Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*)

Alan G. McElligott[1*], Res Altwegg[1] and Thomas J. Hayden[2]

[1]*Zoological Institute, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*
[2]*Mammal Research Group, Department of Zoology, University College Dublin, Belfield, Dublin 4, Republic of Ireland*

Survival and reproduction are key features in the evolution of life-history strategies. In this study, we use capture–mark–resighting and multi-state models to examine survival senescence and reproductive senescence in six successive cohorts of fallow bucks that were studied for 16 years. We found that the overall age-specific survival probabilities of males were highly variable and the best-fitting model revealed that fallow bucks have four life-history stages: yearling, pre-reproductive, prime-age and senescent. Pre-reproductive males (2 and 3 years old) had the highest survival. Survival declined sharply after the age of 9 years, indicating that senescence had begun. When we considered reproducing and non-reproducing males separately, there was no evidence of senescence in the former, and steadily decreasing survival after the onset of social maturity in the latter. Reproduction probability also declined in older males, and thus we provide very strong evidence of senescence. Reproducers had a greater chance of reproducing again in the following year than non-reproducers. Furthermore, there were differences in the survival probabilities, with reproducers consistently surviving better than non-reproducers. In our study population, reproducers allocate more to the effort to reproduce than non-reproducers. Therefore our results indicate the generally higher phenotypic quality of reproducing males. These results, along with earlier studies on the same population, could indicate positive relationships between fitness correlates.

Keywords: Akaike Information Criterion; capture–recapture; MARK program; multi-strata models; reproduction

1. INTRODUCTION

Survival and reproduction probabilities in relation to age and condition are key features in the evolution of life-history strategies (Stearns 1992; McNamara & Houston 1996). Senescence refers to a reduction in either survival or reproduction with increasing age, and life-history models predict its occurrence. Two of the main mechanisms used to explain the evolution of ageing are the 'antagonistic-pleiotropy' and 'mutation-accumulation' theories (Medawar 1952; Williams 1957; Hamilton 1966; Partridge & Barton 1993; Kirkwood & Austad 2000). However, these mechanisms are not considered to be mutually exclusive, and both are thought to contribute to senescence (Zwaan 1999).

Until recently, evidence for senescence in wild living animal populations has been ambiguous because of some important impediments. If mortality rates are high throughout life, the probability of an animal reaching an age at which senescence is apparent is very low (Comfort 1979). Therefore, detecting senescence in long-lived animals requires long-term monitoring of marked individuals in order to accumulate the required data (Newton & Rothery 1997; Loison *et al.* 1999). In addition, there were analytical problems that included, for example, the use of age-specific changes in mortality as a measure of senescence, the inappropriate analysis of life-tables, and the use of maximum lifespan as a measure of longevity. These difficulties have now been overcome with the recent developments in capture–mark–recapture (CMR)/resighting models (Lebreton *et al.* 1992; Gaillard *et al.* 1994; Nichols *et al.* 1997).

Ungulates are ideal study organisms for examining senescence, with some long-term studies already providing evidence for its occurrence (Gaillard *et al.* 1998; Loison *et al.* 1999; Mysterud *et al.* 2001). However, the best evidence of reproductive senescence to date has been for females (Bérubé *et al.* 1999) because age-specific data on reproduction for males is more difficult to obtain. In this paper we examine for the first time, to our knowledge, the relationship between senescence, survival and reproduction in male ungulates. We present the results of a long-term study (16 years) of six successive cohorts of fallow bucks, for which detailed information is available on death records and reproduction (McElligott & Hayden 2000). We use CMR and multi-state models to examine survival and reproduction probabilities and the occurrence of senescence. A high level of variation characterizes the fallow deer both in mating systems and in individual mating strategies within those systems (Moore *et al.* 1995*a*; Thirgood *et al.* 1999). Competition amongst males for access to mating opportunities is intense and the level of sexual size dimorphism is high; mature males weigh on average 110 kg and females weigh on average 45 kg. In addition, successful males allocate more to reproduction than unsuccessful males (McElligott *et al.* 1998, 1999, 2001; McElligott & Hayden 1999).

Specifically, this study aimed to model accurately the overall age-specific survival probabilities of fallow bucks. The fitted models took into account life-history character-

Proc. R. Soc. Lond. B (2002) **269**, 1129–1137
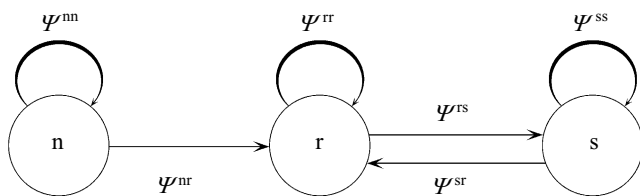DOI 10.1098/rspb.2002.1993

1129

© 2002 The Royal Society

Figure 1. Definition of reproductive state in male fallow deer. The first state describes non-reproducers, n, the second state describes reproducers, r, and the third state describes secondary non-reproducers (individuals that do not reproduce during the current season, but have reproduced previously), s. The arrows show the possible transition probabilities of changing from one state into the other, Ψ. Survival in the three strata is modelled independently, and transition probabilities are conditional on survival in the current year. Therefore, $\Psi^{nn} + \Psi^{nr} = 1$, $\Psi^{rr} + \Psi^{rs} = 1$, $\Psi^{ss} + \Psi^{sr} = 1$, and only three transition probabilities are modelled explicitly.

