

Cumulative reproduction and survival costs in female red deer

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Successful reproduction in a single breeding event has consistently been shown to reduce condition, fecundity and survival to the following breeding season. Few studies have examined the cumulative costs of frequent reproduction on survival. Here we use a dataset of female red deer (*Cervus elaphus*) from the Isle of Rum, Scotland, to model survival probability within a mark–recapture framework. By including both recent reproduction and long-term cumulative reproductive effort in the models we tested whether knowledge of lifetime reproductive effort improves our estimates of survival probability. We found that the fit of the model was significantly improved with the inclusion of longer-term measures of reproductive history. Heterogeneity in the reproductive performance of individuals influenced the expected survival cost of reproduction, with high cumulative reproductive effort associated with high survival, except with individuals reproducing in their first year where reproduction was associated with a decrease in survival. This work emphasises the need to account for reproductive history when estimating the survival probabilities of animals.

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Maximising reproductive success over an individual's lifetime involves a series of tradeoffs between breeding at each available opportunity and surviving between breeding events. Successful reproduction in one breeding occasion has consistently been shown to reduce body condition, survival and fecundity during the following breeding season in several vertebrates (Clutton-Brock et al. 1983, Boyd et al. 1995, Woodroffe and Macdonald 1995, Golet et al. 1998, Ruusila et al. 2000, Hanssen et al. 2003, Koivula et al. 2003). The severity of the cost of reproduction on survival is dependent on individual attributes such as weight and age and environmental factors such as population density (Tatar et al. 1993, Woodroffe and Macdonald 1995, Clutton-Brock et al.

1996, Festa-Bianchet et al. 1998, 2003, Lambin and Yoccoz 2001, Pilastro et al. 2003). Most analyses have focussed on the costs of single breeding events, but there may also be cumulative costs of frequent reproduction throughout life. In this paper we examine the effect of these costs on survival.

Evolution is expected to favour reproductive strategies that contribute most genes to subsequent generations (reviewed by Roff 1992, Stearns 1992). A consequence of this can be that individuals make decisions about whether to reproduce at a particular time as a function of their condition, which in turn may be a function of previous reproductive effort (Clutton-Brock et al. 1983, Pilastro et al. 2003). Different decision rules

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consequently generate different life history strategies. In seasonally breeding long-lived species, like red deer (*Cervus elaphus*), where gestation is comparatively long, there is only a limited time window during which breeding females have the opportunity to regain condition following the end of lactation before reproducing in the next season (Clutton-Brock et al. 1982). If a female does not reproduce, thus preventing contribution of genes to subsequent generations in that year, survival and fecundity may be increased in subsequent years; if a female does breed, she may have an elevated probability of mortality during gestation or lactation, and this is interpreted as a tradeoff between reproduction and survival. Such tradeoffs are at the heart of life history evolution, so it is perhaps surprising how little research has been conducted on the cumulative costs of reproduction.

Life history strategies can depend on the age at first reproduction and ages at subsequent reproduction. In Scotland, most red deer hinds first reproduce between three and five years old, although it has been known for first reproduction to be delayed until the age of six or seven. Variation in the timing of first reproduction may also have consequences for future survival or fecundity (Tavecchia et al. 2001, Kruger 2005, Tavecchia et al. 2005). Red deer commonly skip breeding events for one or more years and this can depend on investment in their offspring. In the population we examine in this paper, previous work has focused on the direct costs of reproduction (Clutton-Brock et al. 1983, Catchpole et al. 2004). Red deer have been found to suffer costs of reproduction in terms of reduced body condition and fecundity in the next year, and increased mortality rates (Clutton-Brock et al. 1983, Catchpole et al. 2004). Body condition of dead animals was assessed by using measurements of carcass weight, kidney fat and rump fat from culled animals. These measures of condition were shown to be significantly lower in milk hinds (those with a calf that year) than in yield hinds (those without a calf that year), although these condition effects were predominantly in winter months and by the next calving there did not appear to be a reduction in body condition in response to previous reproduction (Clutton-Brock et al. 1983). The costs of reproduction were found to vary considerably and were strongly dependent on extrinsic (population density and quality of home range) and intrinsic (sex, birth date and weight of calf) factors (Clutton-Brock et al. 1983).

Large mammals, such as red deer, are often considered to be capital breeders as they rely largely on accumulated energy reserves for reproduction (Festa-Bianchet et al. 1998), conversely small mammals are usually considered as income breeders, where reproduction relies on recent energy acquisition rather than a long-term stored energy reserve. These differences are predicted to result in contrasting life history strategies; energy expenditure in

a previous reproductive event should affect future reproduction more in capital breeders than income breeders. Experiments are most effective at accurately assessing costs of reproductive effort and have been used extensively with birds and mammals (Dijkstra et al. 1990, Barber and Evans 1995, Golet et al. 1998), but manipulations are usually very difficult to do with capital breeders, especially if the species is studied in the wild. Observational studies are more common in capital breeders; however, often costs of reproduction have not been detected (Berube et al. 1999, Toïgo et al. 2002), possibly due to the variation in previous energy expenditure or individual quality and reproductive potential (Festa-Bianchet et al. 1998, Yoccoz et al. 2002). Despite these problems, the most effective non-experimental method of assessing the effect of reproduction on future survival in capital breeders is by modelling survival with individual measures of reproductive effort (Lebreton et al. 1992, Berube et al. 1999).

