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DEMOGRAPHY BEYOND THE POPULATION

Bayesian estimates of male and female African lion mortality for future use in population management

Julia A. Barthold[1,2]*, Andrew J. Loveridge[1], David W. Macdonald[1], Craig Packer[3] and Fernando Colchero[4]

[1]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK;* [2]*Max-Planck Odense Center on the Biodemography of Aging and Department of Biology, Uiversity of Southern Denmark, Campusvej 55, 5230, Odense M, Denmark;* [3]*Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN55108, USA; and* [4]*Department of Mathematics and Computer Science and Max-Planck Odense Center on the Biodemography of Aging, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark*

Summary

1. The global population size of African lions is plummeting, and many small fragmented populations face local extinction. Extinction risks are amplified through the common practice of trophy hunting for males, which makes setting sustainable hunting quotas a vital task.

2. Various demographic models evaluate consequences of hunting on lion population growth. However, none of the models use unbiased estimates of male age-specific mortality because such estimates do not exist. Until now, estimating mortality from resighting records of marked males has been impossible due to the uncertain fates of disappeared individuals: dispersal or death.

3. We develop a new method and infer mortality for male and female lions from two populations that are typical with respect to their experienced levels of human impact.

4. We found that mortality of both sexes differed between the populations and that males had higher mortality across all ages in both populations. We discuss the role that different drivers of lion mortality may play in explaining these differences and whether their effects need to be included in lion demographic models.

5. *Synthesis and applications*. Our mortality estimates can be used to improve lion population management and, in addition, the mortality model itself has potential applications in demographically informed approaches to the conservation of species with sex-biased dispersal.

Key-words: African lions, age-specific mortality, dispersal, Hwange, lion population management, Serengeti, Siler model, sex differences in life history, sex differences in mortality, social carnivores

Introduction

Estimates of mortality for wild animal populations are important to test ecological and evolutionary theory, and to project future population size and structure for population management measures (Griffith et al. 2016). Such measures are needed, for example, for many populations of African lions *Panthera leo* that are facing local extinction (Packer *et al.* 2011; Riggio *et al.* 2012; Packer *et al.* 2013). Populations are further decimated through the common practice of shooting males for trophies (Packer *et al.* 2011). Trophy hunting is an important yet controversial conservation tool and setting shooting quota at sustainable levels a vital task (Loveridge *et al.* 2007; Lindsey *et al.* 2012). Consequently, multiple demographic models evaluate consequences of male offtake on lion population growth (Whitman *et al.* 2004, 2007; Becker *et al.* 2013), but none of these demographic models use unbiased estimates of male age-specific mortality, because such estimates do not exist. Male mortality estimates inferred using the conventional Cormack–Jolly–Seber models (Cormack 1964; Jolly 1965; Seber 1965) are biased, because these models cannot account for male dispersal. More specifically, they are unable to derive mortality information from records of males that disappeared from monitored populations around the age

*Correspondence author. E-mail: jbarthold@biology.sdu.dk

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of maturity with uncertain fates (i.e. the males have died or dispersed out of the study area).

The most common answer to male data deficiency in population ecology is to ignore males altogether and to model only the dynamics of the female population (see for notable exceptions Schindler *et al.* 2015; Childs et al. 2016). This can be a legitimate approach depending on the study question and species. However, for lions it is generally recognized that male mortality may affect population dynamics via the mechanistic link of infanticide (Whitman *et al.* 2004; Caro *et al.* 2009). Frequent deaths of adult males disturb the social structure of prides and male coalitions and result in a higher frequency of male takeovers with subsequent deaths of young infants, premature evictions of juveniles with low survival probability and a risk of injuries for females trying to protect dependent young (Elliot *et al.* 2014). Furthermore, for many applications of demographic models of lions, males are the sex of interest, because the models aim to address issues of sustainable shooting quota in populations hunted for trophies (Whitman *et al.* 2007). Existing studies of lion population dynamics therefore use various approaches to overcome the lack of male age-specific mortality estimates. Some use population summary statistics without further differentiating the age or sex structure of the population (Packer *et al.* 2011), others structure their model in a way that makes a distinction of uncertain male records into deaths and dispersal superfluous (Whitman *et al.* 2004, 2007), or use female mortality estimates for both sexes (Becker *et al.* 2013). The development of a model that can provide estimates for both sexes is therefore a significant addition to the toolbox available for species management.

Among dioecious organisms, sex differences in life history are the norm. In mammal species that exhibit a polygynous or polygynandrous mating system in which males compete for access to receptive females by physical combat, males are commonly larger than females, mature later, reproduce for fewer years and die younger than females (Promislow 1992; Andersson 1994; Clutton-Brock & Isvaran 2007). Lions are a prominent example of this type of mating system, and a shorter male than female life span in this species is well known (Packer *et al.* 1988). Yet the degree to which mortality of males and females differs at different ages, and whether sex differences are stable across populations, is poorly understood. Without this knowledge, the management-relevant consequences of sex differences in mortality cannot be unveiled.

Here, we develop a mortality analysis method that can incorporate uncertain male records for species with male natal dispersal. In this model, dispersal state (i.e. whether a male with an uncertain fate dispersed or died) is imputed as a latent state jointly with the coefficients of a parametric mortality model in a Bayesian hierarchical framework. The parameters of the mortality model have a distinct biological interpretation (see Data section in Materials and methods), and the mortality model thus decomposes mortality into age-dependent and age-independent mortality (Siler 1979). Age-independent mortality represents mortality due to external sources that kill regardless of age (Pletcher 1999). The mortality decomposition therefore allows comparison of mortality between the sexes or populations not only in terms of different levels but also in terms of differences in underlying processes. Furthermore, we extend the basic framework of the model to also account for possible secondary dispersal, where immigrants to the study area out-migrate again after a period of residency.

Using the model, we estimate age-specific mortality rates for males and females for two populations of African lions that varied with respect to environmental factors, densities and human impact. The first population was hunted for trophies at its boundary, was subjected to killings in accidents and human–wildlife conflicts, and lived in a food-scarce environment at low densities (the "disturbed" population). The second population was hardly impacted by humans and lived in a nutrient-rich environment at high densities (the "undisturbed" population). We compare age-specific mortality between these two populations with particular focus on a possible signature of human impact. We expected to find higher levels of mortality, and particularly of age-independent mortality, in the disturbed population compared to the undisturbed one. We also expected to confirm previously observed sex differences in mortality (Packer *et al.* 1988) and to observe an amplification of this difference in the population impacted by humans, since males were the primary target of trophy hunting and had a higher risk of being killed by farmers in retaliation for raided livestock.

