
**Demographic and evolutionary implications of lion
(*Panthera leo*) body size: The application of an
integral projection model to a large carnivore.**

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Abstract

Correlations with body size are ubiquitous across all levels of biological organisation and have been widely researched and documented. This study utilises these associations with body size to parameterise an integral projection model (IPM) for a population of lions (*Panthera leo*). Such a model can be employed to calculate the key quantities of both population ecology and evolutionary biology, therefore providing insight into the eco-evolutionary dynamics of the population. The model can have applications in predicting and exploring dynamical responses to environmental change. An IPM was parameterised for the whole study area to assess its predictive potential and then an IPM was subsequently constructed for grassland plains and another for woodlands to demonstrate its functionality. Survival, successive body size and probability of reproduction all demonstrated significant relationships with body size, whereas litter size and offspring body size exhibited independence. The model was able to predict most quantities to a reasonable level of accuracy but evidence would suggest that substantially more accuracy would be gained through the inclusion of social structure. This provisional construction of an IPM does, however, indicate that both ecological and evolutionary processes affecting body size are important to the dynamics of a large carnivore.

Keywords: integral projection models; body size; African lion; *Panthera leo*; eco-evolutionary dynamics.

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1. Introduction

Body size is frequently a central consideration in studies of predatory performance, having notable effects on fitness, motility and supremacy (MacNulty *et al.* 2009), but also has an important influence on their potential prey niche (Funston *et al.* 1998, 2001), territory size (Reiss 1988) and intra- and inter-specific competition (Stamps & Krishnan 1994). The African lion (*Panthera leo*) is no exception to these effects yet there has been little research conducted on their body size and, being social carnivores, it is possible that complex correlates of body size exist. There is an ongoing concern surrounding hunting of lions which is closely linked to body size, particularly in males where the largest are most desirable, and so any insight into how dynamics will change with the removal of a particular subset of the population could be particularly valuable. It should therefore prove interesting to examine the ultimate impact that body size has on lion dynamics, not only for furthering our understanding, but also in terms of applied science. This study will aim to gain insight into the influence lion body size has by modelling the consequent dynamics.

The most fundamental association with body size is that of fitness (Brown *et al.* 1993); how do survival and reproductive success correspond to body size? The individual consequences of having a larger body size on vital processes, for example hunting, pursuing, capturing and killing prey, are what determine the impact on overall fitness. MacNulty *et al.* 2009 addressed these relationships in wolves (*Canis lupus*) finding that the net predatory benefit of possessing a larger body size is limited by the consequent hindrance on mobility. A larger body size can increase strength allowing larger prey to be overcome, but this causes an associated reduction in the ability to pursue prey; this therefore imposes an evolutionary limit on how large the predator can become. In lions, the smaller females are superior at hunting the fleet-footed prey, whereas the larger males tend to stand and fight (Funston *et al.* 2001). Lion sexual dimorphism (Schaller 1972), with males and females exhibiting different hunting behaviours, emulates that observed in wolves between differential body sizes (MacNulty *et al.* 2009).

In addition to impacting on their capacity to hunt, body size is also likely to influence lion interactions with other lions and other species. The African lion is nominally a social carnivore living in prides of typically about 13 individuals consisting of a male coalition, a group of females and any associated offspring (Starfield *et al.* 1981). To takeover a pride, and furthermore maintain their residence, a male coalition must fight with any competing males (Packer & Pusey 1983a) so an increased body size is likely to be an advantage. After a takeover, the new males will kill any existing cubs to bring the females back into oestrous enabling them to sire their own

cubs (Packer & Pusey 1983b). The females may be able to prevent this by grouping together and defending the cubs (Packer & Pusey 1983a) rendering an increased body size favourable to females as well. A lion will try to appropriate a kill in preference to hunting their own, particularly from leopards and cheetahs (O'Brien *et al.* 1986), and will also suffer from the same threat shrouding their food, namely from spotted hyenas, African wild dogs and vultures (Schaller 1972), and, as a result, being the largest predator in the African savannah has its benefits for both sexes (Owen-Smith & Mills 2008).

The link between body size and resource availability is intuitive. Since all lions within a pride share a kill equally (Caraco & Wolf 1975), the influence of resource availability should have a homogenous effect on body size across a pride but will differ between prides. Packer *et al.* (2005) observed dissimilarities in population dynamics between Serengeti prides inhabiting plains and woodland territories. The degree to which the vast Serengeti migration of wildebeest, zebra and Thompson's gazelle visits each habitat is dependent on rainfall, therefore environmental conditions influence the relative food availability between different prides. This effect is not so abrupt in the lions of the Ngorongoro Crater due to the resident herds (Kissui & Packer 2004). It has also been documented that lions hunt more successfully under increased vegetative cover (Hopcraft *et al.* 2005). Dynamics influenced by body size should be accordingly disparate in areas with differing distributions of body size and could consequently go some way to describing any observed distinctions (Packer *et al.* 2005).

There is clearly a wealth of support for the possibility that body size influences fitness in lions, manifesting as survival and reproductive success, and therefore affects the population growth rate and structure. This implies that some form of selection acts on body size and that the distribution of body sizes in the population changes over time. Being able to consider all of these interactions and processes together crosses the border between population ecology and evolutionary biology (Pelletier *et al.* 2009). Although traditionally considered to be separate disciplines, they can both provide an insight into the dynamics of a population, despite having apparently contrasting focuses (Ezard *et al.* 2009). The collusion of these two areas of research recently resulted from the realisation that ecological and evolutionary processes can actually occur on the same timescale (Hairston *et al.* 2005), as opposed to differing by an order of magnitude (Slobodkin 1961), consequently formulating the theory of eco-evolutionary dynamics (Dercole *et al.* 2006; Pelletier *et al.* 2009; Schoener 2011). This study will utilise this new angle for researching population dynamics to investigate the influence body size holds in a population of lions and, hence, calculate the focal quantities of both disciplines by employing an integral projection model (IPM).

An IPM tracks the distribution of a quantitative character over time and hence the population size, which can then provide insight into the dynamics of the character, population structure and life history variables (Easterling *et al.* 2000; Caswell 2001). This model structure can therefore offer the insights desired by both population ecologists and evolutionary biologists, as well as the potential for understanding the associations between all the quantities calculated from the model and how these responses interact (Coulson *et al.* 2010).

Traditional matrix models require that the character falls into discrete classes, which means continuous traits have to be classified into distinct groups. In most cases, these will not be classes defined by the life history of the species, but rather arbitrary groups to meet the purpose, therefore unavoidably generating some degree of error. The IPM avoids this inaccuracy by maintaining the continuous nature of these traits, which also improves the comparability of multiple models applied to the same or different species (Ellner & Rees 2006). This IPM will use lion body size as the quantitative trait, represented by heart girth measurement. Adult males weigh approximately 170kg and females 120kg, but with significant variation, and individuals continue growing until they are six years old (Schaller 1972). Body size is a relatively useful quantity within a population as it is continuous, universal and can be measured consistently. These properties are valuable in that they allow this measurement to be interpreted in a mathematical manner (Peters 1983), in addition to being particularly practical in matrix population models (Caswell 2001).

As eco-evolutionary dynamics is a comparatively new concept, models linking ecological and evolutionary change exist (e.g. Hairston *et al.* 2005) but essentially remain an untapped resource, having only been applied to a small subset of all the populations and systems with sufficient available data (Ezard *et al.* 2009). This situation is exacerbated further with IPMs, which have been mostly unexploited despite the vast potential they provide for studying the influence of environmental change on population dynamics. They have predominantly been employed to address questions concerning plant species (e.g. Rees & Rose 2002; Childs *et al.* 2003; Kolb *et al.* 2010) but have recently been applied to mammalian species (Coulson *et al.* 2010; Ozgul *et al.* 2010).

Ozgul *et al.* (2010) used two IPMs parameterised for a yellow-bellied marmot (*Marmota flaviventris*) population to identify the key factors behind the observed sudden increase in the population growth rate. The marmots were found to have been emerging prematurely from hibernation and to be weaning their young earlier, which both contributed to allowing more time for growth. The consequent increased average body mass conferred an increase in adult survival and, hence,

the inflated growth rate of the population. This study thus demonstrated how observed shifts in population dynamics can be as a result of simultaneous ecological and evolutionary changes.

Coulson *et al.* (2010) provide an example of how IPMs can be effectively used to make predictions of population structure and growth and for key life history quantities by making matrix approximations of the model. In the illustrative IPM, the associations between body mass and: survival, ontogenetic development, fertility and inheritance were parameterised for a population of Soay sheep (*Ovis aries*). The predicted response of various properties of the population were then calculated by individually and independently perturbing each parameter within the associations to isolate which aspects of the assembled population are most influential over dynamics.

An important feature of Coulson *et al.*'s (2010) study is the comparison between observed and predicted quantities indicating that IPMs can make reliable estimates demonstrating the potential value they can present to studies aiming to quantify how population dynamics are affected by phenotypes and environmental factors (Ezard *et al.* 2009). This consequently implies that an IPM could serve as a proxy for traditional population ecology and evolutionary biology methods for making the same calculations allowing speculative conclusions to be drawn from populations and systems lacking the same degree of data availability. Applying IPMs across a broader range of species populations, and even systems, should therefore be a primary aim to investigate the applicability of the method and to quantify truly its potential. The study conducted here will thus endeavour to contribute to this objective by extending into carnivores, which has not previously been attempted. The IPM will be parameterised for the lion population spanning Serengeti National Park and Ngorongoro Conservation Area taking a similar approach to that applied by Coulson *et al.* (2010).

