pendula* Roth, juniper *Juniperus communis* L. and hawthorn *Prunus spinosa* L.; (5) dense Douglas fir or Norway spruce plantations; (6) plantations of beech, hornbeam *Carpinus betulus* L., Norway spruce or fir less than 10 years of age; (7) mixed forest comprising large oak *Quercus robur* L., beech, hornbeam and pine *Pinus sylvestris* L.; and (8) regenerating forest similar to habitat type (7) but with an additional, intermediate, layer of young growing trees (mainly beech, hornbeam, spruce and fir).

The red deer population in PPNR has been managed by the ONCFS since 1977 and is hunted each autumn, both by professionals and for sport. For every deer shot ONCFS managers record the sex; the age according to three age classes (calf, yearling and adult, i.e. 2 years of age and older; Hamlin *et al.* 2000); dressed body mass; and the hind's reproductive status from post-mortem inspection of the uterus. Hinds culled before mid-November are excluded from uterus inspections in order to avoid errors in the assessment of female reproductive status. Between 1977 and 1999 fecundity data were obtained for 102 females and only singletons were produced (Bonenfant *et al.* 2002). Yearling females were excluded from the analysis because too few were hunted each year (average 3.4 yearlings year⁻¹).

DEFINITIONS OF PROBABILITIES AND PROPORTIONS

A record of a female with a calf at heel can be viewed as the outcome of two events: (i) the identification of female reproductive status (IRS); and (ii) the occurrence of a calf at heel (OCH). $P(\text{IRS})$ is thus the probability of identifying female reproductive status and $P(\text{OCH})$ the probability of a female having a calf at heel. Hence, the event 'female seen with her calf at heel' should occur with a probability $P(\text{IRS} \cap \text{OCH})$, equal to $P(\text{IRS}) \times P(\text{OCH} | \text{IRS})$. It follows from this that the proportion of females counted with their calves is an estimate of the joint probability $P(\text{IRS} \cap \text{OCH})$. Given the relatively high sample size ($n = 1917$), we assessed the two probabilities of interest $P(\text{OCH})$ and $P(\text{IRS})$ using field observations as unbiased estimators: (i) IRS is the proportion of females for whom the reproductive status is known, i.e. $1 - P(\text{reproductive state unknown})$; (ii) OCH is the proportion of mothers seen with their calves among females of known reproductive status. Because $P(\text{OCH} | \text{IRS})$ is a conditional probability (the probability that a female of known reproductive status has her calf at heel), this value is higher than $P(\text{OCH})$ (the probability of a female having a calf at heel whatever her reproductive status).

An additional parameter derived from observations of marked deer provides an estimate of another conditional probability of $P(\text{OCH})$, that is the $P(\text{OCH})$

given that the female successfully raised her calf to weaning [hereafter $P(\text{OCH} | \text{WEA})$]. $P(\text{OCH} | \text{WEA})$ must therefore be higher than $P(\text{OCH} | \text{IRS})$.

STATISTICAL ANALYSES

We investigated the temporal patterns of IRS and OCH (binary response variables taking values 0 or 1) by fitting generalized additive models (GAM) with a logistic link and a binomial error distribution (Hastie & Tibshirani 1990). The complexity of the curve, i.e. the number of degrees of freedom (d.f._{spline}) associated with a smoothing spline (which defines how close to the observed values the curve passes through), was selected by repeated GAM fitting. We fitted the same model with varying d.f._{spline} for time. We pooled all years and the Julian date was entered in the model as a covariate taking 1 May as the origin (i.e. Julian date 1). Thereafter, we tested the fit of the different models in an ANCOVA setting (Venables & Ripley 1999).

We explored the influence of year (a 20-modality factor) and habitat type (an eight-modality factor) on the proportion of females for which reproductive status was known (IRS) and on the proportion of reproductive females (OCH) using a generalized linear mixed model (GLMM) and a logit link function. Female identity (97 individuals) was treated as a random factor. We accounted for the effect of time by entering linear and polynomial (from second order to fourth order) functions of Julian date (normalizing polynomial terms). Some of the possible interactions among variables were discarded because of the high number of degrees of freedom associated with each factor. We did not include third-order and all second-order interactions because the model would have been overparameterized. We only considered the most a priori biologically relevant interaction, i.e. the two-way interaction between habitat and year (Table 1).