istics of fallow bucks, such as the age of social maturity, and they allowed us to determine if senescence (in terms of a reduction in survival) occurred, and furthermore, if it started at the onset of social maturity. We then examined the transition probabilities for a change in the reproductive status of socially mature males from one year to the next. Reproductive status was determined by the mating success (yes/no) of males in each year. This allowed us to determine if senescence was manifest in a decline in the reproduction probabilities of males with age. Finally, we tested if socially mature males that reproduced in a given year had different survival probabilities during the following year compared with those that did not reproduce, and at each specific age-class. As reproducing males allocate more in the effort to reproduce, this analysis could indicate if any trade-offs existed. Earlier studies indicated that males consistently failing to reproduce are of lower quality than those that reproduce at least once during their lifetime (McElligott & Hayden 2000). Such heterogeneity can obscure the detection of costs of reproduction (van Noordwijk & de Jong 1986) and complicate patterns in the age-specific survival rates (Vaupel & Yashin 1985). Therefore, we considered three different reproductive states (figure 1). The first state, called non-reproducers, n, accommodates males that do not reproduce in the current season and have never done so before. The second state, called reproducers, r, consists of males that reproduce in the current season. In the third state we consider males that do not reproduce in the current season, but have reproduced earlier in their lives, and call them secondary non-reproducers, s. We examine age-specific survival of males in the three reproductive states separately, and we examine age-specific patterns of the six possible transition probabilities between the reproductive states (summarized in figure 1). To our knowledge, there are no other studies that have used the latest CMR and multi-state models to examine senescence in terms of survival and reproduction in males of a highly polygynous and long-lived mammal.

2. MATERIAL AND METHODS

(a) *Study site, observations and population*

We conducted the study on a herd of European fallow deer in Phoenix Park, Dublin, Ireland (709 ha, 80% pasture, 20%

woodland; 53°22′ N, 6°21′ W). The observation schedule, and data on population size, structure and changes for all years except one, have already been given elsewhere (Moore *et al.* 1995*a*; McElligott *et al.* 1998, 1999, 2001; McElligott & Hayden 2000). In November 2000, there were 152 fawns, 223 females (1 year old or older) and 180 males (1 year old or older). Although the population density has changed during this study, natural food is plentiful and therefore additional supplements are not necessary (Hayden *et al.* 1992). Matings occur from mid-October until the beginning of November each year. The mating success of each male is based on the number of directly observed copulations and in our study population, 84% of females only mate once within the same oestrous cycle (McElligott & Hayden 2000). Therefore, as is the case with red deer (*Cervus elaphus*), directly observed matings are thought to provide a very good estimate of reproductive success (Pemberton *et al.* 1992). We used data from males born from 1984 to 1989 (*n* = 56, 68, 67, 67, 60, 73 respectively; total *n* = 391). In total, 48 (12.3%) of these males gained all the matings (*n* = 1126) recorded for these cohorts.

Fawn ear tagging in June of each year has been carried out since 1971. When observations of this population began in 1988, the males from the 1984 cohort were the oldest at 4 years old. Males younger than 4 years rarely mate (McElligott & Hayden 2000), and therefore we assumed that none of the males in this study had mated prior to 1988. Males that were not tagged were recognized using a combination of coat colour and antler characteristics. The complete population was captured in 1991 and any untagged individuals were tagged and their age was determined (Moore *et al.* 1995*b*). A large number of fawns born in each year (1984–1989) were tagged shortly after birth (*n* = 488). However, it was not possible to catch and tag all the young born. Therefore, the ratio of tagged to untagged fawns was used to estimate the total number born in one year, and then the sex ratio of tagged fawns was used to estimate the total number of males. Before 1988, deer deaths were recorded by the Phoenix Park authorities (T. J. Hayden, unpublished data). Since 1988, male deaths have been recorded using a combination of data on when dead animals were found, and dates when individual males were last observed. The most common cause of death among mature deer is collisions with road vehicles (McElligott & Hayden 2000). However, it is not unusual for humans to be the main source of mortality in an ungulate population (Ericsson *et al.* 2001). Fawns are also predated by foxes (*Vulpes vulpes*) and domestic dogs (*Canis familiaris*), although the level of this predation is difficult to quantify. Deer do not move outside Phoenix Park.

(b) *Statistical analyses*

We used CMR methods to estimate age-specific survival and reproduction probabilities, and to test specific hypotheses of survival patterns (Lebreton *et al.* 1992; Nichols *et al.* 1997). We chose this approach even though our resighting rate was 1 (no marked male was missed one year and subsequently resighted), because it is very flexible and allows a fit to a large variety of models. Data were analysed using the program MARK (White & Burnham 1999). All individuals were followed from birth to death except for four males from the last two cohorts that were still alive at the time of the analysis. Four animals that were removed or died during capture were withdrawn from the sample in the relevant year.

The CMR modelling approach makes the underlying assumptions of equal survival and resighting probabilities across individ-

uals that are normally tested with a goodness-of-fit test for the Cormack–Jolly–Seber model, which is then used as a starting point for fitting to other models (Lebreton *et al.* 1992). This model assumes complete time dependence in survival and resighting rates, but does not take into account age-specific variation. As we expected such variation to be strong in our data it was not a suitable starting model. Therefore, as a starting point, we chose a constant resighting model and a survival model which allowed for full age dependence and for differences between the cohorts, and assessed its goodness of fit using the parametric bootstrap procedure in the program MARK (White & Burnham 1999). Based on 5000 bootstrap replicates, this test suggested an acceptable fit of this general model ($p = 0.17$).

Recently, the CMR approach has been extended to accommodate different strata, with the possibility to estimate not only survival and resighting rates for individuals living in either stratum, but also transition probabilities from one stratum into the others. These models were used to estimate survival and migration probabilities in metapopulations (Spendelow *et al.* 1995), but the strata can also be used to define different states of the individuals, such as reproducer and non-reproducer within one population (Nichols *et al.* 1994). Transition probabilities then refer to the probabilities of changing from one state into the other. We used this class of models to estimate age-specific reproduction probabilities. With this approach, survival and transition probabilities can be separated under the assumption that survival from one time-step to the next only depends on the stratum in which the individual is currently located, and not on the stratum in which it will be next (Nichols *et al.* 1994). In our study, this assumption is reasonable because future reproductive status is unlikely to affect present survival.