Materials and methods

DATA

We used life-history data from two free-living lion populations that have been monitored for many years. The "disturbed" population lives in the northern range of Hwange National Park in north-western Zimbabwe. The study area extends to 7000 km^2 and receives 600 mm rainfall seasonally. Vegetation is a mosaic of mixed deciduous woodland and scrubland with limited areas of open or bushed grassland (Rogers 1993; Loveridge *et al.* 2007). Water is artificially supplied during the dry season, and the prey assemblage is largely resident. The park borders on hunting concessions in the north and north-east. Human settlements occur on the north and east of the park and are mainly used for subsistence agriculture and wildlife exploitation under the Communal Areas Management Plan for Indigenous Resources (CAMPFIRE) scheme (Frost & Bond 2008). The park shares a border with wildlife management areas in Botswana to the west. Life-history data were collected between 1999 and 2013. One female per pride and some resident male nomads and males of male coalitions wore a radiocollar. These prides, resident male nomads and male coalitions were located by radiotelemetry and

censused approximately once per month. Other males were monitored by opportunistic sightings and photographs collected from tourists and guides. Field staff identified individual lions other than the collar-wearing ones from markings such as whisker spot patterns, scars and teeth characteristics (Pennycuick & Rudnai 1970; Smuts, Anderson & Austin 1978). A summary of the data used is given in Table 1.

The "undisturbed" population occupies a 2000 km^2 study area in the Serengeti National Park, Tanzania. The area has a south-east to north-west gradient in vegetation from short to tall grassland to open woodlands (Packer *et al.* 2005; Mosser *et al.* 2009). Most rainfall occurs during the wet season, when large herds of migratory herbivores pass through. In response to an increasing abundance of migratory prey, the study population has grown since the start of the study in 1966 (Packer *et al.* 2005, C. Packer, unpublished data after 2005). We used life-history data collected between 1966 and 2013. During the early years of the study (1966–1984), observers gathered data from opportunistic sightings, about 1–3 times per month for most individuals. Since 1984, tracking the signal of at least one radiocollared female per pride, observers have sighted each pride 2–6 times per month. The observers identify individuals from natural markings (Packer *et al.* 1991) and deduce birth dates of cubs born in the study area from lactation stains on the mothers. A lot of nomadic males enter the area, most of them migrate through without taking up residence in the study population. Because of the sparse information on these males, our analyses excluded all nomadic males that never became residents (n = 548). A summary of data is provided in Table 1.

In both studies, trained observers estimate age of individuals with unknown dates of birth using age indicators such as relative body size, nose coloration and eruption and wear of teeth (Smuts, Anderson & Austin 1978; Whitman *et al.* 2004). Furthermore, both data sets contain individuals that died at young ages before sex could be determined (unsexed records). For all data, we identified male records as uncertain (i.e. the male may potentially have dispersed) if missing males that were born in the study area (native borns), and whose deaths were not observed, were older than 1·5 years at disappearance (minimum age at dispersal). Finally, secondary dispersal has rarely been observed in the Hwange population (A. Loveridge, unpublished data). However, the head of the Serengeti study indicated 90 out of 348 immigrants to possibly have out-migrated again ("potential secondary dispersers", C. Packer, unpublished data). This opinion was formed based on the circumstances accompanying the disappearances. We added these 90 records to the uncertain male records for which the dispersal state needed to be imputed.

MORTALITY ANALYSIS

The parametric mortality and dispersal models

We fitted a parametric model for age-specific mortality. With X being a random variable for ages at death, the mortality function, or hazard rate of death, for continuous age x was

$$\mu(x|\boldsymbol{\theta}) = \lim_{\Delta x \to 0} \frac{\Pr(x \leq X < x + \Delta x | x \leq X, \boldsymbol{\theta})}{\Delta x}, \qquad \text{eqn 1}$$

where $\boldsymbol{\theta}$ was a vector of mortality parameters (see Table 2 for a summary of all random variables, parameters and indicators). From the mortality rate, the probability to survive from birth to age x, or survival function, could be calculated as

$$S(x|\boldsymbol{\theta}) = \Pr(X \geq x) = \exp\left[-\int_0^x \mu(z|\boldsymbol{\theta})\mathrm{d}z\right]. \qquad \text{eqn 2a}$$

And the probability that death occurred before age x, or the cumulative density function (CDF), was

$$F(x|\boldsymbol{\theta}) = \Pr(X < x) = 1 - S(x|\boldsymbol{\theta}), \qquad \text{eqn 2b}$$

with the probability density function (PDF) of age at death of

$$f(x|\boldsymbol{\theta}) = \frac{\mathrm{d}}{\mathrm{d}x}F(x|\boldsymbol{\theta}) = S(x|\boldsymbol{\theta})\mu(x|\boldsymbol{\theta}). \qquad \text{eqn 2c}$$

To capture the bathtub shape of lion mortality (Packer, Tatar & Collins 1998), and to allow for the estimation of age-independent mortality, we used the Siler model (Siler 1979) in the form

$$\mu(x|\boldsymbol{\theta}) = e^{a_0 - a_1 x} + c + e^{b_0 + b_1 x}, \qquad \text{eqn 3}$$

where $\boldsymbol{\theta}^\top = [a_0, a_1, c, b_0, b_1]$, with $a_0, b_0 \in \mathbb{R}$ and $a_1, c, b_1 \geq 0$. The Siler model is the sum of three additive mortality hazards (Siler 1979). The first summand models the decrease in mortality rates over infant and juvenile ages, with e^{a_0} being the initial level and a_1 modelling the rate of decrease. The middle summand is a constant hazard c, also known as a Makeham term (Makeham 1860), that captures age-independent mortality. The last summand is the Gompertz law of mortality (Gompertz 1825), which captures the exponential increase in mortality rates with age from an initial level e^{b_0} with a rate of increase of b_1.

