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updated population assessment from
photo-id collected at Peninsula Valdez,
Argentina

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ABSTRACT

Photo-id data collected during 1970-2012 on southern right whales (*Eubalaena australis*) in their winter calving grounds at Península Valdéz, Argentina were analyzed using an updated version of the stage structured model, that allows for birth intervals to depend on survival or mortality of the previous calf. The best-fitting model using the AIC criterion contained heterogeneity in capture probabilities between years, life stages and individuals, in addition to annual variability in the calf mortality rate and in the proportion of mothers recorded in association with their calves. The result show that almost all mothers of surviving calves take a resting year before getting pregnant again, whereas only about 40% of mothers who lose their calf take a resting year before getting pregnant again. Following a resting year, the pregnancy rate is over 90%. The calf mortality rate shows substantial variation over time around a median level of ~18%, with no overall upward or downward trend. The proportion of non-surviving calves that are still with the mother when she is sampled also varies over time, with an upward trend. Consequently, the model predicts a steep increase in observable calf mortality since 2000, despite the fact that the population calf mortality rate is not estimated to be higher than in previous decades. The steep rise in observable calf mortality since 2000 is consistent with the trend in recorded strandings in the gulfs of Nuevo and San José during this period. No change in the population growth rate of 6.5 ± 0.2 % p.a. is detected yet, but it is important that recent data be processed and that the population continue to be monitored in the coming years.

INTRODUCTION

Photo-id data have been collected each winter in the southern right whale (*Eubalaena australis*) calving grounds at Península Valdéz, Argentina from 1970 to the present. The nature of the data and collection method were described by Payne *et al.* (1990) and have remained broadly similar (Rowntree *et al.* 2001).

An inter-birth interval model was developed to analyze the data by Payne *et al.* (1990) and further developed by Cooke *et al.* (2001). The model was cast in a transition probability matrix framework by Cooke *et al.* (2003) and extended to allow for random yearly variation in transition parameters between stages. They found significant inter-annual variation in the relative frequency of 3- and 5-year birth intervals. They attributed the 5-year intervals to pregnancy termination and/or cryptic calf loss. Leaper *et al.* (2006) found that the variation was correlated with the El Niño-Southern Ocean Oscillation and also correlated with reproductive success in fur seals and Gentoo penguins at South Georgia, which is known to be a feeding area for at least part of this right whale population. An interim updated analysis using data through 2010 was provided by Cooke (2013).

Since 2000, two new trends have emerged. The proportion of two-year calving intervals, which before 2000 had been only rarely observed, increased. Also, an increasing number of stranded dead calves have been observed in the Golfo Nuevo and Golfo San José (Rowntree *et al.* 2013). So far, no unambiguous cause of the increased rate of stranding of calves has been identified. It has been

suspected that the increase in observed calf mortality is related to the increase in two-year calving intervals, on the grounds that a mother who is spared most of the energy of lactation due to the death of the calf is able to bear the next calf after a shorter interval.

In this analysis, the population model is developed further to allow the birth interval to depend on survival or mortality of the previous calf. The aim is to use the model to help interpret the apparent recent changes in the demography.

MATERIAL AND METHODS

Input data

The data are from the winter seasons for the years 1971-2012. In these years a total of 3,034 individuals were identified and catalogued, of which 1,059 were observed at least once with a calf.

For the purpose of this analysis, the data were summarized as annual sighting histories of identified individuals. Each annual sighting of an individual was classified into one of three categories: (i) mothers (i.e. accompanied by a calf in at least one sighting in the season, and regardless of whether the calf itself was catalogued or not); (ii) calves; and (iii) all others. There were a total of 6,585 annual sightings of catalogued individuals, including 2,402 mothers with accompanying calves.

Many calves lack distinguishing marks, or may lose them subsequently: only for 536 of the 2,402 observed mother-calf pairs was the calf also catalogued. A further 140 lone calves were catalogued.

Model

Demography

The stage-structured model of Cooke et al (2013) is extended here to allow the subsequent reproductive cycle of a mother to depend on the fate of the last calf. For this purpose, the calf stage is divided into two stages: “sickly calf” and “healthy calf”. “Sickly calves” are those which are doomed to die. The distinction between sickly and healthy calves is internal to the model and is not necessarily observable in the field before a calf dies. The “mother stage” is divided into two: “successful mothers” (of healthy calves) and “unsuccessful mothers” (of sickly calves). Successful and unsuccessful mothers are not observationally distinguishable, but a successful mother is, other things being equal, more likely than an unsuccessful one to be recorded in the field as a mother (i.e. associated with a calf), by virtue of being associated with its calf for longer.