We divided the analysis into three steps. In the first step, we focused on estimating survival probabilities for all individuals, irrespective of their reproductive status. The fitted models, age-classes considered and their biological meanings are summarized in table 1. Fawn survival is typically low in ungulates such as fallow deer and therefore most models accounted for this (Gaillard *et al.* 2000*a*). We examined the following models, which correspond to different biological hypotheses. The most restricted model assumed constant survival with age, whereas the most flexible model allowed for full age dependence (models 1 and 2). The other models can be considered special cases of these two models. We examined a three-age-class model considered typical for ungulates (referred to in table 1 as 'Caughley-like' model, after Gaillard *et al.* (2000*a*); models 3 and 4), and a four-age-class model, with the age classes determined by known differences in behaviour and social maturity of males in our study population (McElligott *et al.* 1998, 1999; models 5 and 6). We also considered a possible increase in mortality at social maturity. Ralls *et al.* (1980) highlighted the decrease in survival probability in males of some mammals around the time of the onset of social maturity. This decrease has been reported for a diverse array of male mammals, including fallow deer, but has never been statistically tested with CMR models (see reviews Ralls *et al.* 1980; Clinton & Le Boeuf 1993; Jorgenson *et al.* 1997; McElligott & Hayden 2000). We refer to it as the 'Ralls-like' model or the 'Ralls effect' in table 1 (models 7, 10 and 13). We investigated whether the age-specific pattern of survival differed between the cohorts (model 8). In addition, we considered the hypothesis that survival declined after the age of 4 years according to a Gompertz function (model 11). The Gompertz function has commonly been used to describe senescent decline (Hughes 1995; Loison *et al.* 1999; Pletcher 1999).

Finally, we evaluated the hypotheses that survival declines after the onset of reproduction (here after the age of 4 years) at a constant or an accelerating rate, respectively, as would be expected if the strength of selection decreases with age (models 9 and 12 (Hamilton 1966)).

In the second step of our analysis, we defined reproducing males, r, as those that mated at least once in the current year; non-reproducers, n, as those that did not mate; and secondary non-reproducers, s, as those that did not mate in the current year but have mated earlier in their lives. We assigned the individuals to three strata according to their reproductive status (figure 1). A change in the reproductive status of a male from one year to the next means that it changed its stratum in the analysis. Some transitions are not possible (e.g. from n to s), and were fixed to zero. Starting from the most parsimonious survival model obtained in step one of the analysis, we investigated age-specific patterns in the transition probabilities between the three strata (see table 1 for a summary of the models). In a third step, we investigated whether survival probabilities differed depending on the reproductive status and whether the age-specific pattern in survival differed between the states. We did this by fitting different survival models to the three strata while using the best model for the transition probabilities as obtained in step two.

Model selection was based on the small-sample-size corrected Akaike Information Criterion (AICc) (Lebreton *et al.* 1992; Burnham & Anderson 1998). The AICc is calculated as $-2 \log$ (likelihood) plus twice the number of free parameters of the model, with a correction factor taking into account sample size (Burnham & Anderson 1998, p. 51). The model with the lowest value of AICc is the most parsimonious one, i.e. the one providing the best balance between bias (due to underfitting) and lost precision (due to overfitting; Anderson & Burnham 1999). When two models differ in their AICc values by less than 2 units, the models can be considered competitive. A difference of more than 2 units indicates that one model fits the data considerably more poorly, and a difference of 7 or more units suggests a bad fit of the model with the higher AICc value (Burnham & Anderson 1998). The Akaike weights give the degree to which a particular model is supported by the data, relative to the other models in the set (Burnham & Anderson 1998, p. 123). To test specific hypotheses among nested models, we also used classical likelihood-ratio tests (LRT). Differences in deviance between two nested models follow a χ^2-distribution, with degrees of freedom (d.f.) equal to the difference in number of free parameters.

The data used in this paper differ from an earlier one (McElligott & Hayden 2000) in two important respects. First, we have added the data for an additional complete cohort to our analysis. Second, we have extended our observations to include survival and death records until after the breeding season in 2000 (November). These two measures have had the important effect of increasing our sample size, particularly for animals in the older age classes. This is important for a detailed examination of the occurrence of senescence in a population (Promislow *et al.* 1999).

3. RESULTS

(a) *Overall survival probabilities irrespective of reproductive status*

In a first step, we modelled resighting rates and survival probabilities to search for overall age-specific patterns.

Table 1. *Models fitted to investigate age-specific survival and reproduction patterns.*

model[a]	notation	biological meaning
step 1: survival models		
1	ϕ	no age effects
2	ϕ_{age}	full age dependence
3	$\phi_{0,1,2-9,10+}$	Caughley-like model with three age classes (plus fawns) that differ in survival
4	$\phi_{0,1,2-10+}$	as model 3, without senescence
5	$\phi_{0,1,2-3,4-9,10+}$	four age classes (plus fawns), defined by social maturity that differ in survival
6	$\phi_{0,1,2-3,4-10+}$	as model 5, but no difference between the last two age classes
7	$\phi_{0,1,2-3, 4-9/5,10+}$	Ralls-like model (decrease in survival at intermediate age, here age 5)
8	$\phi_{(0,1,2-3, 4-9/5,10+)*cohort}$	as model 7, allowing for an interaction between age and cohort effects
9	$\phi_{0,1,2-3,4-10+/a1}$	linear[b] relationship between age and survival beyond age 4
10	$\phi_{0,1,2-3,4-10+/5,a1}$	as model 9, but with Ralls effect
11	$\phi_{0,1,2-3,4-10+/Gompertz}$	as model 9, survival following a Gompertz function beyond age 4
12	$\phi_{0,1,2-3,4-10+/a1a2}$	quadratic[b] relationship between age and survival beyond age 4
13	$\phi_{0,1,2-3,4-10+/5, a1a2}$	as model 12, but with Ralls effect
step 2: models for the transition probabilities of changing the reproductive status, conditional on survival to the next time-step		
	$\Psi_{.}$	constant transition probability
	Ψ_{age}	full age dependence
	Ψ_{a1}	linear[b] relationship between age and transition probability
	Ψ_{a1a2}	quadratic[b] relationship between age and transition probability

[a] Survival probability: all survival models accounted for differences between cohorts.
[b] Linear and quadratic on the logit scale. The linear model is mathematically similar to the Gompertz model (Loison *et al.* 1999).