To model the ages at dispersal, we defined the random variable Y for age at natal dispersal (Table 2). It followed $Y \sim G_Y(y)$ for

Table 1. Sample sizes for males (M), females (F) and individuals that died before sex could be determined (U)

	Serengeti			Hwange			Sex ratio
Sample	M	F	U	M	F	U	F:M
Birth*	1466 (316)†	1507	875	174 (32)	244	140	0·51‡
0·5	988 (315)	1095	62	168 (32)	235	60	0·53
1	763 (315)	905	4	157 (32)	225	32	0·55

*"Birth" indicates the sample that includes all individuals. "0·5" and "1" indicate the samples that include individuals that survived to at least 0·5 and 1 year, respectively.
†For males, sample sizes refer to the number of native-born individuals, followed by the number of immigrants in brackets.
‡Female-to-male sex ratio among all native borns (pooled data, excluding immigrants) assuming a sex ratio of 0·5 among individuals that died before sex could be determined.

Table 2. Random variables, observed variables and indicators

Modelled random variables	
X	Random variable for age at death, where x is any age element
Y	Random variable for age at natal dispersal with elements y
Z	Random variable for age at secondary dispersal with elements z
D	Binary random variable for disperser or non-disperser
S	Binary random variable for sex
Observed variables and indicators	
$\mathbf{x}^F$	Vector of ages at first detection ($x_i^F = t_i^F - b_i$)
$\mathbf{x}^L$	Vector of ages at last detection ($x_i^L = t_i^L - b_i$)
$\mathbf{m}$	Indicator vector for immigrants ($m_i = 1$ if immigrant)
$\boldsymbol{\omega}$	Indicator vector for potential natal dispersers ($\omega_i = 1$ if $m_i = 0$, $s_i = 0$, and uncertain fate at $x_i^L \geq \alpha$, and $\omega_i = 0$ otherwise)
$\boldsymbol{\upsilon}$	Indicator vector for potential secondary dispersers ($\upsilon_i = 1$ if $m_i = 1$, $s_i = 0$, uncertain fate at x_i^L, and expert indicated potential secondary dispersal, and $\upsilon_i = 0$ otherwise)
Updated indicators	
$\mathbf{d}$	Indicator vector for dispersers ($d_i = 1$ if disperser and $d_i = 0$ otherwise)
$\mathbf{s}$	Indicator vector for sex ($s_i = 1$ if female and $s_i = 0$ otherwise)
Parameters	
$\boldsymbol{\theta}$	Vector of mortality parameters
$\boldsymbol{\gamma}$	Vector of natal dispersal parameters
$\boldsymbol{\lambda}$	Vector of secondary dispersal parameters
Functions	
Mortality	
$\mu(x\|\boldsymbol{\theta})$	Mortality (Siler model)
$S(x\|\boldsymbol{\theta})$	Survival
$F(x\|\boldsymbol{\theta})$	Cumulative density function (CDF) of age at death ($F(x)$=1−$S(x)$)
$f(x\|\boldsymbol{\theta})$	Probability density function (PDF) of age at death
Dispersal	
$g_Y(y\|\boldsymbol{\gamma})$	PDF of age at natal dispersal (gamma distribution)
$G_Y(y\|\boldsymbol{\gamma})$	CDF of age at natal dispersal
$g_Z(z\|\boldsymbol{\lambda})$	PDF of age at secondary dispersal (gamma distribution)
$G_Z(z\|\boldsymbol{\lambda})$	CDF of age at secondary dispersal

ages $y > 0$, where $G_Y(y)$ was the gamma distribution function with the parameter vector $\boldsymbol{\gamma}^\top = [\gamma_1, \gamma_2]$. The probability density function (PDF) of age at natal dispersal was given by

$$g_Y(y|\boldsymbol{\gamma}) = \begin{cases} \frac{\gamma_1^{\gamma_2}}{\Gamma(\gamma_2)}(y-\alpha)^{\gamma_2-1}e^{-\gamma_1 (y-\alpha)} & \text{if } y \geq \alpha \\ 0 & \text{if } y < \alpha, \end{cases} \quad \text{eqn 4}$$

where α is the minimum age at natal dispersal (α = 1·5 for both populations) and $\gamma_1, \gamma_2 > 0$. We further defined the random variable Z for age at secondary dispersal, where the age at secondary dispersal was $Z \sim G_Z(z)$ for ages $z > 0$, with $G_Z(z)$ being a second gamma distribution with the parameter vector $\boldsymbol{\lambda}^\top = [\lambda_1, \lambda_2]$ (Table 2). Accordingly, the probability density function (PDF) of age at secondary dispersal was given by

$$g_Z(z|\boldsymbol{\lambda}) = \begin{cases} \frac{\lambda_1^{\lambda_2}}{\Gamma(\lambda_2)}(z-\alpha)^{\lambda_2-1}e^{-\lambda_1 (z-\alpha)} & \text{if } z \geq \alpha \\ 0 & \text{if } z < \alpha, \end{cases} \quad \text{eqn 5}$$

where $\lambda_1, \lambda_2 > 0$.

Model variables and functions

In a Bayesian hierarchical framework, the model maximized the posteriors of the mortality and dispersal models, while imputing the dispersal state for uncertain male records (i.e. dispersed or died) and the sex for unsexed records as latent states (see Fig. 1 for a flowchart of the model structure). Contributions to the mortality and dispersal likelihoods varied according to the sex, dispersal state and migration history of the individual. The likelihood for females was constructed as

$$p(x^F, x^L; \boldsymbol{\theta}) = \begin{cases} \Pr(X = x^L \mid X > x^F) & \text{if uncensored} \\ \Pr(X > x^L \mid X > x^F) & \text{if censored,} \end{cases} \quad \text{eqn 6a}$$

where x^L denotes the age at last detection and x^F is the age at first detection. Note that $x^F = 0$ for individuals born in the study area and $x^F > 0$ for both immigrants and individuals born before monitoring began. The likelihood for native-born potential natal dispersers was

$$p(x^F, x^L; \boldsymbol{\theta}, \boldsymbol{\gamma}) = \begin{cases} \Pr(X = x^L, Y > x^L | X > x^F) & \text{if uncensored} \\ \Pr(X > x^L, Y > x^L | X > x^F) & \text{if censored} \\ \Pr(X > x^L, Y = x^L | X > x^F) & \text{if dispersed.} \end{cases} \quad \text{eqn 6b}$$