The stage-structured model is illustrated in Fig. 1. A female is subadult until its first pregnancy. The age at first pregnancy for females is assumed to range from 5 to 13 years, such that there are no subadult females beyond 12 years of age. There is little point in modeling the male population in much detail: males are assumed to be adult from age 8.

The model has no explicit stage for pregnancies that do not reach full term. Pregnancies that terminate early enough for the mother to become pregnant again one year after the start of the failed pregnancy, are subsumed into the “Resting” stage. Pregnancies which reach a later stage such that the mother must miss a year until the next pregnancy, are subsumed into the “Unsuccessful mothers” stage. Consequently, the “sickly calf” stage could include some foetuses that are not born alive.

The probability parameters of the stage-structured model, that are to be estimated by fitting the model to the data, are listed in Table 1. Each “parameter” is actually a set of parameters, that may depend on the covariates listed. Where covariates are fitted, the models for the probability are linear on the log-odds scale, and the covariate coefficients are estimated as random effects.

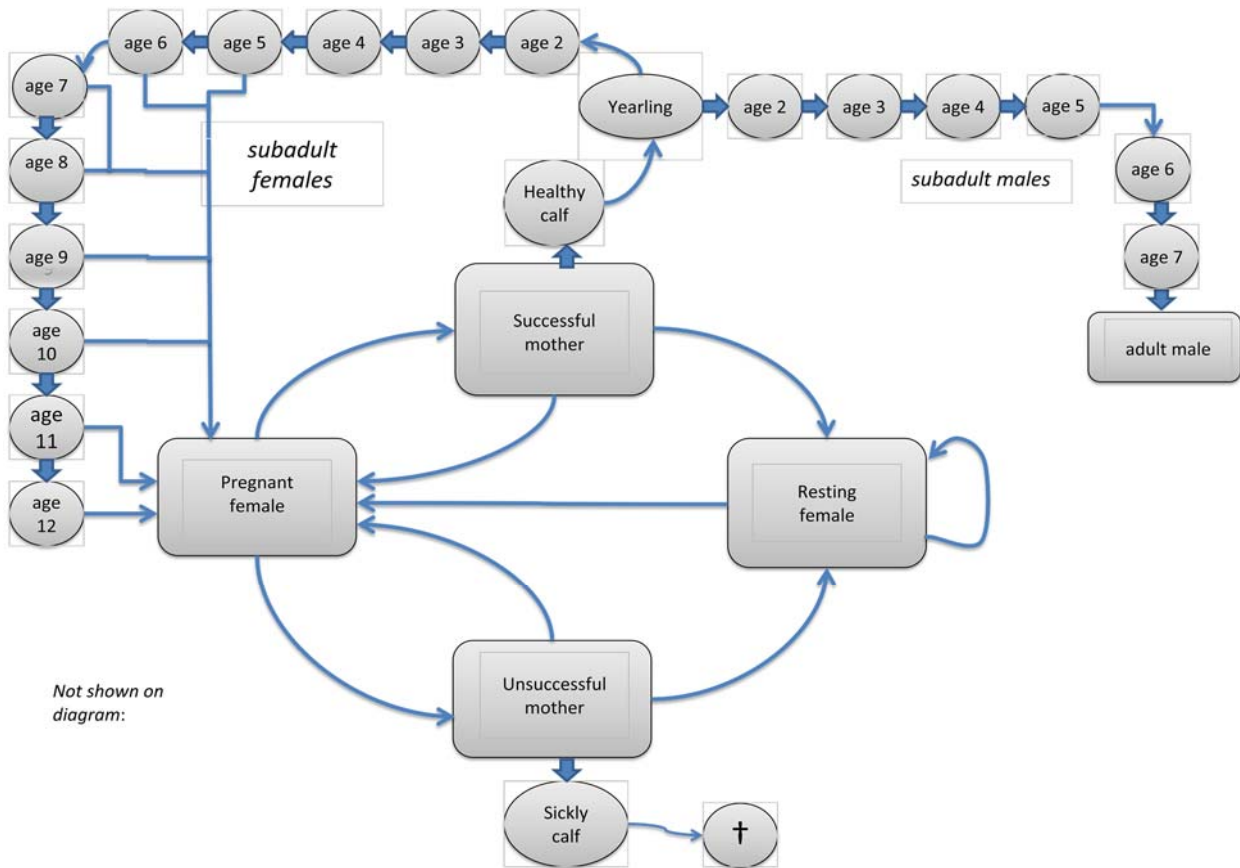


Fig. 1. Stage-structured population model used for the analysis.

