

Modelling Impacts of Poaching on the Sumatran Elephant Population in Way Kambas National Park, Sumatra, Indonesia

Arnold F. Sitompul^{1,2}, John P. Carroll³, James Peterson⁴ and Simon Hedges⁵

¹Conservation Science Initiative, Medan, Indonesia

²Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA, USA

³Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

⁴U.S.G.S. Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

⁵Wildlife Conservation Society, International Programs, Bronx, New York, NY, USA

Introduction

Poaching has been known to have a large impact on elephant populations in both Africa (e.g. Douglas-Hamilton 1987; Poole & Thomsen 1989) and Asia (Sukumar 1989; Sukumar *et al.* 1998). There are fears that poaching of Asian elephants has increased since CITES approved an experimental one-off sale of ivory from Botswana, Namibia, and Zimbabwe to Japan in July 1999, following compliance with a number of agreed conditions. Another one-off sale from South Africa, Namibia, and Botswana was approved in 2002 but that sale has not yet taken place (CITES 2000; Milliken 2004). In Sumatra, during the 1980s and 1990s, poaching was not considered a major threat to elephants (Blouch & Haryanto 1984; Blouch & Simbolon 1985; Santiapillai & Jackson 1990); however it is feared that poaching activity has increased since year 2000 (Sitompul *et al.* 2002; Hedges *et al.* 2005). While poaching activity is predicted to continue increasing, accurate data on poaching is very difficult to obtain. Furthermore, there have been no field studies in Sumatra identifying the impact of poaching on elephant abundance and population trends.

Population modelling has been widely used in wildlife ecology studies for many terrestrial large mammals (e.g. Belovsky 1987; Berger 1990; Rothley *et al.* 2005). Incorporating modelling approaches as part of adaptive management strategies, allows managers to develop more effective conservation strategies (Cromsigt *et al.* 2002) while reducing the uncertainty

about how the system responds to management actions (Williams *et al.* 2002). Furthermore, modelling allows managers to make an empirical assessment of the species of interest and identify and implement the management strategies that are most likely to increase the probability of a species persisting over a given time period. However, developing detailed and accurate population models for many species requires extensive historical baseline data (i.e., population size, age structure, sex-ratio, fecundity rate, and natural survival and mortality rates). In Sumatra, reliable baseline data for Sumatran elephant is uncommon; however the results of a couple of studies (Riley 2002; Hedges *et al.* 2005) provide reliable data for the elephant population in Way Kambas National Park. We believe that modelling of elephant populations and poaching threats will help managers identify key parameters to monitor, and strategies to adopt, in order to minimize extinction threats for Sumatran elephants.

In this paper, we estimate the potential impact of poaching on the elephant population in Way Kambas National Park (WKNP) using a stochastic population model. We projected the population trend under three different poaching scenarios: no poaching, low poaching, and high poaching. For each model, we predicted the population's age distribution, growth rate, and trends in abundance estimates over 50 years. Finally, we calculated the extinction probability for each scenario and conducted sensitivity analyses to identify the parameter that had the largest effect on the model's estimates.

Methods

Study area

Field data used in the model were collected in Way Kambas National Park (WKNP), Sumatra, Indonesia. WKNP is located in eastern part of Lampung Province in south-eastern Sumatra (4°62'–5°26' S and 105°54'–105°90' E), and is 1235 km² in area. The entire park is < 50 m above sea level and annual rainfall is 2000–3000 mm. Vegetation types are typical tropical lowland and swamp forest. Most of the park was logged in the 1960s and 1970s, so most of the forested area in the park is relatively degraded. Nonetheless, the park has still been categorized as the second highest priority for Sumatran elephant conservation (Santiapillai & Jackson 1990). The park boundary is approximately 227 km long and 65% (148 km) of it is bordered by 34 villages. The elephant population in the park was estimated to be 180 (95% CI = [144, 225]) in 2002 (Hedges *et al.* 2005). The government of Indonesia established an Elephant Training Centre (ETC) in the south-eastern area of the park in the early 1980s; the purpose of this ETC was to house “problem elephants” captured as a result of human–elephant conflict and habitat conversion in WKNP and other parts of Lampung Province (Hedges *et al.* 2005). The “problem elephants” were then tamed and trained at the ETC for tourism purposes. The ETC in WKNP is the largest such centre in Sumatra and during 2000–2002 was known to contain about 100 elephants (authors' pers. obs.).