While for immigrants that were potential secondary dispersers, the likelihood was

$$p(x^F, x^L; \boldsymbol{\theta}, \boldsymbol{\lambda}) = \begin{cases} \Pr(X = x^L, Z > x^L | Y = x^F, X > x^F) & \text{if uncensored} \\ \Pr(X > x^L, Z > x^L | Y = x^F, X > x^F) & \text{if censored} \\ \Pr(X > x^L, Z = x^L | Y = x^F, X > x^F) & \text{if dispersed.} \end{cases} \quad \text{eqn 6c}$$

For the imputation of dispersal state for the uncertain male records, we defined a binary random variable D, which assigned 1 if an individual i dispersed in its last detection age x_i^L, and 0 if otherwise. We furthermore defined a second binary variable S ($s_i = 1$ if female, $s_i = 0$ if male) for the imputation of sex as another latent state for unsexed records (Table 2).

Finally, we constructed the full Bayesian model as

$$p(\mathbf{d}_u, \mathbf{s}_u, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\lambda} | \mathbf{d}_k, \mathbf{s}_k, \mathbf{x}^F, \mathbf{x}^L) \propto \underbrace{p(\mathbf{d}, \mathbf{s}, \mathbf{x}^F, \mathbf{x}^L | \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\lambda})}_{\text{likelihood}} \times \underbrace{p(\mathbf{d})p(\mathbf{s})}_{\text{priors for states}} \times \underbrace{p(\boldsymbol{\theta})p(\boldsymbol{\gamma})p(\boldsymbol{\lambda})}_{\text{priors for parameters}}, \quad \text{eqn 7}$$

where $\mathbf{d}$ was the indicator vector of dispersal states and $\mathbf{s}$ was the indicator vector for sex. Each of these vectors had two subsets represented by the subscripts u for unknown and k for known.

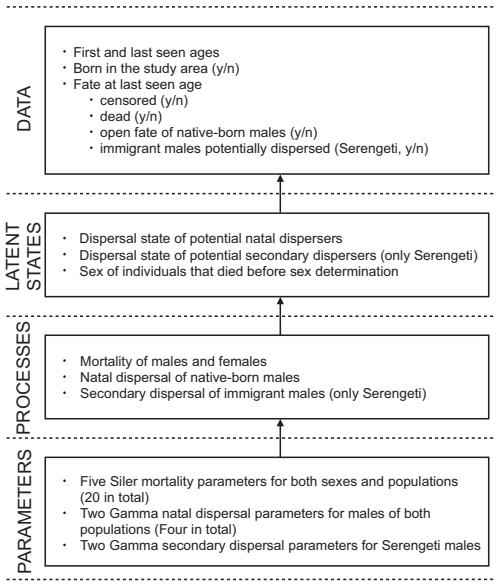

Fig. 1. Structure of the Bayesian hierarchical model to infer age-specific mortality of the Serengeti and Hwange lions.

Model fitting and conditional posteriors

We fitted the model in eqn 7 using a Markov chain Monte Carlo (MCMC) algorithm in four parallel sequences. We randomly drew starting values and set the number of iterations to 15 000 steps with a burn-in of 5000 initial steps and a thinning factor of 20. We used a hierarchical framework that only needed the conditionals for posterior simulation by Metropolis-within-Gibbs sampling (Gelfand & Smith 1990; Clark 2007). This means that, for this particular case, the algorithm divided the posterior for the joint distribution of unknowns into five parts: (i) estimation of mortality parameters, (ii) estimation of natal dispersal parameters, (iii) estimation of secondary dispersal parameters, (iv) imputation of unknown dispersal state and (v) imputation of unknown sexes. We provide details about the conditional posteriors and the acceptance probabilities for the different parts in Appendix S1, Supporting information.

Mortality and dispersal priors

The Siler parameters for the prior for both sexes were $a_{0p} = -3$ (σ = 0·5), $a_{1p} = 0.2$ (σ = 0·25), $c_p = 0$ (σ = 0·25), $b_{0p} = -4$ (σ = 0·5), and $b_{1p} = 0.01$ (σ = 0·25). For dispersal, the gamma parameters (shape and scale) for the dispersal priors were set to $\boldsymbol{\gamma}_p = \boldsymbol{\lambda}_p = \{8, 2\}$ with $\sigma(\boldsymbol{\gamma}_p) = \sigma(\boldsymbol{\lambda}_p) = \{2, 1\}$. All priors for parameters were fairly uninformative and within the bounds given by the life expectancies of medium- to long-lived animals. The priors for sex as a latent state corresponded to the empirical sex ratios at model start ages (Table 1).

Model application and posterior analysis

To study the differences in mortality between the sexes and between the two populations, we fitted the model with both sex and population as covariates and allowed for an interaction effect between sex and population. Since the negative exponential part of the Siler model may have problems in capturing the very steep decline in infant mortality after birth, the mortality at adjacent infant and juvenile ages can be overestimated by models fitted from birth. To evaluate this issue and with the goal of providing the best possible estimates, as well as estimates across the entire life span, we fitted the model from three different starting ages: birth, 0·5 years of age and 1 year of age. Since the latter was not affected by the constraints of the Siler function, we used this model for further investigations.

We predicted mortality rates for each sex and population using the parameter estimates of each MCMC iteration after burn-in and thinning. We then used these predictions to calculate the mean and credible intervals of age-specific mortality rates. Since we were *a priori* interested in the effects of population and sex on mortality, we decided against taking a model selection approach and instead calculated Kullback–Leibler (KL) divergences of the mortality parameter posterior densities (Kullback & Leibler 1951; McCulloch 1989; Burnham & Anderson 2001). The KL divergence compares two probability density distributions and can be interpreted to measure the amount of information lost when using the second probability density distribution to approximate the first one. After a simple calibration of the KL values (McCulloch 1989), the values range from 0·5 to 1, where a value of 0·5 indicates that the distributions are identical, and 1 that they do not overlap at all.