Despite the extensive work on reproductive effort in a range of species, most of these studies have only examined the costs of reproduction to survival in one year of life. There is comparatively little research on the cumulative costs of reproduction over an individual's lifetime. By using information on whether animals have bred in a particular year, their total number of offspring to date and their proportional possible reproductive effort, the causes of reproductive costs can be assessed and life history strategies can be more fully understood.

In this paper, proxy measures of cumulative reproductive effort are used alongside environmental covariates to model survival of female red deer. We found that recent reproduction was the best reproductive covariate for explaining variation in survival, but the fit of the model was improved further with the inclusion of longer-term measures of reproductive history. Heterogeneity in the reproductive performance of individuals influenced the expected survival cost of reproduction, with high cumulative reproductive effort associated with high survival.

Methods

Study area and red deer life history

The Isle of Rum is situated in the Inner Hebrides, Scotland. The island is split into unfenced blocks for deer management purposes. Red deer have been studied intensively in the North block of Rum since 1971 and culling ceased in the area in 1972. Since this time, the population has increased and now fluctuates around ecological carrying capacity. Female red deer can be sexually mature at 2½ years to produce their first calf at 3 years. Females only ever have a maximum of one calf a year. The rut occurs between September and November with calving between May and July. The main mortality

is in winter, in February and March, and this is usually as a result of starvation (Clutton-Brock et al. 1982).

Data collection on Rum

The life history is known for over 95% of animals in the study area, including precise date of birth, maternity and in many cases paternity. Calves are caught, weighed, measured and uniquely marked with ear tags for both sexes and collars for females shortly after birth. Formal censusing began in 1974; the entire study area is censused five times a month for most months of the year and this is carried out by walking a set route and recording any deer seen, their identification code, location, behaviour and proximity to other deer (Clutton-Brock et al. 1982).

Encounter histories

All females are assigned an encounter history: for each recapture occasion “1” indicates the animal was encountered (i.e. “recaptured”) in that recapture occasion and “0” indicates the animal was not seen. For an individual to be encountered in any year, they must have been recorded in a census between July and September inclusive. This small fraction of the year was used to ensure that the encounter occasions did not coincide with mortality; individuals seen at the beginning of the censusing occasion should still be alive at the end, as survival is calculated between rather than within occasions (Lebreton et al. 1992). As there is little mortality in July to September, this avoids individuals dying during the censusing occasion. This prevents bias occurring when using mark–recapture analysis. Only encounter histories of individuals that were encountered in their first year of life were used so first capture defines an individual’s cohort. Censusing formally started in 1974, therefore only individuals born after that time were used in the analysis. After removing the pre-1974 cohorts’ encounter histories and those individuals that were known to be shot outside the study area, 529 encounter histories remained for analysis for 29 annual occasions. Mark–recapture analysis allows estimation of both survival and recapture probabilities. In this paper, both survival and recapture (defined as an individual being resighted) probabilities are annual.

Model construction

Model notation used is found in Table 1. The general model structure was similar to that of a Cormack-Jolly-Seber model ($\phi_t; p_t$), where both survival (ϕ) and recapture (p) are time dependent (Lebreton et al. 1992). Recapture and survival probabilities were initially

Table 1. Symbols used in model notation.

Term	
ϕ	annual survival probability
p	annual recapture probability
NAO	North Atlantic Oscillation
d	population density
R	residual birth weight
TC	total number of calves
PARE	proportional age-specific reproductive effort
PARE _m	status milk
PARE _{mw}	status milk and winter yield
PARE _{all}	all statuses except true yield
CP	calving previous year
a	age group
A	continuous age
\times	interaction effect between covariates
$+$	additive effect between covariates

modelled as time dependent and individual covariates and age structure were added to the model for survival. In a previous model for survival of female red deer in this population (Catchpole et al. 2004), the number of model parameters was reduced by grouping individuals according to age class rather than survival being kept fully age-dependent. The probability of survival was found to increase in the first two years of life, then remain relatively constant from the third to the eighth year and decrease from the ninth year onwards. This increase in survival probability with the early age groups and the decrease with older individuals makes it unrealistic to include age as a continuous covariate over all age groups, however within the older age groups, age can be included as a continuous covariate to test the extent of the decrease in survival with age. Four age groups were consequently identified; calves (1st year), yearlings (2nd year), adults (3rd to 8th year) and seniors (9 years onwards) (Catchpole et al. 2004). Survival probabilities in each age class were regressed logistically on environmental and individual covariates. Despite the adult and senior age groups being the only reproductive groups, survival probability of calves and yearlings was also analysed to assess how environmental covariates influenced survival in each age group and how this compares to the reproducing age groups. Including the non reproducing age groups will not affect the final model for survival for adults and seniors. Dispersal probability was not included in the model as it has been previously (Catchpole et al. 2004). Permanent dispersal of females is minimal; some are occasionally found outside the study area boundary, but are usually seen within the area during the course of a year. Program MARK was used for analysis due to its ease of use with encounter history data combined with individual and environmental covariates (White and Burnham 1999).