Methods

We developed a stage-based stochastic population model to determine the impact of poaching in the park based on known rates of illegal killing of elephants in WKNP (Sitompul *et al.* 2002). Population trajectories and maximum population size under different scenarios were predicted for elephants in WKNP using a Leslie matrix projection model (Leslie 1945, 1948). The model consisted of four different life-history stages: calf, juvenile, subadult, and adult and operated on an annual time step basis (Fig. 1). The calf stage included any elephant <1 year old, juveniles

included ages 1–5 years, subadult elephants included individuals >5–15 years old, and adults included individuals >15 years old (Sukumar 1989). Each simulation began by assigning individuals to one of the four life history stages: calves were 8.04% of the population, juveniles were 28.57%, subadults 50%, and adults 13.39%, based on the demographic configuration of the elephant population in WKNP in Reilly (2002). The number of calves produced each time step was a function of the number of adults and subadults and fecundity. Stage-specific maximum annual fecundity rate was assumed to be constant over time and estimated to be 0.225 for both subadult and adult elephants, and was based on long-term studies of Asian elephants in other regions (Sukumar 1989). Stage-specific natural survival rate was assumed to be similar to Asian elephants in India and averaged 0.85 for the calf, 0.96 for the juvenile, 0.98 for the subadult, and 0.85 for the adult life history stages. We incorporated stochasticity into the model by randomly generating annual survival rates from a beta distribution with the mean specified above and a standard deviation that was 10% of the mean.

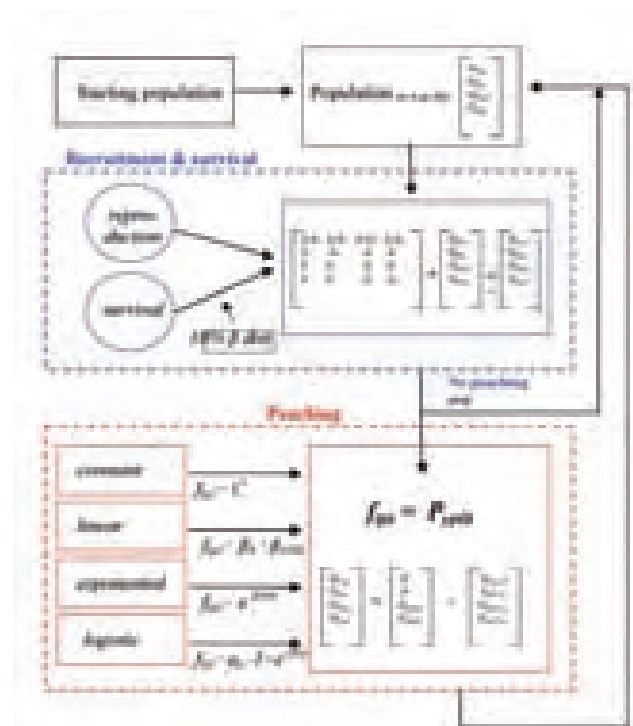


Figure 1. Model flow for population estimation and demographics as a function of recruitment, survival and poaching for elephants projected for 50 years in Way Kambas National Park.

For each simulation scenario, we ran 1000 replicate simulations for a 50 year time period, and observed the final population structure at year 50. Mean and 95% confidence interval (95% CI) of population size, population structure, and population growth rate (λ) were calculated. In addition, a quasi-extinction coefficient (EC) was estimated as the proportion of the 1000 replicate simulations that resulted in extinction before 50 years.

We evaluated the effect of poaching on elephant populations using three different scenarios. The first scenario, which we called the control, assumed that the elephant population in the park was fully protected, resulting in no anthropogenic removal of elephants (no poaching and elephant capture due to conflict with human). The second scenario assumed poaching occurred at a low rate defined as the mean number of elephants known to have been removed from the population per year due to poaching over the years 2000–2004. The number of elephants poached in the park was estimated from the total number of carcasses with signs of poaching activity found in the park in the 2000–2002 period ($n=8$ elephants) plus 8 elephants that had been found killed by poachers in the 2003–2004 period (Sitompul *et al.* 2002; Hedges *et al.* 2005; WCS unpub. data). We assumed only sub-adult and adult elephants were poached. The third scenario assumed that high poaching would occur in the park based on continued human population growth and land use trends in Lampung Province. High poaching was defined as a 2x increase on the previously defined low poaching rate described above. Because the relationship between poaching and population size is unknown, we modelled poaching rates as a function of population size using four alternative functions: (1) poaching was constant over time; (2) poaching was a negative linear function of population size; (3) poaching was an exponential decay function of population size; and (4) poaching was a logistic function of population size. For the high poaching rate scenario, poaching functions were kept the same as in the low poaching rate scenario. For each poaching function, the number of sub-adult and adult elephants poached from the park was randomly assigned using a Poisson distribution and the

scenario-specific rate. Thus, the rate of poaching per year, in the model, was assumed to be additive to the stage-specific natural mortality. We did not include sex-specific differences in poaching rate because there was no information on such sex-specific differences for WKNP. There is evidence that adult female elephants are also poached in Sumatra and their toenails, genitalia, and other body parts are collected for use in traditional medicines (Sitompul *et al.* 2002).