Mortality measures

We report mortality information as mortality rates, defined as the instantaneous hazard of death, and also known as the force of mortality (see eqn 1). From the continuous age-specific mortality rate, the discrete age-specific probability of survival ${}_{\Delta x}p_x$ can be calculated. It is defined as the probability to survive from age x to age $x + \Delta x$, with $\Delta x = 1$ for annual survival. Survival probabilities are a common mortality measure in cap-

ture–recapture studies, where they are also termed survival rate. To make our mortality estimates widely usable, we describe this calculation in Appendix S2. We also calculated life expectancy at the model start age. Finally, we computed the PDFs of age at death for males and females in the Serengeti and Hwange (see eqn 4). All analyses were conducted using the statistical programming language R (R Core Team 2012).

Results

POPULATION DIFFERENCES IN MORTALITY

The models converged for all estimated parameters and all starting ages (Fig. 2, see also Figs S1–S3 for traces). However, the posterior distributions for Hwange were wider than those for the Serengeti, which was expected due to the smaller sample size of the Hwange data (Fig. 2). This is also reflected in the wider confidence bands around the mean estimated mortality rates for Hwange compared to the Serengeti (Fig. 3). A model that allowed all Serengeti immigrants with uncertain fates at the age of last detection to be potential secondary dispersers did not converge. We therefore decided to restrict the potential secondary dispersers as described in the data section. Overall mortality of both sexes was U-shaped in the Serengeti with high initial cub mortality, low mortality of prime-aged adults and an age-dependent increase in mortality during the older ages (Fig. 3, left panels). Hwange lions also showed higher senescent mortality than prime-age mortality, although the confidence bands were wider than for the Serengeti population (Fig. 3, right panels). The main difference in overall mortality between the two populations was that, in Hwange, we could only detect moderately elevated levels of cub mortality compared to the mortality of prime-aged adults. Furthermore, this result only held for the model that estimated mortality from birth (Fig. 3, upper right panel).

The KL divergences comparing Serengeti and Hwange females revealed that mortality of females differed between the two populations (Fig. 2, lower right panel). Females in the Serengeti had higher initial cub mortality (a_0) and a steeper decline in mortality over infant and juvenile ages (a_1), yet slightly lower levels of prime-adult

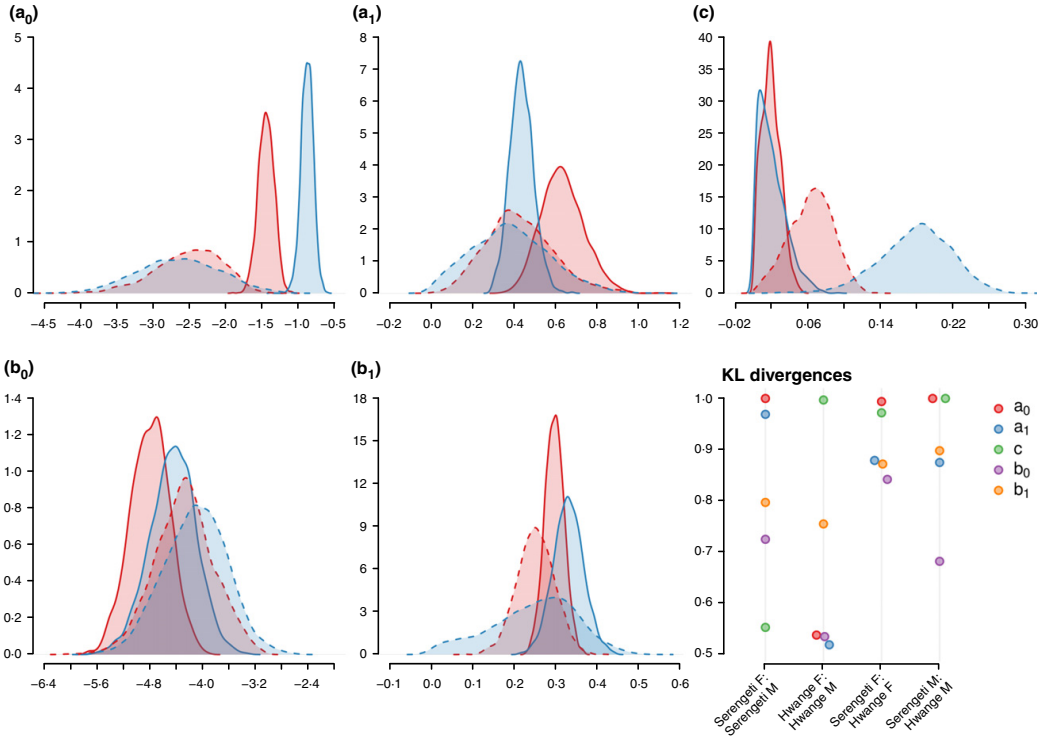

Fig. 2. Posterior distributions of Siler parameter estimates for female (pink) and male (blue) African lions of the Serengeti (solid lines) and Hwange (dashed lines) populations. The Siler parameters and their biological interpretation are as follows: initial level (e^{a_0}) and rate of exponential decrease with age of infant mortality (a_1), age-independent mortality (c), and initial level (e^{b_0}) and rate of exponential increase of mortality with age (b_1). Also shown are Kullback–Leibler (KL) divergences comparing parameter posteriors between females (F) and males (M) within populations, and within sexes between the populations. Note that some KL divergence estimates are jittered in x-axis direction to improve visibility. The analysis was conditioned on survival to the first year of life.