The resighting rate was 1 and thus constant in all models. We did not count it as a parameter. Furthermore, all models accounted for differences in survival between cohorts (LRT $\chi^2 = 16.68$, d.f. = 5, $p = 0.005$).

Table 2 shows a summary over the whole model selection process. There was significant age-specific variation in the survival probabilities (comparing model 1 with model 2, table 2: LRT $\chi^2 = 126.4$, d.f. = 12, $p < 0.0001$) and it was best described by the models with four age classes (figure 2; models 5 and 7; table 2) with or without a drop in survival at the age when the males reach social maturity (Ralls effect). These two models were very similar, and together were 59% supported by the data (combined values for Akaike weights, 0.312 and 0.275), but neither AICc ($\Delta = 0.25$), nor LRT (model 5 versus model 7: LRT $\chi^2 = 2.28$, d.f. = 1, $p = 0.13$) clearly favour one over the other model. The model with three age classes (model 3), considered typical for ungulates (Caughley 1966; Gaillard *et al.* 2000a), was less well supported in our dataset, but still 38 times (ratio of Akaike weights, 0.076/0.002) better than the model with full age dependence (model 2). There was strong evidence for a decline in survival probability beyond age 9 (comparing model 5 with model 6: LRT $\chi^2 = 13.16$, d.f. = 1, $p < 0.001$), indicating that survival senescence had begun (figure 2). Model 10 describing senescence as a linear

decrease in survival after the age of 4 years, and accounting for a Ralls effect (model 10), was 2.3 times less well supported than the model with four age classes (model 7). The remaining models that we tested (4, 8, 9, and 11 to 13) were all poorly supported by the data. All cohorts experienced similar age-specific mortalities as the model allowing for an interaction between cohort and age was poorly supported by the data (model 8).

(b) *Reproduction probabilities*

The probability of becoming a reproducer (Ψ^{nr}, Ψ^{rr}, Ψ^{sr}) was strongly age dependent, regardless of the current reproductive state (figure 3, comparing model 14 with model 21, table 2: LRT $\chi^2 = 101.14$, d.f. = 2, $p < 0.0001$; model 14 with model 22: LRT $\chi^2 = 6.48$, d.f. = 2, $p = 0.04$; and model 14 with model 23: LRT $\chi^2 = 7.50$, d.f. = 2, $p = 0.02$). These transition probabilities were best explained by a quadratic relationship with age for non-reproducers and reproducers, and by a linear decline at older ages for secondary non-reproducers (model 20; figure 3). The probability of reproducing in the following year declined for all groups with old age. However, the probability of reproducing remained highest for reproducers, lower for secondary non-reproducers, and lowest for non-reproducers (figure 3). This is the opposite of

Table 2. Summary of the model selection procedure (resighting rate = constant).

(ϕ^n refers to the survival model for non-reproducers, ϕ^r refers to the survival model for reproducers, and ϕ^s refers to the survival model for secondary non-reproducers. The model with the lowest AICc value is the most parsimonious one among the fitted models and is selected (bold lettering). ΔAICc is the difference in AICc to the selected model. Akaike weights indicate the relative support a particular model has compared with the other models. No. par. is the number of free parameters. Deviance is the difference in -2 log (likelihood) of the current model and -2 log (likelihood) of the saturated model, which is the model with the number of parameters equal to the sample size.)

model		AICc	ΔAICc	Akaike weight	no. par.	deviance
step 1: fitting survival models						
1	ϕ	1445.56	112.25	0.000	6	193.66
2	ϕ_{age}	1343.66	10.36	0.002	18	67.23
3	$\phi_{0,1,2-9,10+}$	1336.14	2.83	0.076	9	78.15
4	$\phi_{0,1,2-10+}$	1350.92	17.61	0.000	8	94.97
5	$\phi_{0,1,2-3,4-9,10+}$	1333.56	0.25	0.275	10	73.54
6	$\phi_{0,1,2-3,4-10+}$	1344.68	11.37	0.001	9	86.70
7	$\boldsymbol{\phi_{0,1,2-3,\ 4-9/5,10+}}$	**1333.31**	**0.00**	**0.312**	**11**	**71.26**
8	$\phi_{(0,1,2-3,\ 4-9/5,10+)*cohort}$	1365.38	32.08	0.000	36	51.15
9	$\phi_{0,1,2-3,4-10+/a1}$	1337.03	3.73	0.048	10	77.02
10	$\phi_{0,1,2-3,4-10+/5,a1}$	1334.99	1.69	0.134	11	72.94
11	$\phi_{0,1,2-3,4-10+/Gompertz}$	1336.04	2.73	0.080	10	76.02
12	$\phi_{0,1,2-3,4-10+/a1a2}$	1337.07	3.76	0.048	11	75.01
13	$\phi_{0,1,2-3,4-10+/5,\ a1a2}$	1338.45	5.15	0.024	12	74.35
step 2: estimating transition probabilities, survival model is $\phi_{1,2-3,4-9/5,10+}$						
14	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1a2}$	1739.64	1.28	0.268	20	360.11
15	$\Psi^{nr}_{age}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1a2}$	1757.24	18.88	0.000	30	356.78
16	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{age}\ \Psi^{sr}_{a1a2}$	1756.64	18.28	0.000	30	356.18
17	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{age}$	1755.70	17.35	0.000	30	355.25
18	$\Psi^{nr}_{a1}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1a2}$	1795.86	57.51	0.000	19	418.40
19	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1}\ \Psi^{sr}_{a1a2}$	1741.81	3.46	0.090	19	364.35
20	$\boldsymbol{\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1}}$	**1738.35**	**0.00**	**0.509**	**19**	**360.90**
21	$\Psi^{nr}_{.}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1a2}$	1836.64	98.28	0.000	18	461.24
22	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{.}\ \Psi^{sr}_{a1a2}$	1741.98	3.62	0.083	18	366.59
23	$\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{.}$	1743.00	4.65	0.050	18	367.61
step 3: different survival models for the three strata (non-reproducers, ϕ^n; reproducers, ϕ^r; and secondary non-reproducers, ϕ^s); transition probabilities are $\Psi^{nr}_{a1a2}\ \Psi^{rr}_{a1a2}\ \Psi^{sr}_{a1}$						
24	$\phi^{n=r=s}_{0,1,2-3,4-9/5,10+}$	1738.35	12.24	0.001	19	360.90
25	$\phi^n_{0,1,2-3,4-9/5,10+}\ \phi^r_{2-3,4-9/5,10+}\ \phi^s_{4-9/5,10+}$	1732.91	6.80	0.012	26	340.88
26	$\phi^n_{0,1,2-3,4-9/5,10+}\ \phi^r_{2-10+}\ \phi^s_{4-9/5,10+}$	1729.21	3.09	0.078	23	343.44
27	$\phi^n_{0,1,2-3,4-9/5,10+}\ \phi^r_{2-10+/a1}\ \phi^s_{4-9/5,10+}$	1731.04	4.92	0.031	24	343.18
28	$\phi^n_{0,1,2-3,4-9/5,10+}\ \phi^r_{2-10+}\ \phi^s_{4-10+}$	1730.89	4.78	0.033	21	349.29
29	$\phi^n_{0,1,2-3,4-9/5,10+}\ \phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1729.15	3.03	0.080	22	345.46
30	$\phi^n_{age}\phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1737.09	10.97	0.002	29	338.74
31	$\phi^n_{0,1,2-3,4-9,10+}\ \phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1729.40	3.29	0.070	21	347.80
32	$\phi^n_{0,1,2-3,4-10+}\ \phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1728.89	2.78	0.091	20	349.36
33	$\phi^n_{0,1,2-3,4-10+/a1}\ \phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1727.77	1.66	0.159	21	346.17
34	$\boldsymbol{\phi^n_{0,1,2-3,4-10+/Gompertz}\ \phi^r_{2-10+}\ \phi^s_{Gompertz}}$	**1726.12**	**0.00**	**0.364**	**21**	**344.51**
35	$\phi^n_{0,1,2-3,4-10+/a1a2}\ \phi^r_{2-10+}\ \phi^s_{4-10+/a1}$	1729.14	3.03	0.080	22	345.46