Several other assumptions were required in constructing the models. Natural mortality rates used were derived from data on Indian elephants, which might be different than Sumatran elephants. However, it is unlikely that they would be substantially different because elephants in India and Sumatra have similar life histories. Furthermore, we did not include a carrying capacity function because the carrying capacity of the study area is not well studied (but is thought to be much higher than the present population size) and because our primary concern was preventing declining populations and local extinction, the effect of density-dependent factors as the population approached carrying capacity was considered unimportant. However, model scenarios projecting increases in population will need refinement and some measure of carrying capacity should be included as those data become available. Finally, potential genetic problems associated with small isolated elephant populations (e.g. inbreeding depression) were not included in our model.

Sensitivity analyses

The purpose of the sensitivity analyses was to determine the relative influence of each parameter and alternative poaching model on model estimates (Williams *et al.* 2002). Relative sensitivity of model estimates can be evaluated by varying model input parameters over a specified range and examining the change in model outputs. For this study, we evaluated the relative sensitivity of the year 50 model estimates to each parameter by calculating a Sensitivity Index (SI) using regression analysis to calculate the slope and uncertainty of each poaching function and then multiplying the slope and uncertainty of

the parameter to calculate the SI following the methods of Wiegand *et al.* (1998). We evaluated the sensitivity of reproductive parameters of sub-adult and adult elephants by varying the reproductive rates from 0.19 to 0.25, with 0.01 increments. We also evaluated model sensitivity to the survival rate parameter for the calf to juvenile transition and the sub-adult to adult transition by varying the survival parameter for each life history stage from 0.75 to 0.90, with 0.05 increments. To understand the sensitivity of the population model to the alternative poaching functions, we varied poaching rate from the low poaching scenario's 50% to 200% of the estimate values in 10% increments. The results of these sensitivity analyses for the high poaching rate scenario will be identical to the low poaching rate scenario since the difference between the low and high poaching rate scenarios is simply the magnitude of the poaching rate. All simulation modelling and sensitivity analyses were conducted using SAS (SAS version 8.2).

Results

Projection of the WKNP elephant population over a 50-year period showed the population increasing from 180 elephants to 594 elephants (95% CI = [570, 618]) if we assumed that poaching stopped. The extinction coefficient for the control population was 0.0 and population growth rate (λ) was 1.02 (0.0001 SE). Under the low poaching rate scenarios we also showed that the elephant population would increase (Fig. 2). The linear poaching function produced an elephant population in year 50 of 422 (95% CI = [403, 441]). The extinction coefficient using the linear function was also 0.0 and λ was 1.02 (0.0002 SE). If poaching in the park behaves as an exponential extinction function, the elephant population in year 50 was estimated to be 325 (95% CI = [308, 342]). The extinction coefficient for this function was 0.009 and λ was 1.01 (0.0002 SE). The constant and logistic poaching functions in the model produced estimates of elephant population size of 253 (95% CI = [235, 271]) and 263 (95% CI = [245, 281]), respectively. The extinction coefficient with constant poaching was 0.099, and logistic poaching resulted in an estimate of 0.086. The population growth rate with constant

poaching was 1.0 (0.0005 SE) and λ with logistic poaching was 1.0 (0.0005 SE; Table 1). The age distribution after 50 years for the control and low poaching rate scenarios changed slightly from one dominated by sub-adults towards one more dominated by adults (Fig. 3).

Population models with high poaching rate scenarios showed a different trend to the low poaching rate scenarios over the 50-year period. In the high poaching rate scenarios, only linear and exponential decay poaching patterns showed that the elephant population in WKNP would increase over the 50 years (Fig. 4). Population size in year 50 for the linear and exponential decay poaching functions was estimated to be 274 (95% CI = [263, 285]) and 217 (95% CI = [211, 226]), respectively. The extinction coefficient for the linear and exponential poaching functions was 0.0 and λ was 1.0 (0.0002 SE). For the exponential decay poaching function, the extinction coefficient was 0.01 and λ was 1.0 (0.0003, SE). In contrast, the constant poaching and logistic poaching functions in the high poaching scenarios showed that elephant population in WKNP would decline dramatically (Fig. 4). Final population size in year 50 for the constant and logistic poaching functions was 41 (95% CI = [33, 49]) and 37 (95% CI = [30, 44]), respectively. The extinction coefficient for constant poaching was 0.75 and for logistic poaching it was 0.76. The population growth rate was 0.97 (0.008 SE) for constant poaching and 0.97 (0.009 SE) for logistic poaching (Table 1). The age distribution in the high poaching rate scenarios showed similar patterns to the low poaching scenarios, with more adult individuals found at the end of each simulation (Fig. 5).