Simple models were constructed using parameter index matrices (PIMs), and then individual and environmental covariates were added using design matrices. Individual and environmental covariates were modelled

on a logit scale for each reproductive age group, for example

$$\phi = \frac{e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \dots)}}{1 + e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \dots)}}$$

Where x_i represents a covariate and β_i represents a linear predictor coefficient of ϕ .

Time-varying individual covariates were modelled by calculating the covariate for each year for each individual and then including this in the design matrix at the corresponding year.

To determine the most parsimonious model, all environmental and individual covariates and their second order interactions were initially included in the model and then progressively removed until no further simplification was possible (Burnham and Anderson 2002, Crawley 2002). Model selection was based on Akaike's information criterion (AIC), giving a compromise between the number of parameters and the deviance of each model. If there is a very small difference in AIC between models (less than 2), it is argued that the models are equivalent and the model with the smallest number of parameters should be used (Lebreton et al. 1992).

Recapture

Recapture probability was initially modelled as fully time-dependent. Recapture probability was assumed not to be affected by individual or environmental factors as it is believed that variation in recapture probability is only due to changes in resighting effort. To further minimise parameters, resighting effort was defined as high, medium or low, and this model was tested against the fully time dependent model and a model with constant recapture.

Covariates

Weather – the North Atlantic Oscillation (NAO) measured between December and March has been shown to be a relatively good predictor of the complex effects of weather on survival for northern ungulates (Coulson et al. 2001, Catchpole et al. 2004, Hallett et al. 2004). The winter index of the NAO between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland was obtained for each year (from <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html>; Hurrell 1995).

Population density – defined as the number of animals that are seen in 10% or more censuses occurring between January and May. As this is the number of individuals in a fixed area throughout the study, this can be defined as population density. Censuses between January and May were chosen in order to exclude

influxes of stags to the study area during the rut. A wide range of census dates were chosen so as to ensure all resident individuals were included and the 10% cut off was used to exclude transients whilst still ensuring all resident individuals were included in the population (Coulson et al. 2004). The value for population density should then include all individuals in the population during the mortality season.

Residual birth weight – approximately two thirds of calves are caught and weighed and only these individuals were used in the full model. As the time at which newly born calves are weighed varies, residual birth weight is usually calculated by linearly regressing weight at capture against time of weighing in hours and subtracting this value from the capture weight (Catchpole et al. 2004, Nussey et al. 2005). The regression equation used in this analysis is:

$$\begin{aligned} \text{residual birth weight} \\ &= \text{capture weight (kg)} \\ &\quad - (6.486 + 0.0154 \times \text{age at capture (hours)}) \end{aligned}$$

Age in years – included for each individual as a time-varying individual covariate.

Reproductive effort covariates

Three reproductive effort covariates were used in the model: one explaining recent reproduction and two explaining cumulative reproductive effort. Reproductive status is known for every hind in every year. Statuses are as follows:

- immature - hind has not previously calved;
- true yield - hind did not calve in that year;
- summer yield - calf died before 1st October of its first year;
- winter yield - calf died in the winter of its first year;
- milk hind - calf survived its first year.

These status records were then used to calculate the reproductive covariates for each hind.

Calving in previous year (CP)

For each occasion, this set of time varying individual covariates was dependent on whether the hind had a calf in the previous spring or not (regardless of how long it survived), and was allocated a “1” or a “0” respectively for each year.

Total number of calves (TC)

The cumulative number of calves a hind has had (regardless of how long the calves survived) up to and including the current year in the encounter history, for each year.

Proportional age-specific reproductive effort (PARE)

This measure is defined as the proportion of years since sexual maturity in which a hind has reproduced. The proportional age-specific reproductive effort was calculated for each year for each hind using the equation:

PARE

$$= \frac{\text{total number of years in particular status to date}}{\text{current age-2}}$$

We considered three different methods of categorising hinds when calculating PARE:

- m – calves survived their entire first year
- mw – calves died during their first winter of life
- all – all calves born regardless of their fate.

For example, for a 6-year-old hind that has had 3 calves at ages 3, 4 and 5, with one surviving its first year, one dying soon after birth and the third dying in its first winter, the PARE_m, PARE_{mw} and PARE_{all} values would be 0.25, 0.5 and 0.75 respectively. In preliminary analyses we fitted PARE calculated for each hind status and fitted each into separate models to establish which version of the PARE variable should be included in the final model.