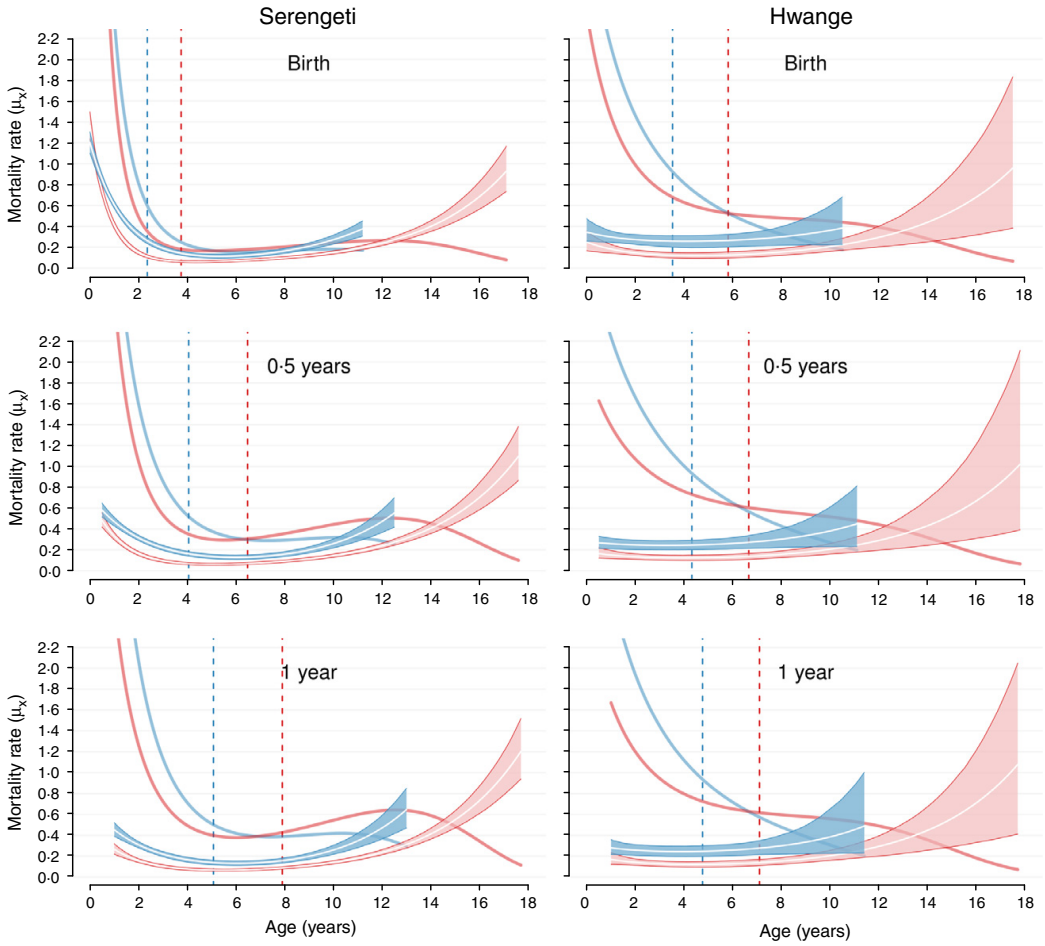

Fig. 3. Age-specific mortality estimates for male (blue) and female African lions (pink) of the Serengeti population (left panels) and the Hwange population (right panels). Polygons represent 95% credible intervals of age-specific mortality rates with white lines indicating the mean. Solid lines indicate the probability density function (PDF) of age at death, scaled so that the areas under the curves are equal and multiplied with a scaling factor of 100 to improve visibility. The dashed lines indicate life expectancy at birth. Mortality rates and PDFs are plotted until the ages when 95% of a synthetic same-sex cohort would be dead. The first row of panels shows results of the model fitted from birth. The second and third rows show results of models fitted to individuals that died or disappeared at ages older than 0·5 and 1 year, respectively.

mortality, and similar levels of senescent mortality, when compared to females in Hwange (b_0 and b_1). Due to higher cub mortality, they also had a shorter life expectancy at birth (or 0·5 years and 1 year of age where applicable) (Fig. 3).

As with females, the mortality of Serengeti males differed from the mortality of Hwange males (Fig. 2). Initial cub mortality and the increase in senescent mortality (a_0, b_1) were lower in Hwange, but age-independent mortality (c) was much higher, resulting in higher mean mortality rates across the prime-adult ages for Hwange males compared to Serengeti males (Figs 2 and 3). The PDFs of age at dispersal for males are illustrated in Fig. S4.

SEX DIFFERENCES IN MORTALITY

Mortality also varied between the sexes. In the Serengeti population, mortality of males was higher than mortality of females across all ages (Fig. 3, left panels). There was an overlapping of confidence bands of male and female cub mortality in the model fitted from birth (Fig. 3, upper left panel). However, this result may stem from the imputation of sex as a latent state for the many unsexed individuals (Table 1), which increased uncertainty. The sex difference in mortality is also reflected in the KL divergences (Fig. 2).

In Serengeti, males and females had identical levels of age-independent mortality (c parameter). The other

parameter estimates showed little or no overlap, with the parameter distributions governing early-life mortality overlapping the least. In Hwange, males also had higher mortality than females. However, the difference in mortality was almost entirely due to different age-independent mortality indicated by the c parameter, which was strikingly higher for males than for females. This indicates a source of age-independent mortality that was sex-selective.

Due to the higher male than female mortality in both populations, life expectancy at birth, or at 0·5 year and 1 year of age for the models fitted from these respective ages, was lower for males than for females in both populations (Fig. 3). For the model fitted from birth, the mean PDFs of age at death showed that more male than female deaths occurred up to the age of about 6 years in both populations, although because of different reasons: higher age-dependent male than female mortality in Serengeti and higher age-independent male than female mortality in Hwange (Fig. 2).

Discussion

Estimates of age-specific mortality, particularly for males and for populations disturbed by humans, are often a missing piece of information for developing demographic models for population management. Here, we found that, contrary to expectation, males in the disturbed Hwange population outlived those in the undisturbed Serengeti population by approximately 1 year, and Hwange females outlived Serengeti females by approximately 2 years, despite Hwange's history of lions being killed in accidents, as trophies and as retaliation for raided livestock (Fig. 3) (Loveridge *et al.* 2007). Although adult mortality was, as predicted, higher in Hwange, the difference was too small to compensate for the much lower mortality of cubs in Hwange compared to the Serengeti. Despite mortality varying between the populations, females outlived males in both of them. However, the sex difference was driven by different mechanisms in each locality: lower age-dependent female than male mortality in Serengeti and lower age-independent female than male mortality in Hwange. In the following, we discuss how possible drivers of lion mortality may explain our findings.