Sensitivity analyses

Sensitivity analyses for each natural parameter revealed high levels of variation in the model. The result of the sensitivity analyses for the sub-adult and adult reproductive parameters showed that small changes in the adult reproductive parameter caused large changes in the final population size. For example, an increase of 6% in the adult reproduction rate could cause a 76.01% change in final population size. In contrast, a 6% change in

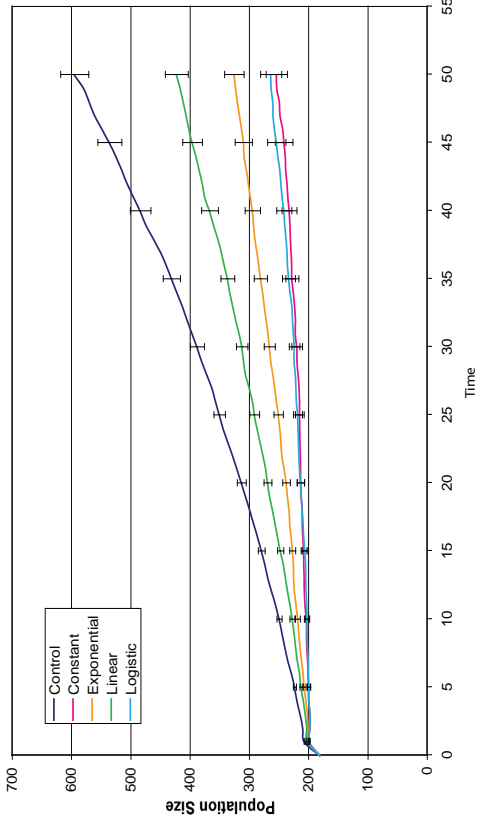


Figure 2. Simulated population trends of Asian elephants for 50 years under control and low poaching scenarios in Way Kambas National Park,. Density dependent effects using low poaching level scenarios were developed (constant, exponential, linear and logistic).

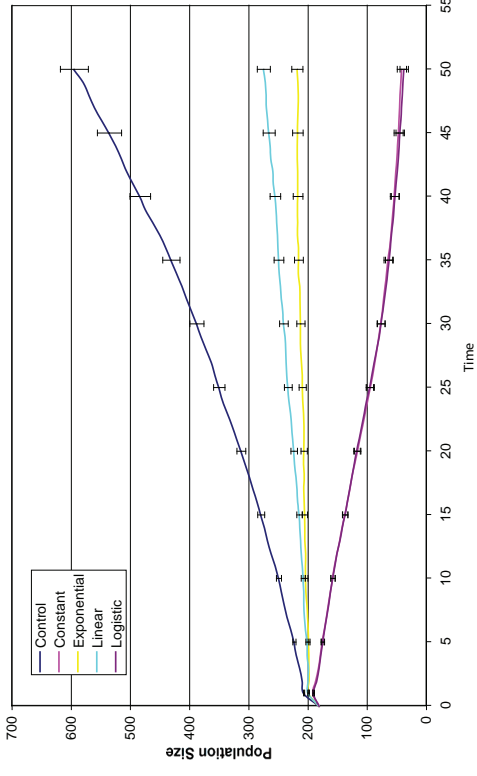


Figure 4. Simulated population trends over 50 years period under control and high poaching scenarios in Way Kambas National Park. Density dependent effects using high poaching level scenarios were developed (constant, exponential, linear and logistic).

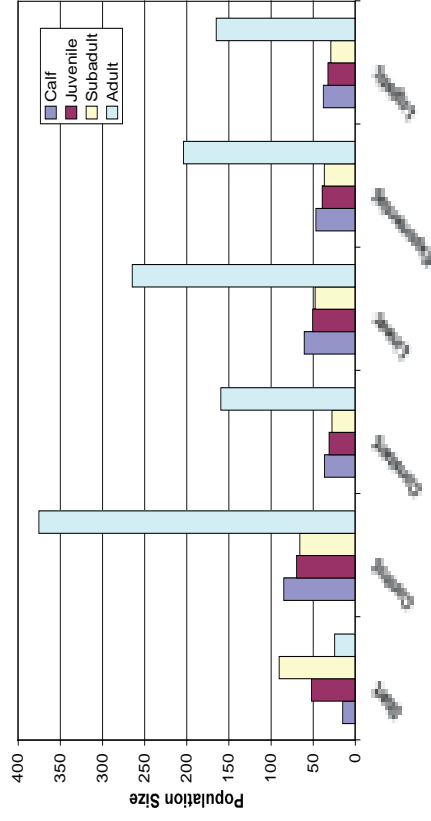


Figure 3. Projection of the age structure of the elephant population in Way Kambas National Park after 50 years of simulation, presented in the current population (start) and in control and low poaching scenarios.