what would be expected if current reproduction led to a reduction in future reproductive output.

(c) State-specific survival probabilities

The aim of this part of the analysis was to investigate whether the age-specific survival patterns depended on the reproductive state of the individuals. Overall, reproducers survived better than non-reproducers and secondary non-reproducers (model 24 versus model 25, table 2: LRT χ^2 = 20.02, d.f. = 7, p = 0.006; figure 4). Survival clearly declined at old age for non-reproducers and secondary non-reproducers, which resulted in a good fit of the models including some form of senescence (models 33, 34; table 2) compared with the models without senescence (models 28, 32). The AICc-selected best models describe senescence as a steady decrease after the age of 3 years, either linear (on the logit scale, model 33) or following a Gompertz curve (model 34). The Akaike weights show that the Gompertz model was twice as well supported as the linear model. We found no evidence for senescence among reproducers. All models assuming some form of senescence in this group were badly supported by the data (models 27, 25, ΔAICc > 4). There was no evidence of a lower survival at the onset of social maturity, as no model accounting for a Ralls effect in any group was well supported by the data.
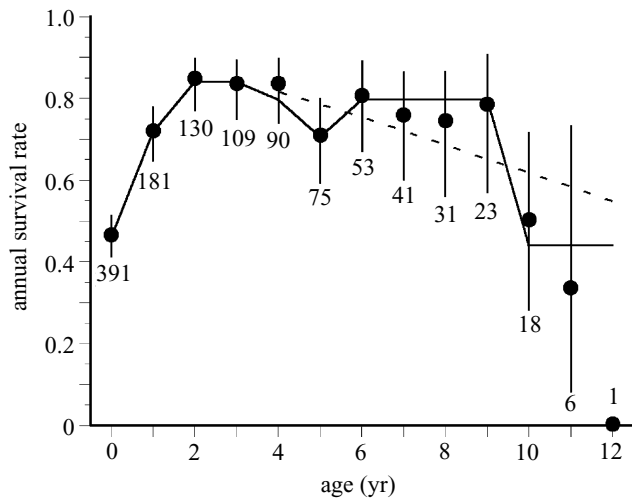
Figure 2. Age-specific survival probabilities for male fallow deer. Vertical lines show 95% confidence intervals. The solid line shows the best-fitting model, and the sample sizes at each age class are also given. The broken line shows the best-fitting Gompertz function beyond the age of 4 years. According to this model, survival drops at a rate of -0.11 ± 0.04 (on the complementary log(log) scale) with age. The figure pools the data from six cohorts that differed in survival (accounted for in the analysis). For example, fawn survival was 0.36, 0.45, 0.48, 0.39, 0.56 and 0.52 in the six successive cohorts from 1984 to 1989, respectively.
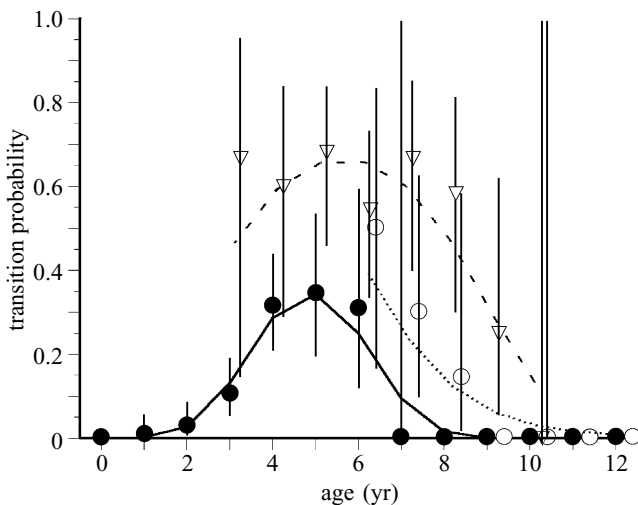
Figure 3. Age-specific probabilities for fallow bucks in three different reproductive states to reproduce during the following year, given that they survived (filled circles, $n \rightarrow r$; open circles, $s \rightarrow r$; open triangles, $r \rightarrow r$). Vertical lines show 95% confidence intervals. The numbers of non-reproducers from age 0 (fawns) to 12 years are 391, 181, 129, 105, 77, 44, 19, 9, 6, 4, 5, 0 and 0, respectively. The numbers of reproducers from age 0 to 12 years are 0, 0, 1, 3, 12, 27, 25, 19, 13, 8, 2, 0 and 0, respectively. The numbers of secondary non-reproducers from age 0 to 12 years are 0, 0, 0, 1, 1, 4, 9, 13, 12, 11, 11, 6 and 1, respectively.