We used spring and summer observations of a subset of 56 individually marked females known from observations in late autumn to have successfully weaned a calf in November and, hence, successfully calved in May. From this we estimated an unbiased probability of observing a female with her calf at heel for each month. We built individual records comprising '0' when the female was seen without her calf at heel or not seen at all, and '1' when the female was seen with her calf at heel. The response variable $P(\text{OCH} | \text{WEA})$ corresponds then to the conditional probability of seeing a female with a calf at heel given her calf has been successfully weaned. We estimated the variation of $P(\text{OCH} | \text{WEA})$ over time (for a definition of the different models see Table 2) with GLMM including female identity ($n = 56$) as the random factor.

MODEL SELECTION

Model selection was based on an Akaike information criterion (AIC; Sakamoto, Ishiguro & Kitagawa 1987;

Table 1. Effects of date (jul), habitat type (hab) and year (year, from 1979 to 1999) on the proportion of females for which the reproductive status was identified with confidence by managers and/or observers, and on the proportion of females with a calf at heel. *k* represents the number of estimable parameters. μ is the intercept, β is the coefficient slope, and ϵ the error term of the fitted model

Model (response variable being either IRS or OCH)	IRS (<i>n</i> = 1116)				OCH (<i>n</i> = 1116)			
	AIC	<i>k</i>	Δ AIC	\hat{w}_m	AIC	<i>k</i>	Δ AIC	\hat{w}_m
logit(response) = $\mu + \beta_1(\text{jul}) + \epsilon$	1429.8	3	103.19	0	858.79	3	34.53	0
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \epsilon$	1424.36	4	97.75	0	858.83	4	34.57	0
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \epsilon$	1367.08	5	40.47	0	860.81	5	36.55	0
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \beta_4(\text{jul}^4) + \epsilon$	1366.04	6	39.43	0	851.45	6	27.19	0
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \beta_{15}(\text{hab}) + \epsilon$	1361.17	8	34.56	0	857.13	8	32.87	0
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \beta_{16}(\text{year}) + \epsilon$	1327.81	24	1.2	0.35	824.26	24	0	0.99
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \beta_{15}(\text{hab}) + \beta_{16}(\text{year}) + \epsilon$	1326.61	27	0	0.64	832.74	27	8.48	0.01
logit(response) = $\mu + \beta_1(\text{jul}) + \beta_2(\text{jul}^2) + \beta_3(\text{jul}^3) + \beta_{15}(\text{hab}) + \beta_{16}(\text{year}) + \beta_{17}(\text{hab} \times \text{year}) + \epsilon$	1372.84	84	46.23	0	868.29	84	44.03	0

Subscript numbers refer to a covariable; Subscript letters to a categorical variable.

Table 2. Modelling the conditional probability of observing a red deer female with her calf at heel over time given that she successfully weaned her calf [$P(\text{OCH} | \text{WEA})$], using GLMM. Models were ranked by normalized weights AIC_c (\hat{w}_m). μ is the intercept, β is the coefficient slope, and ϵ the error term of the fitted model

Model	AIC_c	<i>k</i>	Δ AIC_c	\hat{w}_m	Biological significance
logit(OCH WEA) $p_i = \mu + \beta_1(t_{\text{months}}) + \sigma + \epsilon$	361.53	9	0.00	0.995	The probability of observing a female with a calf at heel changes each month
logit(OCH WEA) = $\mu + \beta_1(t) + \beta_2(t^2) + \beta_3(t^3) + \sigma + \epsilon$	372.34	5	10.81	0.004	The probability of observing a female with a calf at heel changes as a third order polynomial function of time
logit(OCH WEA) = $\mu + \beta_1(t) + \beta_2(t^2) + \sigma + \epsilon$	377.09	4	15.56	0	The probability of observing a female with a calf at heel changes as a quadratic function of time
logit(OCH WEA) = $\mu + \beta_1(t) + \sigma + \epsilon$	394.46	3	32.92	0	The probability of observing a female with a calf at heel increases or decreases as a linear function of time
logit(OCH WEA) = $\mu + \sigma + \epsilon$	392.53	2	31.00	0	The probability of observing a female with a calf at heel is constant over time