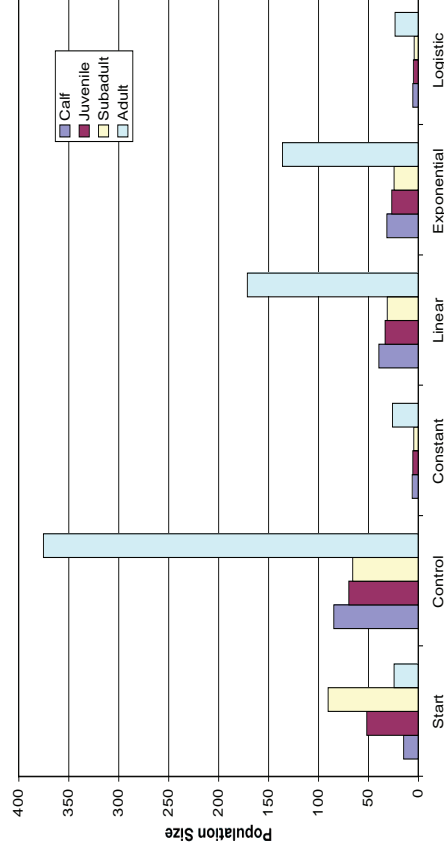


Figure 5. Projection of the age structure of the elephant population in Way Kambas after 50 years of simulation, presented in the current population (start) and in control and high poaching scenarios.

sub-adult reproduction rate only caused a 26.84% change in final population size (Fig. 6). For the survival parameter, sensitivity analyses showed that juvenile survival and young survival rates had relatively similar impact on the final population size. An increase of 5% in survival of young and juvenile elephants independently caused a change of 29.25% and 29.87% in final population size, respectively (Fig. 7). However, the adult survival parameter had a far more sensitive effect on the final population size compared to the sub-adult survival parameter. Changing the adult survival parameter 5% could cause an 86.54% change in final population size. In contrast, a 5% change in the sub-adult parameter only caused a 37.46% change in final population size (Fig. 8).

Sensitivity analysis for the four poaching function parameters showed clear differences in model sensitivity (Fig. 9, Table 2). The logistic poaching function appeared to have the greatest influence, which is shown by it having the lowest index (SI = -2.626) followed by the constant poaching function (SI = -0.013). The linear, constant, and exponential poaching functions appeared to have relatively similar sensitivity in the model (Fig. 9). The level of uncertainty of poaching parameter in the model showed that the exponential parameter had the lowest uncertainty compared to the other three poaching parameters (Table 2).

Discussion

Our model clearly demonstrates that in the control (no poaching) scenarios the elephant population in the park will increase over time. Furthermore, the low poaching rate scenarios also show the

elephant population increasing. These results imply that the low poaching rates observed in the past did not have a serious negative impact on the elephant population in the park. The population growth rate in the low poaching rate scenarios remained about 1.0 or above and extinction encounter rate after 1000 simulations was less than 0.1. However, if we doubled the poaching rate from the minimum known rate observed in 2000–2002, as in the high poaching scenarios, we found that the population could decline dramatically for the logistic poaching and constant poaching functions, with the extinction coefficients for both functions increasing significantly up to about 75%. For both the constant and logistic poaching functions, the magnitude of poaching pushed the population into negative growth rates. In contrast, the linear and exponential poaching functions did not differ much from the lower poaching scenarios. In this situation, poaching (linear and exponential functions) seemed to have little effect on the population even though the magnitude of the poaching increased two fold from the low poaching scenarios. It is clear from these results that further study of the WKNP population, and other Asian elephant populations, is necessary in order to decide which poaching function best describes reality and therefore allow us to better model population trajectories under different scenarios.

The age distribution in the model showed that the proportional representation of the different age stages in the population shifted towards the adult age stage for the low and high poaching rate scenarios. The overall pattern of age distribution for both poaching scenarios was the same, with

Table 1. Summary of model result representing final population size; population growth rate and extinction encounter using all possible scenarios in the model. f = poaching function of population size. N_{50} = population at year 50; λ = population growth rate; EC = Extinction Coefficient.

Scenarios	f	N_{50}	95%CL	λ	95%CL	EC
Control		594	23.59	1.02	0.0002	0
Low-poaching	constant	253	17.87	1.01	0.001	0.099
	linear	422	19.03	1.02	0.0004	0
	exponential	325	16.63	1.01	0.0006	0.009
	logistic	263	17.80	1.00	0.0009	0.086
High-poaching	constant	41	7.86	0.97	0.016	0.75
	linear	274	11.08	1.00	0.0005	0
	exponential	217	9.40	1.00	0.0007	0.01
	logistic	37	7.09	0.97	0.018	0.76