4. DISCUSSION

We found that the survival probabilities of males in our study population were highly variable with age, and the best-fitting model had four distinct phases (figure 2; table 2). The fitted models provide strong evidence for survival
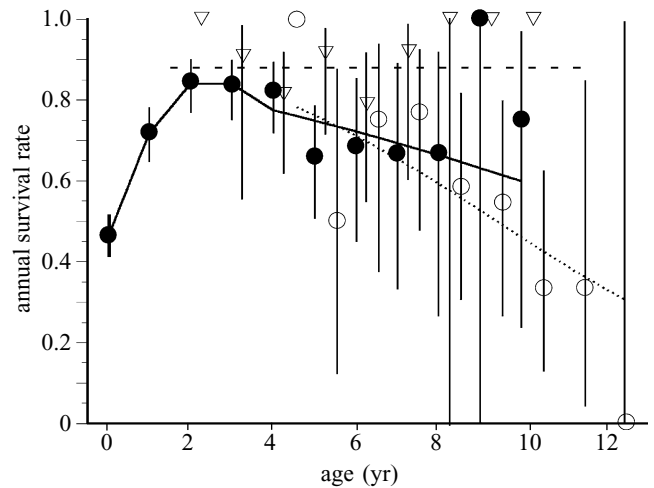

Figure 4. Age-specific survival probabilities of non-reproducers (filled circles), reproducers (open triangles) and secondary non-reproducers (open circles). Vertical lines show 95% confidence intervals. Lines show the best-fitting model. According to this model, survival drops with age beyond the age of 4 years at a rate of -0.11 ± 0.06 (on the complementary log(log) scale) among non-reproducers, and -0.16 ± 0.08 among secondary non-reproducers.

senescence that begins approximately at the age of 9 years if we considered all males as one group (figure 2; table 2), or at social maturity if we divide them according to their reproductive state (figure 4; table 2). Our estimated maximal yearly survival rate was 85%, at the age of 2 years. Therefore, our analysis is not affected by below-threshold mortality, which is a common problem in senescence analyses of organisms with very high survival during early life (Promislow *et al.* 1999). Reproduction probability declined at older ages for all males, indicating the onset of reproductive senescence (figure 3). Thus we provide very strong evidence for senescence in male ungulates.

We found that reproducers had a greater chance of reproducing again in the following year than both types of non-reproducers (figure 3; table 2). There were also significant differences in the survival probabilities, with reproducers consistently surviving better than non-reproducers (again both types) (figure 4; table 2). As reproducers in one year were likely to remain reproducers in the following year and these animals also had higher survival, it could indicate the generally higher phenotypic quality of reproducing males. In our study population, reproduction is associated with higher fight rates and social dominance rank, more vocal display and larger body size (McElligott *et al.* 1998, 1999, 2001). This evidence suggests that phenotypic characters could be linked to longevity in fallow bucks. Evidence for this link already exists for *Drosophila melanogaster,* female bighorn sheep (*Ovis canadensis*) and female roe deer (*Capreolus capreolus*) (Partridge *et al.* 1999; Gaillard *et al.* 2000b).

Age-specific survival probabilities of ungulates are usually best described with a Caughley-like model that incorporates three distinct phases, with lower survival both early and late in life, and relatively high survival during 'middle age' (Caughley 1966; Loison *et al.* 1999; Gaillard *et al.* 2000a). In general our results support this model but also with some important modifications. We found

that survival of fallow bucks could best be described using a model with four phases (figure 2; table 2). We found that males 2 and 3 years old had significantly higher survival compared with all other males, but this was only marginally higher than the survival of males between 4 and 9 years. Males at the ages of 2 and 3 years old are not yet socially mature (McElligott *et al.* 1998, 1999). Thus we have identified two distinct survival levels amongst the age classes that experience generally higher survival. The slight lowering of survival among males aged 4–9 years old could be related to the intense intrasexual competition that they experience (McElligott *et al.* 1998, 1999, 2001). We did not find any evidence to suggest that survival decreased significantly at the onset of social maturity and then increased again afterwards (Ralls *et al.* 1980; Clinton & Le Boeuf 1993; McElligott & Hayden 2000).

Recent evidence for ungulates has shown that senescence does not generally occur at sexual maturity or the age of first reproduction, as predicted by early life-history models (Medawar 1952; Hamilton 1966; Gaillard *et al.* 1994; Loison *et al.* 1999). Similarly, the first step of our analysis, which treated all males equally, indicated that senescence does not begin until well after the ages at which males may have the opportunity to reproduce. We found that survival remained high and stable until the age of 9 years (figure 2), although the proportion of males reproducing in our study population greatly increases at the ages of 4 and 5 years (McElligott & Hayden 2000). However, when we investigated the age-specific patterns in survival for individuals in three reproductive states independently, the results differed. Survival decreased steadily after the age of social maturity among current non-reproducers, regardless of whether or not they had reproduced earlier (non-reproducers and secondary non-reproducers). By contrast, survival stayed high and constant among reproducers. Even though individuals changed their reproductive state repeatedly during their lifetimes, these three groups are likely to differ in phenotypic quality, and our results may be caused by heterogeneity among individuals. Theory shows that population trajectories in survival are complex if they arise from different groups that each follow their own simpler trajectory (Vaupel & Yashin 1985). Successive cohorts of older animals may have increasing proportions of better quality males (McDonald *et al.* 1996; Newton & Rothery 1997) and the population trajectory thus approaches more and more the trajectory of the most vigorous group (Vaupel & Yashin 1985).