Burnham & Anderson 1998). GLMM were run with the ‘glmm’ R function by Lindsey (personal communication) that provides maximum likelihood estimates of the parameters, because AIC requires the computation of the fitted model likelihood (Burnham & Anderson 1998). Following Burnham, White & Anderson (1995), we derived an AIC_c accounting for the effective sample size of our data set, here denoted AIC_c . In both cases, the most parsimonious set of models, i.e. models having the lowest AIC or AIC_c , was selected as the most suitable to describe the pattern of variation in the mother–calf pair sighting probabilities. We followed Burnham & Anderson (1998)’s methodology, also advocated by Johnson & Omland (2004), and used a model-averaging procedure among the set of competing models. The model goodness-of-fit (GOF) for logistic regression was assessed according to Agresti (1990) by transforming the continuous variable Julian date into a 10-level factor. We fitted models including the categorized Julian date and grouped habitat classes (into four categories), and then tested the GOF on the basis of Pearson’s residuals. Both for IRS and OCH, the simple models fitted the data satisfactorily [$\chi^2(27) = 18.47$, $P = 0.888$ and $\chi^2(27) = 14.51$, $P =$

0.975] and we thus assumed adequate GOF for more complicated models (Langvatn *et al.* 2004).

COMPARISON WITH PREGNANCY RATES

For each year of study, the proportion of females seen with a calf at heel was compared with the known pregnancy rate to quantify the potential bias resulting from the use of female : calf ratios in estimating birth rate. Pregnancy rates were estimated from hunted deer shot between September and January (Bonenfant *et al.* 2002). Differences in the proportion of pregnant females and females with a calf at heel were tested with simple non-parametric correlation tests (Sokal & Rohlf 1981). All statistical analyses were performed using the R statistical package (R Development Core Team 2004).

Results

WITHIN-YEAR PATTERN

The raw data giving the overall proportion of females with a calf at heel in the population (all observations combined) was adequately described by a 3 d.f._{spline}

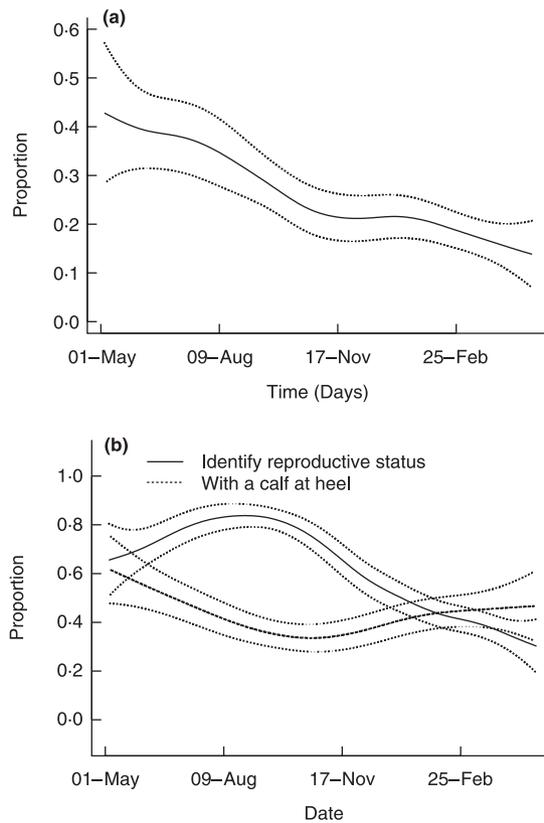


Fig. 1. (a) Within-year changes in the proportion of red deer females seen with a calf at heel in La Petite Pierre National Reserve (France). The solid line is the GAM model prediction (with 3 d.f. used for the smoothing spline function) and the dotted lines are the standard errors of the observations. (b) Temporal changes in both the proportion of red deer females for which the reproductive status has been recorded confidently and the proportion of females seen with a calf at heel corrected for observation quality in La Petite Pierre National Reserve. The solid and dashed lines correspond to the GAM model predictions (5 d.f. for the smoothing spline function) and the dotted lines are standard errors of the observations.