Goodness of fit

Mark–recapture models are commonly checked for lack of fit by calculating \hat{c} , by dividing χ^2 measure for lack of fit of the model by the degrees of freedom (Lebreton et al. 1992). However, with complex life history models such as this, \hat{c} can not be calculated when the model includes individual and environmental covariates. Models were therefore checked graphically and then visually for goodness of fit in a similar manner to Catchpole et al. (2000) and Catchpole et al. (2004). In this way, expected values predicted from the model were plotted against “observed” values calculated by replacing environmental covariates with full time dependence.

Results

Recapture

In the work of this paper, recapture probability was not found to be constant (Table 2 and recapture matrix shown in Appendix 1) and approximately equal to unity as it has been in previous work on the Rum red deer population (Catchpole et al. 2004). This is because censuses were taken from different months to previous work, to ensure the months did not coincide with the main mortality, and those chosen have not been censused with varying effort throughout the study. Recapture is based on resightings and so this probability would not be expected to vary with individual or environmental covariates. As recapture can not be kept constant with time, no more information can be gained from further manipulation of the parameter. However, in order to realise the most parsimonious model, these estimates of recapture probability can be grouped into levels of resighting effort. Recapture was primarily grouped using just two (high and low resighting effort) measures of effort and then by using three recapture parameters (high, low and very low resighting effort) (Table 2). Using three recapture parameters sufficiently lowered the AIC, by using: 20 normal years (recapture probability between 0.955 and 1), 7 low recapture years (recapture probability between 0.884 and 0.955) and one single very low year where recapture = 0.153. This year of very low recapture is due to partial absence of the field assistant. We consequently modelled recapture probability as a function of recapture effort type. Mark–recapture analysis is such that these differences can be modelled to ensure that estimates for survival do not vary due to censusing effort. This grouping of recapture probabilities does not affect estimates of survival and makes little difference to the AIC of the model (Table 2) and so for the purpose of this model, recapture was kept as general as possible and so remained fully time-varying.

Survival

Model selection for estimating survival probabilities started from the most general model with fully time-varying recapture including all individual and environ-

Table 2. Deviance, AIC and Δ AIC of the model using either three recapture parameters (high, low and very low), two recapture parameters (high and low), constant recapture or a fully time-dependent recapture structure, models listed in order of ascending AIC. See Appendix 1 for the number of sightings and resightings in each year.

Model	AIC	Δ AIC	No. parameters	Deviance
With 3 recapture parameters	2975.13	0	16	2942.96
Recapture fully time-dependent	2977.31	2.179	40	2896.3
With 2 recapture parameters	3018.15	43.02	15	2988
Recapture constant	3520.51	545.4	14	3492.38

Table 3. Deviance, AIC and Δ AIC of the model for survival (with recapture as fully time-varying), comparing the use of two environmental and five individual covariates and age groups (a). Model 5 is the most general model.

Model	AIC	Δ AIC	No. parameters	Deviance
1 backwards elimination of insignificant terms from model 5	2979.4	0.00	41	2896.29
2 environmental+individual+a	2989.6	10.21	46	2896.23
3 environmental \times individual+a	2995.3	15.94	54	2885.45
4 environmental+individual \times a	3003.6	24.23	65	2870.91
5 environmental \times individual \times a	3005.2	25.87	81	2839.08
6 individual+a	3057.0	77.65	43	2969.83
7 individual \times a	3064.4	85.06	53	2956.64
8 environmental+a	3075.0	95.69	36	3002.22
9 environmental \times a	3080.9	101.57	45	2989.64
10 a	3172.7	193.30	32	3108.01
11 constant survival	3346.6	367.22	29	3288.04

mental covariates with their second order interactions (model 5 in Table 3). Model 5 was then simplified by progressively removing insignificant terms (model 1 in Table 3). Examples of models tested are shown in Table 3. Not all models are shown here as term elimination involved many steps, but the information in Table 3 shows the importance of including both individual and environmental covariates. Correlation between covariates was checked before and after model selection. Before model selection, the correlation between environmental covariates was 0.056, and between individual covariates was 0.891. After model selection the highest correlation between environmental covariates remained the same and between individual covariates was reduced to 0.599. Correlation is common in complex life history models, but should not affect model selection and in this case is not at a high enough level to affect the estimates from the model after selection.

The most parsimonious model for survival was model 1 in Table 3 (with model notation as in Table 1):

$$\phi_{\text{calves}}(\text{R} + \text{NAO} \times \text{d}), \phi_{\text{yearlings}}(\text{NAO} \times \text{d}),$$

$$\phi_{\text{adults}}(\text{NAO} \times \text{d} + \text{PARE} \times \text{A}),$$

$$\phi_{\text{seniors}}(\text{NAO} \times \text{d} + \text{PARE} + \text{CP} + \text{A})$$

Table 4 shows the coefficients and standard errors for the main effects and interactions used in this model.

Environmental covariates

Our results show that a combination of high population density and positive NAO reduces survival probability. The environmental covariates were found to be best fitted with the same coefficient to all age groups with an interaction between NAO and density. This indicates that a combination of high positive NAO and high population density results in much lower survival (Table 4). High positive NAO is an indication of warmer yet stormier and wetter winters in northwest Scotland.