The probability of becoming pregnant for the first time is assumed to be age-dependent. Subsequently, the probability of becoming pregnant is stage-dependent (i.e. can differ between successful mothers, unsuccessful mothers and resting females), and optionally can vary across years and between individuals.

The transition probability from “Pregnant” to “Successful mother” represents the calf survival probability. A single annual mortality parameter is estimated for all non-calves.

Individual variation in pregnancy rates (optional) is modelled by dividing the population into three productivity classes, where each whale has an equal prior probability of being assigned to each class, but the posterior probabilities are influenced by the recorded calving history of the whale.

Sampling model

The probability that a whale is recorded in each year can depend on its stage. For this purpose, stages are grouped as follows, where group-specific annual sampling probabilities are to be estimated:

- mothers of the year
- pregnant females
- resting females
- calves
- yearlings
- subadults
- adult males

Individual variation in sampling probability (optional) is modelled by dividing the population into three availability classes, where each whale has an equal prior probability of being assigned to each class, but the posterior probabilities are influenced by the sampling history of the whale.

In the case of mothers, there is an additional “dissociation” parameter that determines the probability that a mother is recorded without its calf. The dissociation parameter can differ between successful and unsuccessful mothers and optionally vary over time. In the case of unsuccessful mothers, the dissociation probability will include the probability that the calf was lost before the mother was recorded. In all cases the dissociation parameter will also include the probability that the calf was actually present when the mother was seen, but was overlooked or could not be assigned uniquely to that mother.

Table 1. Model parameters and covariates

Process	Covariates (<i>optional covariates in italics</i>)
Calf survival	<i>Year</i>
Non-calf mortality	
1 st pregnancy	<i>Age</i>
Pregnancy (2 nd and later)	<i>Stage, Year, Productivity class</i>
Sampling	<i>Year, Stage group, Availability class</i>
Dissociation	<i>Stage, Year</i>

Fitting the model

The annual stage transition model and the observation model were used to compute the probability of each observed sighting history. The individual history log-likelihoods were summed to compute a total log-likelihood. Where probability parameters are dependent on covariates, a linear model was assumed for the log-odds ratio, with the covariates modelled as random effects. Random-effect variances were estimated by REML.

Several models were fitted with different combinations of covariates as listed in Table 2 [*at end of document*]. For each model, the REML log-likelihood, the effective number of parameters, and the AIC was computed.

RESULTS AND DISCUSSION

With respect to sampling probability, all the following factors substantially improved the fit and were retained in subsequent fits: year effects ($\Delta AIC = -1\ 886$); stage effects ($\Delta AIC = -4\ 106$); stage \times year interactions ($\Delta AIC = -306$); and individual availability effects ($\Delta AIC = -83$) (models A through E).

Allowing annual variation in calf survival (model F) further substantially improved the fit ($\Delta AIC = -26.8$) and was retained.

Allowing annual variation in pregnancy rates (model G) did not improve the fit ($\Delta AIC = +34.3$). Allowing individual variation in pregnancy rates (model H) did not materially improve the fit ($\Delta AIC = -0.3$). These two factors were not retained in the preferred model.

Allowing for annual variation in the separation probability for calves of unsuccessful mothers (model J) also improved the fit ($\Delta AIC = -8.5$).

Model J was selected as the preferred model. It includes year-stage interaction and individual effects in sampling probability; annual variation in calf survival; no annual or individual variation in pregnancy rates; and annual variation in the separation between mothers and calves.

Estimates of selected parameters of interest from the preferred model are listed in Table 3. The estimated trajectory of population size is shown in Fig. 2.