Parameterising the IPM requires that the associations of body size with: survival, subsequent body size, fertility and offspring body size are found. All of these responses have been shown to demonstrate a positive relationship with body mass in mammals (Blueweiss *et al.* 1978). Ontogenetic development is a function of body mass, meaning current body mass influences future body mass, as are both maximum and average life span, suggesting survival increases with body mass. The ambiguous nature of how body size affects the predator-prey relationship makes it difficult to determine the shape of the association with predatory success. That given, up to a limit imposed by the negative relationship with mobility (MacNulty *et al.* 2009), an increase in body size would be expected to cause an increase in fitness due to improved predatory ability. A positive correlation between body size and fitness infers that a larger body

size would increase an individual's probability of survival which would indirectly increase reproductive success (Gittleman 1985).

Millar (1977) showed there to be no correlation between litter size and body mass but Wootton (1987) demonstrated that age at first reproduction is partially attributed to body mass suggesting there is some significant effect of body size on whether an individual reproduces or not. Both total litter mass and individual offspring body mass supported a good power relationship with maternal body mass (Blueweiss *et al.* 1978); individuals tend to produce offspring of similar body mass to themselves suggesting that body mass is in some part maternally inherited.

This study will, firstly, analyse the nature of the mentioned relationships with heart girth in lions. These associations will then be used as the framework for an IPM enabling the calculation of key population quantities. An IPM will be constructed for the whole lion study population and then each for the population in the plains and woodland habitat. The aim is primarily to develop our understanding of lion body sizes, but furthermore to demonstrate the application of an IPM to a carnivorous mammal population.

2. Methods

2.1. Study system

2.1.1. Study area

The study area covers 2000 km² of Serengeti National Park and the Crater floor within the Ngorongoro Conservation Area in Tanzania (Schaller 1972). This area is comprised of three distinct habitats: grassy plains, wooded grasslands and the Crater floor. The Crater floor is predominantly open grassland with wooded patches and is a closed population (Pusey & Packer 1987). The grassy plains, denoted as plains from here on, are defined as grasslands largely dominated by: *Pennisetum*, *Sporobolus*, *Themeda*, *Andropogon* and *Cynodon* spp. and are consistently frequented by Grant's gazelle and warthogs. In contrast, the wooded grasslands, now referred to as woodland, are grassy regions regularly interrupted by scattered trees, namely *Acacia*, *Commiphora*, *Balanites* and *Albizia* spp. and tend to have larger populations of buffalo, hartebeest and topi. Both the plains and woodland habitats lie within the range covered by the annual migration of wildebeest, zebra and Thompson's gazelle (Schaller 1972; Packer *et al.* 2005).

2.1.2. Study species

The African lion (*Panthera leo*) is a major predator within the Serengeti ecosystem and has been the subject of much research. The population within the study area has been comprehensively studied for multiple generations and has significantly enhanced and expanded our understanding of lion biology and dynamics (e.g. Schaller 1972; Packer *et al.* 2005; Fryxell *et al.* 2007).

Lions are social carnivores and exist as either a member of a pride or a nomad associated with no pride (Schaller 1972). Males tend to form coalitions, where larger groups are more successful in residence (Packer & Pusey 1983a) monopolising a group of females (Smuts 1978). Group living adds considerable complexity to studies of lions and therefore, as the purpose of this study is to trial the IPM method for a large carnivore, this aspect will be omitted from the model to prevent over-complication at this stage.

2.2. Integral projection model

The concept of an integral projection model (IPM) is that the distribution of a continuous, ubiquitous character over discrete time can be utilised to approximate key population values, including life history descriptors and quantitative genetic quantities (Easterling *et al.* 2000). The IPM employed here takes the form of a univariate, deterministic integral model:

$$n(z, t + 1) = \int [S(z', t). G(z|z', t) + R(z', t). D(z|z', t)]. n(z', t) dz'$$

Eqn. 1

The distribution of heart girths within the population at time t , $n(z', t)$, is subjected to the predicted effects of the processes likely to significantly influence the distribution to obtain the distribution of heart girths at time $t+1$, $n(z, t + 1)$ (eqn. 1). $G(z|z', t)$, $S(z', t)$, $D(z|z', t)$ and $R(z', t)$ are approximated through statistical analysis of the long term lion data. The probability of survival given a particular heart girth, $S(z', t)$, is applied to the character distribution and then the heart girth of subsequent survivors at time $t+1$ is predicted given their heart girth at t , $G(z|z', t)$. This is combined with the heart girth distribution after reproductive allocation; the likely number of individuals added to the population is predicted given the heart girth distribution at t , $R(z', t)$, and their likely heart girth is assigned given the inheritance of the trait $D(z|z', t)$. The trait transition rates, $G(z|z', t)$ and $D(z|z', t)$, are probability density kernels which predict the probability of the individual and of their offspring, respectively, having heart girth z at time $t+1$ given having a heart girth of z' at time t .

To enable the IPM to be utilised in the same way as matrix population models, a discrete approximation of the integral was constructed (eqn. 2). The IPM is computed by iterating a matrix but in the traditional way of calculating integrals using very small intervals and would therefore not be considered to be a discrete model (Ellner & Rees 2006).

$$\mathbf{n}(t + 1) = \mathbf{A}(t). \mathbf{n}(t) = [\mathbf{G}(t). \mathbf{S}(t) + \mathbf{D}(t). \mathbf{R}(t)]. \mathbf{n}(t)$$

Eqn. 2

Increasing the matrix dimensions increases the accuracy of the predictions formulated from the model (Ellner & Rees 2006) therefore small heart girth intervals were used as the units of the matrix model. The heart girth values ranged from 90% of the minimum observed value to 110% of the maximum and were divided into 100 equal classes to give an acceptable degree of accuracy. The heart girth distributions at time t and $t+1$ are contained within the vectors $\mathbf{n}(t)$

and $\mathbf{n}(t + 1)$, respectively. The associations of the demographic rates with heart girth, functions $S(z', t)$ and $R(z', t)$, were approximated to diagonal matrices $\mathbf{S}(t)$ and $\mathbf{R}(t)$, respectively. The trait transition rate kernels, $G(z|z', t)$ and $D(z|z', t)$, were approximated to square matrices, $\mathbf{G}(t)$ and $\mathbf{D}(t)$ respectively, with columns summing to unity. These matrices are all incorporated into one matrix, $\mathbf{A}(t)$, which was then employed in matrix multiplication to iterate the model.

2.3. Data

The lions within the study area have been studied in detail at an individual and pride level since 1961 from the Crater and 1966 from the Serengeti (Schaller 1972; Bertram 1978); the study is currently directed by Professor Craig Packer. The demographic data were collected predominantly from direct observations. Each study pride is located about once a week and, since 1984, pride location has been primarily enabled through the utilisation of a single radio-collared female within each pride. The identity of each individual was known from their unique whisker pattern supplemented by any ear notches and obvious scars, so all individuals present at each sighting were recorded. In this way, pride identity and structure was inferred over time. It is significantly more difficult to collect data on males than females due to the differences in life history; males will commonly leave their natal pride when they are between 2-3 years and will remain nomadic until they are able to take over another pride (Pusey & Packer 1987). This difficulty is conveyed in the volume or reliability of data for various variables required for model construction, therefore only data from the female cohort was used.

An individual was classified as having died when it was not seen for over six months, after which the last seen date was taken to be the death date. Maternity was inferred from observations of pregnancy, birth, nursing or lactation stains, or a combination of these indicators. As females within a pride tend to become reproductively synchronised (Estes 1991), it was often impossible to identify an exact mother for each cub so these individuals were assigned multiple mothers to cover all possibilities.

Direct measurement of lion weight was inconvenient or not possible given the associated risks of immobilisation and the sheer size of a lion. It was therefore more practical to use a linear measure of weight and the most consistent measurement of lion body size was found to be the chest circumference around the heart (Bertram 1975). This technique was adopted in 1984 as an additional measurement collected from immobilised individuals, when possible. Radio-collared females were immobilised more frequently than other individuals; the youngest adult female in

the pride was selected due to their long life expectancy, but may occasionally be recently emigrated sub-adult females. Despite heart girth being a reasonable predictor of lion body weight (Bertram 1975), the raw heart girth measurements will be used to avoid incurring further unreliability.

2.4. Model parameterisation

2.4.1. Model fitting

All analyses were run in R version 2.12.1 (R Development Core Team 2010) using the lme4 package (Bates *et al.* 2011). With the exception of the growth function, the details of which are explained below, all associations were tested using a general linear mixed effects model (glme) under the appropriate error structure. Heart girth measure was held as the fixed effect and individual identity, age, measurement year and birth year were added as random effects; all these variables were considered to be potentially influential over heart girth. Individual identity was included to account for repeat data points for the same individual and age to account for the variation in size conferred by different ages. Birth and measurement year also potentially contribute to variance as conditions within these years were likely influence fitness and therefore have some effect on vital rates (Packer *et al.* 2005).

For each model, if the association with heart girth was found to be non-significant, then heart girth was removed from the model with the aim of achieving the minimal adequate model to explain the data (Crawley 2007). It was not tested whether the random terms contributing to the variance were significantly different from zero as, ultimately, the model will be used for making predictions, and not to assess which components are important sources of variation. Any unimportant terms are estimated as essentially zero and therefore have a negligible effect on predictions (Ozgul *et al.* 2010).

2.4.2. Survival function

An individual was considered to have survived if it was recorded as still being alive one year after their heart girth measurement was taken and to have died if its death date was recorded within this time, therefore rendering survival a binary variable. The association describing survival rate of an individual, given their heart girth at t , was found by fitting a glme under a binomial error structure to the survival data.

2.4.3. Growth kernel

The growth kernel required for the IPM must describe the probable heart girths at $t+1$ given the mean heart girth at t ; however, when a repeat measure of an individual's heart girth has been recorded, the time between the measures is not consistent, ranging from months to years. In the absence of suitable data for direct construction of the mean growth function, it can be derived from heart girth as a function of age. Heart girth was fitted as a quadratic function of age at measurement, due to the apparent curvature in the relationship. The data exhibit two distinct growth phases, therefore a separate function was fitted to each phase to capture the data more effectively.