Individual covariates

Birth weight

Residual birth weight only affected the survival probability of calves (Table 4).

Senescent declines in survival

Age was included as a continuous variable to explain decreased survival in the adult and senior age classes (coefficient = -0.380 , SE = 0.045). This was best fitted to both the adult and the senior age group with the same coefficient, (Table 4). Despite age being fitted linearly across both the adult and senior age groups, on the logit scale this translates to survival rates decreasing slowly for individuals in the adult age group and accelerating beyond age 8.

Reproductive covariates

A combination of all three reproductive covariates (CP, TC and PARE) originally provided the best fit for the data (Table 5). However, the calculation of PARE is such that $\text{TC} \approx \text{PARE} \times \text{age}$, without considering the years as immature. Therefore, TC in the model with all three reproductive covariates can be replaced by an interaction between PARE and age. These two models are equivalent as a model with age, TC and PARE as additive effects would have the same number of para-

Table 4. Coefficients and standard errors (in brackets) of the final model, including reproductive covariates.

Effect	Final model	
	age group	estimate
NAO	all	0.651 (0.303)
Density	all	-0.041 (0.215)
NAO \times density	all	-0.241 (0.089)
Birth weight	calves	0.382 (0.076)
Age	adults and seniors	-0.380 (0.045)
CP	seniors	-1.335 (0.323)
PARE	adults	-2.674 (0.489)
	seniors	2.314 (0.851)
PARE \times age	adults	1.066 (0.178)

Table 5. Deviance, AIC and Δ AIC of model subsets containing different combinations of the reproductive covariates; total number of calves (TC), calving in the previous year (CP) and proportional age-specific reproductive effort (PARE) with the continuous age (A) covariate. Models are listed in order of ascending AIC.

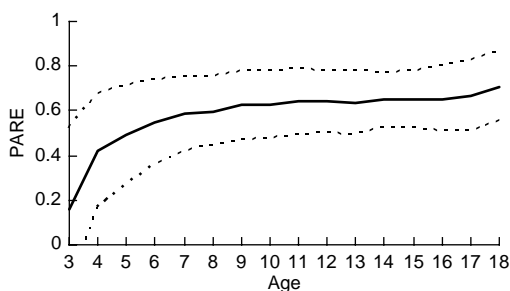
Model	Individual covariate structure		AIC	Δ AIC	No. parameters	Deviance
	adults	seniors				
PARE and CP	PARE \times A	PARE + A	2975.12	0	16	2942.95
TC, PARE and CP	PARE + TC + A	PARE + CP + A	2975.13	0.01	16	2942.96
TC and CP	TC + CP	TC + CP + A	2978.45	3.33	14	2950.32
CP	CP + A	CP + A	2987.83	12.71	14	2959.70
TC and PARE	TC + PARE + A	A	2991.99	16.87	14	2963.86
PARE	PARE + A	A	3000.12	25.00	14	2971.99
No reproductive covariates	A	A	3004.50	29.38	12	2980.41
TC		TC + A	3004.99	29.87	13	2978.88

meters as a model with PARE and age as an interaction. Table 5 shows the differences in the AIC values and deviance of models with different combinations of reproductive covariates. The number of parameters does not necessarily vary as might initially be expected, because in order to get the optimal model for each combination, different covariate combinations have been fitted to different age groups. If only using one reproductive covariate in the model, the lowest AIC value is with CP (Table 5), although the fit of the model is improved significantly using the lifetime measures of reproductive effort from using only recent reproductive history (Δ AIC = 12.702). TC explains least additional deviance; the model with no reproductive covariates is not improved by just adding TC (AIC = 29.864 and 29.374 respectively) and TC is not required in the final model as it is replaced by an interaction between PARE and age.

We now provide further analyses of these effects.

Calving in previous year (CP)

CP was only significant in the senior age group where recent reproduction was shown to be associated with a decrease in survival (coefficient = -1.335, SE = 0.323) (Table 4).



Lifetime reproductive effort measures

The mean of TC increases constantly with age (Fig. 1), whereas PARE increases rapidly with age within the adult age group, and then remains relatively constant with increasing age. Both PARE and TC show a pronounced increase at age 18. The standard deviation of TC also increases gradually with age, whereas the standard deviation of PARE decreases in the adult age group and then remains at this relatively constant level throughout the senior age group.

Initially, the three levels of PARE (all, mw and m) were fitted to each of the reproductive age groups (adult and senior). Raising a calf to any age (PARE_{all}) was shown to explain the greatest deviance, although the difference in AIC was very small between this and the other levels (Δ AIC = 0.945). As the number of parameters are equal between models, PARE_{all} is taken as the best measure. The coefficients for the adult age group for each level of PARE were also very similar.

