Modeling harvest rates and numbers from age and sex ratios: A demonstration for elephant populations

Karpagam Chelliah [a], Harshvardhan Bukka [b], Raman Sukumar [a,*]

[a] Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India
[b] Centre for Neuroscience, Indian Institute of Science, Bangalore 560 012, India

ABSTRACT

Illegal harvest rates of wildlife populations are often unknown or difficult to estimate from field data due to under-reporting or incomplete detection of carcasses. This is especially true for elephants that are killed for ivory or in conflicts with people. We describe a method to infer harvest rates from coarse field data of three population parameters, namely, adult female to male ratio, male old-adult to young-adult ratio, and proportion of adult males in the population using Jensen's (2000) 2-sex, density-dependent Leslie matrix model. The specific combination of male and female harvest rates and numbers can be determined from the history of harvest and estimate of population size. We applied this technique to two populations of elephants for which data on age structure and records of mortality were available—a forest-dwelling population of the Asian elephant (at Nagarahole, India) and an African savannah elephant population (at Samburu, Kenya) that had experienced male-biased harvest regimes over 2–3 decades. For the Nagarahole population, the recorded numbers of male and female elephants killed illegally during 1981–2000 were 64% and 88% of the values predicted by the model, respectively, implying some non-detection or incomplete reporting while for the Samburu population the recorded and modeled numbers of harvest during 1990–1999 closely matched. This technique, applicable to any animal population following logistic growth model, can be especially useful for inferring illegal harvest numbers of forest elephants in Africa and Asia.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

A major challenge in conservation science presently is to come up with robust estimates of illegal harvest of wildlife populations in order to understand the impacts of such harvest on the future trajectory and viability of such populations (Ginsberg and Milner-Gulland, 1994; Allendorf et al., 2008). While broad estimates of the illegal global trade in wildlife are available (Broad et al., 2003), there is an urgent need to assess illegal wildlife harvest patterns regionally (Nijman, 2010; Liberg et al., 2012; Velho et al., 2012) or harvest rates in populations of vulnerable species of wildlife. In fact, a global programme of Monitoring the Illegal Killing of Elephants (MIKE) was established in 2001 precisely to measure elephant offtake in Africa and Asia (Burn et al., 2011). Various approaches from field detection of carcasses and analysis of law enforcement records to population modeling have been used to infer the nature, patterns and reasons for illegal harvest of wildlife species (reviewed in Gavin et al., 2010). In the case of elephants the volume of ivory in the trade has been used as a surrogate of

numbers killed illegally (Pilgram and Western, 1986; Milner-Gulland and Beddington, 1993; Wasser et al., 2008).

Illegal harvest of an animal population is often biased toward a particular age class or sex (Allendorf and Hard, 2009) that may alter its structure, sex-ratio, size and productivity (Ginsberg and Milner-Gulland, 1994; Langvatn and Loison, 1999) with attendant evolutionary consequences (Mysterud, 2011). Thus, it is imperative to monitor harvest rates of a population in order to assess the conservation implications, but this may not be easy in some animal species. For instance, even in large-bodied species such as elephants, estimating the number of animals killed illegally for ivory is a non-trivial issue (Burn et al., 2011), especially in the case of the forest-dwelling populations of the African elephant *Loxodonta cyclotis* and the Asian elephant *Elephas maximus* for which carcasses are difficult or impossible to detect. However, it may be possible to infer unknown harvest rate and number by comparing current age-structure and sex ratio of an elephant population, with age-structure that results from natural mortality alone (Sukumar, 1989; Sukumar et al., 1998).

Characterizing the age-structure of a wild animal population is also non-trivial because classifying individuals into fine age-class bins in the field is often subjective and error prone. A much coarser field classification such as juvenile, sub-adult, young adult and old

* Corresponding author. Tel.: +91 80 2293 3102; fax: +91 80 2360 2280.
E-mail addresses: umiyak@hotmail.com (K. Chelliah), harsh.balu@gmail.com (H. Bukka), rsuku@ces.iisc.ernet.in (R. Sukumar).

adult is easier (Milner-Gulland and Beddington, 1993). Similarly, adult males and females in most mammalian species are morphologically distinct and, therefore, adult sex ratio is also easier to estimate. At the least, three ratios, namely, adult sex-ratio (*asr*), male old-adult to young adult ratio (*moy*) and proportion adult male (*pam*) in the population are fairly easy to estimate and robust against gross classification errors. These three ratios (henceforth referred to as "population signature ratios") can be highly informative about the dynamics of an animal population.

Modeling exercises based on change in ratio (CIR) of adult males to adult females or sub-adult to adult individuals have been used to infer population size, harvest rate, productivity, and survival rates for closed populations (Chapman, 1955; Paulik and Robson, 1969). CIR methods have been extended to open population models (Hanson, 1963; Chapman and Murphy, 1965) but only natural mortality is considered and not recruitment. None of the existing methods has considered age-specific mortality or fecundity, and all are applicable only to short harvest seasons. None of the models has considered all the three population signature ratios *asr*, *moy* and *pam* taken together to understand how they vary with varying harvest regimes.