The mean growth function was then derived using age as a surrogate for time. For the range of heart girths possessed by individuals within each growth phase, the appropriate function was used to predict what the heart girth at time $t+1$ would be. This involved back fitting from the model where the heart girth was given to the function to find the corresponding age, and then a year was added to this age and put into the function to predict the next heart girth. A quadratic function allows the possibility of two valid heart girth measures at $t+1$ for one measure at t , therefore preventing the construction of a smooth function. This was accounted for by fitting a linear model to all the legitimate values predicted by both functions; that is, those steps in heart girth actually exhibited by the lions. The number of points predicted from the function was proportional to the length of time spanned by the associated growth phase; this enabled the mean growth function to be weighted appropriately towards the longest growth period. The linear model fitted to this consequent set of predicted heart girths at time t and their predicted heart girths at time $t+1$ for both growth phases describes the mean growth across the full range of observed heart girth measures.

The variance of the mean growth function was estimated using the data from the few individuals with repeat measures. This was found by fitting a linear model to the second heart girth against the first heart girth, accounting for time between measures and age at first measurement. The minimal adequate regression of the squared residuals against heart girth was used to find the variance around the mean growth function for use in the construction of the growth kernel.

The probability density kernel of the transition rates between heart girths at t and $t+1$ assumed a normal distribution (eqn. 3).

$$G(t, z|z') = \frac{1}{\sqrt{2\pi\sigma_g(z)^2}} e^{-\frac{(z' - \mu_g(z))^2}{2\sigma_g(z)^2}}$$

Eqn. 3

Where $\mu_g(z)$ is the mean heart girth at t+1 predicted using the mean growth function, z' is the original heart girth and $\sigma_g(z)^2$ is the variance.

2.4.4. Fertility function

For each female, it was recorded whether they were observed to have reproduced within the year after their heart girth measurement was taken and, subsequently, the number of female cubs in that litter that survived to their first birthday. As cub mortality is so high (Packer *et al.* 1998), it is common for cubs to die before they are recorded so the presence of a litter was inferred from indicators, as previously mentioned. It was therefore appropriate to divide fertility into a binary variable of absolute reproduction and a count of the number of surviving female cubs. Survival of cubs to their first birthday is considered to be a good marker as the litter size will be accurately known by this time and, after one year, survival greatly increases (Packer *et al.* 1998) suggesting that these individuals are likely to have a significant impact on the total population. In the cases where maternity was not absolutely known, the mothers were taken as having reproduced as the majority will have exhibited signs of reproduction but, due to synchronised births and communal nursing (Packer *et al.* 2001), their exact cubs were difficult to identify. The mother was then assigned cubs in proportion to the number of other possible mothers.

A glme of whether an individual reproduced or not as a function of heart girth was fitted under a binomial error structure and another under a Gaussian error structure to the number of surviving cubs. A Gaussian error structure was used, as opposed to Poisson, due to the proportional litter sizes created by assigned cubs to possible mothers. The probability of reproduction was then multiplied by the mean litter size to give the expected recruitment of an individual with a given heart girth.

2.4.5. Inheritance kernel

There was a subset of measured females for which the heart girth of one of their female offspring was also recorded and these data were used to construct the mean inheritance function. The offspring measures were taken across a range of ages so this was accounted for by using the model of heart girth as a function of age. The actual measured offspring heart girth was taken as

a proportion of the predicted heart girth for that age and this proportion was then applied to the predicted heart girth for a one year old. This approximated heart girth of the one year old offspring was then regressed against the heart girth of the mother using a glme under a Gaussian error structure. The variance was calculated by regressing the squared residuals of the inheritance model against heart girth.

The probability density function describing inheritance rates between mother and daughter was constructed using the same method as for the growth kernel (eqn. 4).

$$D(t, z|z') = \frac{1}{\sqrt{2\pi\sigma_d(z)^2}} e^{-\frac{(z' - \mu_d(z))^2}{2\sigma_d(z)^2}}$$

Eqn. 4

Where $\mu_d(z)$ is the mean heart girth of offspring recruited to the population at t+1 at their first birthday as predicted using the mean inheritance function, z' is the mother's heart girth and $\sigma_d(z)^2$ is the variance.

2.5. Key population biology parameters

2.5.1. Calculation

The matrix approximation of the model was used to predict the values of key quantities. The equations utilised to estimate the quantities are detailed in table 1. The various quantities calculated by the model were also calculated from the data to enable judgement on the integrity of the IPM.

The population growth rate at equilibrium is estimated as the dominant eigenvalue of the matrix and the dominant real right and left eigenvectors are estimated as being the stable distribution and reproductive value of heart girth, respectively. The left eigenvector is the right eigenvector of the transpose of the matrix. The stable heart girth distribution is scaled to sum to unity, as is the actual distribution of heart girths to allow comparison. The reproductive values of the heart girths are scaled to be relative to the first value (Caswell 2001).

Table 1 Key quantities calculated from the matrix approximation of the IPM and, in most cases, also from the data for comparison. Where: \mathbf{z} = vector of heart girth midpoints, $\mathbf{n}(t)$ and $\mathbf{n}(t + 1)$ = vector of number of individuals across heart girth bins at time t and $t+1$ respectively, $\mathbf{n}_o(t)$ and $\mathbf{n}_p(t)$ = vector of offspring and parental population size, respectively, across heart girth bins at time t , \mathbf{x} = vector of ages, $\mathbf{S}(t)$ and $\mathbf{R}(t)$ = matrix of survival and fertility rates.

Quantity	Description	Calculation
\bar{z}	Mean heart girth	$\frac{\sum \mathbf{z}\mathbf{n}(t)}{\sum \mathbf{n}(t)}$
$\sigma^2(\bar{z})$	Variance of mean heart girth	$\frac{\sum \mathbf{z}\mathbf{z}\mathbf{n}(t)}{\sum \mathbf{n}(t)} - \left(\frac{\sum \mathbf{z}\mathbf{n}(t)}{\sum \mathbf{n}(t)}\right)^2$
λ	Population growth rate	$\frac{\sum \mathbf{n}(t + 1)}{\sum \mathbf{n}(t)}$
T	Generation length	$\frac{\sum(\sum(\mathbf{x}\mathbf{n}_o(t))\mathbf{n}(t))}{\sum(\mathbf{n}_o(t)\mathbf{n}(t))}$
\bar{S}	Mean survival rate	$\frac{\sum \mathbf{S}(t)\mathbf{n}(t)}{\sum \mathbf{n}(t)}$
\bar{R}	Mean recruitment rate	$\frac{\sum \mathbf{R}(t)\mathbf{n}(t)}{\sum \mathbf{n}(t)}$
\overline{LRS}	Mean lifetime reproductive success	$\sum \mathbf{n}_o(t)\mathbf{n}(t)$
$\sigma^2(d)$	Dispersion of reproduction	$\frac{\sum(\sum(\mathbf{x}\mathbf{x}\mathbf{n}_o(t))\mathbf{n}(t))}{\sum \mathbf{n}_o(t)\mathbf{n}(t)} - \left(\frac{\sum(\sum(\mathbf{x}\mathbf{n}_o(t))\mathbf{n}(t))}{\sum \mathbf{n}_o(t)\mathbf{n}(t)}\right)^2$
h^2	Heritability	$2 \left(\frac{Cov(z_o z_p)}{Var(z_p)} \right)$
VS	Viability selection	$\frac{\sum \mathbf{z}\mathbf{S}(t)\mathbf{n}(t)}{\sum \mathbf{S}(t)\mathbf{n}(t)} - \frac{\sum \mathbf{z}\mathbf{n}(t)}{\sum \mathbf{n}(t)}$
FS	Fertility selection	$\frac{\sum \mathbf{z}\mathbf{R}(t)\mathbf{n}(t)}{\sum \mathbf{R}(t)\mathbf{n}(t)} - \frac{\sum \mathbf{z}\mathbf{n}(t)}{\sum \mathbf{n}(t)}$

2.5.2. Perturbation analysis

By perturbing individual components of the model, the sensitivity of various quantities to changes in independent variables or transitions can be examined. Transitions within the combined matrix, $\mathbf{A}(t)$, were individually and independently perturbed by 1% and the quantity

was recalculated for each altered matrix (Coulson *et al.* 2010). The sensitivity of a parameter, p , to small increases in transitions rates are given by a partial derivative, where matrix element, a_{ij} , is perturbed to produce a new estimate of the parameter, p' (eqn. 5).

$$\frac{\partial p}{\partial a_{ij}} = \frac{p - p'}{0.01}$$

Eqn. 5

Perturbing individual matrix elements of the model causes the eigenvalues and eigenvectors to be altered, hence changes the population growth rate, stable distribution and reproductive value of heart girth; as a consequence, all the other quantities calculated using these values will also change (Caswell 2001). Perturbation analyses were used to inspect how the predictions for population growth rate, generation length and the strength of selection were influenced.