Table 3. Estimates of selected parameters of interest from the preferred model

Parameter	Estimate	SE
Calf mortality rate (median) /yr	0.179	0.027
Calf mortality rate: SD of annual variation	0.097	0.019
Non-calf mortality rate	0.026	0.003
Mean age at first pregnancy	7.58	0.18
Pregnancy rates:		
- following a surviving calf	0.023	0.009
- following a lost calf	0.596	0.082
- following a resting year	0.911	0.010
Median mother-calf dissociation		
- unsuccessful mothers (calf dies)	0.490	0.072
- successful mothers (calf lives)	0.925	0.016
Annual rates of increase (aged 1+)		
1980-1990	0.064	0.002
1990-2000	0.067	0.002
2000-2010	0.065	0.002

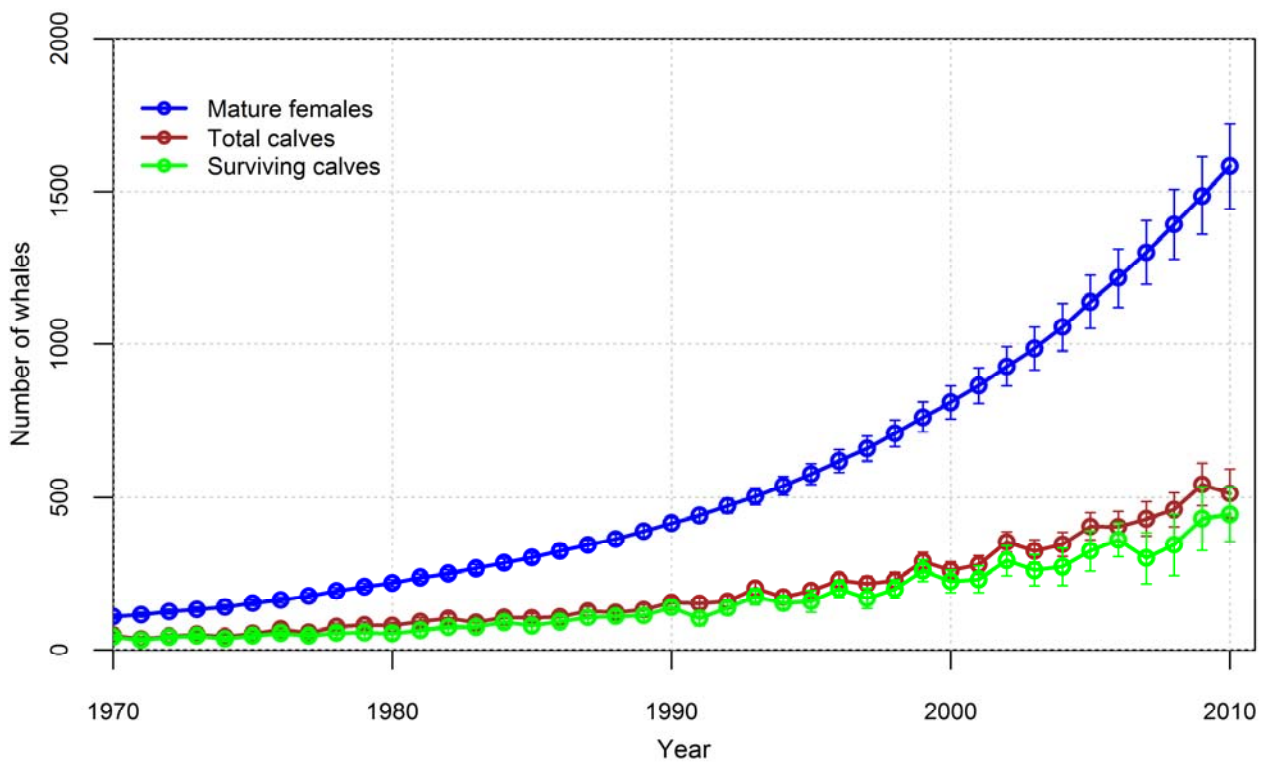


Fig. 2. Population trajectory estimate from preferred model, 1970-2010 (± 2 SE).