smoothing spline for time (Julian date; Fig. 1a). We fitted GAM with 5 and 3 d.f._{spline} for time (Julian date) to model, respectively, the proportion of females with a calf at heel (OCH) and the proportion of females for which reproductive status was determined (IRS). We detected marked variations over time for both OCH and IRS but the patterns differed between the two measures (Fig. 1b). OCH decreased steadily from the calving season (1 May) until the rut peak (25 September), and then increased to reach a plateau by the end of January. In contrast, IRS increased from 1 May, peaked on 25 August and then decreased at a constant rate until the next calving season. Thus, everything else being equal and assuming that both events were independent, the probability of identifying the reproductive status of a female (IRS) was much lower at the end of winter than at the beginning of winter (from 0.62 to 0.35, i.e. a 43% change). This pattern could be accounted for, at least partly, by juvenile mortality (Fig. 1a). However, the decrease in the probability of observing a female with a

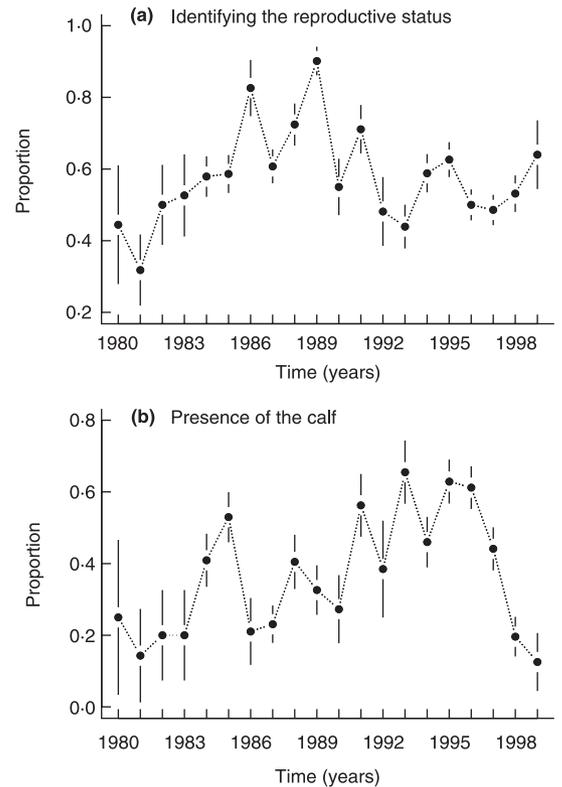


Fig. 2. Annual variations in (a) the proportion (\pm SE) of red deer females for which the reproductive status was identified and (b) the proportion of females seen with a calf at heel in La Petite Pierre National Reserve (France).

calf at heel (OCH), which most probably reflects calf winter mortality, was much lower (from 0.54 to 0.46, i.e. a 14.8% change).

EFFECT OF YEAR, INDIVIDUAL AND HABITAT TYPE

The average model for IRS (models within the range of 4 AIC points from the best model) included both the additive effects of year and habitat (Table 1; coefficients of the average model are given in the Appendix). IRS was highly variable from year to year (Table 1), ranging from 0.31 ± 0.10 in 1981 to 0.90 ± 0.04 in 1989 and averaging 0.57 ± 0.03 ($CV = 4.37$; Fig. 2a). The highest probability of accurately determining a female's reproductive status were found in habitats (3) (open meadows) and (4) (regenerating forest), whereas the lowest probability was found in habitat (7) (mixture of deciduous and coniferous forest; Fig. 3a). These differences could be related to the degree of openness of the vegetation cover affecting the observer's range of sight. We tested this assertion by grouping habitat types into two categories (habitat 1, 2, 3, 4 vs. habitat 5, 6, 7, 8, i.e. open vs. closed habitat types) based on vegetation height and density. However, vegetation density was not a factor explaining IRS variability ($\Delta AIC > 4$ with the best selected model in Table 1). The random factor 'individual' (among female variability) was also significant in explaining IRS variability (Table 1;