3. Results

3.1. Model parameterisation

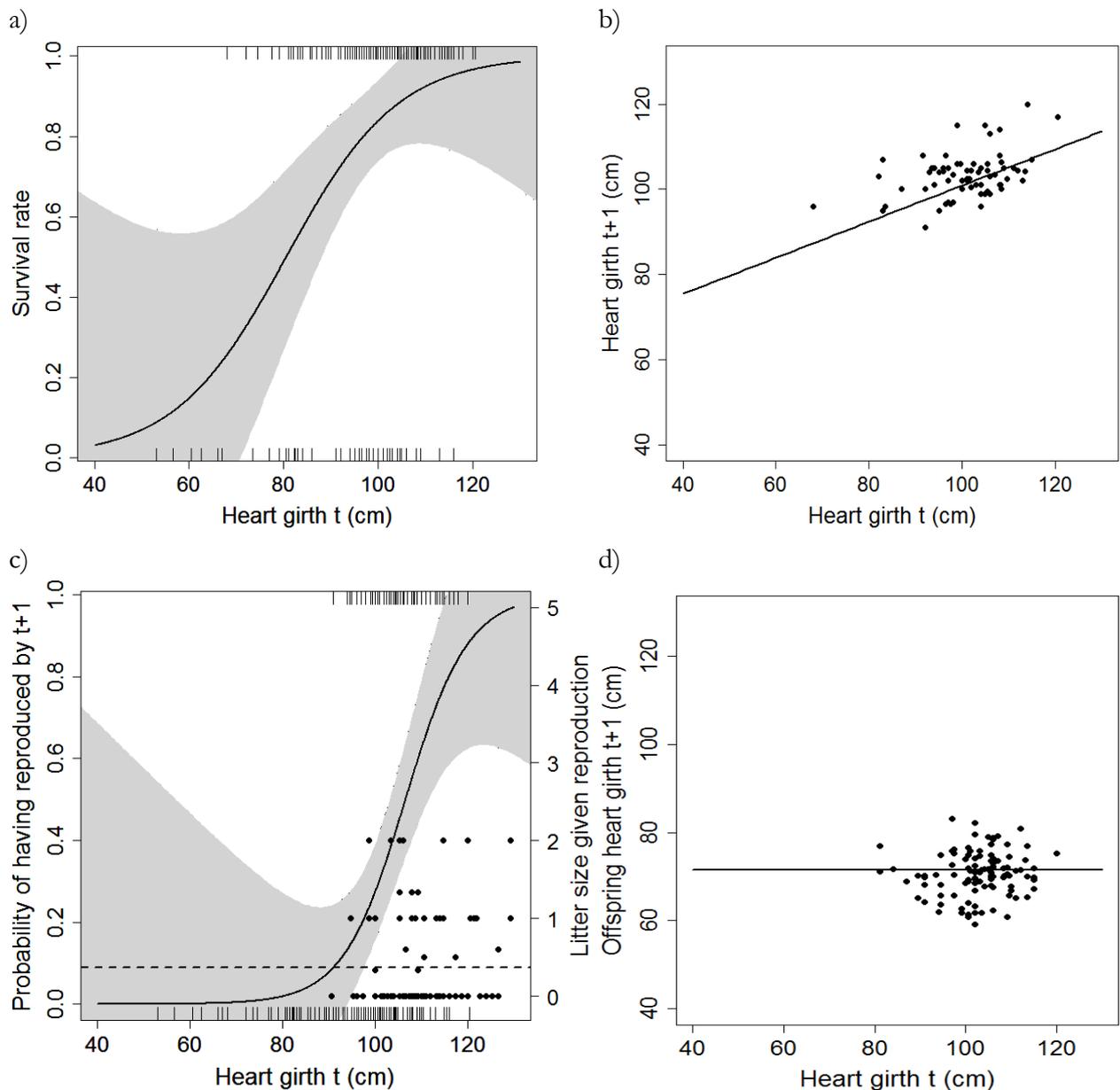


Figure 1 Fitted statistical functions to the data between heart girth measurement at t and: a) probability of survival b) heart girth at $t+1$, c) fertility rate (and consequent litter size) and d) offspring heart girth at $t+1$. Rugs above and below the graph represent the raw data for: a) survival and death and c) reproduction and no reproduction, respectively. Points represent the raw data, lines represent the predictions from the statistical models and the shaded areas indicate 95% confidence intervals; confidence intervals were omitted from the mean growth and inheritance functions as they were at least partially derived rather than fitted. In the case of the fertility function (c), the rugs and line refer to the probability of reproduction (left axis) whereas the points and dashed line refer to the average litter size given reproduction (right axis).

The relationships used to construct the IPM are presented in figure and the parameterised associations are detailed in the appendix (tab. A1).

3.1.1. Survival function

The logistic regression of the probability of survival against heart girth demonstrates that survival rate significantly increases with heart girth size (fig. 1a), rising rapidly from a heart girth of approximately 65cm and reaching a plateau at 102cm. Maximal survival rates are maintained between the ages of 3 and 12yrs (fig. 2) and, as survival increases with heart girth, the highest survival rates are estimated for individuals between 7 and 8yrs which possess the greatest heart girths.

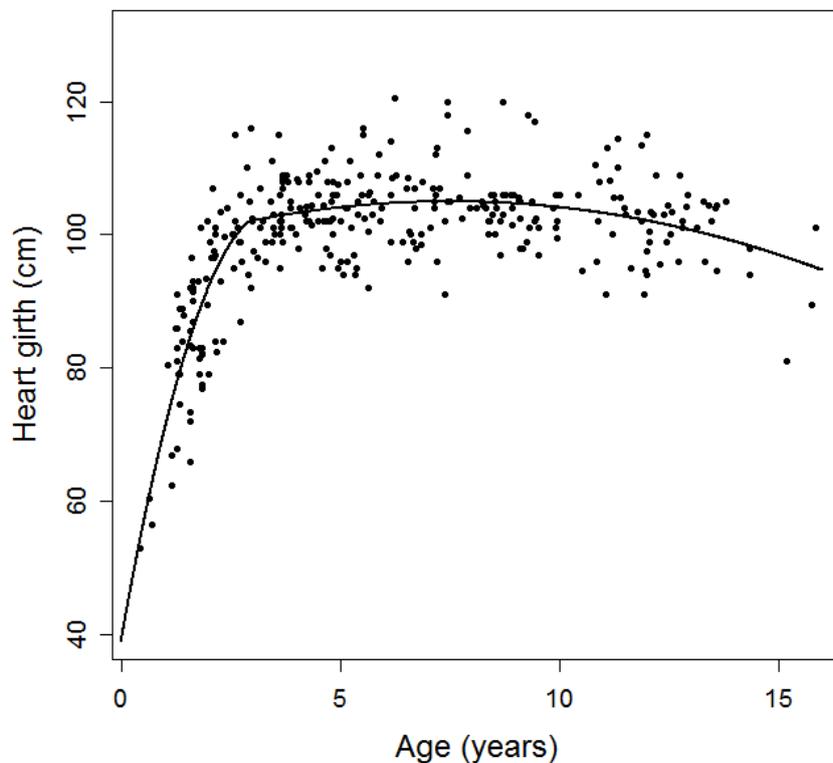


Figure 2 Heart girth measurement as a function of age where the points represent the raw data and the lines represent the fitted functions. For ages ≤ 3 yrs: $z = -5.493x^2 + 37.600x + 39.072$ and for ages > 3 yrs: $z = -0.1424x^2 + 2.1355x + 96.9735$, where z is heart girth measure in cm and x is age in years.

3.1.2. Growth kernel

The relationship between heart girth measurement and age was divided into two sections, below and equal to 3 years and above 3 years (fig. 2), for which both exhibited heart girth measurement to be a quadratic function of age but with differing parameter values. The two functions demonstrate that considerable growth occurs in the first 3 years of a lioness's life, after which

changes in heart girth occur more slowly exhibiting an increase followed by a gradual decline. Maximal heart girths are achieved between the ages of 3 and 12, peaking at approximately 104cm.

The number of growth points predicted from the two functions was relative to the length of the growth period, hence there were proportionally more points from the latter function, which spanned 13 years as opposed to 3, despite covering a smaller range of heart girth measures. The mean growth function fitted to these points predicts that, on average, a lioness will increase in body size each year, gaining more per year at lower body sizes, until a heart girth of approximately 102cm is achieved, after which body size will decline by the next year (fig. 1b; slope=0.441). The linear regression fitted to the repeated heart girth measures exhibited a significant correlation between heart girth at the first time step and that at the next, but was independent of age at the first measure and the time between measures. The squared residuals of this model remained constant with heart girth and therefore the intercept of the regression with 1 was taken as the variance around the mean growth function calculated as 21.05cm² (see appendix; tab. A1).

The mean growth function and associated variance was used to construct the probability density function describing transition rates between heart girth at t and $t+1$ (fig. 3: $G(t, z|z')$). This is based on the normal distribution, therefore assumes heart girth at the next time step to most likely be near the heart girth at t . The kernel predicts that heart girths are expected to mostly fall within the range of 85-120cm, peaking just after 100cm.

3.1.3. Fertility function

A logistic regression demonstrated that the probability of reproduction significantly increased with heart girth, although litter size was found to be independent simply averaging 0.373 female cubs (fig. 1c). A threshold heart girth seems to exist at approximately 80cm, before which an individual will not reproduce and after which the probability of reproduction rapidly increases. Since reproduction is predicted to be more likely at the highest heart girths, the females with the greatest fecundity are estimated to be between 3 and 12yrs (fig. 2). Cub survival is low, with most individuals in a litter not surviving to their first birthday (0.368).

3.1.4. Inheritance kernel

There was no significant association found between offspring and mother heart girth and, therefore, mother's heart girth was eliminated from the model to find the mean offspring heart girth at their first birthday to be 70.74cm (fig. 1d). The squared residuals of the mean inheritance

function remained constant with heart girth so the linear model was reduced to a regression against 1 where the intercept was taken as the variance (14.77cm^2 , see appendix; tab. A1).

The probability density function describing the transition rates of heart girth between mother and daughter estimated that offspring heart girth should fall between 60 and 80cm at their first birthday, with a high probability of being very near to 70cm (fig. 3: $D(t, z|z')$).

3.2. IPM

The parameterised component of the IPM in equation 1 with which the heart girth distribution is multiplied by is presented in figure 3.