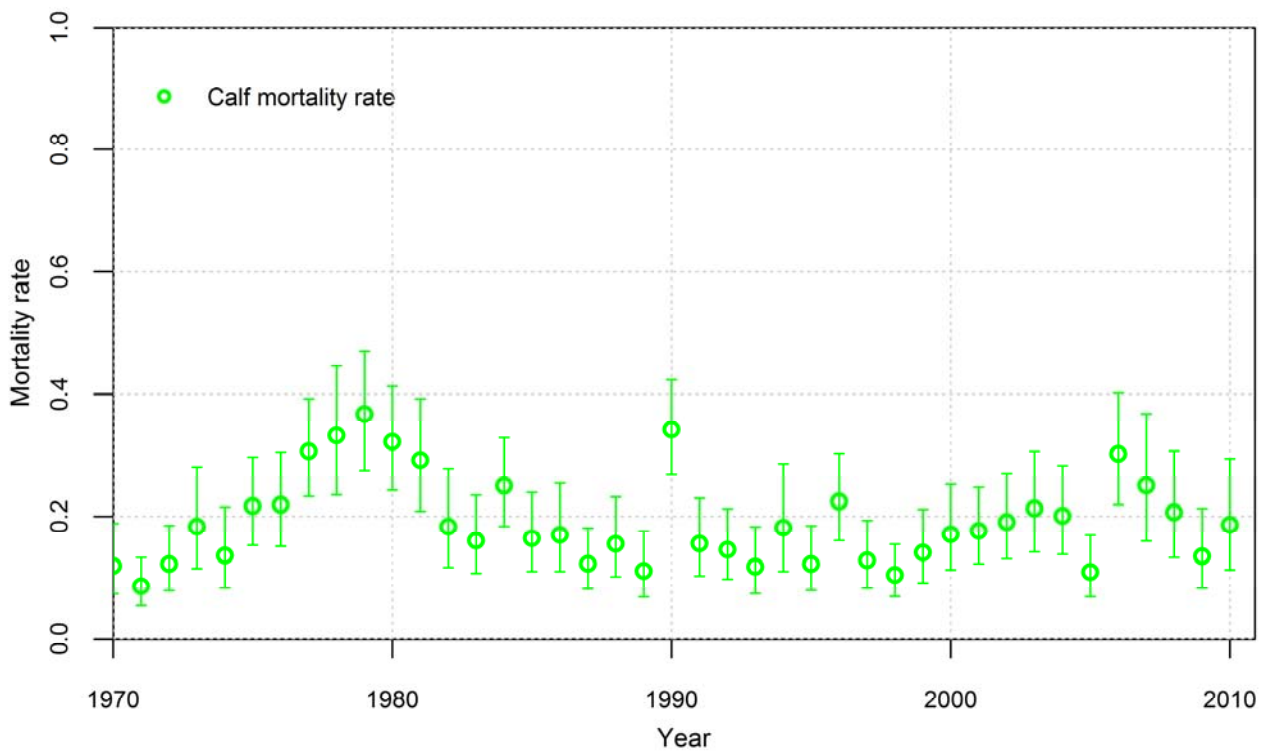


Fig. 3. Estimates of annual calf mortality rates, 1970-2010 (± 1 SE).

The estimated median calf mortality rate is 0.18 (SE 0.03) but there is substantial annual fluctuation with an inter-annual SD of 0.10 and yearly estimates ranging from 0.08 to 0.37 (Fig. 3), but no clear upward or downward trend over time.

Pregnancy rates following a successful calving are low (2% SE 1%) , pregnancy rates following a resting year are high (91% SE 1%), and pregnancy rates following a lost calf are intermediate (60% SE 8%). This means that nearly all mothers take a rest year following a surviving calf, but that only about half or less take a rest year following a lost calf.

Although pregnancy rates by stage do not vary over time in the preferred model, the variation in calf survival induces variation in the population pregnancy rate, because females become pregnant sooner following a lost calf than following a surviving calf. The model therefore predicts that when conditions are poor (low calf survival) population pregnancy will be higher, than when conditions are good (high calf survival). Thus, the effective rate of successful reproduction is predicted to be negatively correlated with pregnancy rates.

The probability of unsuccessful mothers being sampled without their calves is estimated to have decreased over time (Fig. 4). This results in more two-year calving intervals being observed in later years, relative to five-year intervals. Assuming that the decrease is associated with an increased tendency for the unsuccessful mothers to enter the study area before losing their calf, and that calves dying within the study area have a better chance of becoming stranded and found, the change would be predicted to result in increased observed calf mortalities within the study area.

The expected observable mortality predicted by the model can be roughly expressed as the product of the estimated mortality (no. of calves times calf mortality rate) and the estimated proportion of calves that are brought by their mothers into the calving area. The resulting predictions of observable calf mortality are shown in Fig. 5. Also shown for comparison are the recorded calf

mortalities listed by Rowntree et al. (2013). Both the predicted and observed mortalities show a very marked increase since 2000.

The observed calf mortalities were almost entirely in the Golfo Nuevo and the Golfo San José. Calf mortality occurring around the outer cape or offshore would presumably be less likely to result in strandings because of currents and the nature of the coastline. Rowntree et al. (2001) report a shift in distribution of right whales away from the outer coast and into the gulfs during the period 1971-97. The stranding records in the gulfs may have been incomplete prior to 1994, when the first stranding network was established.