The decline in reproduction probability for older age classes (figure 3) does not provide evidence for reproductive senescence in terms of fertility, as for example in female bighorn sheep (Bérubé *et al.* 1999). However, the fall in reproduction in older males does indicate a more general physiological decline that is linked to senescence and is due to competitive exclusion by prime-aged males (Abrams 1991; McElligott *et al.* 1998). This deterioration is also evident in the decrease in body condition and antler size of older fallow bucks (Kelly 1998; A. G. McElligott, personal observation). Thus we provide evidence for senescence in this species even under the most restrictive definition, and this also allows us to distinguish it from non-degenerative changes that could influence mortality (Abrams 1991). The low probability of reproduction in the youngest age classes (figure 3) is also caused by competitive exclusion.

Although senescence is often considered related to the costs of reproduction, there are limitations to the use of phenotypic correlation studies when examining the costs of reproduction (Lessells 1991; Reznick 1992; Mysterud *et al.* 2001). However, when other more robust methods such as experimental manipulations or genetic correlations are not feasible, the use of recently developed CMR and multi-state models provide the best possible alternatives (Nichols *et al.* 1994; Tavecchia *et al.* 2001). The positive association that we found between current and future reproduction suggests that reproducing males have higher phenotypic quality. The multi-state models used here to examine reproduction probabilities have only previously been used for studies of meadow voles (*Microtus pennsylvanicus*) (Nichols *et al.* 1994) and kittiwakes (*Rissa tridactyla*) (Cam & Monnat 2000), and never for a large polygynous ungulate. In fact, Nichols *et al.* (1994) stated that data such as ours are very appropriate for analysis using these models due to the very discrete period of reproduction, and our detailed knowledge of the reproductive status of males in our study population (McElligott & Hayden 2000).

In contrast to the results of other studies, we found no evidence for a drop survival at the onset of social maturity regardless of the reproductive state (Ralls *et al.* 1980; McElligott & Hayden 2000). For example, Clinton & Le Boeuf (1993) found that the overall decrease in survival at the onset of social maturity was mainly due to the lower survival of reproducing males. Although fights and not copulations are considered more costly for male ungulates (Gosling *et al.* 1987; McElligott *et al.* 1998), we use reproduction as a proxy indicator of increased reproductive effort because it indicates an overall level of reproductive effort that includes a very substantial component of vocal display, in addition to fighting (McElligott & Hayden 1999; McElligott *et al.* 1999). It also indicates the costs that may result from growing to a large size and fat storage prior to the breeding season (McElligott *et al.* 2001). Our results add to the theoretical and empirical evidence which already exists for positive relationships between fitness correlates (Houle 1991; Dobson *et al.* 1999). In the case of Columbian ground squirrels (*Spermophilus columbianus*), females that produced larger litters also gained more mass during reproduction than other females.

Recent evidence for male ungulates has indicated that population density, through either tooth wear and diet differences (especially when food is limited) or male–male competition, may also have important influences on senescence (Gaillard *et al.* 1993; Mysterud *et al.* 2001). In our study population, females both live longer and reproduce at older ages than males (McElligott & Hayden 2000; T. J. Hayden, unpublished data). The tooth-wear rates of males are higher than those of females, and fight rates of males are also high (Moore *et al.* 1995*b*; McElligott *et al.* 1998). Therefore, in addition to the influence of dietary differences, tooth-wear rates may also be related to the level of male–male competition if they are related to the higher growth rates and larger sizes that males must reach in order to reproduce (Putman *et al.* 1993; McElligott *et al.* 2001).

This study provides strong evidence of marked sen-

escence in both survival and reproduction of fallow bucks. Our long-term monitoring has revealed four life-history stages of males: yearling, pre-reproductive, prime-age and senescent. Survival senescence appeared to start at the onset of social maturity (Hamilton 1966) but the population trajectory of survival was more complex due to heterogeneity between individuals (Vaupel & Yashin 1985). In addition, current reproducers have both higher probabilities of reproducing the following year and higher survival than all non-reproducers (van Noordwijk & de Jong 1986; Partridge 1987).

REFERENCES

Abrams, P. 1991 Fitness costs of senescence: the evolutionary importance of events in early adult life. *Evol. Ecol.* **5**, 343–360.

Anderson, D. R. & Burnham, K. P. 1999 Understanding information criteria for selection among capture–recapture or ring recovery models. *Bird Study* **46**, S14–S21.

Bérubé, C. H., Festa-Bianchet, M. & Jorgenson, J. T. 1999 Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565.

Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach*. New York: Springer.

Cam, C. & Monnat, J. Y. 2000 Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *J. Anim. Ecol.* **69**, 380–394.

Caughley, G. 1966 Mortality patterns in mammals. *Ecology* **47**, 906–918.

Clinton, W. L. & Le Boeuf, B. J. 1993 Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* **74**, 1884–1892.

Comfort, A. 1979 *The biology of senescence*, 3rd edn. Edinburgh, UK: Churchill Livingstone.

Dobson, F. S., Risch, T. S. & Murie, J. O. 1999 Increasing returns in the life history of Columbian ground squirrels. *J. Anim. Ecol.* **68**, 73–86.

Ericsson, G., Wallin, K., Ball, J. P. & Broberg, M. 2001 Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* **82**, 1613–1620.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B. & Pradel, R. 1993 Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* **62**, 778–791.

Gaillard, J.-M., Allainé, D., Pontier, D., Yoccoz, N. G. & Promislow, D. E. L. 1994 Senescence in mammals: a reanalysis. *Evolution* **48**, 509–516.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N. G. 1998 Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**, 58–63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, L. & Toïgo, C. 2000a Temporal variation in fitness components and population dynamics of large herbivores. *A. Rev. Ecol. Syst.* **31**, 367–393.

Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. 2000b Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond.* B **267**, 471–477.

Gosling, L. M., Petrie, M. & Rainy, M. E. 1987 Lekking in topi: a high cost, specialist strategy. *Anim. Behav.* **35**, 616–618.

Hamilton, W. D. 1966 The moulding of senescence by natural selection. *J. Theor. Biol.* **12**, 12–45.