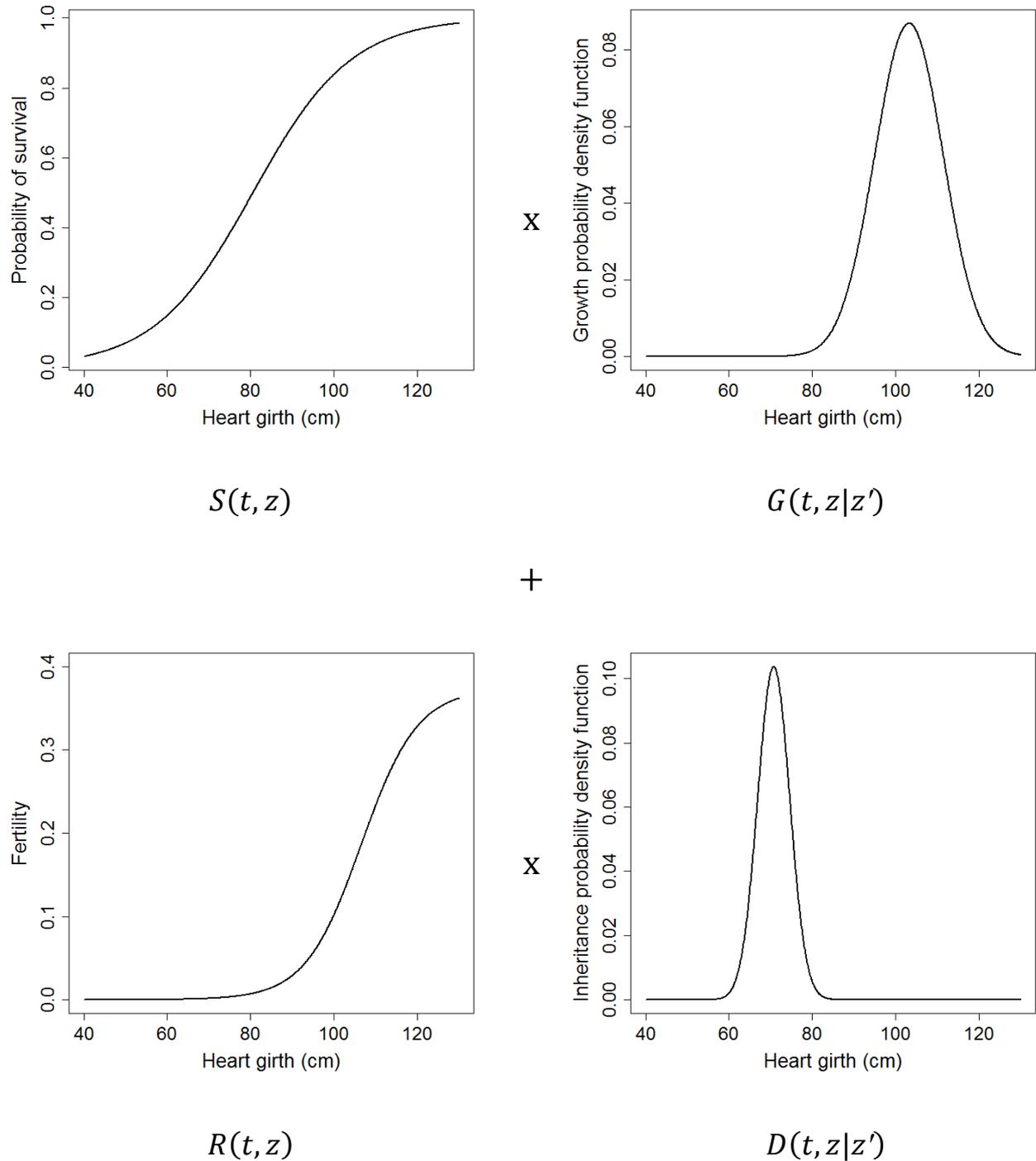


Figure 3 The parameterised IPM with which the distribution of heart girths at t , $n(t, z')$, are multiplied by to find the distribution at $t+1$, $n(t+1, z)$.

3.2.1. IPM predictions

Table 2 The observed values from the data and the predicted values from the model for key quantities. The calculated difference quantifies how the predicted value differs from the observed value with negative values indicating a lower predicted value.

<i>Quantity</i>	<i>Observed value</i>	<i>Predicted value</i>	<i>Difference (%)</i>
\bar{z}	99.9131 cm	97.2085 cm	-2.71
$\sigma^2(\bar{z})$	112.6027 cm ²	128.1526 cm ²	13.81
λ	1.001348 yr ⁻¹	0.880429 yr ⁻¹	-12.08
T	6.8626667 yrs	7.72943 yrs	12.63
\bar{S}	0.805556 yr ⁻¹	0.773694 yr ⁻¹	-3.96
\bar{R}	0.127311 yr ⁻¹	0.106735 yr ⁻¹	-16.16
\overline{LRS}	1.468496	0.647613	-55.90
$\sigma^2(d)$		37.3848	
h^2		0	
VS		2.295057	
FS		5.428868	

The values predicted by the model and those calculated from the actual data are displayed in table 2. Many estimates made from approximating the IPM as a matrix model were reasonably close to the observed values, whilst others corresponded less well. The best approximations were made for mean heart girth and survival rate (<4% difference) but population growth rate, recruitment rate, heart girth variance and generation length were also fairly well predicted (<17% difference). The largest disparity between observation and prediction was in mean lifetime reproductive success where the observed value was two times greater than the predicted value. In general, the model underestimates values but overestimates heart girth variance and generation length.

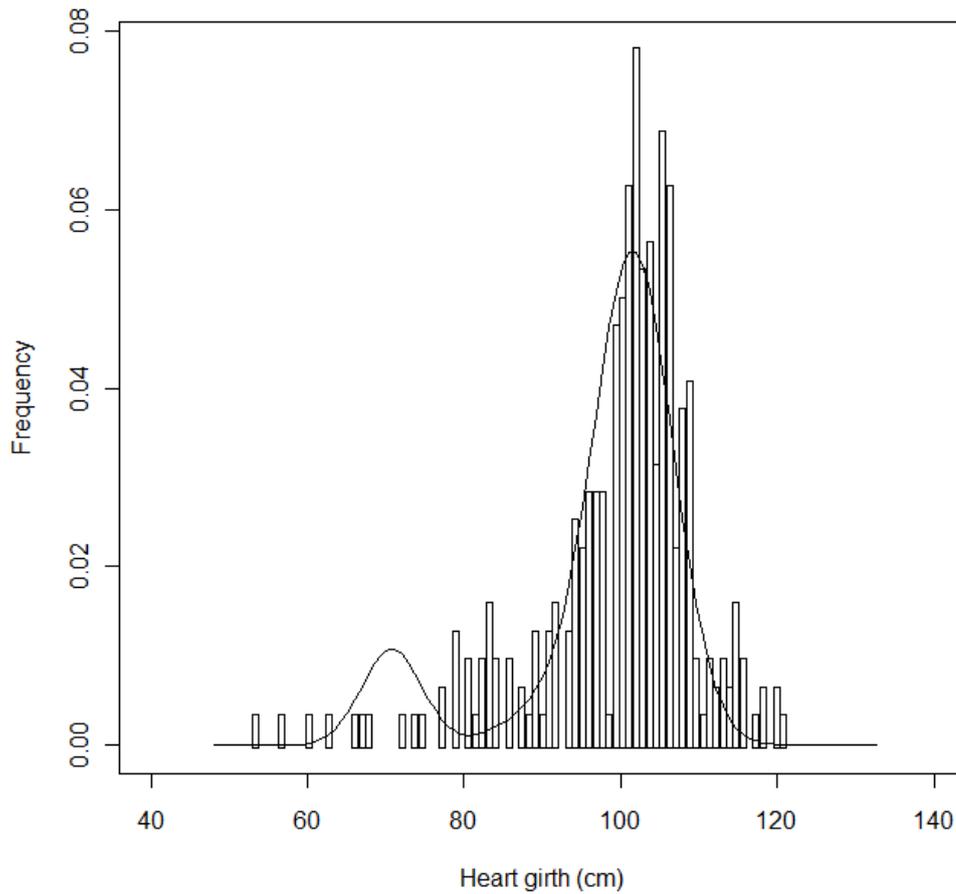


Figure 4 The stable distribution of heart girths as predicted by the right eigenvector of the matrix model is represented by the line whilst the bars represent the actual distribution of heart girths from the data sorted into the same bins as in the model. Both are scaled to sum to unity.

The observed and predicted values for mean heart girth were very similar (tab. 2) and this is represented well in figure 4. The smaller peak in the predicted distribution represents the new recruits to the population where they peak at approximately 70cm, as predicted by the mean inheritance function (fig. 1d); however, the data do not exhibit a similar secondary peak but lie across larger heart girths.

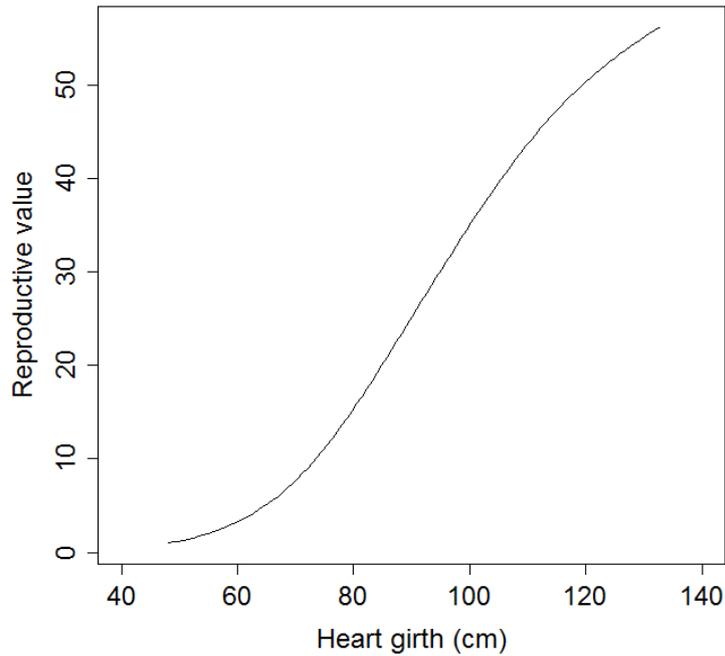


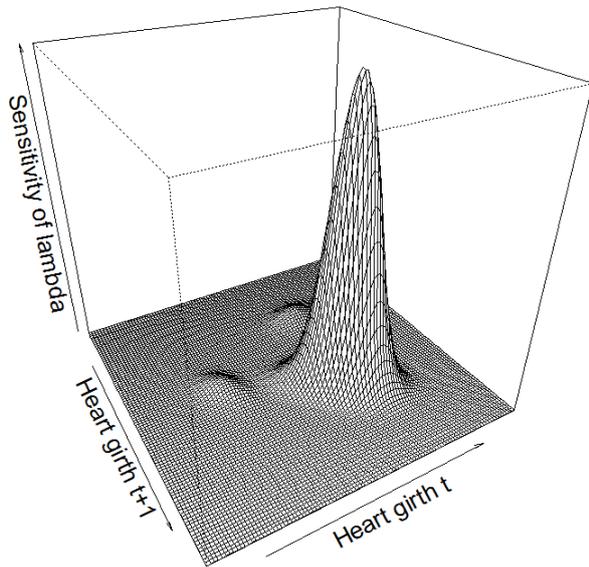
Figure 5 *The reproductive value of the range of heart girths within the population as predicted by the left eigenvector of the matrix model.*