The recent sharp rise in observed calf mortalities is broadly consistent with the model predictions and thus is consistent with a population calf mortality rate that is well within the historical range of variation. This interpretation of the data is still tentative, and further years of data will be needed to confirm this conclusion. Data for 2013-14 are being processed.

The results of this analysis show, as yet, no evidence of a slowdown in population growth rate (Table 3), but this does not rule out a slowdown in recent years not yet detectable from these data. Continued monitoring of the population remains important.

Finally it is instructive to compare the findings of this analysis with the results of Crespo *et al.* (2015) obtained from direct estimation of abundance from airborne and boat surveys. The two methods of monitoring (direct surveys and photo-id) complement each other. Photo-id provides more information on population parameters and processes, but only in retrospect: The demographic parameters for a given year can only be estimated with at least 2-3 subsequent years of data, whereas direct surveys can provide for monitoring in real time.

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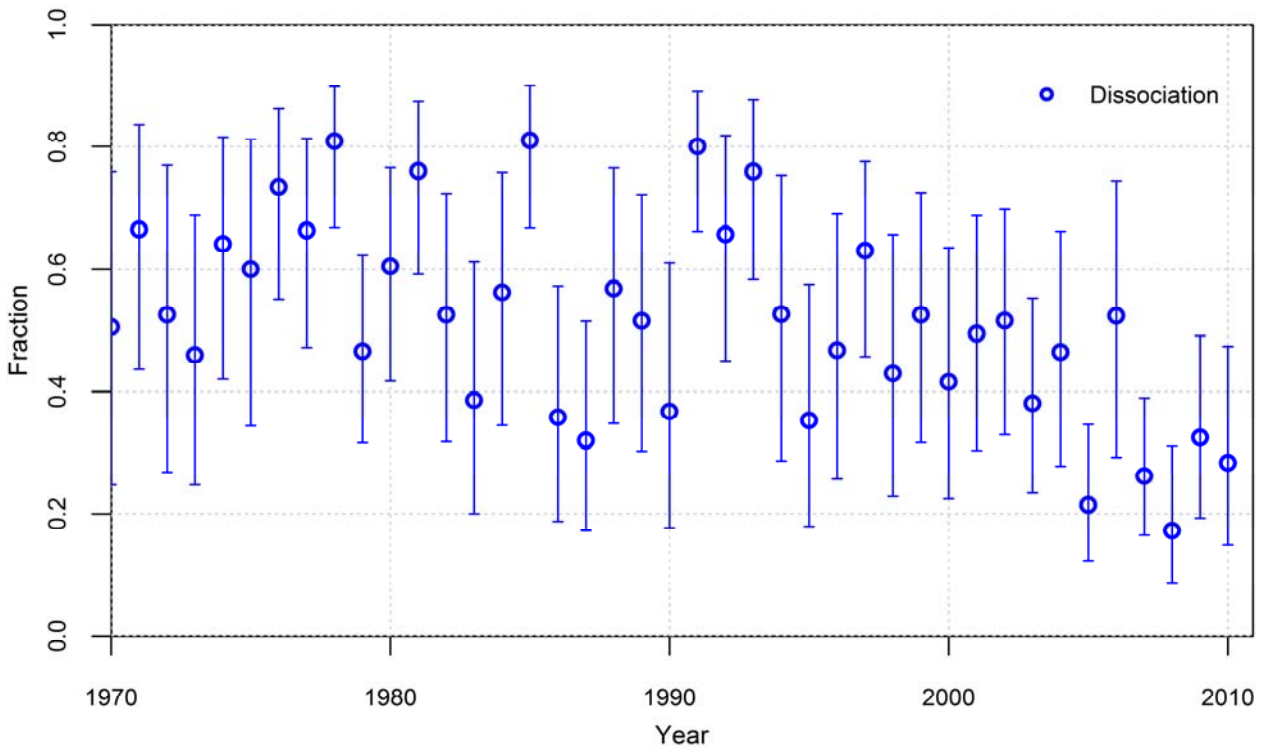


Fig. 4. Estimates of dissociation rate (fraction of unsuccessful mothers observed without calf in the study area).