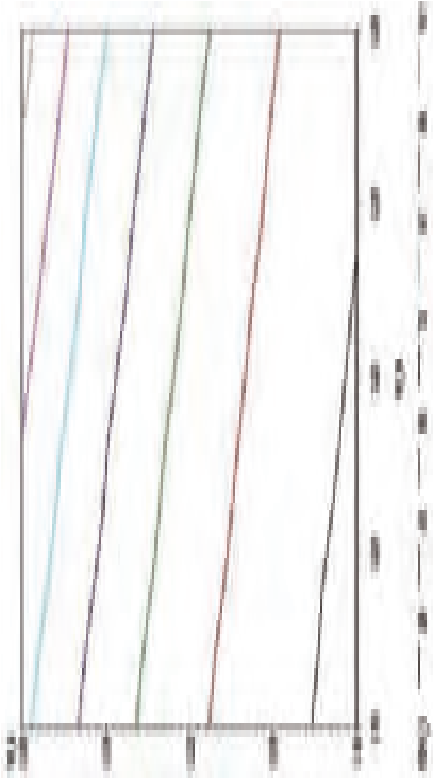


Figure 6. Response on predicted elephant population size in 50 years simulation for various combinations of adult reproduction rate (y-axis) and subadult reproduction rate (x-axis). Line in different color represents elephant population size for specific adult and subadult reproduction rate.

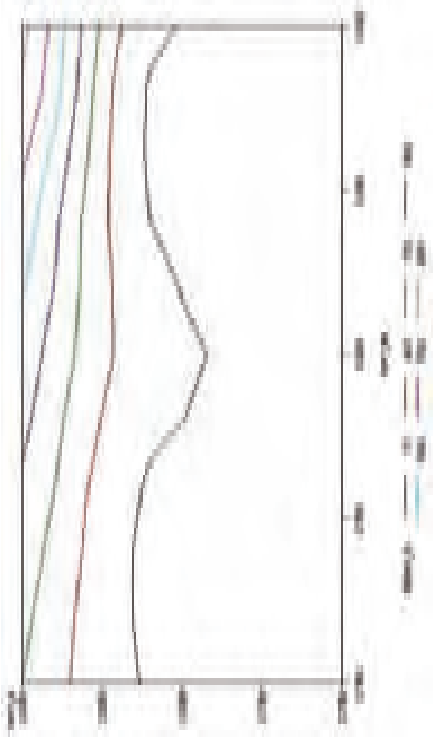


Figure 8. Response on predicted elephant population size in 50 years simulation for various combinations of adult survival rate (y-axis) and subadult survival rate (x-axis). Line in different colour represents elephant population size for specific adult and subadult survival.

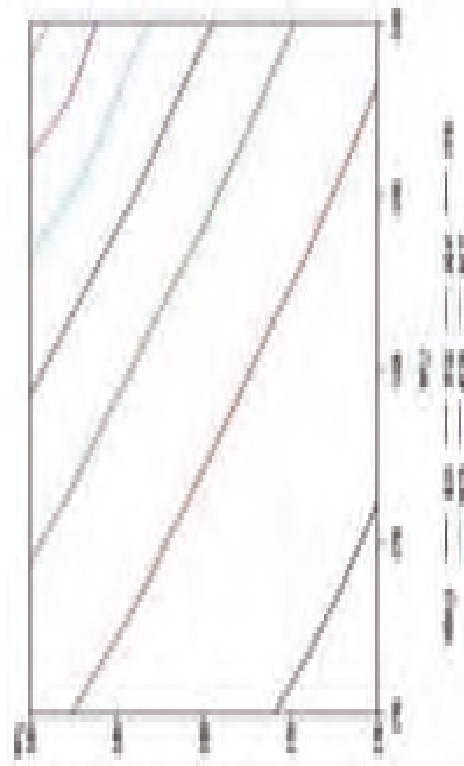


Figure 7. Response on predicted elephant population size in 50 years simulation for various combinations of juvenile survival rate (y-axis) and calf survival rate (x-axis). Line in different color represents elephant population size for specific juvenile and calf survival rate.

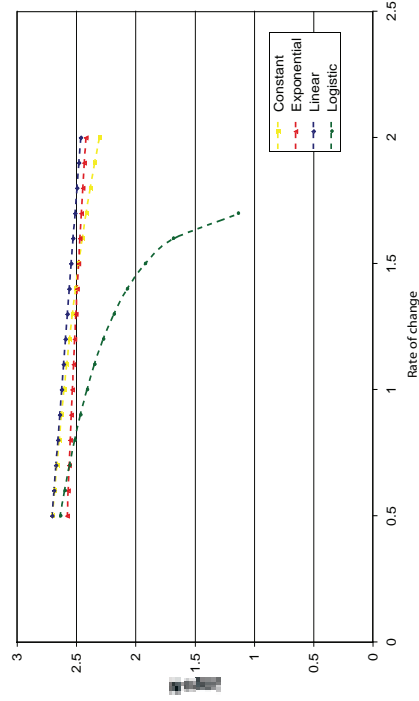


Figure 9. Response of population size in 50 years simulation to the rate of change on the poaching function parameter performed in the model. Different colour line represents different poaching function in the model.