Generation length is predicted as being 7.729 years, whereas the observed value is lower with females giving birth to their first daughter recruiting to the population at an average age of 6.863 years (tab. 2). An individual's reproductive value is predicted to logistically increase with heart girth (fig. 5) and mean fertility of any individual is considered to be approximately 0.11 cubs per year (tab. 2). The dispersion of reproduction was predicted as 37.385 and heritability was estimated at 0 because there was found to be no relationship between mother and daughter heart girth (fig. 1d). The viability selection differential for heart girths of survivors is estimated as being 2.295 whilst the fertility selection differential is higher at 5.429.

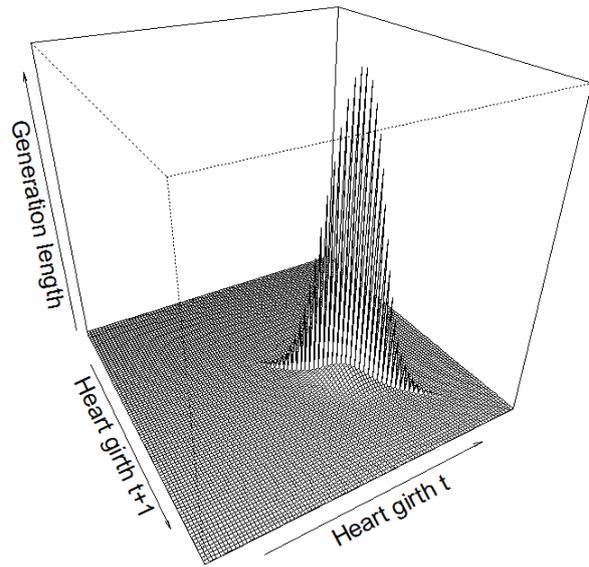
The predicted lifetime reproductive success of 0.648 cubs suggests a declining population, confirmed by the population growth rate below 1 (0.880 yr^{-1}). The actual population is recorded as slightly increasing (1.001) with a mean lifetime reproductive success of 1.468 cubs, greater than replacement.

3.2.2. Perturbation analysis

a)



b)



c)

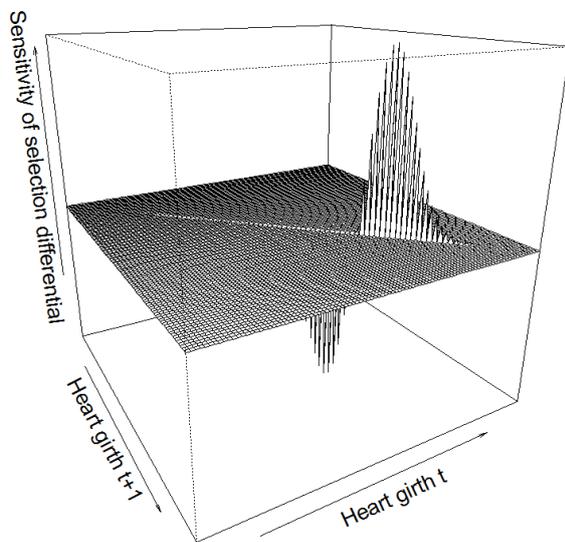


Figure 6 Sensitivity of: a) population growth rate, b) generation length and c) selection differentials to 1% increases in the transition rate between heart girth at t and t+1. Sensitivities are described using a partial derivative given in equation 5.

There is a similar range of combinations between heart girth at t and t+1 to which population growth rate, generation length and strength of selection are most sensitive to transitions between (fig. 6). Population growth rate has three distinct regions of the growth plane, heart girth at t+1 against heart girth at t, where small perturbations will cause a disproportionate response (fig. 6a); the quantities all appear to be most sensitive to larger heart girths. Where the largest response occurs, generation length also appears to be very sensitive, but displays a more linear response

parallel to positive growth (fig. 6b). Both of these parameters increase as a reaction to sensitive growth functions whereas selection decreases initially and then increases but along the same vector as generation length (fig. 6c).

3.3. Habitat comparison utilising an IPM

The two habitats demonstrate relatively similar relationships with heart girth (fig. 7), although there is a significantly different correlation exhibited by the plains and woodland habitat between survival and heart girth (fig. 7a). Individuals in woodland habitats supported a significant logistic regression between probability of survival and heart girth, revealing a steeper increase above 60cm than that of the whole dataset, whilst the plains habitat demonstrated no significant relationship with heart girth, simply averaging a survival rate of 0.79.

The mean growth and inheritance functions (fig. 7b and d, respectively) are essentially the same between habitats, and differ little from those of the whole dataset. The plains females were more likely to reproduce than woodland females up to approximately 105cm when the probabilities switch (fig. 7c) and litter size per year was greater in the woodlands habitats (0.882 cubs per year) compared to the plains females (0.522).

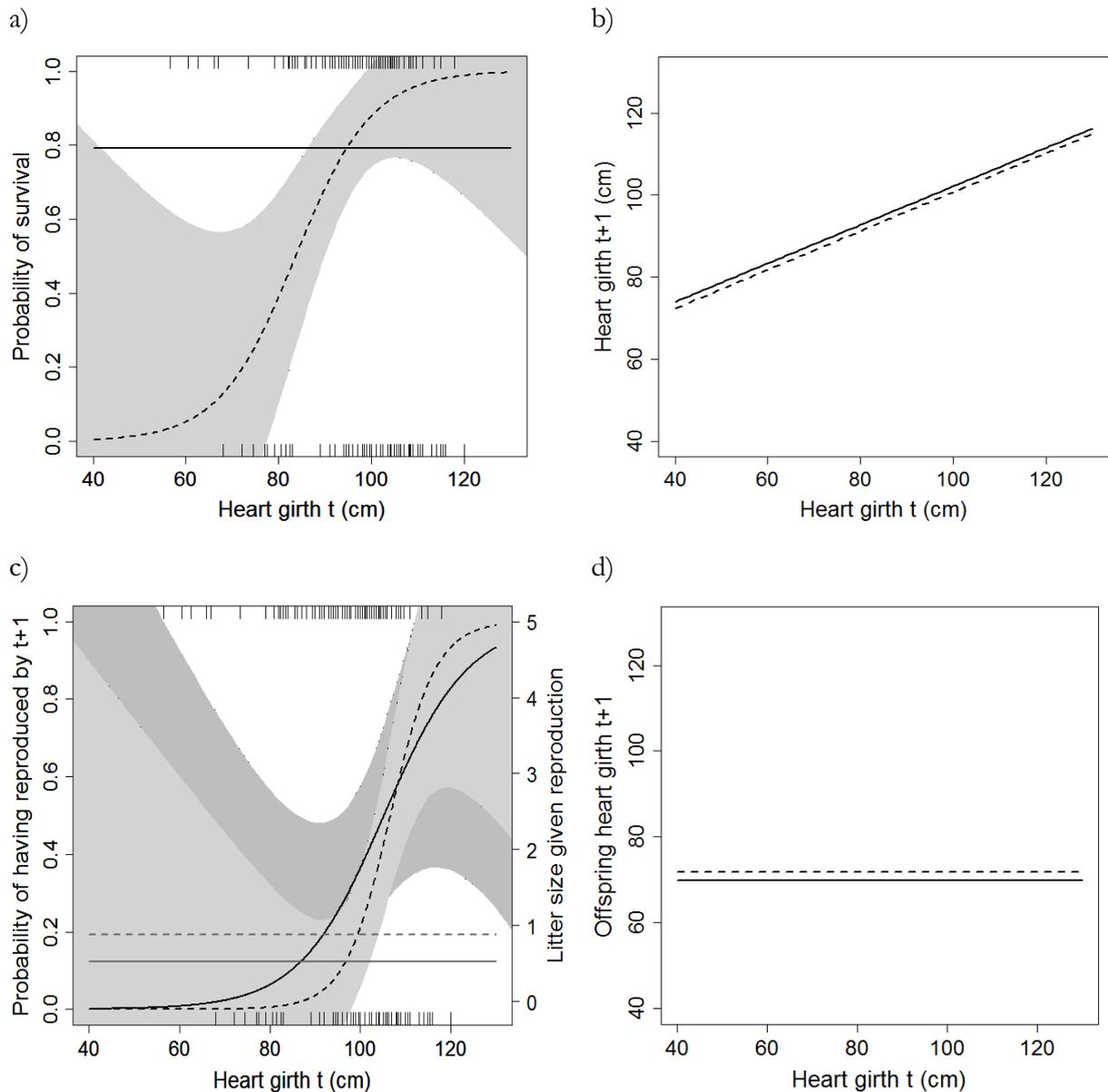


Figure 7 Fitted statistical functions to the data between heart girth measurement at t and (a-d): probability of survival, heart girth at $t+1$, fertility rate (and consequent litter size) and offspring heart girth at $t+1$. The solid lines denote the plains habitat and the dashed lines the woodland habitat. In the case of the fertility function (c), the black logistic lines refer to the probability of reproduction (left axis) and the grey linear lines refer to the average litter size given reproduction (right axis). Rugs at the bottom and top of the graphs represent the distribution of heart girth data for the plains and woodlands respectively. The shaded areas indicate the 95% confidence intervals with dark grey corresponding to plains and light grey to woodlands; confidence intervals were omitted from the mean growth and inheritance functions as they were at least partially derived rather than fitted.