PARE was fitted to both the adult and senior age groups. In the senior age group, survival increases with increasing PARE (coefficient = 2.314, SE = 0.851), showing that a frequently reproducing individual would have higher survival than a less frequently reproducing individual. In the adult age group TC was originally found to improve the model (Table 4) and survival was shown to increase with increasing number of calves (coefficient = 1.066, SE = 0.178). However, as age was present in the adult model, TC could be replaced by

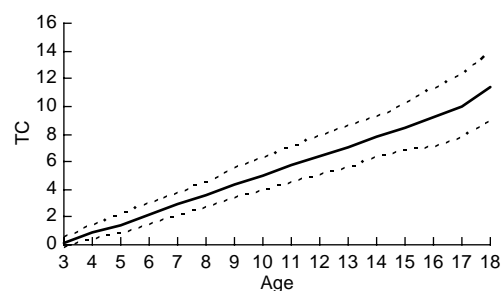


Fig. 1. Mean (bold) and 1 SD \pm mean (broken line) of total number of calves (TC) and proportional age-specific reproductive effort (PARE) with age.

including an interaction between PARE and age, as these are approximately equivalent. This interaction shows that if PARE is initially high at age 3, and therefore the individual calved in that year, survival is low and then increases with age. Alternatively with low PARE, survival is initially high at age 3 before decreasing with age. Older individuals in the adult age class have higher survival with high PARE than individuals with lower PARE (Fig. 2); a similar effect is found within the senior age group.

Goodness of fit

Goodness of fit of the model for survival was examined graphically as in Catchpole et al. (2004). Proxy observed values were calculated by replacing environmental variation in the model with full time-dependence (Fig. 3); this shows the model fits reasonably well. The final model was fitted again, without including long-term reproductive covariates, to compare the fit of the model without these measures. The correlation between the “observed” and expected values decreased when cumulative reproduction was not included in the model ($r^2 = 0.632$, with long term reproductive measures and $r^2 = 0.609$, without long term reproductive measures). The difference between these values is relatively small and most correlation is accounted for by the environmental and recent reproduction covariates. Annual survival estimates from the full model are also compared against a fully time dependent model (Fig. 4). The time-dependent plot for adults shows there is little variation in survival in the

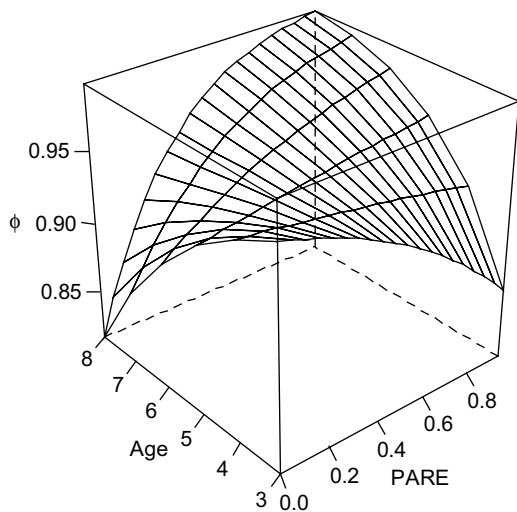


Fig. 2. Plot of survival estimates for adults from $\phi_{\text{adults}}(\text{PARE} \times \text{Age} + \text{NAO} \times \text{Age})$ with respect to PARE and age (A), holding NAO and density (d) constant at NAO = 1 and d = 300 to illustrate the effect of the interaction between PARE and age. The plot shows that with young individuals, PARE is negatively correlated with survival and with older individuals PARE is positively correlated with survival.

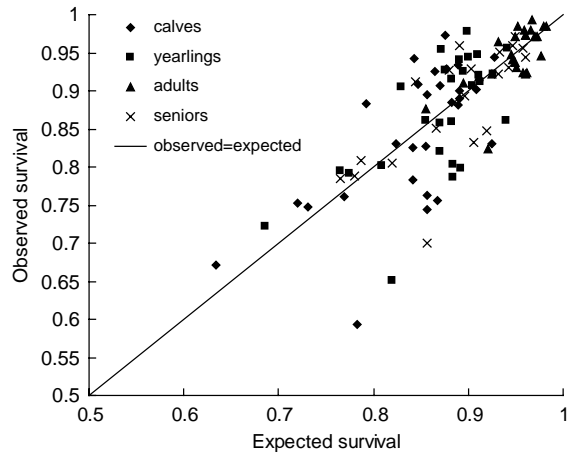


Fig. 3. Goodness of fit of final model, observed survival calculated using a fully time dependent model and expected survival using the final model.

adult age class, but this small amount of variation seems to be explained reasonably well using a combination of environmental and lifetime reproductive covariates.

Discussion

We have used measures of both recent and longer-term reproductive effort as time varying individual covariates alongside environmental covariates in mark–recapture analysis to model survival of female red deer. Environmental covariates and recent reproduction explained a large amount of variance in survival, but further improvement to the fit of the model has been achieved by adding measures of previous reproductive effort. There was little difference in the structure of the models presented here and a previous survival model for female red deer (Catchpole et al. 2004), despite the previous model including data on all months rather than just those between calving and the rut. The most notable differences were that we reported an interaction between NAO and density; we also found that recent reproduction only influenced survival in the senior age group instead of both adult and senior age groups and that age influenced both age groups instead of just the seniors. The addition of cumulative reproductive effort would be expected to affect the inclusion of recent reproduction and an interaction between PARE and age was found to explain more variation in survival with reproductive effort than recent reproduction in the adult age group. Similarly with age, survival was found to vary in the adult age group with age due to the inclusion of PARE. Despite the addition of longer term reproductive covariates and the use of different census months, the coefficients for the corresponding covariates in this and the previous model (Catchpole et al. 2004) agreed reasonably well with each other.