Table 2. Sensitivity analysis of the poaching parameter. Poaching was specified as function of population size. β_0 = parameter value; $\alpha(\beta, \beta_0)$ = slope; $\Delta(\beta)$ = approximate uncertainty in the parameter; $SI(\beta, \beta_0)$ = sensitivity index of parameter β within point β_0

Poaching	β_0	$\alpha(\beta, \beta_0)$	$\Delta(\beta)$	$SI(\beta, \beta_0)$
Constant	2.848	-0.258	0.049	-0.013
Exponent.	2.630	-0.105	0.012	-0.001
Linear	2.780	-0.161	0.000	0.000
Logistic	4.050	-1.802	1.457	-2.626

the highest proportion of the population formed by the adult stage followed by the calf, juvenile, and sub-adult stages. If we examine the relationship between population growth and age structure after simulation, we find that for the low poaching rate scenarios the population is predicted to grow after 50 years. A similar pattern was also found for the exponential and linear poaching functions in the high poaching rate scenario. If the population is growing, that means the population growth rate is equal to or more than one. In this situation we would expect the age distribution at the end of simulation year to be dominated by the younger age classes. However, our models did not predict this, suggesting that improved survival of sub-adult and adult elephants in the population over a relatively short projection period (50 years) relative to an elephant's lifespan provided our populations with much greater numbers of older individuals. As a result, there was not enough new recruitment to shift the age distribution towards the younger age classes.

Sensitivity analyses

Our sensitivity analyses showed that variation in reproduction parameters for adults had the greatest impact on model variability. Relatively small changes in adult reproduction rate could cause a significant impact on final population size. Therefore, reproduction rate of adult elephants needs to be determined accurately if models such as ours are to be useful management tools and to allow the demographic condition of populations of interest to be assessed. If we assumed reproduction rate in the population to be deterministic, and compared the sensitivity of the survival rate, we found the model was more

sensitive to the adult survival parameter compared to the subadult survival parameter. Sukumar (1989) suggested that among adult elephants, female survival rate had a more significant effect on the population than did male survival rate. His study suggested that if adult male elephants have low survival, the population could still grow if female survival rate was high. Similar results have also been demonstrated for other long-lived species such as grizzly bears in Yellowstone National Park (Eberhardt *et al.* 1994).

Sensitivity analyses for the poaching parameter revealed a clear sensitivity to poaching function in the model and this was reflected in the sensitivity index value for the parameter. Sensitivity analyses showed the logistic poaching function was the most sensitive poaching function. This is most likely because the number of elephants poached per year was maintained at the maximum level and at the same time randomization was incorporated into the function. Clear differences can be found if we compare the sensitivity of the logistic to the constant poaching function: the constant poaching function tended to be less sensitive, even though the number of elephants poached per year was maintained at the maximum level, presumably because no randomization was incorporated into this poaching function.

Management implications

Our model suggests that the elephant population in WKNP will not decline over the next 50 years provided poaching rates remain at the low level observed in 2000–2002. While this result is encouraging, there is a possibility that the 2000–2002 poaching rate data used in this study underestimated real poaching rates in the park at that time because they were based on the number of elephant remains found without dedicated carcass searches. There is, therefore, a possibility that the number of elephants killed because of poaching was higher than our estimate, and our models suggest this if this were so the increased poaching could push the population toward negative growth. Moreover, even if the 2000–2002 data were representative of actual poaching rates at that time an evidence-based adaptive management approach to protecting the park's

elephants would require monitoring of poaching rates to determine, for example, whether law enforcement targets were being achieved. Therefore a poaching monitoring program (e.g. systematic carcasses searching) should be established as a priority for management of the park's elephant population. This could perhaps involve the use of detection dogs (sniffer dogs) to improve carcass detection efficiency, as elephant carcasses are surprisingly difficult to find in forested environments. In addition to improving detection rates, the limited number of arrests in relation to elephant poaching and the existence of local ivory markets clearly also need to be addressed (Hedges *et al.* 2005). Interestingly, reducing poaching could also reduce human–elephant conflict around WKNP because research in Africa has shown that poachers hunting elephants in forests can drive them into closer proximity to surrounding farmland thus increasing crop depredation rates (e.g. Nchanji 2005).

Finally, this model did not incorporate habitat degradation or destruction in and around the park. However, illegal killing of elephants and other wildlife is known to be correlated with road building, agricultural encroachment, and other forms of habitat degradation and destruction that facilitate human access into wildlife-inhabited areas (Duckworth & Hedges 1998), and so elephant population management in WKNP and elsewhere on Sumatra should also focus on reducing habitat destruction, especially encroachments into elephant habitat.