Hayden, T. J., Moore, N. P. & Kelly, P. F. 1992 The fallow deer of Phoenix Park: an evolving management plan. In *Proc. 2nd Deer Park Symp.: management, welfare and conservation of park deer* (ed. D. J. Bullock & C. R. Goldspink), pp. 27–45. Potters Bar, UK: UFAW.

Houle, D. 1991 Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution* **45**, 630–648.

Hughes, K. A. 1995 The evolutionary genetics of male life-history characters in *Drosophila melanogaster*. *Evolution* **49**, 521–537.

Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J.-M. & Wishart, W. D. 1997 Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* **78**, 1019–1032.

Kelly, P. F. 1998 Mating success of male fallow deer (*Dama dama* L.): mating strategy, antler geometry and vocal characteristics. PhD thesis, University College Dublin, National University of Ireland.

Kirkwood, T. B. L. & Austad, S. N. 2000 Why do we age? *Nature* **408**, 233–238.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.

Lessells, C. M. 1991 The evolution of life histories. In *Behavioural ecology*, 3rd edn (ed. J. R. Krebs & N. B. Davies), pp. 32–68. Oxford, UK: Blackwell.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T. & Jullien, J.-M. 1999 Age-specific survival in five populations of ungulates: evidence for senescence. *Ecology* **80**, 2539–2554.

McDonald, D. B., Fitzpatrick, J. W. & Woolfenden, G. E. 1996 Actuarial senescence and demographic heterogeneity in the Florida scrub jay. *Ecology* **77**, 2373–2381.

McElligott, A. G. & Hayden, T. J. 1999 Context-related vocalization rates of fallow bucks, *Dama dama*. *Anim. Behav.* **58**, 1095–1104.

McElligott, A. G. & Hayden, T. J. 2000 Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behav. Ecol. Sociobiol.* **48**, 203–210.

McElligott, A. G., Mattiangeli, V., Mattiello, S., Verga, M., Reynolds, C. A. & Hayden, T. J. 1998 Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology* **104**, 789–803.

McElligott, A. G., O'Neill, K. P. & Hayden, T. J. 1999 Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Anim. Behav.* **57**, 1159–1167.

McElligott, A. G., Gammell, M. P., Harty, H. C., Paini, D. R., Murphy, D. T., Walsh, J. T. & Hayden, T. J. 2001 Sexual size dimorphism in fallow deer: do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**, 266–272.

McNamara, J. M. & Houston, A. I. 1996 State-dependent life histories. *Nature* **380**, 215–221.

Medawar, P. B. 1952 *An unsolved problem in biology*. London: H. K. Lewis.

Moore, N. P., Kelly, P. F., Cahill, J. P. & Hayden, T. J. 1995a Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behav. Ecol. Sociobiol.* **36**, 91–100.

Moore, N. P., Cahill, J. P., Kelly, P. F. & Hayden, T. J. 1995*b* An assessment of five methods of age determination in an enclosed population of fallow deer (*Dama dama*). *Biol. Environ.* **95B**, 27–34.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. 2001 Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proc. R. Soc. Lond.* B **268**, 911–919.

Newton, I. & Rothery, P. 1997 Senescence and reproductive value in sparrowhawks. *Ecology* **78**, 1000–1008.

Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L. & Link, W. A. 1994 Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology* **75**, 2052–2065.

Nichols, J. D., Hines, J. E. & Blums, P. 1997 Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina*. *Ecology* **78**, 1009–1018.

Partridge, L. 1987 Is accelerated senescence a cost of reproduction? *Funct. Ecol.* **1**, 317–320.

Partridge, L. & Barton, N. H. 1993 Optimality, mutation and the evolution of ageing. *Nature* **362**, 305–311.

Partridge, L., Prowse, N. & Pignatelli, P. 1999 Another set of responses and correlated responses to selection on age at reproduction in *Drosophila melanogaster*. *Proc. R. Soc. Lond.* B **266**, 255–261.

Pemberton, J. M., Albon, S. D., Guinness, F. E., Clutton-Brock, T. H. & Dover, G. A. 1992 Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* **3**, 66–75.

Pletcher, S. D. 1999 Model fitting and hypothesis testing for age-specific mortality data. *J. Evol. Biol.* **12**, 430–439.

Promislow, D. E. L., Tatar, M., Pletcher, S. & Carey, J. R. 1999 Below-threshold mortality: implications for studies in evolution, ecology and demography. *J. Evol. Biol.* **12**, 314–328.

Putman, R. J., Culpin, S. & Thirgood, S. J. 1993 Dietary differences between male and female fallow deer in sympatry and in allopatry. *J. Zool. Lond.* **229**, 267–275.

Ralls, K., Brownell Jr, R. L. & Ballou, J. 1980 Differential mortality by sex and age in mammals, with specific reference to the sperm whale. In *Report of the International Whaling Commission* (Special Issue), vol. 2 (ed. G. P. Donovan), pp. 233–243.

Reznick, D. 1992 Measuring the costs of reproduction. *Trends Ecol. Evol.* **7**, 42–45.

Spendelow, J. A., Nichols, J. D., Nisbet, I. C., Hays, H., Cormons, G. D., Burger, J., Safina, C., Hines, J. E. & Gochfeld, M. 1995 Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* **76**, 2415–2428.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Tavecchia, G., Pradel, R., Boy, V., Johnson, A. R. & Cézilly, F. 2001 Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. *Ecology* **82**, 165–174.

Thirgood, S. J., Langbein, J. & Putman, R. J. 1999 Intraspecific variation in ungulate mating strategies: the case of the flexible fallow deer. *Adv. Study Behav.* **28**, 333–361.

van Noordwijk, A. J. & de Jong, G. 1986 Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–142.

Vaupel, J. W. & Yashin, A. I. 1985 Heterogeneity's ruses: some surprising effects of selection on population dynamics. *Am. Stat.* **39**, 176–185.

White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139.

Williams, G. C. 1957 Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411.

Zwaan, B. J. 1999 The evolutionary genetics of ageing and longevity. *Heredity* **82**, 589–597.