The growth kernel for the plains and woodland is very similar (fig. 8a), with plains exhibiting a very slightly higher mean heart girth. However, the inheritance kernels are quite different (fig. 8b). The woodland habitat has a greater variance so, although the mean offspring heart girth is

fairly similar between the habitats, the likelihood of a female's offspring having a heart girth different from the mean is much higher in the woodland habitat.

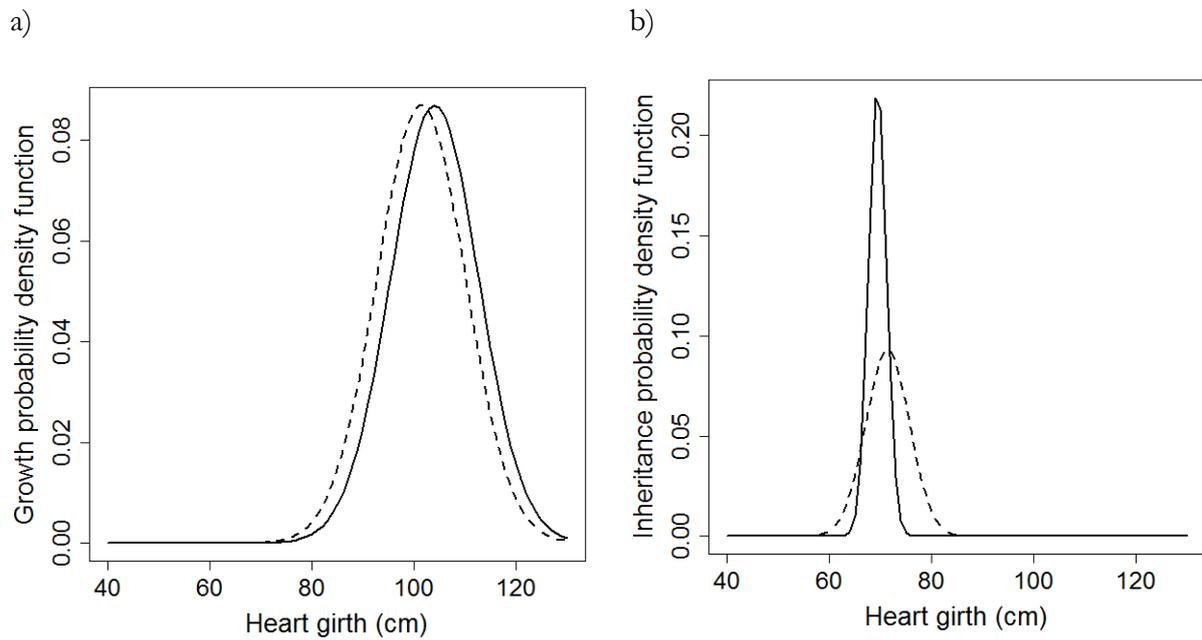


Figure 8 The probability density kernels for: (a) growth and (b) inheritance where the solid line denotes the plains habitat and the dashed line the woodland habitat.

The predictions made by the matrix approximation of the two IPMs parameterised for individuals inhabiting the plains and the woodlands are displayed in table 3. Mean LRS was omitted from these models as it was poorly estimated in the IPM for the whole population therefore would not represent a reliable comparison.

Table 3. The predicted values of key quantities calculated from the habitat IPMs for both the plains and woodland habitats.

<i>Quantity</i>	<i>Predicted value for plains</i>	<i>Predicted value for woodlands</i>
\bar{z}	94.46385 cm	94.43193 cm
$\sigma^2(\bar{z})$	175.3711 cm ²	170.4961 cm ²
λ	0.9544291 yr ⁻¹	0.9177747 yr ⁻¹
T	6.023835 yr	9.746012 yr
\bar{S}	0.790909 yr ⁻¹	0.7226409 yr ⁻¹
\bar{R}	0.1635201 yr ⁻¹	0.1951338 yr ⁻¹
$\sigma^2(d)$	18.55884	62.18826
h^2	0	0

The two habitats were predicted as having similar values for many of the quantities: mean and variance of heart girth, population growth rate and the mean survival and recruitment rates. The mean heart girth was lower than that for the whole population but the variance was greater. Both populations were predicted as being in decline (~ 0.9 for each) but survival rates were comparable to that predicted by the original IPM.

Generation length, recruitment rates and the dispersion of reproduction differed between the habitats with woodland having a higher estimate for each.

4. Discussion

This study ventures into the relatively uncharted realms of lion body size with the aim of gaining some insight into its effect on both an individual and population level. The complex nature of lion life history (Packer *et al.* 1991; Packer *et al.* 2005), as well as the simple fact that lions are large carnivores (Ewer 1973), makes studies of body size quite challenging. These results, however, should provide a preliminary overview of the potentially quite substantial influence body size can confer on a population of lions.

4.1. Associations with body size

Processes that change population density cause the distribution of a character to be altered. Density is modified by adding, removing or transforming individuals within the population, which is achieved through births and deaths and their associated character distribution, in addition to the character changes of existing individuals (Coulson *et al.* 2010). These biological processes are represented in the IPM as the functions of heart girth describing: survival, growth, fertility and inheritance. Immigration and emigration should also be considered as effectors on the character distribution, but are negligible in this lion population as the study area is so large, as well as in the separate habitat IPMs as their social structure dictates that, principally, males might relocate from one habitat to the other (Schaller 1972), whereas only females have been considered in the models parameterised here.

It was found that a female's probability of survival each year logistically increases with heart girth, rapidly increasing above 65cm and stabilising around 105cm (fig. 1a). Packer *et al.* 1998 showed that female mortality rates are high for cubs but minimise between the ages of 3 and 4 resulting in individuals of this age being considered adults. These young adults are predicted as having heart girths approximating 102cm and, at this point, the logistic regression of survival begins to plateau therefore predicting maximal survival rates. Lionesses are expected to maintain a heart girth near to this size until they reach 12yrs, after which survival rates drop once again. The highest heart girths are attributed to 7 to 8 year olds and, as a consequence, are estimated to have the highest survival; however, this ignores the averaged survival of the young and old that both possess the same, lower measurement. It has been shown that mortality rates increase after the age of four (Packer *et al.* 1998) with the average female lifespan being 14 years (Schaller 1977).

In the most part, the plains and woodland habitats demonstrated fairly similar relationships with heart girth (fig. 7), but with survival being the notable exception (fig. 7a). Probability of survival

in the plains habitat was found to be independent of heart girth, whereas survival in the woodlands followed a similar correlation to that demonstrated by the whole study population, but with a slightly steeper increase in survival above 60cm. It is possible that the linear relationship observed in the plains is an artefact of having fewer recordings for lower heart girths. However, prides occupying a territory within the plains are expected to have larger ranges than those in the woodlands linked to resource patchiness and quality (Ogutu & Dublin 2002); the differential resources between the habitats must be in part responsible for the disparity in survival rates. The woodlands habitat has been found to suffer significant losses in prey biomass in particularly wet years, which is likely to be closely linked to the exhibited response of survival rate to body size (Packer *et al.* 1988).

The derived linear regression for growth (fig. 1b) suggests that lionesses experience their highest growth rates when they are small, emulating the rapid growth of cubs, and stabilise around 102cm capturing both the peak heart girth and subsequent heart girth decline of greater measures. Both habitats exhibited effectively the same mean growth (fig. 7b), where the rate of increase was equivalent but the woodlands had a very slightly lower average heart girth (fig. 8a and tab. 3). They both exhibited a marginally faster rate of increase than the mean for the whole population. The growth kernels predicted that heart girths predominantly fall within the range of 85 and 120cm (fig. 3 and 8, $G(t, z|z')$) but that the woodlands are predicted as being very slightly shifted towards smaller measurements. In general though, growth seemed to be fairly consistent across the study area.

Fertility significantly correlated with body size where the probability of reproducing within a year increased rapidly above a threshold of 80cm, before which there was essentially no possibility of reproducing (fig. 1c). The probability of reproducing appears to be highest at heart girths possessed by 3 to 12 year olds (fig. 2) suggesting that this age range is when a female is at her most fecund. It has been documented that females can reproduce from around the age of 3 years, after which maternity rates remain reasonably constant up to 14 years where they begin to decline (Packer *et al.* 1998). This therefore suggests that both age and body size are important factors in determining reproductive potential. The probability of reproducing at a lower heart girth is higher in the plains up to 105cm, above which a woodlands female is more likely to reproduce (fig. 7c). Litter size did not demonstrate a similar correlation with heart girth, but simply predicted that one in three females, given reproduction, would raise her cub to her first birthday. Woodlands females recruited 70% more cubs to the population than the plains females. Females within a pride are considered to be uniformly reproductively successful (Packer *et al.* 1988) and exhibit communal nursing which would support the equal survival of

cubs (Packer *et al.* 2001). Litter size has been shown to significantly decline after 14 years of age (Packer *et al.* 1998), hence the reduced fertility rates at the lower heart girths possessed by older females. In summary, a female's body size is important in determining her likelihood of reproducing, but the dominant factors of lion life history, for example male takeovers (Packer & Pusey 1983b) and communal nursing (Packer *et al.* 2001), control cub survival irrespective of mother's body size.