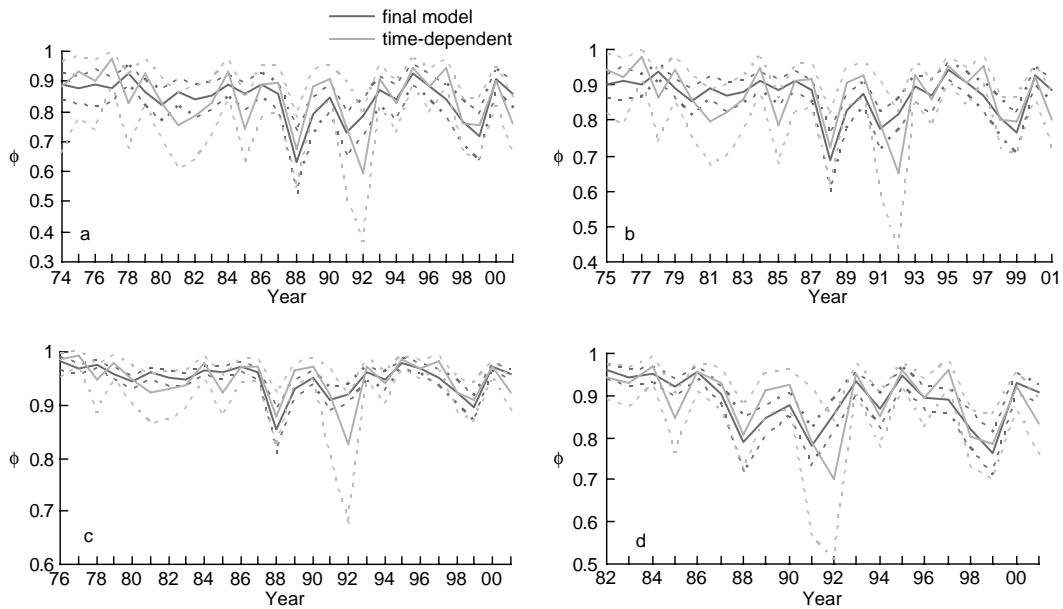


Fig. 4. Comparing model fit of the final model for survival to a fully time dependent model for calves (a), yearlings (b), adults (c) and seniors (d). Solid lines show estimate and broken lines show upper and lower 95% confidence intervals.

Reproducing in the previous year has a detrimental effect on survival, as shown previously by Clutton-Brock et al. (1983) and Catchpole et al. (2004) and longer-term reproductive effort varies in its effect on survival with age. The proportion of possible times an individual has calved (PARE) was used as a measure of longer-term reproductive effort. High PARE in the senior age group was found to be associated with high survival. In the adult age group PARE and age interacted, illustrating that PARE affects survival in a different manner with age within the adult age group. With 3-year-old individuals, those with a high PARE suffer higher mortality than those with low PARE and this effect is reversed within the adult category. The same pattern was not evident in the senior age category. At age 3 PARE is effectively a measure of recent reproduction, therefore survival is lower when individuals calved in the previous year. Also, individuals with an early age of primiparity have a PARE of 1 in this year, but would have a high mortality rate, as previously shown by Clutton-Brock et al. (1983), therefore high PARE negatively affects survival in this age group, as would be expected. This effect does decrease rapidly with age; at age 4, survival is similar between individuals with PARE of 1 or 0 and at age 5, survival is higher in individuals with PARE of 1. Low survival in inexperienced breeders has been found in other species, for example kittiwakes (*Rissa tridactyla*, Cam and Monnat 2000). Here it was suggested that low survival with inexperienced breeders, may be linked to a lower proportion of high quality individuals in the younger age classes (Cam and Monnat 2000). Using all calving events or just considering years when the calf has

been raised to its first year to calculate the proportion of a hind's life spent reproducing, made little difference to the fit of the model for survival. This implies that years when a hind has calved but has not lactated to the calf for a significant length of time does not alter future survival.

The increase in survival with lifetime reproductive effort could be linked to the quality of the individual. For example, an individual of good quality could reproduce more frequently and have a higher survival rate (Clutton-Brock 1985, Yoccoz, et al. 2002). This does not, however, consider the survival of offspring of frequently reproducing hinds. The positive effect of frequent reproduction on survival could be due to some individuals investing little in their calves, resulting in low offspring survival rate and therefore enabling the individual to reproduce more frequently. Previous work has shown that lactation results in higher survival costs than gestation (Clutton-Brock et al. 1989) and so frequently producing calves with low survival and therefore investing little subsequent to birth would not greatly reduce the individual's survival probability. In this dataset, there is an example of a female who survived for 19 years and had 14 offspring in this time, however, only eight of these offspring survived to maturity and only 4 of these reproduced. This individual would have had a high PARE value throughout life and high survival, but with comparatively low reproductive success. The individual would have invested effort in gestation but with little effort in lactation which would have resulted in higher cost. This is not generally the case

with all individuals; a complete range of strategies can be observed with different individuals.