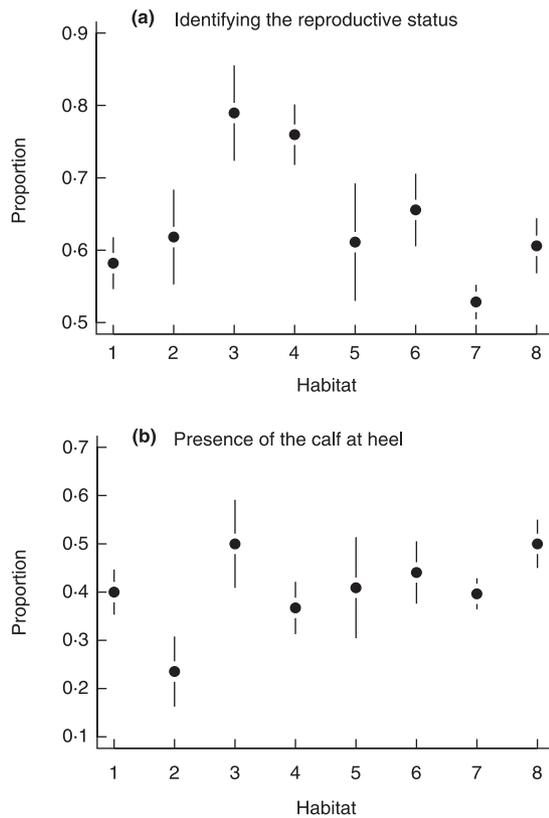


Fig. 3. (a) Effects of habitat type on the proportion of red deer females (\pm SE) for whom reproductive status was determined. The proportion of females with identified reproductive status is strongly affected by the habitat in which the observation was made. (b) Effects of habitat type on the proportion (\pm SE) of red deer females seen with a calf at heel once resighting probability is accounted for. The number of young seen with their mother does not change between habitats, i.e. whatever the density and the degree of openness of the vegetation cover. Habitat type as specified in the text.

standard deviation of the random intercept = 0.335), with an increase of AIC > 10 compared with the best model when this factor was removed (Venables & Ripley 1999).

OCH varied between habitat types and years, although the habitat effect was less obvious (Table 1 and Fig. 3b), as suggested by the AIC relative weights. Yearly variations in OCH (Table 1) ranged from 0.12 ± 0.08 in 1999 to 0.65 ± 0.09 in 1993, and were much lower in OCH (CV = 2.11) than in IRS (Fig. 2b). OCH also differed greatly from one female to another (standard deviation of the 'individual' random intercept = 0.990, with Δ AIC > 35 with the best model). On average OCH was relatively low in PPNR and the overall proportion of females seen with their calf at heel was lower than 0.5 (OCH = 0.42 ± 0.02).

ESTIMATING THE PROBABILITY OF OBSERVING A FEMALE WITH A CALF AT HEEL FROM BIRTH TO WEANING DERIVED FROM INDIVIDUAL DATA

The AIC selection procedure clearly showed the occurrence of non-linear monthly variations in the condi-

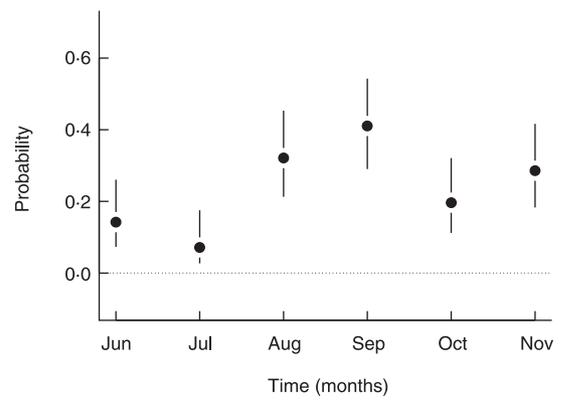


Fig. 4. Monthly probability (\pm SE) of observing a red deer female with her calf at heel conditional on successful weaning with her calf using individually marked females.