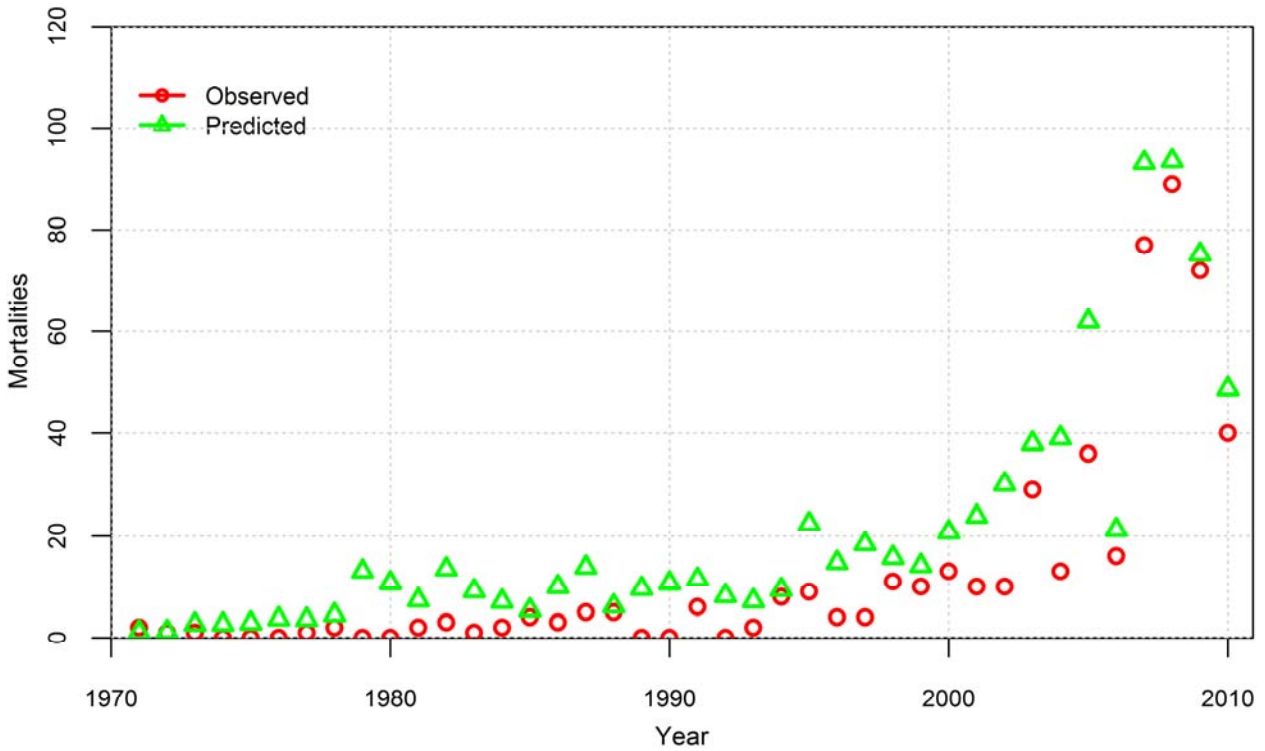



Fig. 5. Observed calf mortalities (Rowtree et al. 2013) and “predictions of observable calf mortalities” from the preferred model 1971-2010.

Table 2. Factors/Terms included in each model

Factor/Term	Case/Model								
	A	B	C	D	E	F	G	H	I
<i>Sampling probability</i>									
Year		•	•	•	•	•	•	•	•
Stage			•	•	•	•	•	•	•
Stage × Year				•	•	•	•	•	•
Individual availability					•	•	•	•	•
<i>Calf survival</i>									
Year						•	•	•	•
<i>Pregnancy</i>									
Age, Stage	•	•	•	•	•	•	•	•	•
Year							•		
Individual productivity								•	
<i>Mother-calf dissociation</i>									
Year									•
Log-likelihood	-7 769.5	-6 785.1	-4 725.2	-4 437.0	-4 398.9	-4 361.7	-4 349.4	-4 360.8	-4 340.2
Effective parameters	10.7	51.9	58.5	193.8	190.6	214.4	243.7	215.1	231.5
AIC	15 560.4	13 674.2	9 567.3	9 261.6	9 178.9	9 152.0	9 186.4	9 151.7	9 143.5
ΔAIC relative to case		-1 886.2 A	-4 106.8 B	-305.8 C	-82.7 D	-26.8 E	34.3 F	-0.3 F	-8.5 F

 Preferred model (AIC)