Acknowledgements

The study was conducted as a collaboration between the Wildlife Conservation Society and the Indonesian Ministry of Forestry's Directorate General of Forest Protection and Nature Conservation (PHKA). The project was funded by the Wildlife Conservation Society and the US Fish & Wildlife Service (through Asian Elephant Conservation Fund grants 1448-98210-00-G496, 98210-1-G806, and 98210-2-G292), the National Geographic Society, and WWF-US. Data analysis was supported by the Warnell School of Forestry and Natural Resources, the University of Georgia,

USA. We thank Clint Moore and Michael Conroy for valuable advice on modelling. Finally we thank Margaret Kinnaird, Tim O'Brien, Josh Ginsberg, and Martin Tyson for support and advice during the project.

References

Belovsky, G.E. (1987) Extinction model and mammalian persistence. In: *Viable Populations for Conservation*. Soule, M.E. (ed) Cambridge University Press. New York. pp 35-57.

Berger, J. (1990) Persistence of different-sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* **4**: 91-98.

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (2000) Experimental trade in raw ivory of populations in Appendix II: interpretation and implementation of the convention. Conservation of and trade in elephants [Doc 11.31.1]. In: *Eleventh Meeting of the Conference of the Parties*. CITES Secretariat, Geneva, Switzerland.

Blouch, R.A. & Haryanto (1984) *Elephants in Southern Sumatra*. Unpublished report, IUCN/WWF Project 3033, Bogor, Indonesia.

Blouch, R.A. & Simbolon, K. (1985) *Elephants in Northern Sumatra*. Unpublished report, IUCN/WWF Project 3033, Bogor, Indonesia.

Cromsigt, J.P.G.M., Hearne, J., Heitkönig, I.M.A. & Prins, H.H.T. (2002) Using models in the management of black rhino populations. *Ecological Modeling* **149**: 203-211.

Douglas-Hamilton, I. (1987) African elephants: population trends and their causes. *Oryx* **21**: 11-24.

Duckworth, J.W. & Hedges, S. (1998) *Tracking Tigers: A Review of the Status of Tiger, Asian Elephant, Gaur, and Banteng in Vietnam, Lao, Cambodia, and Yunnan (China), with Recommendations for Future Conservation Action*. WWF Indochina Programme, Hanoi,

- Vietnam.
- Eberhardt, L.L., Blanchard, B.M. & Knight, R.R. (1994) Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* **72**: 1-4.
- Hedges, S., Tyson, M.J., Sitompul, A.F., Kinnaird, M.F., Gunaryadi, D. & Aslan (2005) Distribution, status and conservation needs of Asian elephant (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation* **124**: 35-48.
- Leslie, P.H. (1945) On the use matrices in population mathematics. *Biometrika* **33**: 183-212.
- Leslie, P.H. (1948) Some further notes on the use of matrices in population mathematics. *Biometrika* **35**: 213-245.
- Milliken, T. (2004) *African Elephants and the Thirteenth Meeting of the Conference of the Parties to CITES, Bangkok, Thailand 2004. A TRAFFIC Briefing Document*. TRAFFIC East/Southern Africa, Harare, Zimbabwe.
- Nchanji, A.C. (2005) Elephant poaching weapons and new experiences from the Banyang-Mbo wildlife sanctuary, Cameroon. *Pachyderm* **39**: 33-42.
- Poole, J.H. & Thomsen, J.B. (1989) Elephants are not beetles: implications of the ivory trade for the survival of the African elephant. *Oryx* **23**: 188-198.
- Reilly, J. (2002) Growth in the Sumatran elephant (*Elephas maximus sumatranus*) and age estimation based on dung diameter. *Journal of Zoology* **258**: 205-213.
- Santiapillai, C. & Jackson, P. (1990) *The Asian Elephant: An Action Plan for its Conservation*. IUCN/SSC Asian Elephant Specialist Group, Gland, Switzerland.
- SAS Institute. *Proc Regression, Version 8.02*. SAS Institute, Cary, North Carolina, USA.
- Sitompul, A.F., Hedges, S. & Tyson, M.J. (2002) *Elephant Deaths in Sumatra as a Result of Poaching or Elephant Capture Operations, 1 January 2000 to 1 November 2002*. Unpublished Report, Wildlife Conservation Society – Indonesia Program, Bogor, Indonesia.
- Sukumar, R. (1989) *The Asian Elephant*. Cambridge University Press, Cambridge, UK.
- Sukumar, R., Ramakrishnan, U. & Santosh, J.A. (1998) Impact of poaching on an Asian elephant population in Periyar, southern India: A model of demography and tusk harvest. *Animal Conservation* **1**: 281-291.
- Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. (1998) Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Application* **68**: 539-570.
- Williams, B. K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, California, USA.

Corresponding author's e-mail:
 asitompul@forwild.umass.edu