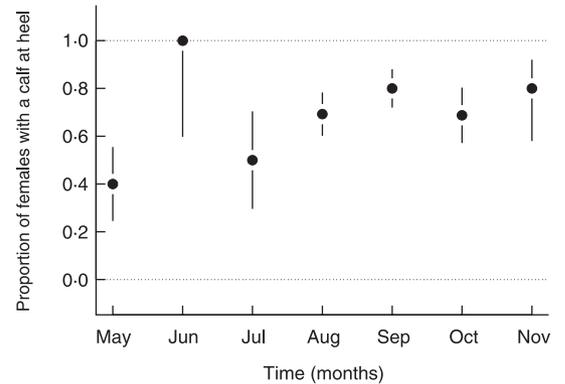


Fig. 5. Monthly variations in the proportion (\pm SE) of red deer females seen with their calves knowing that they successfully raised their offspring by the end of December.

tional probability of seeing a female with a calf at heel from birth to weaning (Table 2), without any competing models (all Δ AIC_c > 10). The highest probability of encountering a female with her calf occurred in September (0.42), whereas the lowest probability (0.06) was in July (Fig. 4). Moreover, as this probability relied on marked individuals successfully weaning their calves, the probability of encountering a female with a calf at heel was likely to be overestimated, as non-reproductive females were not included in the analyses. The selected model fitted the data satisfactorily [$\chi^2(7) = 7.78$, $P = 0.38$]. There was no indication of overdispersion as the residual deviance was smaller than the residual number of degrees of freedom (deviance = 343.1 on 431 d.f.).

To test the reliability of OCH calculated at the population level (Fig. 1b), we compared the temporal pattern of OCH with that of the proportion of females seen with their calves at heel, knowing they had a calf each until December, using individual data (Fig. 5). We failed to show any relationship between the two proportions, either with all months considered (Spearman rank correlation: $R_s = 0.48$, $z = 1.02$, $P = 0.306$, $n = 5$) or when excluding June because of a small sample size ($R_s = 0.1$, $z = 0.1$, $P = 0.920$, $n = 4$). These results illustrate that large

discrepancies occur between the monitoring of individually marked animals and count ratio methodologies.

COMPARISON WITH PREGNANCY RATES

The pregnancy rate of adult females was 0.85 ± 0.05 and was shown to be independent of body size and population density, with the exception of yearling females (i.e. aged 1.5 years during the hunting season; Bonenfant *et al.* 2002). Thus, an estimate based on a calf : cow ratio (averaging 0.62 in May) would lead to an underestimate of the birth rate by about *c.* 15% compared with the original value. On an annual basis, the relationship between pregnancy rates and OCH was weak and not significant ($R_s = -0.196$, $z = -0.69$, $P = 0.489$, $n = 13$). Only pregnancy rates for which we had large sample size ($n = 5$) were considered in this latter analysis.

Discussion

The proportion of females seen with a calf at heel declined steadily from early May to April the following year. Such a decrease could simply be attributed to calf mortality over the first weeks of life (Guinness, Clutton-Brock & Albon 1978). However, by analysing the two components of the observation process, namely the probability of determining a female's reproductive status (IRS) and the probability of female being reproductive (OCH), we found that IRS was highly dependent on the timing of observation. This indicates that the reliability of assessing female reproductive status varies greatly over time. The proportion of females for which reproductive status was recorded ranged from 0.81 in mid-August to 0.33 at the end of the spring. This pattern is likely to be related to changes in the mother-offspring bond over the course of the year as well as to maternal behaviour (Jackson, White & Knowlton 1972; Espmark 1979; Guinness, Hall & Cockerill 1979). On the other hand, the proportion of females seen with a calf at heel (OCH) decreased steadily from the calving season to the end of the rut. Obviously, the observed variations in OCH cannot be accounted for by juvenile mortality alone, because OCH increased following the rut, but may be a result of changes in the mother-young relationship. Newborn red deer remain hidden in cover for 14–21 days after birth (a 'hider strategy'; Bubenik 1965; Guinness, Hall & Cockerill 1979) yet OCH peaked at the beginning of the calving season.