THE EFFECT OF HUNTING AREAS BORDERING ON NATIONAL PARKS

The decomposition of adult mortality rates into age-dependent and age-independent mortality revealed that many Hwange lions die of extrinsic causes that kill regardless of age (high c parameters). Particularly for males, who had a higher c parameter than females, one of these causes is likely trophy hunting that occurs at the park boundary (Loveridge *et al.* 2007). Trophy hunting around Hwange National Park recently made international news when the cherished Hwange lion "Cecil" was lured out of the park and killed (e.g. via The New York Times; Rogers 2015). Hunting threatens males who reside at the park boundary but also those that migrate from deeper in the park to the commonly male-depleted edge (Loveridge *et al.* 2007). The signature that trophy hunting leaves on Hwange mortality in the form of high c parameters becomes strikingly clear in the comparison of the two populations. In contrast to what we found for Hwange lions, mortality due to age-independent, extrinsic causes is low in the Serengeti (low c parameters) for both sexes. Mortality of adult lions is instead dominated by the increase in senescent mortality with age (b_0 and b_1 parameters). The difference in the composition of adult mortality between the populations highlights the threat that hunting poses in areas adjacent to protected areas (Loveridge *et al.* 2007). Given the dominant role of trophy hunting in driving mortality of Hwange males, an important future application of our framework will be to refine our mortality estimates by studying how they vary over time with different hunting intensities.

DENSITY DEPENDENCE AS A DRIVER OF LION MORTALITY

Our results confirmed that adult mortality is higher in the disturbed Hwange population than in the undisturbed Serengeti population; however, the difference in adult mortality would potentially be larger where it not for density dependence effects (i.e. the positive correlation between lion population density and their mortality rates). Since the start of the Serengeti study, the population has been growing due to a long-term increase in prey availability. However, growth did not occur continuously but through stepwise increases in mean population sizes, which remained stable across multiple years (Packer *et al.* 2005). This pattern of population growth is created by the dynamics of between- and within-group competition. Only when an exceptionally large cohort of cubs recruits to a pride can a large enough fraction of the pride split off to successfully compete with other prides for space. In years where these conditions are not met, mortality may be density-dependent due to within-group competition (Packer, Pusey & Eberly 2001; Mosser *et al.* 2009). Density-dependent mortality has been indirectly observed for lions in Kruger National Park, where lion density was positively associated with prey biomass density. As prey biomass increased, lion mortality first declined then increased, indicating that mortality increases at greater lion densities (Ferreira & Funston 2010). Over the past 15 years, the Serengeti population size has remained stable (C. Packer, unpublished data), suggesting that the population may have reached carrying capacity. Therefore, density dependence, alongside epizootic diseases, may cause mortality to be relatively high throughout the study period despite the observed long-term population growth and absence of human impact (Packer *et al.* 1999, 2005).

In comparison, the Hwange population has, because of conservation measures, increased by 46% since 2000, with

a 200% increase in the number of adult males since 2004 (A. Loveridge, unpublished data), when the population sex ratio was heavily skewed towards females due to trophy hunting (Loveridge *et al.* 2007). Since 2004, the trophy hunting regime has changed markedly with smaller quotas now in place. However, other sources of anthropogenic mortality including poaching and conflict mortality remain unchanged. Anthropogenic mortality certainly increases the Hwange mortality rates, yet anthropogenic mortality may also keep the population at low densities and thus in a perpetual state of density-independent growth with the associated low age-dependent mortality. Therefore, the levels of adult mortality in the Serengeti and Hwange populations may be driven by two different mechanisms: density dependence in the Serengeti and anthropogenic mortality in Hwange.

Low density is also the most likely explanation for the observed low cub mortality in Hwange. While estimates of cub mortality in both populations fall within the previously reported ranges for other populations (Van Orsdol, Hanby & Bygott 1985; Becker *et al.* 2013), the difference is remarkable and causes a considerable difference in life expectancy at birth between the two populations. In support of this interpretation, cub survival has previously been shown to decrease in the presence of juveniles and subadults in the pride, which in turn depends on female density (Packer, Pusey & Eberly 2001). However, alternative explanations for the difference in cub mortality are also possible. For example, a larger number of early-occurring deaths may go unrecorded in Hwange because cubs may be older at first sighting in the densely vegetated Hwange landscape when compared to the more open Serengeti. Nevertheless, our findings, both for cub and adult mortality, suggest that density dependence may be an important driver of lion mortality. If this is the case, then density dependence needs to be included in demographic models that aim to determine sustainable trophy hunting quota by projecting the population's development. The impact of density dependence on lion mortality may be quantified in future work by using our model to estimate how mortality varies with density.

COVARIATION OF HUNTING MORTALITY WITH CUB AND FEMALE MORTALITY

Hunting of adult males can decrease population size by more than just the trophy head count if hunting mortality of adult males covaries with male mortality by other causes, or with mortality of females and cubs. With rising adult male mortality, cub mortality can increase because of an increase in the rate of pride takeover and infanticide (Whitman *et al.* 2004). Similarly, juvenile mortality can increase because of the eviction of juveniles that are too young to survive on their own (Elliot *et al.* 2014). It is also plausible that adult females defending their young, and resident males fighting intruders, could be fatally injured. Based on these hypotheses, we expected to find higher cub mortality in the population with higher adult male mortality. However, we found the opposite, which could be explained by other factors including density dependence. Longitudinal analyses within the populations may reveal the expected relationship between cub and adult male mortality. Furthermore, the fact that both Hwange males and females have elevated levels of age-independent mortality suggests possible covariation between male and female adult mortality. By carefully increasing the time resolution of our mortality estimates, our framework could in future help unveil these covariations among age- and sex-specific mortality, which are necessary to project lion population development under changed male mortality rates.

CONCLUSION

We have shown how the combination of a Bayesian hierarchical framework with a parametric mortality model can provide mortality estimates for both sexes in species with sex-biased dispersal. We provided mortality estimates for both sexes from two lion populations that experience varying environments, densities and exposures to human impact. In the undisturbed population, natural mortality governs the mortality trajectory of lions, while in the disturbed population, trophy hunting and other anthropogenic mortality left a clear signature on mortality. Because of the detected variation in mortality between the two populations, we pinpoint the study of lion mortality drivers as an important research area. Our framework for estimating lion mortality can be used to test the role of these potential drivers, including density dependence, trophy hunting and covariation of adult male mortality with cub and female mortality. The framework can therefore be employed to refine demographic models built to make population management recommendations for lions, but can also be applied to other species where dispersal behaviour of one or both sexes has hindered the estimation of mortality.

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Data accessibility

The data and R code used in this study have been deposited in the Dryad data repository: doi:10.5061/dryad.2382q (Barthold *et al.* 2016).