To further explore the effect of reproduction on life history traits, other factors could be considered. Variations in quality of individual has previously been thought to be the cause of not finding costs of reproductive effort (Clutton-Brock and Harvey 1979, Clutton-Brock 1985, Berube et al. 1999, Cam et al. 2002, Yoccoz et al. 2002, Hanssen et al. 2003). A constant measure of quality would be needed to be assigned to each individual to understand fully the effects of lifetime reproductive effort on survival. This could be linked to home range, maternity and paternity, cohort or timing of birth, and addressing this issue is currently work in progress, to both characterise quality of individual and to test if using this in a model of survival would lead to a negative effect of lifetime reproductive effort on survival within "quality" levels. High lifetime reproductive effort could have different implications in terms of survival for poor or good quality individuals, and would enable further insight into life-history strategies. As low quality individuals may invest less than high quality individuals in terms of reproduction, a negative effect of increased reproductive effort still may not be found as individuals could follow an optimum life-history strategy according to their quality (Van Noordwijk and Dejong 1986, Tavecchia, et al. 2005). The finding of a correlation between apparent lifetime reproductive effort in mammals in a long-term study supports previous work mainly on bird populations (Cam et al. 2002, Horak 2003), and the effect could have implications for the population dynamics of the system if some individuals have a disproportionately high genetic representation in future generations due to both longevity and numerous offspring (Bjornstad and Hansen 1994).

Including individual covariates such as the sex of calves, home range and age of primiparity could also improve the fit of the model. In this model all calves in the TC measure are given the same value, but individuals regularly raising a male calf in poor years could pay more of a survival cost. The mother could also be of higher quality than individuals only producing female calves in good years. A further lifetime reproductive effort covariate to consider could be the number of years a hind has bred without a break; as capital breeders utilise energy reserves for reproduction rather than short term energy acquisition, skipping breeding may be necessary to recover condition. Reproducing in several consecutive years may therefore result in lower survival or be an indication of a higher quality individual. An individual may be able to recover fully from previous reproduction by not reproducing in one year, however, without conceiving, a hind may still suffer costs from continuing to lactate to previous offspring, often until the next summer. These factors were not addressed in this analysis as increasing the number of parameters

would make the model overcomplicated and the cumulative effects of reproduction would be more difficult to understand.

A model examining transition probabilities between reproductive status alongside survival probabilities could improve the understanding of the costs of reproductive strategies (Tavecchia et al. 2005), especially as the previous year's reproductive history appears to be the most important parameter in terms of survival. Modelling transitions could also be used to assess the probability of the survival of a calf through its first year of life in relation to the mother's previous reproductive history. These factors could be considered when investigating various life history strategies; however, in this model we were principally concerned with the effects of lifetime reproduction on survival and including extra covariates, states and transitions would greatly increase the number of parameters and the lifetime reproductive costs could therefore be difficult to assess. A model including transition probabilities is currently work in progress. There are various extensions to this work to further understand the effects of various reproductive strategies on survival; however in this model we show that fit of a model is improved by including a measure of cumulative reproductive effort, emphasising the need to account for lifetime reproductive history when estimating the survival probabilities of animals.

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Appendix 1. Recapture matrix – showing the number of individuals originally sighted as calves in each occasion and then their first resighting in subsequent occasions.

Occasion	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Total	
1974	7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	
1975	13	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	
1976	18		16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	
1977	27			25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	
1978	32				28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	
1979	38					34	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	
1980	44						37	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	
1981	48							37	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	
1982	49								41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	
1983	54									48	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	
1984	59										56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	
1985	69											57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57	
1986	64												60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60	
1987	75													66	1	0	1	0	0	0	0	0	0	0	0	0	0	0	68	
1988	76														58	1	1	0	0	0	0	0	0	0	0	0	0	0	60	
1989	74															65	0	0	1	0	0	0	0	0	0	0	0	0	66	
1990	82																76	0	0	0	0	0	0	0	0	0	0	0	76	
1991	97																	10	48	0	0	0	0	0	0	0	0	0	58	
1992	11																		9	0	0	0	0	0	0	0	0	0	9	
1993	66																			61	1	0	0	0	0	0	0	0	62	
1994	78																				67	0	0	0	0	0	0	0	67	
1995	82																					78	0	0	0	0	0	0	78	
1996	89																						70	8	0	0	0	0	78	
1997	80																								79	0	0	0	79	
1998	105																									87	0	0	87	
1999	99																										74	2	1	77
2000	88																											79	0	79
2001	95																												79	79