Experimental studies to assess the accuracy of night spotlighting counts (McCullough 1982) have revealed that the probability of encounters differ markedly in relation to the type of habitat (Hutton & Woolhouse 1989; Whipple, Rollin & Schacht 1994; Härkönen, Härding & Lunneryd 1999), and this is supported by the habitat differences in IRS in this study. As expected, it was easier to assess female reproductive status in open meadows than in heavily forested areas. Indeed, several studies have shown that both female and young

ungulates select habitat with dense cover to reduce both predation risks and disturbance (Bowyer *et al.* 1999; Linnell *et al.* 1999).

There were large among-year variations in OCH patterns that were not related to variations in pregnancy rates, and which were shown to be generally constant in time (Gaillard *et al.* 2000). Previous survival analyses of the PPNR population have shown that winter calf survival does not vary greatly among years (Bonenfant *et al.* 2002). The cause of the high variation in OCH remains unclear, but the lack of relationship between pregnancy rates (from post-mortem inspections of the uterus) and observational data suggest that calf : female ratios are unreliable as a proxy for recruitment rates. We conclude that the calf : female ratio should not be used to estimate juvenile survival rates.

THE MOTHER-OFFSPRING BOND

The conditional probability of observing a female with her calf at heel showed marked variation over time. The shape of the curve we found corresponded with that expected for hider species (Lent 1974; Ralls, Lundrigan & Kranz 1987). The lowest probabilities were found during the first 2 months of life (i.e. during the time when calves are more vulnerable) and a peak occurred in September. Forest-dwelling ungulates typically shelter in dense vegetation when offspring are vulnerable (Lent 1974; Ralls, Kranz & Lundrigan 1986), and at the same time females become more vigilant, react more readily to disturbance and show increased flight distance (Clutton-Brock & Guinness 1975). Therefore, the lowest probability of encounter during visual observations during these early stages is expected. The subsequent increase in the probability of observing a calf at heel corresponds with the young becoming more active and less vulnerable to predators (Jackson, White & Knowlton 1972) and the tighter bond between mother and calf during the lactation period (pronghorn *Antilocapra americana* Ord; Byers 1997). Once calves reach 6 months of age, the pair bond begins to break down as weaning occurs (*sensu* Martin 1984). Calves become more independent from their mothers, and so lower the probability of observing a female with a calf at heel (Guinness, Hall & Cockerill 1979). The lowest probability of observing a calf with its mother occurred during the rut. The decline in the probability of seeing females with calves at heel in September may be a consequence of the rutting behaviour of both adult males and females. For example, rutting males often chase away calves and yearlings in red deer (Clutton-Brock, Guinness & Albon 1982). However, our results contradict observation by Guinness, Hall & Cockerill (1979), who did not report any changes in the association between mother and calf during the reproductive season. A subsequent increase in the probability of observing a female with her calf occurred during the post-rut period, reflecting the continuation of the mother-young bond until the calf reaches at least 1 year of age and the female gives

birth to a new calf (Clutton-Brock, Guinness & Albon 1982). The bond may persist beyond a year for female offspring (Albon *et al.* 1992; L'heureux *et al.* 1995).

SOURCES OF ERROR

The use of individually marked animals minimized errors associated with counts, such as double counts (Gaillard, Loison & Toïgo 2003). It transpired, however, that several problems can arise from the use of calf : female ratios to assess demographic traits in ungulate populations. Temporal changes in the probability of observing a calf at heel showed the same pattern as temporal changes in the proportion of females for whom it was possible to record reproductive status. Such a close correspondence implies that most of the variability in IRS is a result of variations in the probability of observation of a female with her offspring. Thus, observers were unable to record reproductive status because of the absence of a calf at heel, which is confounded with imperfect assignment of reproductive status. This is likely to be even more acute where no distinction in the quality of the observation can be made and where animals cannot be individually recognized.