Matrix models are ideal for simulating the dynamics of age-structured populations (Caswell, 2001) and have been applied to the management of various animals ranging from amphipods to ungulates (Beddington, 1974; Miller et al., 2002; Mantzouni et al., 2007). Jensen (2000) described a simple two-sex, discrete time step, density dependent, Leslie matrix model to simulate white-tailed deer (*Odocoileus virginianus borealis* Miller) population under selective harvest. Intense male-only harvest under the model resulted in deer abundance that was close to carrying capacity but predominated by females. Such demography is very similar to that of heavily poached Asian elephant populations (Sukumar, 1989; Sukumar et al., 1998) indicating that the model may also be suitable for elephants. In fact, an age-structured Leslie matrix model was combined with detailed CIR data to infer that 336–388 tusked male Asian elephants had been poached for ivory over a 20 year period in a southern Indian population for which harvest data were not available (Sukumar et al., 1998).

Being the largest land mammal, long-lived and a slow breeder, it is reasonable to expect elephant populations to be density dependent (Fowler and Smith, 1973; Sukumar, 2003). Therefore, we explored mathematically the relationship between male-female harvest ratio (*hr*) and the resulting adult sex-ratio (*asr*), male old-adult to young-adult ratio (*moy*) and proportion adult male in the population (*pam*), under the Jensen (2000) model. We developed a method to infer the relative male-female harvest rate from these population signature ratios, the age-structure of the population, as well as the absolute number of animals harvested, if population size is known. This method can be applied to populations that may be in stable state (size and structure remain the same) or in a state of transition (size and structure change with time). Although this generic model can be applied to any vertebrate population subject to density-dependent logistic growth, it could be most usefully applied to elephant populations to estimate harvest numbers from sparse field data on age-structure, sex ratio and population size. We applied our model to one wild Asian elephant and one wild African elephant (the savannah elephant *Loxodonta africana*) population for which demography data and possibly incomplete harvest data for multiple years were available in order to test the model validity. These two populations make excellent test cases for our model because they present an interesting contrast in sex-biased harvest; while males of both species are killed for ivory, the tusked female African elephant is also poached but the tuskless female Asian elephant is virtually immune to such harvest.

2. Material and methods

2.1. Description of the matrix model

Jensen (2000) enhanced the basic Leslie matrix age-structured model (Leslie, 1948) by combining it with Williamson's two-sex model (Williamson, 1959). Jensen also incorporated density dependence (population growth is regulated by its size) and an age-specific harvest matrix where different harvest rates may be applied to different age-classes. The resultant model is a discrete time-step, logistic growth model and is expressed concisely as an equation (Jensen, 2000) with matrices:

$$N_{t+1} = N_t + d_t \times (M - I) \times N_t - H \times N_t \qquad (1)$$

where N_t is a vector (*n* rows and 1 column) of number of individuals in each of the *n* age-class bins, at time *t* (even rows are males and odd rows females), d_t is the density factor at time $t = (K - \sum N_t)/K$, where *K* is the carrying capacity, *M* is the Leslie projection matrix of dimension $n \times n$, *I* the identity matrix of dimension $n \times n$, *H* is the age-specific harvest matrix of dimension $n \times n$, and *n* is the number of age-class bins in the age-structure of the population.

Model assumptions are:

a. The model is deterministic with no stochastic processes built into it.
b. The carrying capacity is constant.
c. The birth rate, death rate and harvest rates for a given sex are uniform over time. The harvest rate of males is greater than or equal to the harvest rate of females as is typical of most sexually dimorphic vertebrate species.
d. Birth rate is not affected by skew in sex-ratio.
e. There is no immigration or emigration.

We use the term "stable age distribution" to refer to a population in which the proportion of individuals in different age classes remain constant, irrespective of the sign of the population growth rate, and the term "stable state" to refer to a condition in which a population has attained a stable age distribution and growth rate of zero.

2.2. Computer simulation of the model

Computer simulation of the model was carried out with R 2.15.1 software (R Development Core Team, 2012). Source code developed by the authors is available upon request. Available survivorship data (Table A.1 in Appendix A) for the Asian elephant (Sukumar, 1989; Sukumar et al., 1998) and for the African elephant (Moss, 2001; Amboseli Trust for Elephants, 2012) were used in the simulations. We used an average value of 0.20 calves per adult female per year for the entire reproductive age span for the Asian elephant (Arivazhagan and Sukumar, 2005), and a value of 0.22 for the African elephant (Moss, 2001) based on intercalving intervals of 5.0 and 4.5 years respectively. The reproductive age span was operationally defined as 15–60 years; even though some elephants may give birth at a younger or an older age, the proportions of such individuals are small (Moss, 2001) and can be neglected for our purposes.

We tested the model with data on population structure sampled from:

1. Nagarahole National Park (644 km²; henceforth Nagarahole), India, for the Asian elephant (*E. maximus*); the population was sampled in April–May 2001 (Arivazhagan and Sukumar, 2005).
2. Samburu and Buffalo Springs National Reserves (330 km²; henceforth Samburu), Kenya for the African savannah elephant (*L. africana*); the population was sampled between November 1997 and July 1999 (Wittemyer, 2001).