References

Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ, USA.

Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C. & Colchero, F. (2016) Data from: Bayesian estimates of male and female African lion mortality for future use in population management. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.2382q.

Becker, M.S., Watson, F.G., Droge, E., Leigh, K., Carlson, R.S. & Carlson, A.A. (2013) Estimating past and future male loss in three Zambian lion populations. *The Journal of Wildlife Management*, **77**, 128–142.

Burnham, K.P. & Anderson, D.R. (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, **28**, 111–119.

Caro, T.M., Young, C.R., Cauldwell, A.E. & Brown, D. (2009) Animal breeding systems and big game hunting: models and application. *Biological Conservation*, **142**, 909–929.

Childs, D., Sheldon, B. & Rees, M. (2016) The evolution of labile traits in sex- and age-structured populations. *Journal of Animal Ecology*, **85**, 329–342.

Clark, J.S. (2007) *Models for Ecological Data*. Princeton University Press, Princeton, NJ, USA.

Clutton-Brock, T. & Isvaran, K. (2007) Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 3097–3104.

Cormack, R.M. (1964) Estimates of survival from the sighting of marked animals. *Biometrika*, **51**, 429–438.

Elliot, N.B., Valeix, M., Macdonald, D.W. & Loveridge, A.J. (2014) Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, **123**, 1049–1056.

Ferreira, S.M. & Funston, P.J. (2010) Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, **37**, 194–206.

Frost, P.G.H. & Bond, I. (2008) The CAMPFIRE programme in Zimbabwe: payments for wildlife services. *Ecological Economics*, **65**, 776–787.

Gelfand, A.E. & Smith, A.F.M. (1990) Sampling-based approaches to calculating marginal densities. *Journal of the American Statistical Association*, **85**, 398–409.

Gompertz, B. (1825) On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, **115**, 513–583.

Griffith, A., Salguero-Gómez, R., Merow, C. & McMahon, S.M. (2016) Demography beyond the population. *Journal of Ecology*, **104**, 271–280.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, **52**, 225–247.

Kullback, S. & Leibler, R.A. (1951) On information and sufficiency. *Annals of Mathematical Statistics*, **22**, 142–143.

Lindsey, P.A., Balme, G.A., Booth, V.R. & Midlane, N. (2012) The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PLoS One*, **7**, e29332.

Loveridge, A., Searle, A., Murindagomo, F. & Macdonald, D. (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, **134**, 548–558.

Makeham, W. (1860) On the Law of Mortality and the construction of annuity tables. *The Assurance Magazine, and Journal of the Institute of Actuaries*, **8**, 301–310.

McCulloch, R.E. (1989) Local model influence. *Journal of the American Statistical Association*, **84**, 473–478.

Mosser, A., Fryxell, J.M., Eberly, L. & Packer, C. (2009) Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**, 1050–1060.

Packer, C., Herbst, L., Pusey, A., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgerhoff Mulder, M. (1988) Reproductive success of lions. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* ed. Clutton-Brock. T.H., pp. 363–383. University of Chicago Press, Chicago, IL, USA.

Packer, C., Pusey, A.E., Rowley, H., Gilbert, D.A., Martenson, J. & O'Brien, S.J. (1991) Case-study of a population bottleneck – Lions of the Ngorongoro Crater. *Conservation Biology*, **5**, 219–230.

Packer, C., Tatar, M. & Collins, A. (1998) Reproductive cessation in female mammals. *Nature*, **392**, 807–811.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brien, S.J., Roelke-Parker, M., Hofmann-Lehmann, R. & Lutz, H. (1999) Viruses of the Serengeti: patterns of infection and mortality in African lions. *The Journal of Animal Ecology*, **68**, 1161–1178.

Packer, C., Pusey, A.E. & Eberly, L.E. (2001) Egalitarianism in female African lions. *Science*, **293**, 690–693.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. (2005) Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, **307**, 390–393.

Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011) Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*, **25**, 142–153.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M. *et al.* (2013) Conserving large carnivores: dollars and fence. *Ecology Letters*, **16**, 635–641.

Pennycuick, C.J. & Rudnai, J. (1970) A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, **160**, 497–508.

Pletcher, S. (1999) Model fitting and hypothesis testing for age-specific mortality data. *Journal of Evolutionary Biology*, **12**, 430–439.

Promislow, D. (1992) Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **247**, 203–210.

R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project. org/.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A. *et al.* (2012) The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, **22**, 17–35.

Rogers, C.M. (1993) *A Woody Vegetation Survey of Hwange National Park*. Published report. Department of National Parks and Wild Life Management, Harare, Zimbabwe.

Rogers, K. (2015) August 29, American hunter killed cecil, beloved lion who was lured out of his sanctuary. The New York Times, p. A4. http://www.nytimes.com/2015/07/29/world/africa/american-hunter-is-accused-of-killing-cecil-a-beloved-lion-in-zimbabwe.html?_r=1.

Schindler, S., Gaillard, J.M., Grüning, A., Neuhaus, P., Traill, L.W., Tuljapurkar, S. & Coulson, T. (2015) Sex-specific demography and generalization of the Trivers–Willard theory. *Nature*, **526**, 249–252.

Seber, G.A. (1965) A note on the multiple-recapture census. *Biometrika*, **52**, 249–259.

Siler, W. (1979) A competing-risk model for animal mortality. *Ecology*, **60**, 750–757.

Smuts, G.L., Anderson, J.L. & Austin, J.C. (1978) Age determination of the African lion (*Panthera leo*). *Journal of Zoology*, **185**, 115–146.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985) Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, **206**, 97–112.

Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004) Sustainable trophy hunting of African lions. *Nature*, **428**, 175–178.

Whitman, K.L., Starfield, A.M., Quadling, H. & Packer, C. (2007) Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology*, **21**,591–601.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed description of the conditional posteriors and acceptance probabilities.

Appendix S2. Method to convert continuous mortality rate into discrete probabilities of survival.

Table S1. Estimated Siler model coefficients for the models fitted form birth, 0·5, and 1 year of age, respectively.

Figs. S1–S3. Traces of mortality and dispersal parameter estimation (models fitted from ages 0, 0·5, and 1, respectively).

Fig. S4. Probability density functions of age at dispersal (model fitted from 1 year of age).