We suggest that the best time to estimate the proportion of reproductive females reliably is early September, prior to the rut. At the end of the summer the probability of observing a calf at heel is highest and the matriarchal group is well established (Clutton-Brock & Guinness 1975). However, this probability remains low (0.42), and the chance of seeing a mother with her calf is less than 50%. It is important to note that observations made at different times of the year are not comparable. Thus, to be meaningful, population monitoring protocols need to be standardized from year to year and carried out at the same time of the year (McCullough *et al.* 1994).

In PPNR, where trees cover more than 80% of the area, a single observation is not informative unless a particular calf is seen clearly following its mother. It was not possible to tell whether a female was reproductive or not when seen alone. Repeated observations provided more information and improved the accuracy of the data. In this study, after three consecutive observations of the same female, the percentage of females correctly classified for their reproductive status included 95% of the females known to have raised their calves in December (Fig. 6). Given the relatively high percentage of female–calf pairs seen from August to October (between 70% and 80%), we suggest that repeated observations provide a reasonable and attainable procedure for managers. Hence, except in open grassland areas, where the probability of observing a mother–calf pair is substantially higher (McCullough 1994; Whipple, Rollin & Schacht 1994; this study), we cannot place confidence in studies reporting recruitment rates where data are derived from helicopter or road night counts (or any similar methodology), where deer are observed just once.

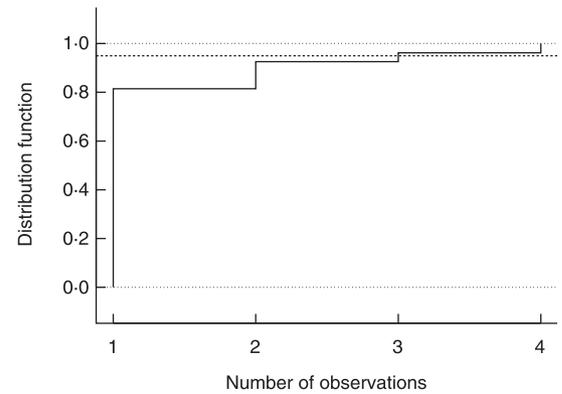


Fig. 6. Cumulative proportions of red deer females seen with their calves as a function of the number of observations made (from 1 to 4 successive observations) and independently of observation time. For instance, the proportion of females correctly assigned for their reproductive status increases from 81% when seen just once to 92% when seen twice. The dashed line represents the 95th percentile, i.e. the number of observations necessary to establish the reproductive status of a given female with a 95% probability.

MANAGEMENT IMPLICATIONS

Managers of commercial forestry plantations aim to maintain deer population levels below that defined as the economical carrying capacity (Caughley 1977), i.e. a density at which the economical consequences of deer browsing on young shoots or bark are not a concern. Despite the fact that they are not very informative, count-based methods are the most widely applied technique used to monitor population levels in the field, because of their ease of use (Smart, Ward & White 2004). Previous studies have warned against the use of counts for estimating population growth rate (Downing, Mickael & Poux 1977), survival (Gasaway & Dubois 1987) and sex ratios (McCullough 1994). In this study, we have demonstrated that the use of young : female ratios does not provide a reliable proxy of recruitment rate.

Alternative methods include monitoring changes in age- and sex-specific traits, such as body mass and pregnancy rate (Eberhardt 1977, 2002) and using an index of browsing pressure where biometric data are unavailable (Cederlund *et al.* 1998; Augustine & DeCastela 2003). Whenever large-scale marking experiments are impractical, we advocate a fine-scale approach to population monitoring based on fewer marked females (around 30). Taken together with the sampling of foetuses from hunted females, this should provide more reliable estimates of survival and pregnancy rates and will be preferable to large-scale count ratios.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE1008/JPE1008sm.htm>

Appendix. Paramater estimates of the average model.

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