No correlation was found between mother and daughter heart girth, signifying that body size is not inherited (fig. 1d and fig. 7d), but rather that females are expected to measure between 60 and 80cm at their first birthday (fig. 3: $D(t, z|z')$). Interestingly, this infers that body size is not inherited in lions but is most significantly determined by other factors. Within a pride, all individuals are permitted access to a kill evenly (Caraco & Wolf 1975), which may help equalise body sizes to give the average observed here as opposed to a correlation. The variation of one year old heart girths was much greater for the woodland indicating that a more heterogeneous distribution of heart girths exists in the plains habitat.

4.2. IPM predictions

The model provides a reasonable approximation of the key quantities of interest, with the exception of mean lifetime reproductive success which is very poorly estimated. In most cases, the model underestimated the actual value but overestimated the standard deviation in heart girth and generation time. As the growth function was derived and not actually fitted to exact data of heart girth at t and $t+1$, it is foreseeable that some disparities will exist. The impact falls within acceptable limits as the predicted mean heart girth is very close to that given by the data and the standard deviation differs by less than 14%.

The stable heart girth distribution in the population is reasonably well predicted (fig. 4), with the largest frequencies being found for the same range of heart girths as in the data. The overestimated heart girth variance may be preventing the data from being fully captured by restricting the peak. The secondary peak, representing the cubs in the population, is less accurately captured; the likely explanation is that there are very few measurements for individuals at 1 year therefore creating an absence where the peak should be. The apparent delayed peak is possibly an artefact of scaling data that does not consistently cover all heart girth measures.

Reproductive value is conventionally expected to decline after a certain age threshold as their future potential reproduction decreases and mortality rates increase (Packer *et al.* 1988). This is not exhibited by this model (fig. 5) as it is not age structured and therefore only accounts for

associated survival and fertility rates of the heart girth. The reproductive value of individuals with heart girths ranging between 80 and 100cm represents the average reproductive value between young females, expected to have high potential reproduction but still suffer from lower mortality rates, and senescent females, expected to have low reproductive value. The selection differentials are predicted as being quite high at 2.30 for viability and 5.43 for fertility implying that the mean heart girth changes to this degree after survival and reproduction, respectively (Gillespie 2004). The true values are unlikely to be so great but the results do suggest that there is selection acting towards larger body sizes within the population for both survival and recruitment. Selection, as with population growth rate and generation length, was most sensitive to transitions between larger heart girth sizes as a positive shift in the distribution of body sizes in the population confers an associated increase in survival and fertility.

The two habitats were predicted as having the same average heart girth measurements and associated variance and a similar population growth rate. Slightly higher survival was predicted in the plains but the woodlands are estimated as having longer generation times and increased recruitment rates. Woodland prides are not as severely affected by rainfall as the plains prides, which is evident in cub mortality during the dry season (Packer *et al.* 1988) and are therefore slightly more reproductively successful.

4.3. Conclusions, implications and recommendations

Body size has been found to be an important determinant of lioness survival and their probability of reproduction; however, there is a limit to body size where, if exceeded, a lioness will experience a probable reduction in size. Conversely, litter size is not affected by mother's body size and genetics were found to not determine subsequent distributions of body size.

The predictions obtained from the IPM support the premise that eco-evolutionary dynamics are acting on lion populations, with both ecological and evolutionary factors acting on body size. It is well documented that hunting ability is influenced by body size (MacNulty *et al.* 2009) although, since all members of a pride feed equally (Caraco & Wolf 1975), this is likely to have a negligible within pride effect but will have implications on fitness between prides. Evolutionary pressures have driven the divergence of body size in males and females with consequential differences in predatory capabilities (Funston *et al.* 2001), whilst ecological factors simultaneously act to create disparities in body size, exemplified by rainfall patterns, which have a palpable effect on different habitats (Packer *et al.* 1988).

Modelling body size dynamics can expose an assortment of otherwise intangible interactions that can be used to identify the foundation of ecological or evolutionary changes and responses. Employing an IPM similar to those parameterised here may prove insightful in isolating the key factors behind the dynamics observed in the Serengeti lion population. Packer *et al.* 2005 described how the population exhibits sudden jumps between long periods of stability attributed to the properties conferred by group living. For a pride to persist, it must dominate an area with sufficient resources to support the likely number of lions within the group (Orsdol *et al.* 1985). Gradual variations in ecological factors meant environmental conditions eventually improved to levels where territories could be subdivided; this was linked to the original territory being able to support a sufficient prey community to allow whole new prides to be formed. It was, however, found to be the short-term improvements in conditions behind the abrupt shifts to new equilibria as a direct consequence of increased young survival. Changes in the migratory wildebeest population have the most significant influence on the dynamics of the Serengeti lion population. Events having substantial effects on the wildebeest population size, such as their release from rinderpest infection and unusual rainfall years, were found to have parallel effects on the lion population correlating significantly with cub survival. Simulated population dynamics demonstrated abrupt changes only when group living behaviour was incorporated (Packer *et al.* 2005).

There is also potential for this type of dynamical modelling to be utilised in assessing the impact of hunting. There is an adequate quantity of data for male lions in the Serengeti population, although considerably less than for females, which could be used to parameterise an IPM. Paternity is largely unknown but cubs could be assigned between a resident coalition and it could be reasonably assumed that no correlation exists between father and son heart girth. The effect of the focused removal of males averaging 5 years on population dynamics could then be explored further. Males around this age are most likely to be in residence therefore are contributing to the reproductive success of the pride; their removal greatly increases the likelihood of a male takeover by another coalition and consequent infanticide (Loveridge *et al.* 2007). In species where paternal care exists, the age of hunted males has a highly significant impact on the population (Whitman *et al.* 2004). This may suggest that the removal of particular body sizes may also be of significance, specifically as the larger males are likely to be targeted. There will consequently be a delayed change in the age structure where there will be fewer older males, which are known to father greater numbers of surviving cubs (Packer *et al.* 1988). An evolutionary pressure will be conferred upon these males ultimately feeding back on dynamics (Loveridge *et al.* 2007).

The main issue concerning the model is that it ignores any social attributes exhibited by lions. Although yellow-bellied marmots also possess a social life history and the IPM predicts accurately in the absence of this trait (Ozgul *et al.* 2010), it has been well documented that social structure has a highly significant influence over lion population dynamics and is therefore likely to have some effect on model predictions (e.g. Packer *et al.* 1990; Scheel & Packer 1991; Packer *et al.* 2005; Fryxell *et al.* 2007). As an example, all cubs within a pride up to the age of at least 18mths are killed after a male takeover (Packer & Pusey 1983a) and, as a consequence, cub survival in those years is zero irrespective of any other factors. For this reason, it is quite possible that a facet of the model inaccuracies could be rectified by incorporating social structure into the model in some form and would therefore be a recommendation for model improvement. It does, however, provide the promise of being effectively applied to large, solitary carnivores where their life history is less complex.

5. Acknowledgements

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7. Appendix

The parameterised associations in table A1 are implemented in the IPM to model how the distribution of heart girth measures in the population varies over time.

Table A1 Parameterised associations between heart girth measurement (z) and: survival, growth among survivors, fertility and offspring heart girth measurements. Survival, fertility and offspring character values were all modelled using generalized linear mixed effects models of heart girth measurement under the appropriate error structure where individual identity, age, birth year and measurement year are taken to be random effects. The growth function was derived using the non-linear regression of heart girth with age.

<i>Transition rate</i>	<i>Function</i>	<i>Parameter values</i>
Survival	$S(t, z) = \frac{1}{1 + e^{-(\alpha + \beta \cdot z)}}$	$\alpha = -6.83430$ $\beta = 0.08485$
Growth	$\mu_g(z) = \alpha + \beta \cdot z$	$\alpha = 57.730463$ $\beta = 0.440843$ $\sigma^2 = 21.05$
Fertility	$F(t, z) = \frac{1}{1 + e^{-(\alpha + \beta \cdot z)}}$	$\alpha = -15.82165$ $\beta = 0.14841$
	$\psi(t, z) = \alpha + \beta \cdot z$	$\alpha = 0.37308$ $\beta = 0$
Inheritance	$\mu_d = \alpha + \beta \cdot z$	$\alpha = 70.7426$ $\beta = 0$ $\sigma^2 = 14.770$

The parameterised associations in table A2 were implemented in two IPMS: one for the plains habitat and another for the woodland habitat to model how the distribution of heart girth measures in each population varies over time.

Table A2 Parameterised associations between heart girth measurement (z) and: survival, growth among survivors, fertility and offspring heart girth measurements for the plains (P) and woodlands (W). See legend for table A1 for details of methods.

Transition rate	Function	Parameter values
Survival	$S(t, z) = \frac{1}{1 + e^{-(\alpha + \beta \cdot z)}}$	P: $mean = 0.790909$
		W: $\alpha = -10.16829$ $\beta = 0.12154$
Growth	$\mu_g(z) = \alpha + \beta \cdot z$	$\alpha = 55.31555$
		P: $\beta = 0.46844$ $\sigma^2 = 21.05$
Fertility	$F(t, z) = \frac{1}{1 + e^{-(\alpha + \beta \cdot z)}}$	W: $\alpha = 53.507032$ $\beta = 0.472575$ $\sigma^2 = 21.05$
		P: $\alpha = -11.21571$ $\beta = 0.10656$
Inheritance	$\psi(t, z) = \alpha + \beta \cdot z$	W: $\alpha = -21.15475$ $\beta = 0.19828$
		P: $\alpha = 0.5217$ $\beta = 0$
Inheritance	$\mu_d = \alpha + \beta \cdot z$	W: $\alpha = 0.8820$ $\beta = 0$
		P: $\alpha = 69.414$ $\beta = 0$ $\sigma^2 = 3.1422$
Inheritance	$\mu_d = \alpha + \beta \cdot z$	W: $\alpha = 71.451$ $\beta = 0$ $\sigma^2 = 18.391$